EDITED BY

Devra G. Kleiman, Katerina V. Thompson, *and*
Charlotte Kirk Baer

Wild Mammals in Captivity

Principles & Techniques for Zoo Management

2nd Edition

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Principles and Techniques for Zoo Management, *Second Edition*

Edited by Devra G. Kleiman, Katerina V. Thompson, and Charlotte Kirk Baer

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This book is dedicated to the memory of our mentor, colleague, and cherished friend, Devra Kleiman, in recognition of her lifelong devotion to conservation. Her tireless effort to understand and conserve the natural world has inspired an international community of zoo and conservation biologists to perpetuate her life's work. The scientists she worked with and the animals she studied will forever be the fortunate heirs of her scientific labors. Aside from her professional endeavors, she also gave selflessly of her personal life to ensure that all those around her could learn, grow, and enjoy. This publication is but one example of the enormous contributions Devra made to the realm of our current knowledge of zoos and animal management for the betterment of all species on Earth. It is our hope that readers of this text will use it with the same rigor, enthusiasm, and passion with which Devra developed it.

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Foreword

George Rabb

President emeritus, Chicago Zoological Society

Many readers and users of this great assembly of current knowledge concerning mammalian biology and behavior are responsible in some fashion for maintaining one or more species in long-term and limited conditions of captivity. It is therefore fitting that almost every chapter of this volume comes with 3 values. One value is information directly relevant to keeping individual animals in good circumstances during their time in captivity. Another benefit is the readers' implicit obligation to confirm findings reported here and extend them appropriately. The third value is that of a resource for meaningful responses to the ever-growing challenge of biodiversity conservation facing zoological parks, aquariums, and related facilities.

This extraordinary challenge is to maintain the diversity of a class of vertebrates by securing their survival in suitable settings in our institutions while we and others try to provide for their future in their native natural environments. Several such undertakings for notable species have been successful over the last century—Père David's deer, Przewalski's horse, addax, and Arabian oryx among them. However, the survival of other large species is still problematic—for instance the giant panda, cheetah, great apes, and rhinos. And we must recognize that the endangerment problem is very much greater, with about 1500 species of mammals considered threatened with extinction in the latest global assessment of their status. As to whether such species diversity, especially of rodents and bats, warrants the investment of people and capital for their conservation, species richness is known to be important for the existence and resilience of ecosystems. Given the current and increasing pressures of anthropogenic climate change on ecosystems everywhere, further losses in species richness will affect the capacity of ecosystems and their component species to adapt in the near future.

Other dimensions of this enormous conservation challenge require attention if we are to respond adequately. One is much more cooperation among our institutions in sharing the recovery programs for species. Another is better linking to field conservation agents and agencies, engaging with them for recovery of species and their native environments. Such cooperative actions will also involve linking with people and communities cohabiting or using the natural environments of species of concern. An overriding dimension of the challenge is more successfully linking urban peoples to such conservation actions. Most captive collection institutions are public entities serving for the education and biophilic entertainment of usually local people. Given the greater general public awareness of the threat to much of the fauna and flora of the world, most urban people would likely take ethical pride in having their local institutions be part of a conservation network preventing further losses of the diversity of life.

Regional and international zoological park and aquarium associations as well as organizations of both professional and lay conservationists are already committed to conserving biological diversity. However, as indicated here, the support of urban communities is essential; and therefore I hope that readers and users of this volume will themselves be inspired to act as conservation advocates, reaching out to neighbors and teachers, and to governmental, political, and societal leaders in their communities.

Preface

Devra G. Kleiman

More than 40 years have passed since the original *Wild Mammals in Captivity*, written by Lee Crandall, was published. This masterwork was a taxonomically organized treatise that included everything we knew about captive exotic mammals at that time. When deciding to revise the book in the 1980s, my colleagues and I realized that repeating its taxonomic approach would not be possible, and chose instead to focus on important topic areas. The book was a major success, providing in one thick volume summaries of important areas of concern to zoo professionals, including mammal husbandry, nutrition, exhibitry, population management, behavior, reproduction, and research. By 1996, there had already been a quantum change in the focus of zoos, along with the recognition that zoos could and should contribute to *in situ* conservation and use the animals in their care to increase and diffuse knowledge about their collections.

The 1996 *Wild Mammals in Captivity* volume took almost 10 years from initial concept to publication and had 48 chapters, 5 appendixes, and 78 authors. Ten years later, I realized that the previous decade had brought additional massive change in the management of zoo mammals and started discussing a revision with colleagues. We first sought feedback on which sections and chapters in the original volume were most useful to zoo professionals. Additionally, we did a "needs assessment" to determine what vacuums in that first edition needed to be filled. My initial intention was to have the original authors (if available) revise and update their chapters, but it soon became clear that (1) some chapters needed no updating or revising, (2) there were unmet needs from the first edition, and (3) several major conceptual and technological shifts within the zoo community needed to be addressed. Thus, this edition of 34 chapters and 4 appendixes is quite different from the first. More than 75% of the chapters and appendixes have substantially new content when compared with the original, or else present the material in substantially new ways. With fewer chapters, we still have 78 authors, and have attracted them much more from the international zoo community (contributors derive from Asia, Australia, North and South America, and Europe).

Probably the most notable change in the past decade has been an increased focus on integrated zoo management such that exhibitry, education, conservation, and research staff work more closely together as they develop the conceptual frameworks for new initiatives. Thus, this volume contains chapters on topics that have emerged as critical to the modern zoo mission during this period, including the integration of zoo in-house activities with *in situ* programs occurring far afield. For most topics, we have tried to pair the conceptual approach to a zoo problem with the practical applications. As a result, this volume contains less theoretical material and is much more management oriented, with the hope that zoos in both developed and developing countries will find all its content useful.

For example, the pressure on zoos to ensure that their programs are of the finest quality in the profession and that their collections are maintained with the highest possible standards of welfare has resulted in much greater attention to the evaluation of zoo programs. We thus include an overview of accreditation processes and 3 short chapters on approaches to the evaluation of zoo facilities, from authors on 3 different continents.

The past decade has also seen an explosion in concern about animal welfare, so this volume provides leading-edge techniques for measuring welfare and improving the environmental conditions of mammals in the zoo staff's care. The recent focus on animal enrichment to enhance animal welfare, both conceptually and methodologically, is well represented throughout this volume. Additionally, the increase in the use of training techniques for animal management, including for the provision of health care, has been extraordi-

Capybaras swimming at the Smithsonian's National Zoological Park, Washington, DC. Photography by Jessie Cohen, Smithsonian's National Zoological Park. Reprinted by permission.

nary. Enrichment and training have together transformed mammal management in zoos.

Another area of focus is the expansion of collaborative management programs across regions, well represented by the chapters on population management and regional collection planning. The species and taxon management programs flourished through the 1990s, and today the vast majority of animals, especially endangered species, are managed locally, regionally, and internationally. Also noteworthy are the emergence and widespread use of software to manage zoo populations.

Finally, the critical role that education programs play in changing the perceptions of zoo visitors and encouraging a conservation ethic in our citizenry is acknowledged through this edition's greater focus on visitor research and conservation learning. Education is now integral to the zoo mission and all its programs.

Note: The mammalian taxonomy used throughout this book is that of Wilson, D. E., and Reeder, D. M. 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference.* 3rd ed. 2 vols. Baltimore: Johns Hopkins University Press.

Acknowledgments

We would have been unable to undertake this revision without the helpful guidance and input of individuals who provided us with valuable feedback on our initial inquiries concerning what would be most useful in a second edition of Wild Mammals in Captivity. The people who responded with helpful comments that informed our revision include Govindasamy Agoramoorthy, Kurt Benirschke, Kathy Carlstead, Jon Coe, Carolyn Crockett, Scott Derrickson, Jim Doherty, Jack Grisham, Georgina Mace, Jill Mellen, Don Moore, Dave Powell, Mike Quick, Franz Schwarzenberger, Richard Snider, Pat Thomas, Steve Thompson, Duane Ullrey, and Sally Walker. In addition, we acknowledge Mary Allen for her efforts in initiating the nutrition section of this new edition.

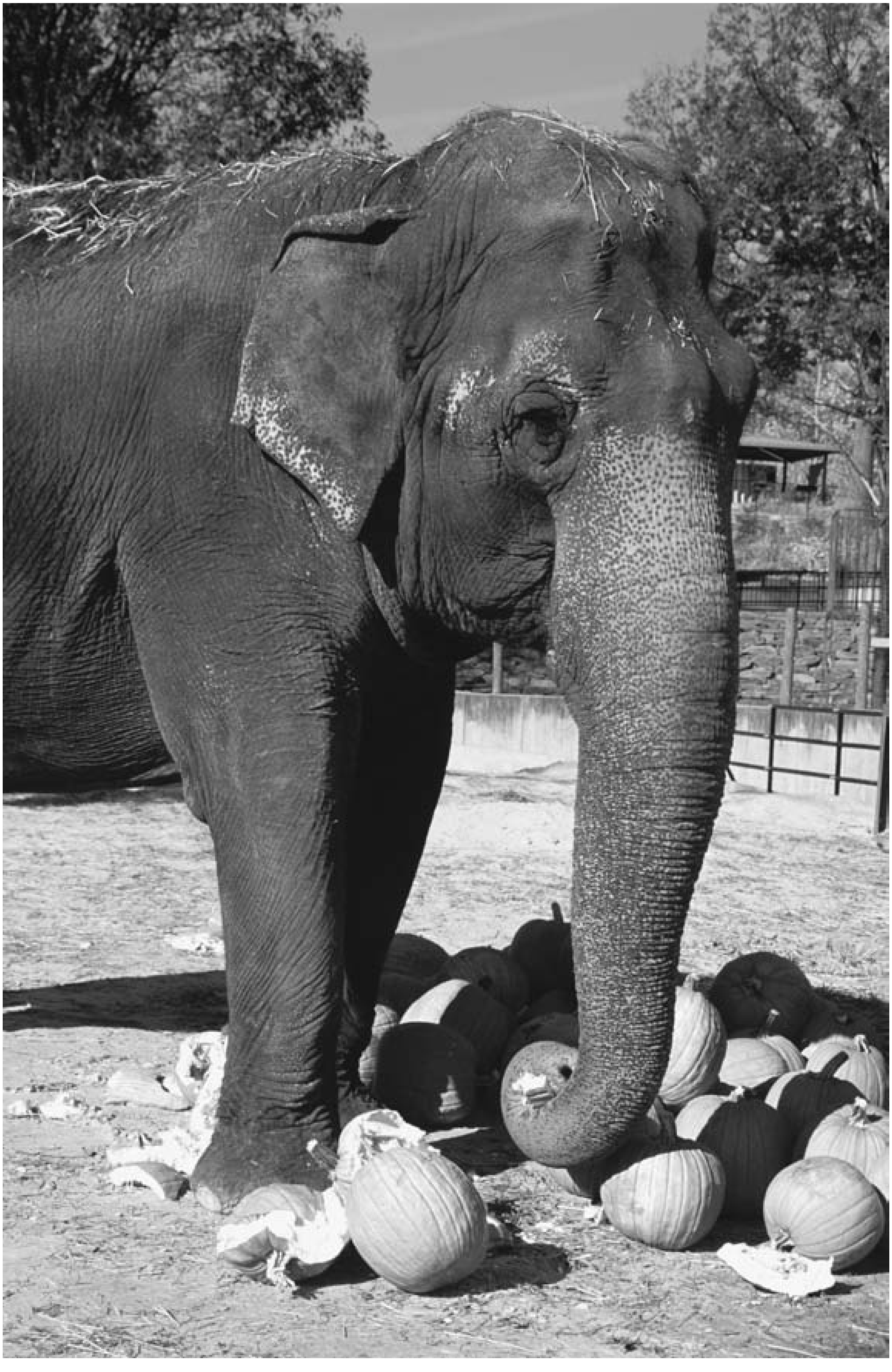
We had numerous reviewers, to whom we are profoundly grateful. We thank the following individuals for reviewing chapters and providing constructive suggestions to authors (asterisks indicate those who reviewed more than one chapter): Joseph Barber*, David Barney, Meredith Bashaw*, Karen Bauman, Benjamin Beck*, Henry Bireline, Randy Brill, Janine Brown, Paul Calle, Bryan Carroll*, Tracy Carter*, Jon Coe*, Nancy Czekala, Shelli Dubay, Mark Edwards, David Field*, Debra Forthman, Elizabeth Frank, Laurie Gage, Tom Goff, Karen Goodrowe*, John Gwynne*, David Hancocks*, William Karesh, Elizabeth Koutsos, Laurie Bingaman Lackey, Kristin Leus*, Donald Lindburg*, Terry Maple, Sue Margulis, Jill Mellen, Axel Moerhenschlager, Donald Moore, Linda Penfold*, David Powell*, Mark Rosenthal*, Anne Savage*, David Selk, Michelle Shaw, Deb Schmidt, Phil Seddon, David Shepherdson, Alan Shoemaker*, James Sikarskie, Patrick Thomas*, Steve Thompson, Kathy Traylor-Holzer, Leon Venter, Cynthia Vernon, Kathleen Wagner, Ann Ward, and Bob Wiese.

Several authors provided contributions that ultimately could not be included in this volume for a variety of reasons. We thank Frank Göritz, Thomas B. Hildebrandt, Katherine Jewgenow, and Kris Vehrs for their time and effort.

Finally, we thank Kerri Donner for her editorial assistance, and the University of Maryland for providing us with some of her time. This volume would never have been published without the professional assistance of Christie Henry at the University of Chicago Press, who supported our concept of a revision. Sandra Hazel did a superb job of copyediting. Anthony Rylands did the indexes, a rather immense task for a book this size. I am especially grateful to Anthony for his eagle-eyed assistance in finding a multitude of inevitable errors, especially with the taxonomy.

A work of this magnitude involves substantial effort on the part of many. It is impossible to list every important contribution to the production of this volume, so whether mentioned here or not, we sincerely thank all who have participated.

Wild Mammals in Captivity



Part One

Ethics and Animal Welfare Standards

Introduction

Devra G. Kleiman

Zoos, unlike museums, have the unique challenge of maintaining living collections. They are charged with the humane treatment and daily maintenance of the animals in their care. The level of sophistication in the husbandry of zoo animals has progressed substantially in recent years, as has the recognition that animal caretakers have a responsibility not only to provide humane treatment for zoo animals, but also to create captive conditions which actually enhance their quality of life. Improvements in animal management have resulted from an increasing awareness of both the physical and the psychological needs of captive animals. Part 1 deals with the ethics of maintaining mammals in captivity as well as the challenges zoo staff have to enhance the welfare of the animals in their care. Additionally, standards for the accreditation of zoos have and are being developed by regional zoo professional associations as a way to improve the functioning of zoos and animal care.

This volume, *Wild Mammals in Captivity: Principles and Techniques for Zoo Management*, appropriately begins with a chapter on the ethics of maintaining mammals in zoos and aquariums, a continuing and evolving controversy. In chapter 1, Kreger and Hutchins discuss the ongoing dialogue concerning what roles zoos should play in society, including historical and modern cultural differences in attitudes toward animals. They also consider whether there should be limits on which species are maintained and exhibited, and the potential conflict between the conservation and exhibit functions of a modern zoo. In chapter 2, Kagan and Veasey provide a history and the foundations of the animal welfare movement and challenge the zoo and aquarium community to increase the

Asian elephant smashing pumpkins at the Smithsonian's National Zoological Park, Washington, DC. Photography by Jessie Cohen, Smithsonian's National Zoological Park. Reprinted by permission.

resources devoted to researching and improving animal welfare. Of great importance is the need to identify and implement methods to measure and improve animal welfare, an area of research that seems to be more developed in Europe compared with the United States. In chapter 3, we have 3 regional approaches to the evaluation of zoos and the development of industrywide standards (Lewis, North America; Agoramoorthy; Southeast Asia; Stevenson, Europe), with an introductory overview by Barber of the challenges associated with setting guidelines and assessing zoos. Clearly there are regional approaches to the evaluation of zoos and aquariums, and these are still evolving, with differences in the degree of government involvement and the degree to which the evaluation is voluntary or mandated. Some of these differences may derive from cultural differences in how nonhuman animals are viewed within a society, and also from the degree of "modernization" and development within a region. The challenge for zoos as stated by Barber (and also Kagan and Veasey) is to determine how best to measure the welfare of animals in our zoos in a quantitative manner, rather than via subjectivity alone, and then to ensure that we provide the best possible conditions for the expression of natural behaviors.

1

Ethics of Keeping Mammals in Zoos and Aquariums

Michael D. Kreger and Michael Hutchins

INTRODUCTION

Ethics is about what is right and what is wrong. Rather than focusing on "what is," which is the realm of science, ethicists focus on "what ought to be" (White 1981). However, when it comes to moral issues, one size does not fit all. Human beings are not moral absolutists; our ethical decisions are complex, and ethical standards often vary with context. For example, while killing a rare animal may represent a loss to biodiversity and may even be against the law, killing a rare animal in self-defense may be considered morally justifiable. Similarly, while a zoo may not be ethically justified in maintaining an endangered wild animal purely for entertainment or profit, many believe that it would be justified for research, educational, or conservation purposes (Hutchins, Smith, and Allard 2003). In bringing wild animals into captivity, important questions are raised that sometimes polarize segments of society and at other times create consensus. When is it morally acceptable to remove an animal from the wild and place it in captivity? Are zoos bleak prisons for wild animals, or are they a comfortable shelter from a potentially cruel and threatening world? Some critics have denounced zoos as exploiters and traffickers of wildlife, while supporters have countered that zoos are champions for wildlife conservation (Mench and Kreger 1996; Hutchins, Smith, and Allard 2003). Animal advocates, philosophers, scientists, conservationists, animal caretakers, and the visiting public are asking difficult ethical questions. There is ongoing debate about what roles zoos should play in society, which species should or should not be exhibited, how animals ought to be exhibited and cared for, and what should be done with animals that are no longer needed for zoo programs.

This chapter will outline some of the ethical concerns associated with keeping and managing wild mammals in captivity. We will describe philosophical differences in ethical perceptions, discuss how ethics affect the conservation mission of zoos, as well as other ethical issues, and address what zoos can do to bridge the ethics gap. We use the term *zoo* to refer to any professionally managed zoological institution, including aquariums, that holds live wild mammals in captivity. We define wild animals as representatives of nondomesticated species, that is, species that have not undergone generations of selective breeding to emphasize particular traits (artificial selection). Professionally managed zoos are those that are accredited by international, regional, or national zoo associations (www.eaza.net; Bell 2001). Examples of international or regional associations include the World Association of Zoos and Aquariums, the European Association of Zoos and Aquaria, and the Association of Zoos and Aquariums (AZA). AZA accredits about 10% of all animal exhibitors in the United States (approximately 214 out of over 2,500 exhibitors) licensed by the U.S. Department of Agriculture (see Lewis, chap. 3b, this volume); however, these include most major metropolitan zoos in the United States and Canada. The Sociedade de Zoológicos do Brasil is an example of a national zoo association.

Almost all these associations require their member institutions to abide by a code of ethics. While such codes vary among associations, institutional missions and good animal care are at the core of the codes. Nevertheless, codes may represent minimum rather than optimum standards or goals. Effectiveness in exceeding codes and standards is often limited by resources (e.g. technical, financial, space). Nonprofessionally managed exhibitors include most roadside zoos, circuses, private animal educators and trainers, wildlife rehabilitation centers, and sanctuaries. The ethics codes, among other professional standards, separate professionally run institutions from nonaccredited facilities.

ETHICAL PERCEPTIONS

Historically, humans have worshipped animals, hunted them for food or sport, domesticated them, eaten them, worn them, made them companions, and wondered about their and our place in the natural world. Humans have also captured and collected them for amusement or scientific study. The history of the world's zoos and their justification through time has been reviewed elsewhere (Mullan and Marvin 1987; Mench and Kreger 1996; Bell 2001; Hanson 2002). From the collection of the Egyptian queen Hatshepsut (1490 BCE) through the European menageries of the 1600s, the earliest collections of captive wild animals were private menageries, assembled mostly to satisfy curiosity or as symbols of wealth and power. Beginning in the late 1700s, public recreation, education, and scientific research separated the Western zoological parks from menageries. However, it was not until the late 1900s that conservation—whether through research, species reintroduction programs, genetic management, or educating visitors about species or habitat conservation—assumed a more central role for the metropolitan zoo. Zoos shifted from large collections of many species, often held in small, sterile cages, to smaller collections of fewer species, exhibited in larger, more naturalistic enclosures (Mullan and Marvin 1987; Hancocks 2001; Hanson 2002). Zoos exhibited species to educate the public and cultivate its appreciation of conservation or research programs. Zoos offered their visitors "edu-tainment" through shows, contact areas, and interactive exhibits. They also began to reflect on their reason for being, along with issues related to animal welfare, such as behavior, exhibit design, and nutrition. This process is ongoing and is proceeding slowly as the zoo community continues to debate ethical differences related to meeting the biological needs of individual animals while still meeting institutional missions.

Today there exists a continuum of ethical perspectives, ranging from the abolitionist view of no animal use (including as pets, for food, and in zoos) to the extreme utilitarian view in which humans are free to use animals regardless of the cost to the individual animal. Two prominent ethical philosophies have emerged regarding the keeping of wild animals in captivity: animal rights, the absolutist approach, and animal welfare, a more utilitarian view. Animal rights advocates focus on whether or not animals should be in zoos at all. As cognitive research has indicated the existence of subjective states in nonhuman animals (Griffin 1984; Bekoff, Allen, and Burghardt 2002), animal rights philosophers have argued that animals must be given moral consideration equal or similar to that given humans (Regan 1983). Those who share this perspective have argued that nonhumans should be given moral and legal consideration equal to humans (i.e. "legal personhood": Wise 2000). In animal rights philosophy, sentience (or the ability to feel pain) is the only characteristic required for full moral consideration. Thus, holding nonhumans in captivity is viewed as "speciesism," that is, one species (humans) giving less moral consideration to other species based solely on taxonomic status (Regan 1983).

The philosopher Peter Singer also espouses moral consideration for nonhumans but has a less absolute approach. He recognizes that humans utilize animals for a variety of purposes. However, to be morally justifiable, the benefits to humans must far exceed the costs to individual animals (Singer 1990). It would be unusual for animal rights advocates to support keeping wild animals in zoos, even if they contributed to species survival (Regan 1995). Indeed, Regan (1983) has labeled any attempt to usurp the rights of individual animals to save species or ecosystems as "environmental fascism." In this view, the welfare of individual common animals also trumps the survival of endangered species and ecosystems. This has caused some to characterize animal rights as anticonservationist or antienvironmental (e.g. Hutchins and Wemmer 1987; Norton 1987; Hutchins 2004b). In general, animal rights advocates oppose zoos because of the belief that any form of human use of animals is intrinsically wrong, especially if it results in any harm whatsoever. In addition, Jamieson (1995) has argued that education of the public and conservation of species can be conducted without keeping animals in zoos, thus questioning the need for zoos. Thus zoos, even nonprofit ones, are seen as exploiting animals for financial gain, while at the same time harming the interests of individual animals that should be allowed to live their lives undisturbed in nature.

Animal welfare has philosophical and scientific components (see Kagan and Veasey, chap. 2, this volume). First, it is based on the assumption that it is ethical for animals to be used by humans. Criteria used to support this ethical decision range from the roles that zoos play in educating visitors and conserving wildlife and wildlife habitat, to arguments that few animals are removed from the wild for zoos; many have been bred over generations and are nearly domesticated; and human managers are providing the animals a better life in captivity than they would have in the wild (a paternalistic attitude: Bostock 1993; Hutchins and Smith 2003). Thus, there are benefits to humans and nonhumans from the existence of zoos. Many definitions of animal welfare have been put forward by philosophers, veterinarians, and applied ethologists, but most share the concept that pain, suffering, and loss of life should be minimized to the extent possible. Some have argued that animal welfare is about how an animal "feels"—in other words, whether it is sentient and has the capacity to suffer (Dawkins 1990; Duncan 1993). This assumes that animals do not simply react to a stimulus, but actually think about the stimulus and react according to their perceptions (Rogers 1994). Zoos must make a moral judgment to determine if an animal's welfare level is acceptable. If it is not, the animal welfare philosophy would insist that behavioral and psychological needs be met. Using the disciplines of ethology, neuroscience, endocrinology, genetics, and immunology, animal welfare science can be used to determine the level of animal welfare by identifying how an animal perceives and responds to environmental stimuli (Mench 1993).

Animal welfare, or quality of life, is enhanced by more than the simple provision of adequate food, water, living space, and veterinary care. However, animal welfare, like animal rights, also is laden with human values (Mench 1993), and has evolved as more information about the needs of animals has been discovered. For example, some early zoo managers believed that barren cages with ceramic tile walls and concrete floors promoted animal welfare, as these facilities were easily cleaned and sanitized, thus reducing the risk of disease (Hancocks 2001). For veterinary procedures, barren cages also appeared to make capture easier and seemed less traumatic to the animals. In essence, early zoos simply wanted to keep the animals alive and, if lucky, to breed them. However, others, such as T. H. Gillespie, director of the Edinburgh Zoo in the 1930s, realized that meeting zoo animals' minimum health and safety needs was simply not enough, and believed that quality of life was also an important consideration. In his 1934 book *Is It Cruel?* he states: "The kind of captivity I am considering must imply good and sufficient food, and such degree of shelter, sunshine, shade, fresh air, room for exercise, and generally, such conditions as are desirable for that particular animal's welfare—such as it naturally desires"(p. 25). In the 1940s, Heini Hediger, then director of the Basel Zoo, recognized that despite some improvements, zoos were still not meeting the basic biological and psychological needs of captive wild animals. In 1942 he stated: "A fundamental problem of zoo biology is how to neutralize as far as possible all modifying (non-hereditary, externally conditioned) and mutative (hereditary) degeneration phenomena in captivity" (Hediger 1969, 63).

Like Hediger and Gillespie, animal welfarists argue that meeting an animal's most basic health and safety needs is not enough. For zoos, the goal of maximizing animal welfare is not as easy or straightforward as it may seem (see Kagan and Veasey, chap. 2, this volume; Barber, chap. 3a, this volume). Many compromises must be made between the competing goals of ensuring animal safety and health versus those of providing an interesting and species-appropriate quality of life (Kreger, Hutchins, and Fascione 1997; Kreger and Hutchins 1998). These compromises, however, only need to be made in captivity, which raises the very issue of the ethics of keeping mammals in captivity. For example, some risk of disease or injury may be necessary in order to give captive animals the ability to perform a greater range of normal behaviors. The provision of substrate for burrowing, branches for climbing, water for bathing and interactive play, or social companions substantially increases the risk of disease or injury for zoo animals, but also has the potential to enhance the quality of an animal's life. Yet precisely how much risk to an individual animal's health should zoo managers tolerate to ensure that psychological well-being is maximized is an ethical question with no clear answer. Indeed, *quality of life* itself is a subjective term, often interpreted differently among humans. For example, some people are most comfortable living in the city and would be bored or frustrated by rural life, whereas others have strong preferences for rural life. Answers may also vary depending on the specific taxon and individual animals involved (Kreger and Hutchins 1998). In addition, the ultimate goal of modern zoos is not necessarily to maximize longevity or eliminate any risk of pain or suffering (Hutchins 2007).

Zoos have frequently been placed in a defensive position as the media, animal protectionists (particularly animal rights advocates), and some scientists criticize zoos on animal welfare issues (e.g. Jamieson 1985, 1995; Malamud 1998; Clubb and Mason 2002; PETA 2005). These issues range from the causes of injuries or mortality, to animal escapes, to the disposition of surplus animals, to the size of animal enclosures. Indeed, media characterizations of zoo and aquarium animal deaths for a 20-month period (September 2003–May 2005) indicated that while most articles were either dispassionate and objective or sympathetic, nearly a third were either accusatory or attempted to balance the accusatory statements of animal rights activists with sympathetic statements from zoo professionals (Hutchins 2006a). The vast majority of these accusations involved the death of charismatic megavertebrates such as elephants, great apes, dolphins, and big cats.

ELEPHANTS

Of the terrestrial vertebrates in zoos, perhaps the elephant, the largest land mammal, has attracted the most attention. Criticism of elephants in zoos has come not only from the public, but from some elephant field researchers as well. Given the great body of research conducted on wild elephants, it is no wonder that zoo exhibitions of these biologically complex creatures draw criticism (Wemmer and Christen 2008). A study commissioned by the Royal Society for the Prevention of Cruelty to Animals (Clubb and Mason 2002) has been used by animal protectionists to argue that elephants in captivity live miserable and greatly shortened lives. Zoos have responded by critically examining such reports to determine their scientific veracity, addressing animal welfare concerns, and debating the education and conservation benefits of having elephants in captivity (Smith and Hutchins 2000; Hutchins 2006b). Scientific discussions have examined captive versus wild longevity of elephants (Wiese and Willis 2004), the use of nature as the sole metric for evaluating animal welfare (Hutchins 2004a), spatial needs and complexity in captivity (ibid.), appropriate group sizes (Mellen and Keele 1994; AZA 2001), and training methods (Desmond and Laule 1991; Hutchins, Smith, and Keele 2008).

Scrutiny of whether elephants should be in captivity and, if so, how they can be managed to provide for their welfare has resulted in husbandry guidelines and policies developed by a variety of organizations (e.g. AZA, the Elephant Managers Association, International Elephant Association, European Association of Zoos and Aquaria, Australasian Association of Zoos and Aquaria, and the U.S. Department of Agriculture) (Olson 2004; Wemmer and Christen 2008). In the United States, only the Animal Welfare Act (1966 as amended) carries the weight of law (7 U.S. Code 2131-2157). However, these guidelines are often based on experience, not science, and are not always in agreement. A zoo in one part of the world may not meet the standards of a zoo in another part of the world. Some zoos are deciding not to keep elephants, because they cannot meet the standards (Kaufman 2004; Strauss 2005). Other facilities are being renovated to upgrade elephant exhibits, increase living space, and maintain appropriate group sizes (Hutchins, Smith, and Keele 2008). Certainly, research is needed to determine how best to meet elephant welfare needs in captivity.

Even if animal welfare needs of elephants are met in the zoo, is it still ethically acceptable to maintain elephants in captivity? Can animal welfare be compromised if there are other benefits of keeping elephants? These are points of ongoing debate, both within the zoo community and in the public arena. Some critics have argued that captive elephants should not be in captivity, because they contribute nothing to conservation since they are not being bred for reintroduction to the wild. In contrast, zoo elephant advocates maintain that zoo elephants serve as conservation ambassadors for their wild counterparts. By exhibiting live elephants, visitors can be moved or educated to support elephant conservation in the field (Smith and Hutchins 2000; Hutchins, Smith, and Keele 2008). Simply having elephants at the zoo helps attract visitors. In fact, when the Maryland Zoo in Baltimore informed the public that it might have to move its 2 African elephants to another zoo because of budget shortfalls, the outcry was so great that local business leaders and the governor raised the necessary funds to operate the zoo and keep the elephants (*Zoo News Digest* 2003). In effect, the threat of removing the elephants contributed to rescuing the zoo. Revenue generated from admissions and concessions from visitors who come to see the elephants can then be funneled into zoo-sponsored research and conservation projects. Indeed, between July 2002 and December 2003, AZA zoos either initiated or supported at least 87 such projects that were elephant related (Hutchins, Smith, and Keele 2008).Some of this research is relevant to field conservation. For example, population control is becoming increasingly necessary to reduce human-elephant conflicts (Pienaar 1969), and contraceptive techniques developed at zoos offer a potential nonlethal option for population reduction (Fayrer-Hoskin et al. 2000). Infrasonic communication in elephants was first discovered and studied in zoo elephants (Payne, Langbauer, and Thomas 1986). This knowledge is vital for understanding how wild elephants communicate and coordinate their movements over great distances. Nevertheless, for zoos to be able to use elephants for research or to educate the public, they must have elephants (Smith and Hutchins 2000). The ethical question is, do these benefits to wild elephants justify keeping some individuals in captivity?

ETHICS AND THE ROLE OF SPECIES CONSERVATION IN ZOOS

One of the missions of zoos is conservation. Conservationists seek to ensure a future for naturally occurring biological diversity (Primack 2002). The term *natural* is used here to distinguish between diversity that has occurred as the result of natural ecological/evolutionary processes (i.e. speciation, colonization, and "natural" extinction), and that which has occurred because of relatively recent human interventions (i.e. introduction of non-native invasive species, human-caused extinctions) (Aitken 1998). Decisions regarding the future of wildlife and their habitats are becoming increasingly complex, particularly as human populations grow, become more affluent, and use more natural resources.

In some instances, the animal rights ethic and the conservation ethic will lead to the same conclusions, and may even result in coalitions between zoological and animal protection organizations. For example, both ethics would consider it wrong for humans to destroy critical wildlife habitat. Both ethics would support conservation training, finding alternatives for communities that market bushmeat, and supporting antipoaching patrols. But when the 2 viewpoints are compared, it is evident that disagreements will arise when the "rights" of individual, sentient animals come into conflict with using zoo animals in efforts to conserve populations, species, habitats, or ecosystems (Hutchins and Wemmer 1987). Even from an animal welfare perspective, many zoo professionals would argue that zoos should prioritize the welfare of the individual animals in the collection over what is good for the herd (with dominant and subordinate animals) or animals used for conservation projects.

Ideological differences between animal rights and conservation ethics are evident in their contrasting view about how to rescue endangered species. While both ethics favor saving threatened or endangered species or populations, they differ in their reasons for doing so. Regan (1983, 360) argues that we must conserve endangered species "not because the species is endangered, but because the individual animals have valid claims and thus rights against those who would destroy their natural habitat, for example, or would make a living off their dead carcasses through poaching and traffic in exotic animals, practices which unjustifiably override the rights of those animals." Thus, all sentient animals, regardless of species, rarity, or other considerations, are to be given equal moral consideration. In contrast, proponents of the conservation ethic argue that endangered populations or species should be given special status solely because of their scarcity (Callicott 1986; Norton 1987; Aitken 1998). That is, extraordinary efforts need to be made to preserve rare populations or species, especially when an organism has become scarce due to some action on the part of humans (e.g. as the result of overexploitation, pollution, or habitat loss or alteration).

Modern zoos use animals as conservation tools in many ways. Animals are used to educate visitors, in fund-raising for *in situ* and *ex situ* conservation projects, and for research or reintroduction. Some zoo-based conservation programs involve welfare risks. A good example is the reintroduction program (see Earnhardt, this volume, chap. 22). Reintroduction is an attempt to establish a species in an area that was once part of its historical range, but from which it has been extirpated or become extinct (IUCN 1998). However, the risk to individual animals during reintroduction through morbidity and mortality may be considerable, especially in a program's early stages (Beck 1995). Reintroduction release candidates must be able to avoid predators, acquire and process food, interact socially with conspecifics, find or construct shelter, move on complex terrain, and orient and navigate in a complex environment (Kleiman 1996). Zoos must decide how to provide animals with the challenges they are likely to encounter in the wild while minimizing potential harm to the release candidates. For example, to teach the reintroduction candidates to fear humans, avoid predators, and shun inappropriate habitat, it may be necessary to provide negative experiences in captivity (Griffin, Blumstein, and Evans 2000).

To ensure that captive-reared black-footed ferret release candidates could recognize and kill their primary food, prairie dogs, they were given the opportunity to hunt and kill live prairie dogs (Miller et al. 1998). While this experience was critical for the success of the reintroduction program, there is no doubt that it violated the "rights" of the individual prairie dogs.

OTHER AREAS OF ETHICAL CONCERN

How animals are selected for exhibit and how they should be exhibited are also areas of ethical concern. There may be species that are too specialized nutritionally or behaviorally to be maintained in captivity. New multi-institutional studies of the behavioral needs of animals (e.g. Shepherdson, Carlstead, and Wielebnowski 2004; Swaisgood and Shepherdson 2005) have led some zoos to question whether or not they can provide for some animals already in their collections. Should a zoo exhibit an animal whose welfare is compromised simply by the presence of visitors? During periods of high visitor attendance, gorillas, *Gorilla gorilla*, at the Belfast Zoo displayed more intragroup aggression, stereotypies, and autogrooming (Wells 2005). Similarly, visitor presence increased abnormal behaviors by 30% in lion-tailed macaques, *Macaca silenus*, over the long term and decreased the use of enriched parts of the exhibit (Mallapur, Sinha, and Waran 2005). While the degree that these behavior patterns vary among individuals and across species, this kind of research can be used to make informed management decisions about the ethics and method of exhibiting these species. Thus, zoos should be proactive by examining their collections and determining if they have any species for which animal welfare needs cannot be met, even if it means that they will close exhibits and relocate animals to more appropriate facilities.

Another area of ethical concern is the use of animals in shows, rides, and contact areas (Kreger and Mench 1995; Mench and Kreger 1996). Animals used in educational demonstrations, petting zoos, rides, and shows often interact with their caretakers and the visitors to a greater extent than those placed on exhibit. They may also be housed very differently from animals on exhibit. When does training, handling, or other interactions for such activities compromise or enhance animal welfare, and what kinds of techniques are appropriate? Some zoos have policies regarding how and when animals may be used for such interactions, as well as which individual animals are more suitable for handling by the visitors than others (Kreger and Mench 1995; AZA 2006).

When is the use of animals in entertainment (including on-site shows and television programming) educational, and when is it exploitative and/or harmful to public attitudes? Visitor studies evaluate the effectiveness of animal exhibits, shows, and visitor contact with animals on visitor knowledge and awareness (see reviews in Kreger and Mench 1995; AZA 2003). Some argue that zoos may unintentionally be portraying animals as glorified pets. Visitors simply observing animal caretakers interacting with animals may engender compassion, but they may also develop the misperception that wild animals are tame.

Ethical decisions also must be made about captive population management. Decisions include which animals should be removed from a group and relocated to another zoo for breeding, when to separate mothers from young, how and where to house offspring that are surplus to the genetically managed population (see Carter and Kagan, chap. 21, this volume), and what to do with postreproductive animals. Relocation of favorite animals has attracted media scrutiny and sometimes ignited debates between zoo managers and animal protection groups. While there are animal welfare issues regarding the transport of live animals, the transport of semen from one zoo to another in itself does not reduce animal welfare, but it may deprive the animal of the experience of breeding. The World Association of Zoos and Aquariums' Code of Ethics and Animal Welfare acknowledges the welfare benefits of reproductive behavior, including courtship, pair formation, mother-infant attachment, and socialization of the young (WAZA 2005). There are also potential welfare benefits arising from genetic management (Hutchins 2001). In small, unmanaged populations, animals may become highly inbred. Inbred individuals are known be at higher risk of congenital abnormalities (i.e. birth defects), have lower reproductive rates, and experience higher rates of neonatal mortality (Ralls, Ballou, and Templeton 1988), all of which could diminish welfare.

Sufficient space for maintaining a sustainable and genetically viable population of rare species is often limited in zoos (Soulé et al. 1986). Removal of genetic surplus, postreproductive, unhealthy, or behaviorally incompatible animals is a difficult decision that sometimes must be made for veterinary, population management, or conservation reasons. Relocation to other zoos, sanctuaries, or private individuals is among the first options considered, as is controlling reproduction through contraception programs (Porton 2005; see also Asa and Porton, chap. 34, this volume). Some zoos retain large holding areas to house animals that are no longer needed for breeding or exhibition programs, and some zoo professionals have argued for the establishment of "retirement homes" for such animals (Lindburg and Lindburg 1995). A final alternative is culling surplus individuals (Lacy 1995). There are policies describing when and how this option can be implemented (AZA AWC 2005; WAZA 2005). As the term *euthanasia* implies, the death must be quick, painless, and as stress-free as possible. It should also be a last resort and in conjunction with careful, long-term population planning.

WHAT CAN ZOOS DO TO BRIDGE THE ETHICS GAP?

The difficulty with zoo ethics is that there is no consensus across institutions worldwide. There are guidelines for animal welfare, environmental enrichment, euthanasia, and reintroductions, but an ethical framework regarding if and how species should be exhibited has yet to be developed. Perhaps part of the debate lies in differences in institution-by-institution priorities. Will the zoo maintain a collection based on what the visiting public expects to see, or will it focus on species of conservation need? How much risk to animal health is acceptable to improve animal welfare? How much, if ever, should zoos engage in debate or collaboration with animal advocacy organizations, particularly animal rights groups? What are the political and financial implications for the institution? Such issues are frequently discussed at professional meetings. There may be more gray areas than black and white views on how zoos should address ethical issues. However, zoos have recognized this, and are moving forward to address the concerns.

Since zoos cannot exist without a collection of live, captive animals (unless it is a virtual zoo), zoo managers obviously cannot adopt a strict animal rights ethic. However, zoos are finding more common ground with animal welfare advocates. In fact, modern, professionally managed zoos consider themselves to be animal welfare advocates (Hutchins and Smith 2003; Stevens and McAlister 2003; WAZA 2005). The AZA has even developed a national awareness campaign with the goal of portraying zoos to the public as animal welfare and conservation organizations (Mills and Carr 2005). In fact, animal welfare has become one of the most important and provocative facets of zoo management. The AZA Animal Welfare Committee (AWC) was established to ensure that AZA institutions identify animal welfare as a top priority. Its purposes are to

> foster a common understanding among AZA members of what animal welfare is, to assist members in their efforts to continually improve the welfare of animals in their care, and to serve as a guide and information resource to member organizations and the public as the AZA and its member institutions engage in cooperative local, national, and international efforts to influence animal welfare issues. (www.members.aza.org/Departments/ConScience MO/animal welfare/)

One of the projects of the AWC is to coordinate the creation of standardized guidelines for animal care by taxa, drawing on the experience of zoo animal managers and the best scientific information available.

The importance of zoo research in meeting ethical obligations cannot be understated. Physiological and behavioral studies measure cognition, motivation, and stress responses. They can be used to determine animal preferences and identify stressors (Fraser, Phillips, and Thompson 1993; Mench 1993). Some studies ask animals to select their preferred food item, social group, or exhibit furniture. For example, giant pandas, *Ailuropoda melanoleuca*, that were given the option to move between exhibit and off-exhibit bedroom areas displayed less behavioral agitation and had lower cortisol levels (a hormonal indicator of stress) than when they were given access to the exhibit area only (Owen et al. 2005). Zoos must encourage these studies and seriously consider the implications of their results.

There are few systematic efforts to examine the welfare of mammals for most taxa. Perhaps the most research has been conducted on the larger, more charismatic species. However, little attention has been paid to small mammals, including lagomorphs, rodents, and bats. Knowledge of what constitutes "normal" behavior can sometimes be difficult, due to lack of species-specific field behavioral and ecological data as well as differences among individuals of the same species. We agree with Swaisgood and Shepherdson (2005) and Carlstead et al. (1999) that future studies, including those of cognition, stereotypies, and environmental enrichment, should strive to increase sample size (e.g. through multi-institutional studies), use appropriate statistical design, and improve descriptions of methods and behaviors in published literature. Further, Swaisgood and Shepherdson (ibid.) envision the development of a predictive science for enrichment, stereotypies, and animal welfare.

Zoos must make animal welfare a research priority that is just as deserving of support as veterinary, nutrition, or any other type of zoo-sponsored research. Too often, such research is underfunded, if funded at all, and results of the studies are often not applied to day-to-day management. Partnerships have been developed with zoo and university researchers to address animal welfare issues; such partnerships should be supported. Indeed, zoo collections can benefit from the results of ethological and physiological studies in laboratory science, animal science, and wildlife biology.

There are other ways zoos can be portrayed as animal welfare advocates. For example, zoos could provide emergency services to nonzoo animals. Animal care staff can be promoted as animal welfare experts. Many zoos dispatch staff to help rehabilitate wild animals affected by oil spills. Aquariums rescue stranded marine mammals. Zoos could do more locally. They can provide advice for care of pets or care and rehabilitation of local wildlife. If they cannot temporarily maintain injured local wildlife or unwanted exotic pets, they can provide contact information for those who need it. Zoos can also partner with wildlife sanctuaries and rehabilitation centers to provide technical assistance or adopt nonreleasable animals if they could be used in zoo programs. Moreover, zoos can take a more active role in identifying exhibitors whose animals live in poor conditions, and either mentor their staff to improve animal welfare or advocate for their closure.

If zoos wish to be ethical institutions, they must also defend animal welfare issues outside their own borders. The AZA Board of Directors approved several specific issue-focused policies that affect animal welfare. These include policies opposing the use of some exotic animals as pets and rattlesnake roundups (Mays 2001). As conservation and welfare institutions, zoos must recognize that there are irreconcilable differences between them and certain animal protection organizations. Zoos should enlist conservation organizations to defend science-based wildlife management decisions that may involve controlling wildlife populations, habitat protection and removal of invasive species, and sustainable use—all of which can result in the death of individual animals, but benefit species and habitats.

Zoos and aquariums exist because of public support. They must be able to demonstrate to the public that their management practices are based on sound scientific principles and are compassionate to the animals in their care. Conservation and animal welfare are moral obligations. As stated by the AZA Animal Welfare Committee, animal welfare belongs to each animal; it is not given to them. Zoos affect the degree of that welfare, but must balance it with their conservation objectives. It is hoped that, as zoos consider the future of their collections and the urgency of their missions in a world of diminishing wildlife species and habitats, they will develop an ethical framework that will have a positive affect on the welfare and conservation of their animal ambassadors.

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2

Challenges of Zoo Animal Welfare

Ron Kagan and Jake Veasey

INTRODUCTION

The public rarely asks questions about the "happiness" of zoo animals using a scientific framework. However, in recent years the scientific community has shown significant interest in and recognition of the cognitive abilities, emotions, and feelings (such as sadness, happiness, pleasure, joy, fear, contentment, and anxiety), even the "mental illness," of animals (Rollin 1990, 2005; Duncan 1993, 2004; Bekoff 1994, 2005; Meyers and Diener 1995; DeGrazia 1996; Broom 1998; Fraser and Duncan 1998; Rushen, Taylor, and de Passille 1999; Hauser 2000; Kirkwood and Hubrecht 2001; Wynne 2002; Cabanac 2005; McMillan 2005b, 2005c; Balcombe 2006; Mendl et al. 2009). Some view these emotional and psychological qualities of animals as subjective, sentimental, and anthropomorphic (Mitchell, Thompson, and Miles 1997).

Animal welfare concerns are important to modern zoos and aquariums (hereafter *zoos*). Where compromised zoo animal welfare exists, it can lead to stress and boredom (Wemelsfelder 2005) as well as aberrant behaviors like swaying (Spijkerman et al. 1994; Wilson, Bloomsmith, and Maple 2004), fur plucking, and pacing (see Welfare Indicators section below; Bashaw et al. 2007; Miller, Bettinger, and Mellen 2008). As zoo professionals we need to understand and effectively address issues of animal welfare in our institutions. In this chapter, we present the primary concepts, challenges, and issues of animal welfare relevant to modern zoos. We also review methods to evaluate the welfare status of zoo mammals, and offer guidelines to advance this vital cornerstone of our profession. Since there are many different cultures, religions, values, and economics in the very human world of zoos, there are typical as well as unusual challenges for captive exotic animal welfare across the globe (Kirkwood 1996; Agoramoorthy 2002, 2004; Almazan, Rubio, and Agoramoorthy 2005; Bayvel, Rahman, and Gavinelli 2005; Jordan 2005; Fraser 2009b).

FOUNDATIONS OF ZOO ANIMAL WELFARE

Over 70 years ago, Gillespie (1934) acknowledged inadequacies in the quality of life of captive exotic animals. In the early part of the twentieth century, animal protection laws (Wild Animals in Captivity Protection Act of 1900/1911 in the UK) and advocacy efforts (Jack London Club in the USA) emerged as the public's concern grew over the treatment of trained and caged animals in both zoos and circuses. European countries have generally led in efforts to improve animal welfare policies and legislation (Leeming 1989; Dol et al. 1997; Radford 2001; Broom and Radford 2001; Bayvel, Rahman, and Gavinelli 2005; Caporale et al. 2005; Anonymous 2006). In 1964, the United Kingdom developed the paradigm of "Five Freedoms" in order to help the agriculture industry simplify welfare concepts, recognize the importance of well-being, and facilitate the adoption of adequate welfare standards. These freedoms include (1) freedom from injury and disease; (2) freedom from hunger, thirst, and malnutrition; (3) freedom from thermal or physical distress; (4) freedom to express most "normal" behaviors; and (5) freedom from fear. By providing for these freedoms, the UK government hoped to achieve the proper care and welfare of farm animals. The UK zoo licensing legislation of 1981 and 2000 also included the Five Freedoms, which if deemed unmet can lead to the denial/revocation of a license.

While the Five Freedoms are limited, and not a framework for measuring welfare, they give structure, context, and accountability to issues of captive animal welfare. Additional freedoms proposed more recently include the freedom of an animal to exert control over its quality of life (Webster 1994) and freedom from boredom (Ryder 1998).

The U.S. Animal Welfare Act of 1970 set the stage for regulating animal care (and, to some degree, for animal welfare) in the United States, including zoos. In 1985, amendments specifically addressed the psychological well-being of captive primates.

While animal care techniques have been improving in zoos for decades, it is only relatively recently that animal welfare has been a significant, separate topic of discussion in the United States (Norton et al. 1995; Rowan 1995; Burghardt et al. 1996; Hutchins 2002; Maple 2007). The Association of Zoos and Aquariums (AZA) created an Animal Welfare Committee in 2000, though in contrast with European zoo associations, there are still no AZA professional awards in North America for animal welfare excellence. In fact, many have published criticisms of zoo animal welfare policies and conditions (Batten 1976; Jordan and Ormrod 1978; McKenna, Travers, and Wray 1987; Malamud 1998; Mullen and Marvin 1999; Margodt 2001; Donahue and Trump 2006).

Public pressure has encouraged much of the current attention on animal welfare, while science has focused on the need to improve the conditions of farm and research animals (Dodds and Orlans 1983; Novak and Petto 1991; van Zutphen and Balls 1997; Ewing, Lay, and von Borell 1998; Rollin 2003; Benson and Rollin 2004; Duncan 2004). Zoo-sponsored research efforts focusing on animal welfare are recent and predominate in the United Kingdom and Europe. The existing challenge for all zoos is to develop both a robust and a rigorous evaluative system to measure well-being, along with a strategy that ensures a good quality of life for each animal (Hosey, Melfi, and Pankhurst 2009).

Zoos have invested in improved exhibit design over the past several decades (see Hancocks, chap. 11, this volume; Coe and Dykstra, chap. 18, this volume), yet exhibit design often attends disproportionately to human needs and wishes, e.g. aesthetics, visitor flow, and ease of cleaning. Since the design of an exhibit can play a critical role in affecting animal welfare, some new exhibits incorporate important elements that address this concern (see Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume). Zoos need to ensure that old and new exhibits meet more than the basic needs of animals.

WHAT IS ANIMAL WELFARE?

The term *welfare* is generally considered synonymous with *well-being*, which is essentially the state of feeling "well-off" (Varner 1996). *Welfare* is not a simply defined term in either philosophy or science (Fraser 1995; Wuichet and Norton 1995; Appleby and Sandoe 2002; Taylor 2003; Haynes 2008; Mellor, Patterson-Kane, and Stafford 2009). It encompasses the condition of good mental, physical, and emotional health (Appleby and Hughes 1997; Bekoff 1998; Dolins 1999; Ryder 1998; Spedding 2000; Nordenfelt 2006). Well-being is a condition that is self-determined by the individual (human or animal) and not by an observer or caretaker—a central challenge for its evaluation.

To provide a good quality of life for captive mammals, we need to understand the main determinants of well-being for each species and, just as important, each individual (Gosling 2001). For example, while the need for food is obviously critical to all organisms for survival, the control over choice of food items, mealtimes, and dining style may be important to some species and/or some individuals, but less so to others (Young 1997; Owen et al. 2005; Videan et al. 2005; Ross 2006).

How can we know if an animal's welfare or state of well-being is good? An understanding of a species' behavioral ecology and natural history is fundamental to identifying those factors likely to be linked with the individual's well-being. Welfare is also dependent on an individual's ability to perform certain species-specific behaviors that it is highly motivated to perform, e.g. nest building or avoiding predators (Gregory 2005; see McPhee and Carlstead, chap. 25, this volume). There should be an absence of signs of distress or severe discomfort and of acute or prolonged stress that results in a reduction in physical and/or mental health (Broom and Johnson 1993; Balm 1999; Moberg and Mench 2000). Thus, good welfare can be demonstrated by the absence of "problems" along with the presence of normal, natural behaviors and good physical condition (Archer 1979; Stoskopf 1983; Wiepkema and Koolhaas 1993; von Holst 1998; Sapolsky 2004; Morgan and Tromborg 2007).

The term *distress* has been suggested as central to characterizing the impact of negative stress (Wielebnowski 2003; McMillan 2005b; NRC 2008). Prolonged distress or severe discomfort will compromise well-being and is measurable behaviorally and/or physiologically. While we are sure that animals deprived of food and water for a prolonged period will ultimately be distressed, we still do not know if (or how much) distress occurs when other, less obvious physical or social needs are not met. If an anteater lives in a zoo without a deep substrate in which to dig, will it be distressed? Do captive polar bears and other marine mammals experience distress when maintained in freshwater as opposed to seawater? We need far more research on hundreds of exotic species to answer these questions.

Individual physical problems, e.g. from disease-related decline, may neither result from poor welfare nor cause a reduction in welfare. For example, an animal's arthritis may not be caused by poor management, but by effective husbandry and care that allow the individual to live longer than is typical in the wild. However, arthritic animals may not only experience chronic pain but also be unable to perform species-specific behaviors, e.g. avoid the aggression of conspecifics, in which case their well-being is likely compromised.

An animal's survival in the wild depends on its successfully reacting and responding to its environment (Poole 1992; Stafleur, Grommers, and Vorstenbosch 1996; Broom 1998; Dawkins 1998). If a zoo animal cannot react appropriately to stimuli in its captive environment, behaviors indicative of "frustration" may result. In addition, the "design" of mammals includes the need to initiate activity (e.g. play, exploration, information gathering) based on changes in motivation, and not just to react to events or circumstances (Mench 1998; Carlstead 1999). Although conditions that compromise well-being do occur in the wild, the animal management staff is responsible for ensuring adequate well-being once an animal enters the care of the zoo. Zoos need to address how they can meet the complete needs of all their mammals, regardless of an animal's age, popularity, or value (Föllmi et al. 2007).

Both the physical and the social environments (Rees 2009) profoundly affect quality of life and therefore state of welfare and sense of well-being. Quality of life and suffering are subjective and relative challenges for animals as they are for humans (Sandoe 1999; Wemelsfelder 1999; Dawkins 1980, 2005; Gregory 2005).

WELFARE INDICATORS

In a very real and literal way, humans are somewhat "blind" to how most other species perceive and experience the world. Our ability to understand the needs of most mammals may also be quite limited. A greater research focus on "soft" psychological characteristics (e.g. animal awareness, consciousness, sentience, emotions, individuality, feelings, and thoughts) may help us better understand the complete needs and complexity of other mammals and therefore how to improve their welfare in captivity (Dawkins 1993, 2001; Capitano 1999; Griffin 2001; Kirkwood 2003; Turner and D'Silva 2006; Powell and Svoke 2008; Fraser 2009a).

Since the thoughts and feelings of animals are largely inaccessible to us, we rely on indirect indicators of an animal's mental state and physical condition to determine its state of well-being. Historically, indicators of zoo animal well-being have included longevity and reproductive success. However, mammals can survive and reproduce over many years, even in the most stressful circumstances. Thus, we need to establish more sensitive indicators.

The challenges scientists face in assessing animal welfare are considerable (Sandoe and Simonsen 1992; Mason and Mendl 1993; Mench 1993; Gonder, Smeby, and Wolfe 2001; Dawkins 2003, 2006; Jordan 2005; Webster 2005). The great number of species, small sample size, limited resources (financial and staff), multiple variables (including individual animal variation), and the unique circumstances of each facility all create additional obstacles when working in zoos. Assessing welfare generally involves measuring behavioral and physiological responses to stressors (Morgan and Tromborg 2007; McPhee and Carlstead, chap. 25, this volume; Hodges, Brown, and Heistermann, chap. 33, this volume). The behavioral and physiological responses of mammals to environmental variables, e.g. insufficient space, that typically have a negative impact on welfare are thought to be their attempts to cope with or eliminate stressors.

PHYSIOLOGICAL INDICATORS

Physiological responses to stress are complex and multifaceted, and they vary according to the species of the animal and the nature of the stressor (Moberg 1985; Touma and Palme 2005; see also Hodges, Brown, and Heistermann, chap. 33, this volume; McPhee and Carlstead, chap. 25, this volume). Exposure to stress generally results in an elevation in glucocorticoids secreted by the hypothalamic-pituitary-adrenal (HPA) axis (Matteri, Carroll, and Dyer 2000; Shepherdson, Carlstead, and Wielebnowski 2004; Carlstead and Brown 2005; Lane 2006). The secretion of these steroid hormones facilitates the mobilization of energy reserves and enhanced cardiovascular tone to prepare the animal for a coping response, such as fight or flight.

Physiological indicators of welfare primarily involve measuring compounds released by the animal in its blood, and/or in excreta and saliva, as well as short-term changes in body temperature and heart and respiration rates (Dathe, Kuckelkorn, and Minnemann 1992; Bauman 2002; Von der Ohe and Servheen 2002; Peel et al. 2005; Stewart et al. 2005; Touma and Palme 2005; Pedernera-Romano et al. 2006; Hodges, Brown, and Heistermann, chap. 33, this volume). However, an elevation in glucocorticoids comparable to that during a stress response can occur seasonally or when an animal is simply excited or has exerted itself. Indeed, the sampling procedure alone, particularly if this involves capture and taking blood, may activate a stress response, potentially invalidating any worthwhile conclusions about other stressors. Further complicating our understanding of the physiological indicators of stress is the finding that in some situations of chronic stress, the HPA response will be depressed (Wielebnowski 2003).

Chronic stress, with a prolonged activation of short-term coping responses, can ultimately harm the health of an individual. The more the animal is required to cope—and the less an animal is able to cope—the more its welfare is likely to be compromised. Chronic physiological stress responses can also be measured, and include immunosuppression, reduced fecundity, reduction in protein synthesis, weight loss, elevated blood pressure, ulceration, thickening of the arteries, and premature death (Coe and Scheffler 1989; Blecha 2000; Elsasser et al. 2000; Shepherdson, Carlstead, and Wielebnowski 2004). Chronic stress reactions may be particularly significant in assessing the level of everyday welfare of zoo animals, because they should reflect welfare status under the prevailing conditions, rather than at the moment of measurement. However, chronic stress indicators are often difficult to measure in live animals. Finally, these measures only result from highly acute or prolonged stressors, and so while they can tell us that the animal is coping poorly, they may be slow to do so.

BEHAVIORAL MEASURES

Since the collection and interpretation of physiological indicators may be difficult, behavioral studies are often a practical approach to evaluating welfare status, particularly in such nonexperimental conditions as are found in zoos. Comparing the behavior of zoo mammals with their wild counterparts can reveal the effects of captive conditions on exotic mammals as we attempt to improve zoo mammal well-being (see also McPhee and Carlstead, chap. 25, this volume).

Time budgets and comparisons with the wild. Time budgets essentially measure how animals allocate their time. Animal care staff can use time budgets of captive mammals as a baseline to assess the impact on behavior caused by changes in management practices or other changes in the animal's physical and social environment. Knowledge of the time-budget differences between wild animals and captive animals can indicate possible problems with captive management (Mallapur and Chellam 2002; Melfi and Feistner 2002), although changes in the frequencies of certain behaviors need not—e.g. it is unlikely that a reduction in vigilance behavior by prey animals would mean that their welfare was compromised.

Preference tests and behavioral needs. Animals can provide insight into their motivations by expressing preferences for certain environmental variables (Fraser, Phillips, and Thompson 1993; Duncan 2004). Thus, preference tests can indicate what animals are motivated to obtain or to avoid. For example, chickens prefer larger cages with a substrate to smaller cages with a wire floor (Dawkins 1983), presumably because the former provide more opportunities to perform species-appropriate behaviors such as dust bathing. However, preference tests only indicate a relative preference. Preferences may vary based on age, season, temperature, social environment, previous experiences, and the availability of different resources. Also, because an animal expresses a preference for a certain variable does not mean that it will inevitably experience reduced well-being in its absence. Finally, animals do not always make choices that are in their individual best interests: e.g. adult male mammals may fight during the breeding season.

The strength of preferences can be measured by making the animal choose to give up resources or perform work for its preference (Consumer Demand Theory: Dawkins 1983, 1990). An individual's unwillingness to sacrifice food, comfort, or social contact, or its willingness to perform "work" such as pressing levers, swimming through cold water, or pushing open heavy doors, is measurable (Van der Harst and Spruijt 2007; Watters, Margulis, and Atsalis 2009) and can demonstrate the strength of its preference. The harder the animal works or the more it is willing to sacrifice, the greater its preference, and hence the greater the likely welfare deficit if the individual is denied access to that resource or opportunity. Such an approach can inform facility design, especially with regard to indoor areas (Ewing, Lay, and von Borell 1998). Species differences are important considerations; a lack of social interaction is likely to be more significant for a social primate such as a chimpanzee than for a solitary predator such as a tiger. Similarly, the compression of an elephant's extensive daily walking routine into 2 or 3 hours in captivity is likely to pose a greater welfare challenge than altering a captive snake's mobility or feeding ecology.

There are certain behaviors (termed behavioral needs) that we believe animals must perform for satisfactory well-being. Such behaviors may be of a long duration, energetically demanding, and internally stimulated (i.e. not reliant on external stimuli). For example, if members of a species typically forage for 14 to 20 hours per day in the wild, limited foraging opportunities in a captive environment may lead to reduced well-being. Zoo professionals should develop creative ways to compensate for such a large discrepancy in the time budget (McPhee and Carlstead, chap. 25, this volume).

Animals usually exhibit escape behavior in the presence of the appropriate external stimuli, e.g. a predator. Nevertheless, many zoo exhibits house animals in close visual, auditory, and olfactory proximity to machinery, visitors, and other species, including their natural predators (Hosey 2000; Birke 2002; Davey and Henzi 2004; Davey 2006; Owen et al. 2004; Davis, Schaffner, and Smith 2005; Powell et al. 2006; Sellinger and Ha 2006; Davey 2007; Kuhar 2008). While the actual risk of being attacked is low (though there are risks of predation in zoos), an animal may exhibit predator avoidance behaviors, e.g. hiding. This important behavioral need can collide with the zoo's wish to have animals in full view during visitor hours.

Abnormal behaviors. We can also document the frequency and duration of "abnormal" behaviors, the most obvious of which are stereotypic behaviors (Meyer-Holzapfel 1968; Dantzer 1986, 1991; Mason 1991a, 1991b, 2006; Mason and Latham 2004; Wechsler 1991; Lawrence and Rushen 1993; Gruber et al. 2000; Rees 2004; Wilson, Bloomsmith, and Maple 2004; Montaudouin and Le Page 2005; Shyne 2005; Tarou, Bloomsmith, and Maple 2005; Swaisgood and Shepherdson 2005; Renner and Kelly 2006; Ross 2006; Elzanowski and Sergiel 2006; Soriano et al. 2006; see also McPhee and Carlstead, chap. 25, this volume). High levels of stereotypy may indicate that an individual has experienced a welfare challenge and has been coping for a prolonged period (Wilson, Bloomsmith, and Maple 2004). These unvarying behaviors have been correlated with poor welfare, as they are typically seen in animals housed in small enclosures. However, stereotypies, like physiological changes, can also occur when an animal is simply excited (Veasey 1993). It has been suggested that stereotypic behaviors may be satisfying or soothing to perform in that they provide a controllable (albeit high) level of stimulation that helps the individual animal cope with unpleasant or uncontrollable conditions (Rushen 1993). Thus, some animals exhibiting stereotypies may actually have lower heart rates, higher levels of circulating endogenous opioids, and reduced cortisol levels in comparison with animals in similar conditions not exhibiting stereotypies (Dantzer 1986; Mason 1991a).

A factor complicating the relationship between stereotypies and animal welfare is that even after conditions improve, stereotypies often persist (Mason 1991b). Therefore the presence of stereotypies may not always reflect the prevailing conditions experienced by the individual. Assessing and addressing the welfare (and especially stereotypies) of primates, elephants, bears, and marine mammals, with their complex behavioral needs, is especially challenging (Novak and Suomi 1988; Kiley-Worthington 1990; Schmid 1995; Galhardo et al. 1996; Baker 1997; McBain 1999; Waples and Gales 2002; Clubb and Mason 2003; Swaisgood et al. 2003; Hosey 2005; Cheyne 2006; Hutchins 2006; Meller, Coney, and Shepherdson 2007; Wemmer and Christen 2008; Forthman, Kane, and Waldau 2009). Instances of apparent stereotypic behaviors have been described in wild animals (Veasey, Waran, and Young 1996).

Behavioral indicators of poor welfare or distress can also include vocalizing, extreme timidity, aggression, escape behaviors, self-mutilation, fur plucking, pacing (Boinski, Gross, and Davis 1999; Wielebnowski et al. 2002; Peel et al. 2005), and decreased performance of behaviors critical to survival and reproduction, e.g. grooming, mating, and foraging/feeding. The context is important when attempting to attribute a cause to the behaviors.

COMPENSATING FOR STRESS

Enrichment is one method of compensating for compromised conditions in captivity. Environmental enrichment programs (Markowitz 1981; Markowitz and Aday 1998; Maple 1996; Robinson 1997; Young 2003; Shyne 2005; Shepherdson, chap. 6, this volume; Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume) continue to evolve as an important way to address challenges created by captive environments.

For zoos, environmental enrichment has traditionally not been as rigorously and consistently applied as has "basic" management, i.e. husbandry, nutrition, and preventive medicine. "Basic" animal care (e.g. feeding, housing, and transport) has tended to be separated from animal welfare (i.e. *how* an animal is fed, housed, and transported) (Dembiec, Snider, and Zanella 2004; Broom 2005; Iossa, Soulsbury, and Harris 2009). Zoos need to allocate more staff time and expertise to enrichment and engage welfare professionals who have been scientifically trained (see Shepherdson, chap. 6, this volume; Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume).

Although counterintuitive to some degree, exposure to a certain amount of stress, even in captivity, may be good for animal well-being (McEwan 2002), since stress in nature helps individuals build a healthy capacity to cope with dynamic physical and social environments. Some of the stress in captivity is similar in frequency, quality, and magnitude to the stress of living in the wild; but captive animals face many additional artificial stressors, e.g. confined space, close proximity to conspecifics, constant human presence, unnatural diets, and exposure to chemicals for cleaning enclosures, among others (Morris 1964; Hosey 2008).

Providing zoo mammals with choice in addition to the Five Freedoms discussed earlier is an enormous challenge (Laule 2003; Owen et al. 2005; Videan et al. 2005; Schapiro and Lambeth 2007) and requires significant rethinking and reengineering of space and other resources for many mammalian species. Control, choice, and decision making represent important biological needs, since they are characteristics that animals exhibit regularly in the wild (Meyers and Diener 1995).

INDIVIDUAL VERSUS SPECIES WELFARE

Conway (1976) suggested that focus on the welfare of individuals is antithetical to the conservation of species, and creates a conflict between the welfare of individuals and that of populations. Thus, the argument implies that consideration for the welfare of many, including future individuals, should outweigh consideration for the welfare of an individual (Lacy 1991, 1995). Animal welfare groups, the media, and the general public often focus their attention on individual animals. And some in the conservation community (including zoos) may essentially contribute to welfare "speciesism" in that the charismatic megavertebrates often benefit more from attention and investment than other species (e.g. giant pandas [*Ailuropoda melanoleuca*] and gorillas [*Gorilla gorilla*]). Zoos' conservation education programs that encourage a greater focus on species survival and habitat preservation may not overcome the great value the public places on individual animals, especially large mammals (Conway 1976; Lewandowski 2003). Zoos can, however, take on this challenge and engage the public in a discovery of, and dialogue about, the relationship between individual animal welfare and conservation, including the complicated choices and significant costs of achieving well-being for all individuals.

Conway (1976), Lacy (1991), and Lindburg (1991) argue that an aesthetic appreciation of individual animals can lead to enhanced appreciation of and support for species. This may be a major contribution of zoos, and the foundation for much support for wildlife conservation and animal welfare (see Routman, Ogden, and Winsten, chap. 12, this volume). Ideally, we should develop solutions that benefit both individuals and populations, although strategies and practices that fully embrace both animal conservation and animal welfare can be difficult to achieve (Kagan 2001; Maple 2003). For instance, consider the dilemma faced by a zoo asked to provide space and resources for a rescued pet tiger of uncertain ancestry. By accommodating this animal, the zoo now may have less space available for captive breeding of genetically valuable tigers capable of making substantial contributions to conservation.

ZOO ENVIRONMENTS FOR IMPROVED ANIMAL WELFARE

The design of exhibits and the interaction of keepers with the animals in their care are central determinants of the quality of a captive animal's life (Shepherdson, Mellen, and Hutchins 1998). For some exhibits, an important distinction between captivity and confinement can be made (Wemelsfelder 2005). Some zoo mammals may be so limited and restricted by their physical environment that they are indeed confined, and not simply captive (Bostock 1993).

Decisions of animal care staff essentially replace many important decisions the animal would have made in the wild. For example, choosing a mate or when and what to eat are important life experiences that we, not the captive animal, determine. Providing significant choice and control to the animal may improve its situation quite dramatically. Current management protocols for elephants, including maintaining them in chains—though banned in the United Kingdom by elephant management guidelines established by the British and Irish Association of Zoos and Aquariums—and the use/threat of physical discipline including electric shock—current AZA elephant standards—are vivid examples of how intensive our control is over some zoo animals (Schmid 1998; Friend and Parker 1999; Gruber et al. 2000; Elzanowski and Sergiel 2006).

Greater knowledge of and sensitivity to how animals (not humans) perceive and experience life in a captive environment could help prevent a host of stressors from dramatically compromising the well-being of zoo animals (Wemelsfelder 1999). For example, while humans' sensory abilities include detecting certain air pollutants, we may not detect many odors (or their relative intensity) or realize that prolonged, even chronic, exposure to fumes from cleaning solutions, urine, dust, and excreta in a holding barn could be extremely challenging for many animals. Moreover, captive animals are often subjected to loud noises (Birke 2002; Owen et al. 2004; Coppola, Enns, and Grandin 2006; Patterson-Kane and Farnworth 2006; Powell et al. 2006), inappropriate temperatures (Lindburg 1998; Rees 2004), unnatural light cycles and/or artificial lighting, and forced human proximity (Rushen, Taylor, and de Passille 1999; Fernandez et al. 2009). Since we humans are usually only temporarily exposed to these stimuli within exhibits, we may not perceive the stimuli as strong, offensive, or even detect them at all.

Similarly, zoos with relatively spacious natural and complex outdoor exhibits may not allow their animals to remain outdoors 24 hours a day for reasons of visibility, security, weather, and ease of maintenance. Some zoos "rotate" individuals within exhibits several times during the day to ensure that the animals that are on display are always active. Thus, some individual animals may spend the vast majority of their lives, by design, off exhibit in small, sterile holding cages (Sommer 1973; Coe 2003), not significantly different from what was provided 50 years ago. We need to provide mammals that climb, dig, fly, run, hide, swim, and burrow with ample and appropriate opportunities to express their behavioral needs. For convenience, we feed some zoo animals at set times in specific locations, not the way most animals feed in the wild. As a consequence, we increase predictability and the passive time in the animals' daily time budget, and we may facilitate aggression in group-dwelling species.

Finally, the impact of weather and climate on captive exotic animal welfare needs significant scientific attention.

THE FUTURE

The environments of zoo animals have improved over the years and, it is hoped, not only appear better to visitors, but also are better for the animals. But, as Mench and Kreger (1996, 10) so poignantly wrote in the first edition of this book, "The natural habitat created in a zoo environment is an illusion . . . real to the visitor but to the animal . . . restrictive, monotonous, lacking most of the niches in nature." While hard to admit, zoo professionals' assumptions, best intentions, expertise, and great affection for animals do not necessarily mean that all individual captive animals are thriving. Our challenge is to develop and utilize accurate measurements of well-being and to provide conditions that will promote welfare for all animals in our care.

Today, while exhibits are larger and more cosmetically appealing to humans, they still may not be fully relevant to their residents. A mowed grassy area may be enticing to humans, but does not offer a natural home to most animals (see Hancocks, chap. 11, this volume). We believe that if each zoo maintained fewer species in truly appropriate physical and social conditions, captive animals would experience better well-being.

Our own sensory limitations as well as the costs of change retard progress in developing new approaches. Providing a full, 24-hour, enriched, stimulating, and relatively uncontrolled life experience for zoo mammals mandates sophisticated, complex environmental design and significantly different animal management practices, developed from extensive, professionwide collaborative research efforts and evaluations (Smith 2004; Wells and Irwin 2008; Wells 2009). Our goal should be to establish institutional policies and professional standards that provide animals with a full range of opportunities, choice, and control.

Of course, we need to avoid creating exhibit features that can pose serious risks for our animals. For example, water moats may be more attractive and less expensive to build than dry moats, and they are effective at containing almost all primates. But, they led to drownings in half of all U.S. water-moated chimpanzee exhibits during the 1990s, even where compensatory safeguards such as underwater nets were installed (data from Chimpanzee SSP). While costly and logistically challenging, we also need to provide mammals with opportunities to be rough on their environments, e.g. to destroy trees (Maki and Bloomsmith 1989). Hot-wired trees and other inaccessible naturalistic exhibit features afford little value to the nonhuman primates.

Our focus should be on optimum, not minimum, conditions. We need to consider that even a successful record of increasing investment in *ex situ* and *in situ* conservation (improving the welfare of a species) does not necessarily mean that individual zoo animals have been adequately provided for (Kirkpatrick 1996). Saving a species may be a hollow conservation success, and ethically questionable, if we harm individual captive animals in the process. We need to advance both the science and the policy of zoo animal welfare (Jordan 2005; Defra 2005, 2006); otherwise, our public standing as "the" animal experts, advocates, and preservers is vulnerable.

ASSOCIATIONS/WEB SITES FOCUSING ON ANIMAL WELFARE

Important associations/Web sites that focus on animal welfare research and issues include the Scientists Center for Animal Welfare (SCAW—www.scaw.com), Universities Federation for Animal Welfare (UFAW—www.ufaw.org.uk), Society and Animals Forum (formerly Psychologists for the Ethical Treatment of Animals, www.psyeta.org), and the International Society for Applied Ethology (ISAE—www.applied-ethology.org). Related journals that regularly publish captive animal welfare studies include *Applied Animal Behaviour Science*, *Animal Welfare*, *Journal of Applied Animal Welfare*, and *Zoo Biology*.

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3

Setting Standards for Evaluation of Captive Facilities

Joseph Barber, Denny Lewis, Govindasamy Agoramoorthy, and Miranda F. Stevenson

Overview

Joseph Barber

INTRODUCTION

The establishment of zoo and aquarium (henceforth *zoo*) accreditation programs is a critical milestone in the history of zoo associations, and plays an important role in promoting the welfare of captive wild mammals. In the following subchapters, 3 similar approaches to assessing the level of care offered by individual zoos are discussed from different regional perspectives. Each author identifies the development of high-level animal care standards as an integral component of accreditation or welfare assessments. Since accreditation relies on this development, and since our understanding of animal care and welfare continues to change with new research findings, zoos are faced with an ongoing commitment to updating these standards of care. In this introduction, the process of accreditation will be discussed in terms of its purpose and its ability to offer valid insights into animal welfare. The challenges associated with accreditation and the process of developing animal care standards will also be highlighted, and possible solutions to these challenges identified.

ACCREDITATION

In the following subchapters, the authors describe a mostly qualitative approach to evaluating the level of animal care offered by zoos, believing it to be the most effective tool to ensure that institutions are meeting appropriate care standards (Lewis, chap. 3b, this volume). This approach involves onsite examinations of animal, personnel, and storage areas, interviews with animal care staff, and a review of documented zoo records (ibid.; Agoramoorthy, chap. 3c, this volume; Stevenson, chap. 3d, this volume). Written materials, policies, programs, and philosophies are reviewed in comparison to general standards of care identified by the zoo associations. Many of the animal care recommendations featured within the accreditation standards discussed are based on the concepts described in the Five Freedoms (Brambell 1965; Farm Animal Welfare Council 1992; see Kagan and Veasey, chap. 2, this volume). The creation of accreditation programs that expand on and formalize these guiding principles within a framework of general animal care standards is a very important step. However, these "freedoms" only offer general guidelines, and there are challenges associated with applying these standards of care consistently and interpreting them objectively during any accreditation or welfare inspection.

If one of the goals of accreditation is to improve standards of animal welfare (Lewis, chap. 3b, this volume; Stevenson, chap. 3d, this volume), then it will be necessary to be able to measure welfare. True assessments of animal welfare are based on detailed quantitative analyses of the behavior, physiology, and physical health of individual animals (Dawkins 1976, 1983, 1998; Broom 1991a, 1991b, 1996; Rushen and de Passille 1992; Mason and Mendl 1993; Clark 1997; Clark, Rager, and Calpin 1997; see also Kagan and Veasey, chap. 2, this volume). Since no new quantitative information is collected during the accreditation processes described by the authors, and the time actually spent observing animals over a 2- to 3-day inspection is minimal, accreditation can only offer an indirect assessment of animal welfare. For example, during a qualitative assessment, an accreditation inspector may look for evidence of an effective nutrition program, but will have no direct way of determining whether each animal is experiencing any nutrient deficiencies unless veterinary records are readily available. When looking at animal exhibits, inspectors may also look for evidence that enrichment has been provided to the animals, but the presence of enrichment initiatives does not show the inspectors whether that enrichment is truly effective at promoting species-appropriate behaviors. Thus, the concepts addressed in the Five Freedoms are only really suited to evaluations of whether captive conditions are theoretically suitable for animals to experience good welfare, in that they represent ideal states rather than specific animal care standards (Farm Animal Welfare Council 1992).

Without strict criteria to evaluate collected information (similar to that dictated by the statistical analysis of quantitative data), qualitative assessments run the risk of being subjectively interpreted. The challenges associated with these assessments are underscored by the example provided by Agoramoorthy (chap. 3c, this volume), where in-house zoo evaluators, in reviewing their own institutions, identified fewer welfare concerns and chose better-constructed exhibits to assess than did evaluators from outside institutions. Nonetheless, there is little doubt that zoo professionals are particularly qualified to determine the suitability of animal care, given their experience working with wild animals in captivity. Using accreditation inspectors from the zoo community, who understand the very real limitations that zoos face, is perhaps the most feasible way for a zoo association to conduct an accreditation or welfare inspection. However, it may not be the only or the best method to achieve the goal, identified by Stevenson (chap. 3d, this volume), of consistently applied standards leading to high-quality zoos. The fact that a zoo lacks the money or space to build larger exhibits, or faces restrictions in how it houses more tropical species during cold-weather months, or is limited in how much browse it offers to a browsing species throughout the year because of its locale, are certainly realities of captive animal management. However, these issues are not sufficient by themselves to justify any variance from professionally developed animal care standards that are focused on the welfare of animals. Assessments of animal welfare should be made independently of the limitations that zoos face, and animal care standards implemented equally in all situations. The effectiveness of accreditation programs will always be judged based on how objectively they address situations where zoos cannot meet the needs of certain species because their limitations are too great. The need for a consistent approach is critical to ensure that professionals outside the zoo community can see that good science is not being ignored in the interest of institutional solidarity.

The accreditation and inspection programs discussed in the following subchapters are currently not set up to offer insights into the actual welfare status of zoo mammals (Agoramoorthy, chap. 3c, this volume), as this would require inspectors having specific knowledge of every species in the collection, and significant periods of time to research the conditions. As an indirect measure of welfare, qualitative accreditation programs are limited to an assessment of "welfare potential"—the potential that captive animals will experience good welfare based on the conditions they are provided. For example, the more effective the animal care programs are at an institution, the greater the potential that the animals will be housed, fed, trained, and enriched in the most appropriate manner. Since animal welfare is a property of individual animals (Broom 1996), we can never assume that recommended standards of animal care will be sufficient to meet the needs of all animals in all situations. Indeed, without a quantitative assessment of the impact that recommended standards of animal care have on the welfare of individual animals, it is difficult to determine the efficacy of any standards. There is a great opportunity for this type of data to be collected by all zoo associations.

Qualitative assessments may currently be the only way for inspectors to get a snapshot of the animal care offered by zoos, but the question remains whether assessments of "welfare potential" represent the end of the road when it comes to evaluating captive facilities, or simply a step in the right direction. As the techniques used to assess the welfare of captive mammals become more readily available, should the measurement of *actual* welfare be a key consideration in the improvement of zoo accreditation programs?

A FUTURE APPROACH

It is important to acknowledge the significant progress that zoo associations have made in establishing and implementing accreditation programs; but while it is tempting to say that accreditation differentiates good zoos from bad zoos, the reality is slightly more complex. For example, there are instances of animals performing abnormal stereotypic behaviors within both accredited and unaccredited facilities (e.g. Carlstead, Brown, and Seidensticker 1993; Stoinski, Daniel, and Maple 2000; Bashaw et al. 2001; Jenny and Schmid 2002; Tarou, Bashaw, and Maple 2003; Rees 2004). These behaviors can be interpreted either as coping responses (Cronin, Wiepkema, and van Ree 1986; Jones, Mittleman, and Robbins 1989; Zanella et al. 1996), or as indicators that the needs of the animals are not being met (Mason 1991; Wechsler 1991; Vickery and Mason 2004). If the latter interpretation is valid for animals in accredited zoos, then there would seem to be a disconnect between what has been judged by accreditation as appropriate from a "welfare potential" perspective, and what the animals are actually experiencing. If these types of disconnects do exist, then the need to assess the actual welfare of mammals is vitally important.

Incorporating more quantitative assessments of welfare into qualitative accreditation programs will certainly be a challenging endeavor. Small steps will be necessary, such as the creation of species-specific animal care standards (Lewis, chap. 3b, this volume). Although still not a measure of welfare, such standards of care would offer much more objective information to accreditation inspectors—and the more objective the information they have, the more consistently it can be applied.

Creating species-specific standards is not without its challenges, however. The behavior of mammals can show a great deal of plasticity (Komers 1997; Reader and Laland 2001), and not all animals within the same species will respond to the same conditions in the same way. Deciding how best to combine the knowledge of animal care professionals with information from the scientific literature to create these standards also requires considerable deliberation. All standards of care will need to be validated by quantitative assessments if they are to become more objective.

The validity and objectivity of any species-specific welfare standards would be effectively illustrated if all regional zoo associations endorsed them. Since a Thomson's gazelle or an elephant will have the same needs in whichever country or latitude they are housed, the development of different regional standards would seem counterintuitive. This is the current reality, though. Stevenson (chap. 3d, this volume) describes the difficulty that neighboring countries have in agreeing on the same set of general standards within a region, let alone finding a consensus between regions. In the absence of scientific data, experiential and intuitive knowledge remains a key component of animal care. However, the more scientifically based that standards can be made, the more likely it is that proponents and opponents of zoos can debate the issues behind the management of captive mammals in more objective rather than subjective terms—not a common occurrence at present (Agoramoorthy, chap. 3c, this volume).

CONCLUSION

The information in the following subchapters chronicles the progress of 3 different regional associations in developing formalized accreditation programs. There is little doubt that accreditation programs do improve the conditions for captive mammals, and zoo associations should clearly document the evidence to support this belief. Nevertheless, while many of the programs implemented in zoos over the last 30 years have focused on providing more effective animal care (maximizing "welfare potential"), the ability of animal care staff within zoos to assess animal welfare quantitatively has yet to show a similar advancement—nor have the tools or training needed to do so become more available within the community. Thus, the creation of species-specific animal care guidelines in tandem with the further development of tools and methods needed to assess animal welfare, and not just "welfare potential," will be fundamental to the continued improvement of welfare standards for evaluating the captive facilities for wild mammals.

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North America

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INTRODUCTION

Until professional standards were established in the early 1970s, zoological parks and aquariums in North America were governed according to the varying objectives of their individual governing bodies and staff. The creation of standards was a recurring topic of discussion, but individual goals and interests at each institution remained the driving force in making choices regarding animal housing and care.

In 1965, the call for an accreditation-like program began in Great Britain, where the Federation of Zoos (now known as BIAZA—the British and Irish Association of Zoos and Aquariums) administered its development. In the United States, several states passed legislation that included a system of inspection and licensing embodying the public's rightful concern about the well-being of animals in zoological collections. On a federal level, the passage of the Animal Welfare Act in 1966 reflected the nation's growing concern about animal care.

The zoo and aquarium community in North America recognized that the time had come for development of a system for evaluating the quality of institutions holding wildlife in the United States, and that its own professional organization, the Association of Zoos and Aquariums (AZA—then known as AAZPA, the American Association of Zoological Parks and Aquariums), was best qualified to accomplish this task. AZA members had long expressed a collective belief that institutions maintaining wildlife must recognize and accept common goals, and seek to advance those goals by adhering to professional standards for maintaining quality and performance.

AZA and its members believe that assuring high standards of animal management and husbandry is paramount in the operation of collections of living creatures, and that good conscience permits no higher priority. In addition to enhancing animal care, AZA recognized that an unbiased and thorough review of zoos and aquariums, measured against written standards and performed by experts within the profession, would provide a service in assuring the public that excellent care was indeed being provided to the collection housed within. AZA also understood that providing quality animal care was dependent on an institution's entire operation, including areas not directly related to animal care, such as governance, finance, maintenance, and the support organization. And finally, by encouraging strong programs in education, conservation, and other scientific studies designed to benefit animals, the importance of maintaining such collections for reasons beyond simple recreational purposes would be increased.

In the early 1970s, AZA developed an accreditation process and appointed an Accreditation Commission to oversee its administration. The twelve-person body consists of a chairperson and eleven commissioners usually serving 2 consecutive 3-year terms. In addition to the chair and commissioners, several advisors are appointed to serve, without vote. Advisors expand the overall body of expertise of the commission, and are appointed from among past commissioners to enhance continuity. Those appointed to serve on the commission are selected from among the top authorities in their fields of expertise, including zoological and aquarium operations, animal management and husbandry, and veterinary medicine, representing zoos and aquariums of all sizes. Currently, commissioners and advisors serving on the Accreditation Commission comprise over 450 collective years of professional training and experience, on which they draw when considering each case and making decisions.

In addition to possessing expertise within the profession, commissioners must approach each case without bias and judge each institution based on factual information substantiated by inspectors. Anything less compromises the integrity of the accreditation process, negates its purpose, and removes its value from every institution that has earned the credential.

Accreditation is granted to institutions judged as meeting or exceeding the professional standards developed by AZA. The process itself is a rigorous one, taking upward of a year to complete, and in some cases longer. Accreditation is good for 5 years, at which time an institution must complete the entire process again.

ASSESSMENT PROCESS

Accreditation begins with the completion of an application, and assembly of documentation. The application package contains copies of institution policies, procedures, personnel information, animal inventory, financial statistics, reports from outside agencies, master plans, and much more—all key elements in measuring the quality of a professional operation. Months of preparation go into the application prior to submittal, after which an intense, 6-month evaluation is conducted by the Accreditation Commission and its expert team of inspectors.

Undergoing an accreditation inspection is analogous to an audit or a physical examination: all require individuals with the proper training and experience in the applicable field to conduct the investigation. Inspectors are selected by the commission from within the ranks of the zoological and aquarium profession based on a demonstrated level of expertise in their chosen field, as well as a set of specific criteria. Each team member must remain impartial and measure an institution solely against standards. It is also important that *all* team members agree that an institution is meeting a standard before approving it as such. Teams are composed of experts in *3* primary fields: operations, curatorial/husbandry (animal management), and veterinary medicine. Inspection teams range in size from 2 to 4 inspectors depending on the size of the institution being assessed, and always include a veterinarian.

After evaluating the institution's application, teams spend 2 to 4 days inspecting the institution in light of professional standards and generally accepted modern zoological practices and philosophies. Team members spend several months preparing for the inspection by studying all the institution's internal materials submitted with its application, and draw on their professional expertise and experience in making their judgments. Examples of materials inspectors review in advance include all internal policies and procedures, reports, staff resumes, long-range and master plans, animal inventories, departmental programs, maintenance programs, finances, and educational materials. While on site, inspectors examine all areas of the physical plant, including exhibits, holding and service areas, food preparation and storage areas, the animal hospital and quarantine areas, public amenities, eateries and restaurants, maintenance areas, administrative offices, and off-site facilities if any exist. Additionally, inspectors review animal records, diets, medical reports and records, and reports of outside agencies such as the U.S. Department of Agriculture. Inspectors also conduct private interviews with staff at all levels, as well as with the governing authority and support organization.

At the conclusion of the inspection, the inspection team presents the institution director with a list that must be addressed before the institution can be granted accreditation. Based on the team's observations, the list includes both major and lesser concerns, and also identifies areas in which the institution is judged as excelling. Each institution is expected to provide the Accreditation Commission with a written account documenting how those concerns are being addressed. Finally, representatives of the institution appear in person before the commission to answer questions and receive the commission's decision. The commission considers all factors when determining the outcome of a case, including the number *and* the nature of the concerns, and how they have been addressed.

After the hearing is concluded, the institution receives a copy of the inspection report. This report is tied to the list of concerns generated by the team at the end of the inspection, and is submitted to the Accreditation Commission along with a letter containing the team's recommendation. Although this recommendation is important, it only is a piece of the overall information considered by the commission in making its final decision. On occasion the commission takes action that is different from what the inspection team recommends. This occurs when information surfaces that the team did not have access to, or when events take place that affect the outcome positively or negatively after the inspection is completed, including how well the institution has addressed the list of concerns developed by the inspection team.

Decisions made regarding the granting or denial of accreditation are based on conditions at the institution *at the time the evaluation is conducted*—not on future plans or past events. When making its decision, the commission considers all information that has been confirmed and evaluated during the 6-month review process, including

- materials submitted by the institution,
- materials submitted by outside sources,
- reports of other agencies,
- the on-site inspection,
- the inspection team's written report and recommendation,
- the institution's response to the list of concerns, and
- the interview with institution representatives conducted by the commission at the end of the process (AZA 2009).

ACCREDITATION STANDARDS

While animal care is recognized as the single most important section of the standards, and the driving force behind their creation, all branches of an institution must function well to assure top-quality animal care.

When developing professional standards, AZA recognized the need to build in flexibility so that one set of standards could apply to both small and large institutions. Standards dealing with such things as research, public amenities, staff, and conservation projects, for example, are areas where judgment of adequacy is directly related to the size of the institution. For instance, the standard requiring that the education program "be under the direction of a paid staff person" deliberately does not specify that the staff person be dedicated to the position on a full-time basis. When considering this issue, the inspection team and the Accreditation Commission will factor in the size of the institution. A small facility with a part-time staff person directing the education program might prove acceptable, whereas the program at a medium-to-large facility would require someone full time. However, while it is helpful to remain flexible and consider an institution's size and nature when evaluating requirements, standards dealing directly with animal care are firm in their application to institutions of all sizes. Standards dealing with such things as living environment, physical comfort, health, nutrition, social and biological needs, and enrichment activities are not based on an institution's size or the nature of its collection.

At present, professional standards for evaluating zoos and aquariums are divided into the following sections: animal collection, veterinary care, staff, governing authority, physical facilities, guest services, safety/security, finance, conservation, education and interpretation, research, and other programs/activities. As both the zoological and aquatic professions are dynamic fields of study in which new discoveries are continuously being brought to light, so, too, are professional standards being evaluated and revised regularly. The Accreditation Commission reviews its standards continually, and issues its standards each year.

ANIMAL COLLECTION

Accreditation standards (AZA 2009) are especially concerned with assuring high standards of animal management and husbandry. Accreditation inspectors evaluate all animal areas, including exhibits, holding areas, and all the institution's off-site facilities at which animals are kept. Among the things closely examined is the institution's Acquisition and Disposition (A&D) policy for animals. The written A&D policy of an accredited institution must, at minimum, incorporate all requirements contained in AZA's A&D policy. Animal records are examined, and accredited institutions are encouraged to place animals only at other accredited institutions. If an animal is placed at a nonaccredited institution, documentation must be obtained verifying that the receiving institution has the expertise, records management capabilities, financial stability, and facilities to provide for the animal's health and comfort. There must also be evidence that the nonaccredited facility balances public exhibition of animals with efforts in conservation, education, and science. In addition, the receiving institution's mission (stated or implied) must not be in conflict with AZA's mission or A&D policy.

Under the animal collection section, the accreditation team assesses exhibits to ensure that they are of a size and nature sufficient to provide for the psychological and physical well-being of each specimen. Inspectors check to ensure that animals are protected from excessive heat and cold, that exhibits replicate natural habitats and contain appropriate furniture and sufficient shade, and that animals are kept in numbers adequate to meeting their social and behavioral needs. Display of single animals is acceptable *only* when biologically correct for that species.

Enrichment is also considered important for the proper care of animals in captivity, particularly mammals; and each institution is expected to have an active program in place for the enrichment of all the animals in its collection, including a system for documenting behavior that can be shared with other institutions. Other areas addressed under animal care standards include collection planning, permits, food storage and preparation areas, and the use of animals in touch tanks and other programs in which animals interact with the public (including appropriateness of species used and frequency of rotation).

VETERINARY CARE

Standards in the veterinary care section require that each institution's animal heath care program be under the direction of a licensed veterinarian. The program must follow the guidelines of the American Association of Zoo Veterinarians. Veterinarians are required to be properly qualified to care for exotic collections, and there must be an adequate number of them on staff based on the size of each institution and its collection. The support staff provided to the veterinarians is also assessed as to number and experience. In addition, standards in this section address veterinary records, quarantine procedures, nutrition programs, emergency procedures, alarm systems, necropsy policies, drug storage, authorization, and use protocol, and all related inspection reports of the U.S. Department of Agriculture, Animal and Plant Health Inspection Service.

STAFF

A key element of an institution's successful operation is maintaining a staff sufficient in qualification and number to meet the needs of the institution's collection. Effective communication, good working relationships, and regular training are the basic essentials on which good animal care begins.

SAFETY AND SECURITY

The security program employed by an institution should be sufficient to provide appropriate, 24-hour protection for the animal collection, its staff, and the visiting public. Perimeter fencing must be 2.4 m high, surround the institution completely, and be separate from exhibit fencing. The perimeter fence should be checked regularly and fixed immediately to deter vandals, feral animals, and effectively contain the collection. Also required are appropriate safety procedures to deal with potentially dangerous or venomous animals, natural disasters, power outages, and animal escapes (see Rosenthal and Xanten, chap. 8, this volume).

CONSERVATION, EDUCATION, AND RESEARCH

Standards also consider the future of animal care, including educating the public about the needs of animals and participating in conservation and research efforts both locally and *in situ*. Education must be a key element in the mission statement of the institution. Standards target both on-site and off-site programming for audiences such as school groups and families, and interpretive methods such as graphics, exhibits, program animal use, and docent/keeper talks. Each institution must have a written education plan, and the education program must be under the direction of a paid staff person with appropriate experience or training. Institutions are required to evaluate their education programs regularly for effectiveness, content, and the use of current scientific information. Conservation is a requirement in education messages so as to foster concern about disappearing biodiversity and to elevate the environmental knowledge of individuals in the field, the institution, and the visiting public.

Participation in conservation efforts must also be a mission of the institution, and each facility is expected to contribute at an appropriate level, based on the size of its budget and number of staff. Participation in field conservation is strongly encouraged, particularly ecosystem conservation. Examples of such involvement are (1) conducting educational programs in the targeted areas, (2) contributing to the establishment or continued support of reserves, (3) conducting conservation research in the field, (4) supporting ecotourism so that indigenous individuals derive a value from preserving their natural environment, (5) conducting or supporting conservation training in the targeted areas, and (6) technology transfer. Institutions are expected to work with local colleges and universities on conservation efforts, and to encourage the next generation of conservationists.

ADDITIONAL CONSIDERATIONS

While some sections of the standards do not relate directly to animal care, it is important that each institution function efficiently in *all* areas in order to ensure its ability to provide its collection with a high level of care. Areas of this nature covered by the standards include the governing authority, finance, guest services, and overall physical facilities (including preventive maintenance).

GUIDELINES FOR INDIVIDUAL SPECIES

Leaders within the zoo and aquarium community in the United States are now turning their attention to creating more-specific guidelines of care for all vertebrates in captivity, beginning with mammals. The creation of these guidelines is a huge undertaking involving experts in each taxonomic group and animal welfare specialists from accredited institutions around the country, and will require several years to complete. The guidelines will identify the most suitable and appropriate conditions for management of species in captivity, and will supplement current accreditation standards in the United States. Based on a standardized template that includes information on the physical, biological, social, and psychological needs of animals, the guidelines are intended to complement current husbandry manuals (Moore, Barber, and Mellen 2004). In addition to being used as a blueprint for daily care, the guidelines will stand as a common source of documented information to supplement the professional knowledge and experience of accreditation inspectors when assessing adequate or proper care of a particular species within an institution, thus further enhancing the welfare of animals managed by AZA-accredited institutions.

With an increasing focus on conservation, accreditation standards can help to ensure that accredited institutions remain actively involved in efforts to save and conserve animals and their habitats in the wild. Certainly, a good accreditation program is never finished, nor should it be. Only by constantly raising professional standards can leaders in the zoo and aquarium community throughout the world promote continuous improvement in providing humane, healthy, and stimulating environments for mammals, and all animals held in captivity.

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Southeast Asia

Govindasamy Agoramoorthy

INTRODUCTION

Southeast Asia is known for its unique diversity of fauna and flora (Myers et al. 2000). Yet the region is losing its forests faster than any equatorial region for reasons that include increasing human population density, habitat destruction, unsustainable use of natural resources, poaching, and trade in endangered species. Zoos play a crucial role in Southeast Asian countries by promoting public awareness campaigns to minimize human impact on natural resources and conserving animals in captivity to safeguard endangered species from extinction. Major zoos and recreational parks are associated with the Southeast Asian Zoos Association (SEAZA), which is the major zoological union in the region (Agoramoorthy and Hsu 2001a). It was officially formed in 1990 with the objectives to strengthen *in situ* conservation, increase captive breeding, improve standards of animal welfare, provide better recreational experiences for zoo visitors, and educate the public about wildlife conservation. Since 1993, SEAZA has comprised 12 countries and territories, including Brunei, Cambodia, Hong Kong, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Taiwan, Thailand, and Vietnam.

All member institutions are obligated to sign the association's code of conduct and to ensure the minimum ethical and welfare standards required by SEAZA (1998). Despite the fact that recognized zoos in Southeast Asian countries work hard to improve standards of animal welfare and ethics, certain resorts, recreational theme parks, and even restaurants are increasingly displaying wildlife with less legal, ethical, and professional scrutiny. As a consequence, stringent ethical and welfare evaluations have become crucial to maintain high professional standards among member zoos.

To promote the continued advancement of animal welfare, SEAZA has adopted the zoo evaluation procedure as an accreditation process, and all institutional members are required to obtain the certificate affirming that their zoo has fulfilled the minimum welfare standards, a document that is valid for 5 years. In order for zoos to obtain this accreditation certificate, they must go through a voluntary evaluation first and be reevaluated later by SEAZA, to assess whether they complied with the suggestions made in the initial assessment reports. Upon satisfactory completion of the evaluations, SEAZA's Ethics and Welfare Committee will recommend the zoo to the Executive Board, which in turn issues the certificate, signed by the president and the chair of the Ethics and Welfare Committee.

ETHICS AND WELFARE EVALUATIONS IN ZOOS

Since 1998, I have been leading SEAZA's Ethics and Welfare Committee in conducting zoo evaluations. The objective of the zoo evaluation is not to measure animal welfare scientifically, but to identify, rectify, and prevent ethical and welfare-related problems in zoos. Between 1999 and 2005, at the invitation of the local zoos and zoo associations, SEAZA has assessed 14 zoos in countries such as Malaysia, Thailand, and Indonesia. So far, 5 zoos in Thailand have been awarded certificates for passing the minimum welfare standards. In the meantime, zoo assessments and reassessments continue, and qualifying institutions will be awarded with certificates in due course. In this chapter, a summary of the procedures of such evaluations is provided, including their importance in improving ethical and animal welfare standards in zoos in Southeast Asia.

EVALUATION METHODS

Data on animal welfare and ethics are collected using questionnaires and data forms. Representatives from the SEAZA Executive Board, local animal welfare/conservation organizations, and the zoo community participate in the evaluation process (Agoramoorthy 2002, 2004, 2008; Agoramoorthy and Harrison 2002). Usually, a maximum of 6 representatives form a team to conduct evaluations; the idea of including local zoo staff is to understand how they would evaluate their own zoo. The evaluators' experiences range from basic animal welfare to specialized training in husbandry and veterinary care. Each evaluator also targets a single exhibit/species to assess welfare problems thoroughly, and all taxa are considered equally. In an ideal exhibit, animals should have access to sufficient food and drinking water, shelter from inclement weather conditions, a clean enclosure to reduce the spread of infectious diseases, and responsible staff to care for them; and finally, the animals displayed should exhibit normal behavior. The animal exhibit should be as large as possible, with adequate environmental and behavioral enrichment devices following internationally accepted minimum husbandry and welfare standards (e.g. AZA 1997). The most contentious ethical issues facing zoos are the acquisition of animals for captive breeding, disposal of surplus animals, basic animal care and husbandry, and use of animals for research and recreation (Hutchins and Fascione 1991; Agoramoorthy 2002, 2004; Agoramoorthy and Hsu 2005; WAZA 2005)—all are carefully reviewed during the evaluation process.

A few months prior to the evaluation, all data collected are translated into local languages such as Thai, Bahasa Indonesian, or Bahasa Malaysian and forwarded to the respective zoos. Before each evaluation, a meeting is held with the director, curators, veterinarians, animal keepers, and administrative staff. After the completion of the evaluation, staff members of each zoo are briefed on the major findings. A total of 94 questions are asked during data collection (Agoramoorthy 2002, 2004, 2008), and the questions are organized into 7 broad categories, such as (1) freedom from hunger and thirst, (2) freedom from thermal and physical discomfort, (3) freedom from pain, disease, and injury, (4) freedom to express normal behavior, (5) freedom from fear and distress, (6) animal welfare and zoo management, and (7) animal welfare and zoo responsibility (adapted from Thorpe 1969 and Spedding 1993). The last 2 categories are mainly to understand whether or not member zoos realize the importance of welfare improvements in respective member zoos, and their responsibility for them. While recording data in each category, an evaluation score such as 5—excellent, 4—good, 3—average, 2—poor, and 1—not acceptable is given. Once the data are entered into a computer, statistical analyses are performed using Statistical Analysis Systems software (SAS Institute 2000). The effect of zoos and evaluators are tested using analysis of variance in general linear model. Duncan's multiple range test is used to test the differences in mean scores. If the results indicate below-average scores, the zoos will be asked to make appropriate changes based on the evaluation report. SEAZA cannot issue the certificate until further improvements are made to upgrade welfare standards to the satisfaction of the Ethics and Welfare Committee.

WELFARE AND ETHICAL PROBLEMS IN ZOOS

The most serious problems that the zoos face are overcrowding of animals in small cages (often resulting from the rescue of confiscated and abandoned animals such as gibbons, macaques, orangutans, and various species of birds and reptiles), poor hygiene associated with overcrowding, lack of enrichment, old/unsuitable indoor animal enclosures, use of animals in shows and photography, and lack of policies to take responsibility for animals that are traded or exchanged to other zoos (Agoramoorthy 2008). These problems are seen even in well-managed zoos. There are 3 pressing concerns that need to be tackled swiftly in Southeast Asian zoos: (1) rebuilding decades-old indoor enclosures; (2) addressing the problems created by confiscated and abandoned animals that are regularly dumped on zoos by the general public, the government, and nongovernment agencies; and (3) monitoring the use of animals in photography and shows. Financial support and policies related to ethics, welfare, and management are essential to solve these crucial problems. The minor problems are usually associated with the lack of enrichment for animals in exhibits and holding areas.

EVALUATIONS ENHANCE WELFARE STANDARDS IN ZOOS

Being in the tropics, zoos in Southeast Asia usually have fast-growing, lush green vegetation; thus, most outdoor exhibits tend to have naturalistic surroundings. But animal enclosures regularly lack behavioral and environmental enrichment devices to stimulate natural behavior among animals. This could be easily improved by adding ropes, artificial vines, branches, and other furniture to encourage activity (Markowitz 1982). Some zoo employees reacted swiftly to rectify basic problems by adding more ropes in gibbon enclosures to stimulate behavioral enrichment, and socializing macaques and chimpanzees that were kept alone in small cages (Agoramoorthy and Harrison 2002). Furthermore, all zoo directors submit reports on how they solve problems and what measures are being taken to solve major issues that might otherwise require more time and funds. During zoo evaluations, I often had productive interactions with the employees, who took the criticisms constructively by showing immediate progress in solving some issues. This indicates that zoo managers not only are concerned about problems related to animal welfare, but also demonstrate their ethical/professional obligations to provide humane care for animals in their facility.

Following evaluations, zoo directors are advised to conduct courses on environmental/behavioral enrichment for their staff to serve as a catalyst for creativity, since enrichment activities often need to be provided on a variable schedule to minimize boredom among animals. Institutional members and national zoo associations are encouraged to conduct zoo biology courses, and in fact, enrichment courses are being conducted regularly in countries such as Malaysia, Thailand, Taiwan, and Indonesia.

Zoos in Southeast Asian countries continue to rescue and receive from the public various species of animals, both common and endangered, which triggers overcrowding and other welfare-related problems due to insufficient space and staffing. Similar instances have been reported in other regions as well (Cuaron 2005). Instead of waiting for funds to rebuild cages and increase staffing, zoos should embark on projects to relocate rescued animals to more-specialized centers that maintain better welfare standards (Agoramoorthy and Hsu 2001b). Zoos have been involved in releasing healthy animals back into their natural habitats for some time. This practice must strictly follow the guidelines established by the International Union for Conservation of Nature (IUCN 1998, 2002) for the release of confiscated species and the reintroduction of animals.

During evaluations, recommendations are made to rebuild old/outdated enclosures; it can sometimes take 5 years to see any improvement, as this involves major construction work. For example, in 2000 the evaluation team recommended that the Zoological Parks Organization of Thailand rebuild an animal holding area, hospital, quarantine area, and sun bear exhibit in Dusit Zoo (Agoramoorthy and Harrison 2002). The zoo used the evaluation report to convince the government of Thailand to provide the funds needed to rebuild exhibits and other facilities. When Dusit Zoo was reevaluated in 2005, all problems identified in the 2000 report had been rectified. This is an example of the success of the ongoing evaluations in Southeast Asia in upgrading zoo standards.

In inspecting their own zoos, local evaluators gave high scores and underestimated the extent of welfare issues. Furthermore, they selected the best exhibits for evaluation, while outside evaluators chose exhibits with major welfare concerns, indicating that the local evaluators were biased and reluctant to look critically at welfare problems in their own institutions. The role of outside evaluators therefore is crucial to make the assessment procedure fair, efficient, and successful.

CRITICISMS OF ZOOS IN SOUTHEAST ASIA

Recently, animal rights activists and conservation groups have criticized zoos in Thailand, Indonesia, Malaysia, and

Singapore, highlighting various concerns. The crackdown on private zoos in Thailand by law enforcement officials was unprecedented—armed policemen raided various zoos, including Safari World, which harbored over 100 orangutans, of which only 44 were legally registered (Agoramoorthy 2004). These zoos are still part of the Thai Zoo Association, so there is an ethical issue for this local zoo organization having jurisdiction over the investigation. In Singapore, local activists asked the Singapore Zoo and Night Safari to ban all animal shows, citing cases of animal attacks and raising welfare, ethical, and safety concerns.

Animal rights and conservation groups tend to voice armchair philosophy and may even be sarcastic, but they do little that is practical to alleviate animal suffering in zoos. Most animal rights groups do not provide applied support for the care of animals in zoos, as they are philosophically against the idea of animals in captivity. They tend to believe that zoos will never be able to provide appropriate conditions, management, and care to meet the needs of their animals (see Kreger and Hutchins, chap. 1, this volume).

Many animal rights groups also comment on welfare issues (e.g. the report *Caged Cruelty* published by the World Society for the Protection of Animals), and they then have campaigns that likely bring in substantial donations from the public (WSPA 2002). But their condemnation alone will not help in relieving animal suffering in our zoos.

In contrast, only a few animal welfare organizations have been willing to conduct constructive dialogue with us and work closely to improve welfare conditions in our zoos. For example, the International Fund for Animal Welfare and the Royal Society for the Prevention of Cruelty to Animals supported our evaluation efforts financially by providing small travel grants to conduct animal welfare evaluations; these ultimately contributed to improved zoo animal welfare standards in SEAZA zoos (Agoramoorthy 2002, 2004).

Over the last decade, SEAZA has permitted animal rights groups to participate in its conferences and workshops. International organizations such as the World Society for the Protection of Animals and other smaller animal rights groups from Malaysia, Hong Kong, and Singapore participated in our workshops and conferences, yet do not provide financial support to SEAZA to upgrade welfare standards in zoos; moreover, they continue to criticize our zoos. If constructive progress in animal welfare is to be made in our zoos, animal rights and animal welfare organizations need to be more balanced in addressing the issue.

ZOO EVALUATIONS AND FUTURE PROSPECTS

SEAZA's Ethics and Welfare Committee does not discriminate against poor zoos or favor rich ones. Opinions from zoo managers, conservationists, and animal rights activists are held in equal regard. Customarily, these independent stakeholders of the world's wildlife diversity seldom work closely together, and instead are often in conflict. Over the last 2 decades, I have had the opportunity to work with this outwardly incompatible trio. As a rule, the focus of each group is to denounce the inadequacies of the other in a process that often results in intimidating conflicts and an ultimate loss of headway in alleviating animal suffering. Therefore, a synergistic approach to accomplishing the shared, yet seemingly conflicting, objectives of the various groups is essential. I am confident that such a binding adjudication among different conservation, zoo, and animal rights interest groups can be accomplished, consequently enabling them to focus much more on welfare standards.

Conducting zoo evaluations in the culturally diverse countries of Southeast Asia is a complex task, and presenting evidence of animal suffering in a cordial manner without being openly unpleasant is even harder. However, in the course of zoo evaluations I have been astounded at how open our zoo community is to constructive criticism. Several of our zoos operate with insufficient funds and thus face the dual challenge of maintaining welfare standards and keeping the economic bottom line. Yet the zoo managers are willing to commit their efforts to upgrade welfare standards in their zoos. SEAZA members that do not and cannot afford to provide sufficient care in general for all animals (or in certain cases even with only a few animals) are not given a pass—their membership is not renewed if necessary changes to upgrade welfare are not made.

On the recommendations of the Ethics and Welfare Committee of SEAZA, zoo associations in Malaysia, Thailand, and Indonesia have already set up ethics and welfare committees, and are enthusiastically carrying out their own assessments on a regular basis (Agoramoorthy 2008). Certificates for fulfilling the requirement of meeting the basic professional standards of ethics and welfare were awarded for the first time in SEAZA to 5 institutional members in Thailand—Dusit Zoo, Songkhla Zoo, Chiang Mai Zoo, Nakhon Ratchasima Zoo, and Khao Kheow Open Zoo—during the joint conference of SEAZA and the Australian Regional Association of Zoological Parks and Aquaria (ARAZPA) held in Melbourne, Australia, in May 2005. More SEAZA member zoos are destined to undergo the evaluation process to be qualified for the ethics and welfare certificates in the near future. I find the current SEAZA evaluation process adequate, since it facilitates zoos' understanding of basic animal welfare and ethical problems, which in turn leads to an improvement in professional standards. Thus, I am confident that the future prospects for improving animal welfare standards in South Asian zoos look bright.

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Europe

Miranda F. Stevenson

INTRODUCTION

Compliance with set standards can be achieved through legislation and the membership of national and regional zoo and aquarium associations, which apply certain minimum criteria as a condition of membership. Apart from direct zoo-related standards, zoos and aquariums, regardless of country or region, have to comply with a plethora of legislation. These range from employment of staff, health and safety of public and staff, animal health and transportation, restrictions on performing animals, Convention on International Trade in Endangered Species (CITES) and other international conventions, and legislation specifically aimed at zoos and wildlife. Nonetheless, there can be no hope of consistency of zoo and aquarium quality, in terms of welfare and conservation criteria, throughout a country or region without some form of enforceable legislation.

Much of the current legislation has evolved through the setting of standards by zoo associations. For example the Federation of Zoological Gardens of Great Britain and Ireland (now BIAZA, the British and Irish Association of Zoos and Aquariums) was formed in 1966 with the objective "to encourage the proper care of wild animals in captivity by laying down minimum standards of management of animals' husbandry and transportation and by encouraging acceptance and maintenance of these standards." The federation ensured that members complied with its objectives through an inspection system. BIAZA was also one of the organizations that assisted in the preparation of the standards (DETR [Defra] 2000) accompanying the U.K. Zoo Licensing Act (Zoo Licensing Act 2002), which first came into force in 1984 (Olney and Rosevear 2001). This was one of the first pieces of zoo legislation in Europe that involved a system of zoo inspection for its implementation.

The main legislation in the European Union is the EU Zoos Directive.[1] Prior to the introduction of this Directive in 1999, the situation varied from countries that had strict legislation of zoos, e.g. Britain (Kirkwood 2001a, 2001b), to other countries with little or none. If legislation exists within a country which applies standards with regular inspections, then zoo associations may not need to have an inspection regime (e.g. BIAZA no longer inspects licensed zoos that apply for membership). However, the problem with legislation is that it applies minimum standards, so something else is needed if standards are to continue to improve. Legislation might be regarded as a stick, and the accreditation systems of zoo associations more of a carrot.

EUROPEAN LEGISLATION

In order to understand zoo regulation variations throughout the European continent, it is necessary to have some understanding of what constitutes Europe—and as with most things European, this is not entirely clear. Europe is geologically and geographically a peninsula that forms the western portion of the Eurasian landmass. It has clear boundaries on the north (Arctic Ocean), west (Atlantic Ocean), and south (Mediterranean Sea), but to the east the boundary is unclear, with the only definite geographic border being the Ural Mountains. Lack of clarity over what is Europe and what is Asia combined with the legal entities of some of the smaller states results in

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[1] The European Union, or EU, is an intergovernmental and supranational union of (currently) 27 democratic countries (nations) known as Member States. (It is important to note that these are nation-states.) The European Union was established under that name in 1992 by the Treaty on European Union. It has a complex system of internal law, which has a direct effect on the legal systems of Member States. Zoo legislation is based on economic, social, and environmental policies and comes under the EU's Environmental Law.

TABLE 3D.1. Member (nation) states of the European Union as of the end of 2007

Status	Year of joining	Countries
Member states	Founder states 1952	Belgium, France, Germany, Italy, Luxembourg, Netherlands
	1973	Denmark, Ireland, United Kingdom
	1981	Greece
	1986	Portugal, Spain
	1995	Austria, Finland, Sweden
	2004	Cyprus, Czech Republic, Estonia, Hungary, Latvia, Lithuania, Malta, Poland, Slovakia, Slovenia
	2007	Romania, Bulgaria
Candidate states—i.e. hope to become members in time		Western Balkans, Croatia, Macedonia, Turkey
Special relationship states	Current	Iceland, Norway, Liechtenstein, Switzerland

some fuzziness over the number of countries (states) in the Continent. Many changes have taken place since the dismantling of the Iron Curtain in the early 1990s, resulting in much political unrest and the formation of new nation-states. This event also brought the zoos of Eastern and Western Europe closer together. For the purpose of this publication, the number of countries in Europe is taken as 48 (including the Vatican City, Georgia, Armenia, and Azerbaijan). Twenty-seven of these countries form the Member States of the European Union (EU); a list of these (2009) is provided in table 3d.1. Within the mass of the EU there are also territories that are not members, but that have some sort of relationship status, e.g. Monaco, San Marino, Jersey, Guernsey, Isle of Man, and the Faroe Islands.

The European Union has various levels of legislation that apply to all Member States. Treaties and international agreements form its primary legislation. Secondary legislation comprises binding legal instruments, which take the form of Regulations, Directives, and Decisions. The zoo legislation is a Directive; as such it is designed to align national legislation and is binding on Member States in terms of the results that are to be achieved, but it leaves them the choice of the form or methods to adopt to realize the objectives of the Directive. Members have a time frame in which to transpose a Directive into national legislation; e.g. the Zoos Directive (EU Council 1999) came into force in 1999, but Member States had until 2002 to implement it. Some Member States incorporated the Directive into existing legislation (e.g. Scotland, England, and Wales incorporated it into the existing Zoo Licensing Act), whereas other countries prepared new legislation—the very nature of a Directive means that it will not be applied identically throughout the EU. Another problem, specific to the Zoos Directive, is that the agreement that it hinges on is Article 9 of the Convention on Biological Diversity (CBD), which is primarily environmental and conservation, not welfare, legislation.

Article 3 of the Directive deals with ensuring that zoos (1) comply with conservation measures, (2) accommodate their animals under conditions which "aim to satisfy the biological and conservation requirements of the species," and (3) keep good records. In order to ensure compliance, the Directive requires the Member States to introduce licensing and inspection systems for its zoos and aquariums. The Directive also enables Member States to have the power to close noncompliant facilities. Member States, therefore, individually decide on the criteria that they will apply to ensure that enclosures satisfy the "biological needs" and "conservation requirements" of species.

Zoo legislation also exists in non-EU countries in Europe. For example, Switzerland has an Animal Protection Ordinance that ensures minimal requirements for the keeping of wild animals (Peter Dollinger, personal communication). It has undergone several revisions since coming into force in 1981. This is federal legislation which is implemented by the Swiss Cantons, and involves licensing and annual inspections. However, in general few non-EU countries have a licensing and inspection system (Walker 2001; Walker and Cooper 2001).

Zoo licensing legislation can only be implemented through the drawing up and application of standards evaluated by an inspection process, and herein is the main basis for inconsistency. Key areas are the standards themselves, the nature and frequency of inspections and license renewals, and subsequent review processes to ensure that any license conditions are met. The standards produced by Britain (England, Scotland, and Wales) are particularly detailed and helpful, and are used along with a comprehensive inspection and licensing system (DETR (Defra) 2000). The welfare standards are based on the Five Freedoms, as mentioned in Barber (chap. 3a, this volume) and Kagan and Veasey (chap. 2, this volume). These have been modified, termed "principles," and refer specifically to species maintained in zoos and aquariums. There are also conservation, education, research, and veterinary standards and appendixes providing more details in specific areas such as animal contact and certain specialist exhibits such as invertebrates, reptiles/amphibians, aquariums, and marine mammals. A comprehensive bibliography lists the many husbandry guidelines currently available. These standards, originally produced in the early 1980s, were completely revised and republished in 2002, and are frequently revised and updated by the Zoos Forum, the latest version being 2004.

The Zoos Forum (www.defra.gov.uk/wildlife-countryside/protection/zoo/zoo-forum.htm) is an independent body set up to advise the U.K. government on matters pertaining to zoos. The terms of reference of the forum are to encourage the role of zoos in conservation, education, and scientific research; to keep under review the operation and implementation of the zoo licensing system in the UK; and to advise or make recommendations to government ministers of any necessary legislative or other changes. The forum has produced a handbook (Defra 2002), which is designed to aid in the implementation of good standards and legislation. This handbook is a living document, with chapters added and updated over time. It is designed to assist inspectors in applying consistent standards when carrying out inspections under the legislation. The forum also arranges training for inspectors, zoo and aquarium operators, and those who implement the licensing system. This training covers the inspection process, criteria of judging and expected standards, and the implementation of the licensing system.

The EU has not, as yet, carried out a review on the level of implementation of the Directive in Member States. There are known problems and inconsistencies (Eurogroup 2008). Some countries have implemented the Directive but not initiated inspection systems, and as of 2009 others had not even implemented the Directive (e.g. the commission started proceedings against Germany, Italy, and Greece in 2004 for failure to transpose certain measures under the Directive). The frequency of inspections also varies, from regular intervals (Britain, Finland) to more ad hoc systems. Moreover, the organization responsible for licensing varies within each country, from local (e.g. Austria, Britain, Germany) to central government implementation (e.g. Belgium, Republic of Ireland, Netherlands). Thus, the Zoos Directive is not yet fully or consistently implemented throughout the EU, but it has the best potential for ensuring national and regional welfare and conservation standards for zoos and aquariums—especially since, with the increasing expansion of the EU, more countries will have to implement the Directive. This should eventually result in more consistent standards for zoos throughout Europe.

ZOO ASSOCIATIONS

In 1990, the countries of Eastern Europe formed EARAZA, the Euro-Asian Association of Zoos and Aquariums (Spitsin 2001), which is also working toward improving standards in its member collections.

In Europe, as in other parts of the world, much of the progress in improving management of species in zoos is a result of accreditation systems of national and regional zoo associations. Many European countries have national zoo associations; these vary enormously in their ability and influence. EAZA, the European Association of Zoos and Aquariums (Nogge 2001), is the only regional association for all of Europe, and has over 300 members in 35 countries. Since 2000, it has required all potential new members to pass an accreditation process. This process involves the submission of a portfolio of information; compliance with various EAZA codes of practice, including the standards for the Accommodation for the Care of Animals in Zoos (www.eaza.net); and undergoing an inspection. The inspection process is very rigorous and culminates in a report, which is then reviewed by the association's Membership and Ethics Committee and then by its council.

One of EAZA's committees, Technical Assistance and Animal Welfare, helps potential members, especially those from countries with particular problems. For example, training workshops have been held for zoos in Hungary, Bulgaria, Greece, Macedonia, Croatia, and Albania. The committee also provides guidance and support to candidate members of EAZA, i.e. those collections who wish to be members, but have not yet reached EAZA standards.

EAZA and the national zoo associations in Europe expect their members to carry out the recommendations from the World Zoo and Aquarium Conservation Strategy (WAZA 2005), and assist them in doing so.

Standards applied by legislation ultimately tend to be the minimum; zoo associations expect their members to uphold standards exceeding these. Realistically, however, only about 25% of zoos or fewer will become members of national or regional associations. Therefore, legislation is required to ensure that all zoos and aquariums reach minimum standards, and zoo associations should lead and support their members in achieving exemplary standards, far in excess of these minimal levels.

GENERAL LEGISLATIVE COMMITMENTS

As in all regions, zoos and aquariums in Europe have to comply with international conventions (CITES, CBD, CMS, RAMSAR, etc.) to which their respective countries are signatories. Compliance with CITES (especially within the EU) may also involve minimum standards for the keeping of certain species (Cooper and Rosser 2002). Moreover, zoos and aquariums have to comply with animal health and transport regulations, and once again, within the EU these frequently take the form of directives and regulations.

Although efficiently implemented legislation is probably the only way of ensuring consistently good standards in zoos within a country or region, it can also hinder and/or delay animal movements and other aspects of animal management that benefit species conservation and welfare. CBSG—the Conservation Breeding Specialist Group of the International Union for Conservation of Nature/Species Survival Commission—recently ran workshops to address this conundrum and highlight the problem (CBSG 2002, 2004). This circumstance further emphasizes the importance of good zoos working together within national and regional associations to ensure excellent standards of welfare and positive contributions to conservation, and their significant ability to influence decision makers and assist zoos in their important conservation work.

DOES SETTING STANDARDS IMPROVE ZOOS AND AQUARIUMS?

In his introduction, Barber (chap. 3c, this volume) rightly points out that inspection systems tend to involve qualitative rather than quantitative assessment processes. There is probably no alternative to this, as the inspections realistically can only take 1 or 2 days at most. However, the inspection process can check any auditing practices that the zoo carries out and also recommend that auditing take place. A good example of this is detailed in the welfare assessment chapter in the *Zoos Forum Handbook* (Defra 2002). Here parameters and methodologies for assessing welfare in zoos are presented. The inspection process can include requesting evidence that this sort of quantitative evaluation has been carried out by the zoo or aquarium. This marks the next stage: the evaluation of standards to see if they are sufficiently high to satisfy the welfare needs of the species concerned. Quantitative evaluations often involve behavioral research projects, which may involve many collections; e.g. in 2005–6 a Defra-initiated elephant project was being carried out by the University of Bristol on the welfare of elephants in zoos (now online; see Defra 2009). Research and good data collection can result in the production of husbandry guidelines, which can then be used to set standards for the relevant species. For example, the EAZA elephant guidelines (Terkel 2004b), developed through the Elephant Taxon Advisory Group, demand that zoos place potential breeding animals in breeding situations. This has resulted in an increase in births and herd size. Those collections that commit to keeping elephants must focus on larger herds in larger areas (Terkel 2004a; Dorresteyn 2004).

Similarly, better understanding of the needs of the polar bear, *Ursus maritimus*, has resulted in a decrease in the number of collections keeping them (e.g. only one polar bear remains in zoos in Britain and Ireland) and the construction of much larger and more complex enclosures by those zoos that have decided to continue to keep the species.

The challenge of improving conditions for captive mammals will persist, which is why husbandry guidelines and standards must be living documents and frequently updated. Also, zoos have to get better at auditing and evaluating their collections, covering all aspects of welfare (behavioral, environmental, husbandry, and health). One of the main roles of zoos is to inspire their visitors with the wonder of nature through their living collections. This can only be done if the animals are kept in natural environments with excellent welfare. Zoos and aquariums must also evaluate their contributions to conservation, to fulfill the aspirations of the World Zoo and Aquarium Conservation Strategy: achieving seamless and integrated conservation from the zoo to the wild. To accomplish all this we need legislation, zoo associations that encourage the aspirations of their members, and a commitment from zoos and aquariums to evaluate all their actions to achieve the highest standards of welfare, conservation, and environmental education.

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Part Two

Basic Mammal Management

Introduction

Devra G. Kleiman

Since the first version of *Wild Mammals in Captivity*, the zoo and aquarium communities have become ever more professional in their organization and function. One measure of that is the increasing number of guidelines, frameworks, and processes for carrying out various regular as well as rare activities. Zoo professional staffs now have in place in their zoos written methods for dealing with many of the daily aspects of managing mammals, as well as for coping with emergencies. This section provides chapters on the processes involved in restraining and moving mammals, incorporating enrichment into husbandry, responding to threats from emerging diseases, and developing safety programs to reduce the risk that either animals or humans will be harmed through their regular interactions. Of note is the greater consideration given to developing clear goals and objectives, preplanning, and using collaborative interdisciplinary teams in planning and implementation, all of which were less common a decade ago.

For mammals in captivity, we remove many of the choices that they face in nature: we provide food, shelter, and medical care, establish breeding pairs, and make decisions about group composition. Zoos today are much more "hands-on" than even a decade ago, frequently needing to handle or examine individuals in their animal collections. Zoo staff also regularly moves individual animals both within a zoo and between zoos to optimize genetic diversity in species that have long-term breeding programs and Masterplans. Frequent transfers increase

A rufous elephant shrew being weighed at the Smithsonian's National Zoological Park, Washington, DC. Photography by Jessie Cohen, Smithsonian's National Zoological Park. Reprinted by permission.

the importance of understanding and properly organizing the move as well as the socialization processes that accompany moves or introductions.

Christman focuses on the capture, handling, and restraint of mammals and provides a process for choosing the appropriate restraint (e.g. physical, pharmacological, or behavioral options), the processes involved in planning it, and the tools and team needed to implement any restraint procedure for different sizes and types of mammals. Careful planning and design can eliminate injuries and deaths of animals in shipment, especially in light of the dramatic increases in animal shipments.

Powell's chapter provides a framework for implementing successful introductions and socializations, and emphasizes the need for significant planning along with a stepwise process to achieve success. He also stresses the need to identify goals, organize and prepare the team, prepare the enclosure, and evaluate and adjust tactics on an ongoing basis, as well as know the species biology and the individual(s)' temperament and history.

In chapter 6, Shepherdson provides an overview of the conceptual and theoretical framework for environmental enrichment. Enrichment is a method of mimicking nature by fulfilling behavioral and information needs, and providing control and choice for captive animals. A significant problem with enrichment is measuring its effectiveness; currently used guideposts include a reduction in abnormal behavior, an increase in behavioral diversity, and a decrease in physiological indices of stress. Finally, Shepherdson discusses the research methodology typically used in environmental enrichment studies and their flaws, chief among them the small sample sizes most zoo professionals have available to them.

The Travis and Barbiers chapter discusses emerging diseases and methods for preventing and controlling disease. As a surprising 75% of emerging pathogenic diseases are zoonotic, disease management must be a high priority for all zoological institutions despite the large information gaps. The authors emphasize the need for science-based health surveillance and monitoring systems for disease management, including early identification, rigorous investigations, and assessment of risk. They discuss options for prevention, control, and management of disease.

Risk assessments are also key to the management of safety issues, as presented in the chapter by Rosenthal and Xanten. Zoos need to conduct regular safety analyses, including the likelihood of injuries caused by human error (both staff and visitor), animal escapes, natural disasters, and other potential emergencies. Today's zoos look at safety issues much more closely and carefully than even a decade ago, and many have dedicated safety officers or safety committees to evaluate potential safety problems routinely.

4

Physical Methods of Capture, Handling, and Restraint of Mammals

Joe Christman

INTRODUCTION

HISTORY OF CAPTURE, HANDLING, AND RESTRAINT

Physical manipulation has its limits as the sole means of handling and restraining large, dangerous, or temperamental animals (Kleiman et al. 1996). During the last third of the twentieth century, great advances were made in pharmacological restraint techniques to deal with these limitations. New drugs were discovered, and new methods of administering these drugs were developed and refined. These developments have made the use of immobilization drugs safer and economically feasible for exotic animal restraint. In zoos around the world, many husbandry and veterinary procedures (e.g. dental care procedures in large carnivores) that were not previously possible due to the size and/or dangerous nature of the species involved can now be performed safely, both for the animals and for the handlers (Fowler 1995). The use of chemical restraint is effective, relatively easy, and often faster and more efficient than traditional restraint methods. Its use greatly advanced the scope of animal care and gives animal managers a powerful means of extending their ability to meet the needs of their animals.

Additionally, husbandry training techniques in use today provide a means of behavior modification and desensitization to procedures that in the past would have required physical restraint. All 3—husbandry training, physical restraint, and pharmaceutical restraint—should be considered complementary and applied as a continuum in deciding the most appropriate method of restraint (Mellen and MacPhee 2000; Mellen and MacPhee, chap. 26, this volume).

Due to the efficacy of pharmaceutical restraint, it has almost entirely supplanted physical and mechanical restraint techniques, which require training and practice (Kleiman et al. 1996). As staff members with hands-on experience in traditional physical restraint methods leave the profession, that experience is often lost from institutional memory.

Every restraint event is different and almost always will permit the use of multiple methods. There is no hard-and-fast rule that a particular method must be used with a particular species. Each species and each scenario require careful planning, consideration, and evaluation of the resources and experience at hand to determine the most appropriate or preferred method of restraint. In many cases, the "best" method will involve a combination of several different methods applied at the appropriate time and place. Safety for both the personnel and the animals involved should always be the first consideration in choosing a restraint method (Fowler 1995).

DEFINITION OF RESTRAINT: PHYSICAL, MECHANICAL, CHEMICAL, AND BEHAVIORAL

Any restraint procedure involves a capture and some degree of handling. For the purposes of this chapter, the 3 elements—capture, handling, and restraint—will be combined and referred to as the single process of restraint. *Physical restraint* refers to any circumstance where physical force alone is used to restrain an animal. This can be in the form of hand restraint, where an animal is captured, restrained, and handled using only the handlers' bare hands. Depending on the situation, it could involve the use of a variety of handheld capture and safety equipment (e.g., gloves, ropes, noose poles, baffle boards, shields, and nets). All these equipment items require training and practice to master; an excellent reference for their use can be found in Fowler (1995).

Mechanical restraint refers to the use of restraint systems such as a squeeze box, drop-floor chute, or hydraulically operated restraint chute (sources for equipment mentioned here can be found in appendix 4.1). For small mammals, mechanical restraint may be in the form of a Plexiglas (Perspex) box, with a panel providing a squeeze action. The Plexiglas allows the handler to see the animal for positioning. Small wire cages may be used for species such as mink, *Mustela vison* (see Fowler 1995). These cages limit the animal's movement while protecting the handler and allowing necessary access for exams and procedures.

Large-mammal mechanical restraint systems are for the most part stationary or fixed systems incorporated into a containment or handling facility and require a degree of cooperation on the animal's part. There are portable systems available, but their application is more limited than the traditional stationary devices due to the need for supporting pens and runways. The primary goals of a mechanical restraint device are to counter the size and strength of larger animals, protect handlers, limit the movement of the animal, and safely and humanely allow access to various parts of the animal. Figures 4.1 through 4.4 show examples of 4 systems in use. While greatly increasing the range of procedures that may be performed on an animal, they cannot entirely eliminate the need for chemical immobilization. As a complement to physical restraint and/or chemical immobilization, zoo staff often uses husbandry training to desensitize and habituate animals to the restraint system and to facilitate an animal's entering it on cue. However, emergencies may occur that will not allow an animal to be shifted into an area where a mechanical restraint or husbandry training can be used.

CHEMICAL RESTRAINT

Chemical restraint should only be performed by, or under the direct supervision of, a trained veterinarian. Many drugs are legally regulated and require licensing and registration for use. For specific drugs and dosages, please refer to a qualified veterinarian. Information regarding drugs and dosages can be obtained from several sources (e.g. Kleiman et al. 1996; Thurmon, Tranquilli, and Benson 1999). During chemical restraint procedures, physical restraint may or may not be used in the process of administering the drugs used for tranquilization or immobilization.

BEHAVIORAL "RESTRAINT"

Behavioral restraint refers to situations where husbandry training, desensitization, and/or operant conditioning are used to facilitate or perform a procedure. By definition, this is not restraint—this is cooperation. Should the animal involved choose not to cooperate, the procedure cannot be completed using the training alone. Regardless, training and desensitization should always be the first consideration in developing a restraint plan, in order to reduce stress and desensitize the animal to the procedure. For example, an animal may be trained to enter a restraint device voluntarily where it can then be mechanically restrained or chemically immobilized. A backup method or methods should be available if the training does not accomplish the goals. Today, many procedures that in the past would have required full immobilization (e.g. collecting blood samples from large cats or apes) are now accomplished through husbandry training (see Mellen and MacPhee, chap. 26, this volume). There is a time factor—an

Fig. 4.1. White rhinoceros, *Ceratotherium simum simum*, mechanical restraint and training backstage at Disney's Animal Kingdom, Orlando, Florida. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

Fig. 4.2. Nile hippopotamus, *Hippopotamus amphibius*, backstage training at Disney's Animal Kingdom, Orlando, Florida. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

acute illness or emergency may not allow the time required to develop, implement, and establish the degree of training needed for such voluntary procedures.

In this chapter, I do not advocate any one method of restraint over another. Rather, my purpose is to discuss the options available for any restraint procedure and to assist in applying a problem-solving tool for each case. Knowing what method of restraint to use, and when and how to use it, require experience that can only be obtained through staff training and practice. The more tools managers have available to them, the better will be their ability to meet the needs of their captive animals.

When deciding on a restraint method, factors to consider include the goal of the restraint, the conditions (both climatic and facilities), the resources available, and the nature of the animal (Leuthold 1977). Choosing the appropriate method or combination of methods should always begin with the rule of least force; i.e. the chosen method of animal capture, restraint, and handling should involve the least amount of force possible to achieve the desired result. For example, a physical exam that can be done at a distance using binoculars is preferable to any restraint, if it can achieve the objective. In contrast, some procedures, such as dental or surgical operations, may require chemical immobilization as the least force needed.

Regardless of the situation or the restraint method chosen, certain common elements should always be discussed before deciding on a method of restraint. These include the following.

Fig. 4.3. African elephant, *Loxodonta africana*, training in mechanical restraint device backstage at Disney's Animal Kingdom, Orlando, Florida. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

Fig. 4.4. Javan Banteng, *Bos javanicus*, mechanical restraint training backstage at Disney's Animal Kingdom, Orlando, Florida. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

Safety. The choice of whether or not to restrain an animal, and the method of choice, should always have safety as the first consideration. The safety of the personnel should always be the primary consideration, with the safety of the animal next. The immediate and long-term physical, psychological, and social effects on the animal should be taken into account also.

Fig. 4.5. Impala, *Aepyceros melampus*, mechanical restraint for physical exam backstage at Disney's Animal Kingdom, Orlando, Florida. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

Reduction or removal of unwanted stimuli. In all restraint procedures, visual and acoustic stimuli should be controlled and minimized. Enclosing an animal in a darkened stall reduces stress in some species, and the use of a blindfold during handling is recommended for most species (Fowler 1995) (fig. 4.5). Earplugs (e.g. rolls of gauze) can be used for certain species, but care must be taken to remove them after the procedure (Fowler 1995).

Use of voice, body language, and posture. How animal care staff uses voice and body language is critical in restraint situations (Fowler 1995). Much of an animal's communication is through its posture and expressions, and they are very sensitive to the body language and cues of people. Most animal staff has seen situations where an intractable animal has been soothed and handled by an experienced and confident staff member. This confidence, and the ability to convey it to the animal, cannot be taught but can be developed through experience. It is essential for everyone involved with a restraint procedure to be comfortable in his or her abilities. A lack of comfort and confidence is immediately perceived by the animal and can result in an increase in its anxiety and stress levels.

Clarifying the goal for restraint, capture, and handling. The reason for and goal of the restraint procedure should be clear in everyone's mind, although the goal may change during a restraint. For example, upon routine examination an animal might be found to require surgical intervention or be in need of treatment for a previously undisclosed or unnoticed injury. If possible, these potential issues should be considered before the procedure, and preparations made for as many possibilities as are practical. The staff needs to know what is intended, but there should be plans for contingencies.

Natural history of the species and the specimen. Knowing as much as possible about the natural history, capabilities, behavior, and nature of the species and the individual animals involved is critical to the planning of the restraint procedure (Leuthold 1977). In some situations, an otherwise timid animal that would be expected to turn and run may stand its ground or even attack (e.g. a mother defending a newborn calf). Zoo staff should know whether the animal has experience with restraint, i.e. is it naïve or has it been restrained many times?

Physical surroundings, climate, and resources. Staff needs to consider the physical condition of the restraint location, including the climate, the terrain, and the facilities and equipment. Some options for restraint may be precluded by the setting. For example, if animals are maintained on expansive open-range facilities, the only option available for restraint might be a drug administered with a dart. If veterinary support is unavailable, physical restraint may be the only option. If a species or specimen is heat- or cold-weather intolerant, it may not be safe to attempt a restraint procedure during extreme temperatures. Sometimes the best choice is not to perform the procedure.

Being prepared for emergencies. No matter how well animal care staff plan and prepare, restraint procedures will occur because of an emergency, e.g. an animal escape. Procedures should be in place to address escapes in general, but no amount of planning can cover every eventuality. Careful preparation and training of staff using drills and brainstorming sessions can assist staff in thinking about their role in an emergency. Training the animals for specific behaviors, such as shifting, stationing, and emergency recalls, can be helpful in resolving emergency situations.

Release and recovery. In many, maybe even most, restraint events, release and/or recovery is the most critical and dangerous point of the procedure. The transition of an animal from a controlled situation of physical restraint or complete immobilization to a state of freedom must be done carefully. Many animals may react according to their nature—either a flight or a fight response—and either response can result in injury if not anticipated, controlled, or directed (Leuthold 1977). All personnel should be aware of the likelihood of the response upon release and be prepared for every eventuality. Staff escape routes should be discussed as a group and clear to everyone. As an animal is released, it should be directed toward an area that minimizes the risk of injury to it or others. Maintaining a calm, quiet environment that allows an animal to act rather than react is essential to good release and recovery.

TOOLS FOR PLANNING

Emergencies forestall the planning process, but even they can be anticipated and a partial response to them planned. In the collection planning process, the restraint needs for each species should be identified and adjusted to work with the facilities and resources available. When planning a new facility, there should be physical and chemical restraint designs for every species and specimen it houses. A good reference for hoofstock loading and handling facilities can be found at www.grandin.com, the Web site for Dr. Temple Grandin. Any design should incorporate facilities to allow training and behavioral conditioning or modification; these designs should include structures that facilitate husbandry training that is safe for staff and animals.

It is essential that animal managers with restraint experience be included in the design process, and for everyone involved in the design to understand the critical and essential need for restraint systems. Having a clearly outlined and documented restraint plan allows for clear communication between all parties involved, and any differences in philosophy can be identified and agreements reached before the animal care staff actually needs to restrain an animal. An example is given in box 4.1.

Another tool for problem solving, goal setting, evaluation, and improvement is the SPIDER model (adapted from Mellen and MacPhee 2000; see Mellen and MacPhee, chap. 26, this volume). This tool provides a systematic framework for analysis, problem solving, reassessment, and adjustment of procedures, as needed.

Box 4.1 Capture Restraint and Handling Guidelines

Species: Meerkat, *Suricata suricatta* (Wilson and Reeder 1993)

Preferred Restraint Method: As a defense mechanism, this species' natural tendency is to escape by hiding, and individuals will voluntarily enter a crate or container to escape pursuit. This species can be readily trained to enter holding and transport crates. Establishing a training routine to have animals voluntarily enter a transport container on cue can mitigate stress. If physically restrained, the specimen should be held with gloved hands, one hand restraining the head at the neck, the other around the hips to control the hind limbs. With gloves, the danger of injury from claws is minimal.

Equipment and Staff Needed: For restraint, this species will require gloves, long-handled net(s), shipping crates, and 2 keepers.

Safety Concerns: These animals are capable of inflicting bite wounds and, to a lesser extent, scratches from claws. Individual crates are recommended to prevent injury following capture.

Techniques for Capture: A program to train the specimens to enter a carrier on cue should be designed, developed, and implemented. In the event of an emergency or if training is not successful, an empty, open carrier should be placed in the enclosure. Two keepers working together as a team can carefully herd the animal(s) into the carrier or carriers. A meerkat group will usually move together. It may be necessary to catch the entire group and remove the individual(s) desired. If herding is not successful, a long-handled net can be used, and the meerkat captured as it runs along an enclosure wall. Care must be taken to avoid injuring them with the net hoop and to avoid being bitten when removing the animal from the net. Wrapping a meerkat in net fabric and carefully inverting the net into an upended carrier is recommended.

Release and Recovery: Upon completion of the procedure, the individual animal should be returned immediately to the group (if possible) by releasing it into an open portion of the exhibit with the other specimens present. If a specimen is to be held away from the group for more than 24 hours, another member or members should be held with it for company. Due to the social nature of meerkats, introduction and reintroductions can be problematic—meerkats are intolerant of specimens outside their social group.

RESTRAINT AND HANDLING GUIDELINES FOR SPECIFIC TAXA

COMMON MAMMALIAN ORDERS AND SUGGESTED HANDLING AND RESTRAINT METHODS

Table 4.1 organizes most mammalian orders commonly maintained in zoos and aquariums into separate groups, followed by their restraint and handling guidelines (taxonomy adapted from Wilson and Reeder 1993; also Nowak and Paradiso 1983). These orders are included as a basic point of reference; every institution should evaluate all restraint procedures involving any of these species in relation to the principles stated earlier, which are a baseline: resources available; level of staff training, knowledge, and experience; local conditions; and reason for the restraint.

Each taxonomic group has been organized according to the average size, temperament, and nature of the majority of the species classified in the group. The selections are arbitrary and done solely for the ease of use. This is not an exhaustive list, but rather is intended to be representative of as many taxonomic groups as possible.

GROUP 1: SMALL MAMMALS

Suggested restraint methods. Because of their size, hand restraint is the primary means of capture and initial restraint for animals in this group. If chemical restraint is required for more extensive or invasive procedures, an anesthesia box can often be used. Simple restraint devices such as handling crates or cages are suitable in many cases, but a net or gloved hands is the first choice for general exams and minor non-pain-inducing procedures. Often, small mammals can be trained to enter transfer crates voluntarily (Fowler 1995).

Safety concerns. Again, because of their small size, many of these species are very difficult to hand restrain. Their strength in relation to their size is considerable, and most are capable of injuring themselves in attempts to escape. Species such as lagomorphs may struggle to the point of extreme stress and death.

TABLE 4.1. Organization of mammalian orders into categories having similar restraint characteristics

Group 1. Small mammals:
These are mainly noncarnivorous, nonprimate mammals weighing less than 5 kg (with some exceptions, e.g. capybara, giant armadillo, and beaver). Included in this group are

- Lagomorpha—rabbits and hares
- Monotremata—platypus and echidna
- Didelphimorphia—opossums
- Insectivora—hedgehogs, tenrecs
- Scandentia—tree shrews
- Chiroptera—bats
- Pholidota—pangolin
- Hyracoidea—hyrax
- Dermoptera—colugo
- Rodentia—mice, squirrels, capybara, porcupines, agouti, cavys, guinea pigs
- Xenarthra—sloth, armadillo

Group 2. Hoofstock and similar species under 900 kg:
This category includes all members of the order Artiodactyla, and Perissodactyla that average less than 900 kg. The Tubulidentata (aardvark) are included in this group.

- antelopes
- camels
- pigs
- peccaries
- deer
- chevrotain
- zebras, horses, and asses
- tapirs
- aardvark

Group 3. Carnivores:
All carnivores described in this section are further divided into small (<5 kg) or medium to large (>5 kg).

Group 4. Primates:
The primates are divided using the same criteria as set up for carnivores—small (<5 kg) and medium to large (>5 kg).

Group 5. Megavertebrates:
This category includes the following species groups:

- giraffe
- elephant
- rhinoceros
- hippopotamus
- large bovids

Group 6. Cetacea, Sirenia and Pinnipedia:

- dolphins, whales
- manatees
- walrus, seals, and sea lions

Defense adaptations vary widely within these species. Monotremes (echidnas and platypus) have spines and venomous spurs, respectively, and require great care during the restraint process. Pangolins have heavy scales that make it difficult to grasp the animal and can cut an unwary handler. Many species (e.g. flying foxes, shrews, rodents, hyrax, and opossums) are armed with sharp and in some cases impressive teeth that can be used to great effect in the animal's defense.

GROUP 2A: HOOFSTOCK AND OTHER HERBIVORES WEIGHING <5 KG

Suggested restraint methods. Physical restraint in the form of hand restraint is the first choice for most situations that do not require anesthesia. Transfer to a small, confined space should occur before hand restraint. As with other small mammals, these animals can be trained to enter a transfer crate on cue. A darkened stall, approximately 3 m^2 and heavily padded with hay, straw, or other suitable substrate, is ideal. One animal at a time should be enclosed in the stall, with a single trained handler entering after it. As the animal circles the stall, the handler scoops the animal from the floor, supporting the midsection. The hind limbs are restrained at the flanks, and the forelimbs and head restrained with the other hand, while cradling the animal against the handlers' body to support the spine. With practice, this technique can be completed in a single fluid motion. As a second choice, a transfer crate can be used to trap and contain the animal, and as the crate is slowly opened, the animal can be captured and restrained as it is released.

Nets are not recommended for small hoofstock, as most will struggle dramatically, with hooves and horns becoming entangled in the mesh (Fowler 1995). Many species can break one or more legs or rupture a tendon when struggling against a net. Most mechanical restraint devices do not have the range of adjustment to accommodate very small ungulates, and therefore their application is limited.

Safety concerns. The safety of the specimen is the major concern for this group. Only the force necessary to restrain an animal without injuring it should be used. Because of their small size, staff may underestimate the potential for serious personal injury from these animals. Many males in this group (e.g. most gazelles, duikers, and klipspringers) are pugnacious. Some small species of deer have antlers or tusks that can inflict wounds, and all small antelope can use their sharp hooves to injure unwary or untrained handlers.

Following chemical immobilization, staff must be careful to prevent the animal from being injured during recovery, either from group mates or itself. Staff should confine the specimen to a dark, quiet transport crate or kennel and closely monitor it until it has fully recovered, after which it can be returned to its enclosure and social group.

Special considerations. When performing a hand restraint, the handlers need to be aware of potential dangers to the animals. All watches, bracelets, necklaces, belts, and earrings should be removed, as these can potentially catch an animal's leg and cause injury. Long-sleeve shirts are recommended, but buttoned cuffs should be unbuttoned to prevent catching a foot. Shirttails should be untucked to prevent a foot from being caught in the tops of trousers. Coveralls with no pockets are ideal attire during a hand restraint procedure.

GROUP 2B: HOOFSTOCK AND OTHER HERBIVORES WEIGHING FROM 5 TO 900 KG

Suggested restraint methods. This group contains a wide array of species that comprise the majority of animals found in zoo collections today. All are potentially dangerous to themselves, conspecifics, or their handlers and should always be approached with caution. In conjunction with husbandry training, mechanical restraint is recommended as the primary restraint method for most medium and large ungulates. Many types of restraint chutes have been developed and are in use throughout zoos and aquariums (see figs. 4.1–4.4). Physical restraint can be used on many species and/or specimens in this group, and depending on the situation may be the preferred method. The use of hand restraint, or of lariats or nets, should be balanced against the safety of all involved. Some animals can be trained to submit to routine husbandry procedures using operant conditioning techniques. Hand restraint techniques for medium-sized ungulates are similar to those described for small antelope. More personnel may be required to achieve restraint, and it may not be possible to lift the animal off the ground. In this situation, care should be taken to keep the restrained animal from striking anything (or anyone) with its legs and hooves. Staff should support the animal's spine from the back by holding its body against the handlers, with the legs extended away from the handlers. The animal's head should always be maintained at a level above the rumen to avoid regurgitation and inhalation of ingesta.

Safety concerns. Personnel safety is more of a concern when restraining this group of animals, but there is still danger of injury to the animal itself. An animal in this size class is capable of severely injuring or even killing itself through trauma. Some species in this group are extremely aggressive by nature or too big to be restrained by hand. The species in this group pose the greatest risk of injury for personnel: because of their medium size, it is unclear whether it is safer to use chemical restraint, manual restraint, or pure physical restraint for any given individual. In the absence of appropriate mechanical restraint equipment, chemical restraint may be the only safe alternative for extremely large and/or aggressive ungulates.

Special considerations. Capture myopathy brought on by overexertion can occur in a restraint situation (McKenzie 1993). Staff must be careful to limit the duration of a manual or physical procedure to minimize the potential for this and other injuries. When in doubt, or if time is an issue, chemical immobilization should be the method of choice. Afterward, the procedure should be evaluated to determine if husbandry training could have provided an alternative method. When releasing an animal, everyone should be aware of its potential reaction (e.g. fight or flight) and have an escape route in mind.

GROUP 3A: CARNIVORES WEIGHING <5 KG

Suggested restraint methods. Physical restraint is not a first choice, but an option to consider for this group. Many small carnivores can be restrained sufficiently for routine examination using nets and transport crates or kennels. For procedures involving manipulation or for handling more intense than simple examination, chemical immobilization is recommended. Many individual small carnivores can be trained to enter transport crates or kennels voluntarily.

Safety concerns. Injury to the handler is a major concern. Most small carnivores are aggressive and fight back if threatened or cornered. Mustelids and viverrids are particularly aggressive and agile, and react quickly to perceived threats. Many small carnivores are difficult to hand restrain, and are able to turn and bite the handler. The otters, raccoons, mongooses, and many other species have very loose skin, making them even more difficult to handle.

Special considerations. The animals in this group are borderline from those animals that can be reasonably restrained physically when husbandry training is not an option. Experience of the handler, knowledge of the subject, conditions, goals, and resource availability should dictate the method used.

GROUP 3B: CARNIVORES WEIGHING >5KG

Suggested restraint methods. Carnivores weighing more than 5 kg are dangerous if handled without anesthesia, and chemical restraint should be the primary restraint method. Mechanical restraint in the form of remote or protected squeeze chutes is most often the means for administering immobilizing agents. Wherever possible, staff should use husbandry training/operant conditioning to facilitate the administration of drugs. Training can greatly reduce stress to the animal (and staff), and may reduce the amount of drug needed to achieve the appropriate anesthesia. During transport and treatment of immobilized animals, staff should be careful to position the head and neck to maintain an open airway at all times, and to avoid being bitten or clawed if the animal is aroused or has a seizure during the procedure. A trained and experienced handler should be responsible for holding the head of the animal at all times to monitor its anesthetic state and alert the medical staff if needed.

Safety concerns. For many medium and large carnivores, the initiation of immobilization can be dangerous for both for staff and animal. During the early stages of anesthesia, an animal may become recumbent in a position that compromises its airway and requires assistance. If the animal is large and/or dangerous, it may be difficult or impossible to gain access to it to provide aid. Some species (e.g. polar bears, *Ursus maritimus*) have been observed to fake an anesthesia response (Neiffer, personal communication; Mellen, personal communication). All anesthetized large carnivores should be carefully checked to ascertain the level of anesthesia and to determine when it is safe to enter the enclosure with them.

Release and recovery is potentially the most dangerous period of large carnivore restraint. After completion of the procedure and before full recovery, most large carnivores require careful monitoring to watch for the return of the swallow reflex. If an animal has been intubated, the intubation tube is left in place until this reflex returns. Staff must take care to avoid the animal biting though the tube and inhaling it. If an animal should partially recover and fall in a position that compromises its breathing, it is extremely dangerous to reenter the enclosure to assist it. Further stimulation may be needed, but this should only be done remotely.

Special considerations. Since most large carnivore restraints are performed in the animal's enclosure and access points are limited, minimal numbers of personnel should be in the enclosure. All staff should have a clearly designated escape route, and each escape route should have a person stationed outside to assist and secure the door as needed. As in all restraint procedures, noise, light, and all other unwanted stimuli should be minimized. The use of a bite stick should be considered to prevent injury to the teeth.

GROUP 4A: PRIMATES WEIGHING <5 KG

The restraint of all nonhuman primates (NHP) is of particular concern due to the risk of disease transmission, from NHP to human and vice versa. The U.S. Occupational Primate Disease Safety Guidelines for Zoological Institutions (www.aazv.org/associations/6442/files/primate_safety_guidelines.cfm) provides a standardized framework for managing nonhuman primates, and should be consulted and incorporated into all primate restraint plans. All personnel involved in primate restraint should be familiar with the disease risks and trained in proper techniques to minimize the risk of transmission. Proper protective equipment should be worn at all times.

Suggested restraint methods. For primates less than 5 kg, the use of hand restraint and nets is the first choice. Most small primates are agile, fast, and very difficult to net. Hand restraint using gloves is an option, but should only be attempted by trained staff. Hand restraint without gloves should not be done. The potential for receiving a bite or a scratch is high, and disease transmission is a serious issue.

Safety concerns. For this group, the risk for serious injury to the animal is higher than the risk for serious injury to the handler. An added concern is the dexterity of small primates and their ability to grasp with both hands and feet. Knowing the medical status of all primates in the collection is essential. Some diseases carried by primates pose a severe health risk to humans. All equipment used for restraint (e.g. nets, gloves, and transport containers) should be carefully cleaned and disinfected after each use.

GROUP 4B: PRIMATES WEIGHING >5 KG

Suggested restraint methods. Physical restraint is very difficult and should not be attempted unless absolutely necessary in special circumstances. Attempting to hand restrain any ape species is not feasible and extremely dangerous to both the handler and the animal. Because of the species' intelligence and the stress that is caused, involuntary mechanical restraint is not a method of choice, and should be avoided. Mechanical squeeze systems can be used together with husbandry training that may alleviate the stress. Primates can learn behaviors that facilitate many procedures, including hand injection of immobilization drugs (Colahan and Breder 2003). Many large primates are attuned to human behavior and are capable of knowing the difference between a training procedure and a real restraint. Practicing and training for restraint procedures should be a standard part of a husbandry training program, including all steps leading to the restraint procedure itself. Any changes in routine, no matter how subtle, may give the animal a cue that a restraint rather than a training session is planned.

Safety concerns. Large primates can be extremely dangerous due to their strength, agility, and intelligence. Disease transmission is especially problematic with this group.

Special considerations. As large primates recover from anesthesia, care must be taken by staff to avoid being grabbed and/or bitten. During recovery, I recommend confinement in a smaller enclosure. An area that does not allow climbing is preferable, because a recovering primate may attempt to climb before being fully recovered and could fall and injure itself.

GROUP 5: MEGAVERTEBRATES (ELEPHANTS, RHINOCEROSES, GIRAFFES, AND OTHER LARGE BOVIDS)

Restraint methods. Mechanical restraint is the method of choice in most institutions. Many types of specialized handling and restraint devices allow procedures to be performed safely on this group of animals. Due to their size and strength, those procedures that cannot be performed without cooperation must be conducted with some sort of mechanical assistance and potentially with chemical restraint.

Safety concerns. With modern mechanical restraint devices, the primary concern is for the safety of the animal involved. Human safety is less of a risk if involved zoo staff is adequately trained and the equipment has been tested and maintained.

Special considerations. Husbandry training is critical. Any animal being restrained in a mechanical chute should be desensitized to the area, and to the sounds, smells, and movement of the restraint equipment. These animals should be trained so that they calmly and voluntarily enter the restraint area on cue. Most large-mammal restraint devices are not intended to press on an animal physically, but instead limit the space available for retreat (figs. 4.6 and 4.7). I suggest that staff estimate the space needed by the animal before the procedure, and then adjust the size of the chute and allow the animal to enter on its own. Some specimens may voluntarily enter into a space barely large enough to allow passage, yet object to any movement of the chute once they are inside.

Animal care personnel should be sure to have an emergency release wall or door. If an animal becomes overly excited or startled or goes down in the chute, a means of quickly releasing it is necessary.

Fig. 4.6. Giraffe, *Giraffa camelopardalis*, mechanical restraint and training at Disney's Animal Kingdom, Orlando, Florida. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

Fig. 4.7. Okapi, *Okapia johnstoni*, mechanical restraint training backstage at Disney's Animal Kingdom, Orlando, Florida. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

GROUP 6: CETACEANS, MANATEES, AND PINNIPEDS

Restraint methods. Physical restraint is not a first option. If animals are in water sufficiently deep to allow them mobility, restraint will require their removal from the water (Fowler 1995) by husbandry training, using nets and slings, or draining the tank to a level that will allow manipulation of the subjects.

Safety concerns. Overheating and respiratory distress of a restrained animal are the primary concerns. Because marine mammals are voluntary breathers, chemical immobilization is especially risky. Procedures must be carefully timed and monitored to prevent injury to the subject. While out of the water, many species of cetaceans have enough mobility to bite unwary bystanders. Manatees are very powerful and may roll onto their back, catching handlers by surprise and pinning them.

Special considerations. Husbandry training is essential in the preparation and implementation of restraint procedures for animals in this group. Pinnipeds are agile both in and out of the water, difficult to restrain physically, and capable of inflicting serious injury. Attempting to restrain a manatee or cetacean without desensitization to the process, removing it from the water, or severely restricting its movement in a sling can cause severe stress and/or injury.

DISCUSSION AND CONCLUSIONS

Husbandry training, physical restraint, and pharmaceutical restraint should be seen as a continuum, and the appropriate method or combinations of methods for restraint should always be available for consideration. Restraint methods should, and are, continuing to evolve to meet the needs of managing animals in our collections. Advances in mechanical restraint systems have greatly enhanced our ability to care safely and humanely for elephants, rhinoceroses, hippopotamuses, giraffes, and large bovid species on a routine basis. Advances in drug regimens increase the efficacy of chemical restraint options and allow us to perform safer procedures. There are now husbandry training programs being used with many species to aid in restraint procedures.

Together with these advances, it is important to remember and retain the animal handling skills they have supplanted lest they become lost over time. Skills such as roping or the use of nets require practice to maintain the levels of proficiency and confidence required to use them effectively. All animal husbandry personnel should be trained in the proficient use of these varied methods through formal staff training programs.

The process for selection of a restraint method must always consider a hierarchy of criteria. First among these is safety—safety of the personnel and of the animal. Depending on the conditions, the resources available, and the purpose of the restraint, the best restraint method may not be an option at a particular facility. Having as many viable alternatives as possible should provide a level of flexibility that can greatly enhance an institution's capability to meet the needs of the animals in its care.

APPENDIX 4.1

Sources for Equipment Mentioned in the Text

Fauna Research
8 Bard Avenue
Red Hook, NY 12571-1108
marknmartv@yahoo.com
Manufacturer of handling equipment for nondomestic hoofstock, hydraulic tamer, standard mechanical tamer, giraffe tamer, rhinoceros crates and restraint, bison and large-bovid head gates, etc.

Powder River Livestock Equipment
www.powderriver.com
Manufacturer of livestock chutes and restraint equipment

Fuhrman Diversified Inc.
2912 Bayport Blvd
Seabrook, TX 77586
www.fieldcam.com
Manufacturer of Flexinets and other animal handling and capture equipment

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5

A Framework for Introduction and Socialization Processes for Mammals

David M. Powell

INTRODUCTION

For the modern zoo, construction of new, naturalistic exhibits or renovation of existing facilities represents one of the most important tools for ensuring animal well-being. Exhibit designers today seek to create an exhibit that not only displays animals, but also minimizes stress and challenges them physically and psychologically.

New tools for small population management now enable managers to make scientifically based decisions about the breeding of species in captivity to ensure their long-term genetic and demographic health (see Ballou et al., chap. 19, this volume). Ironically, those management tools that should ultimately contribute to the well-being of animals in captivity may also cause them stress in the short term, e.g. placing animals into novel environments or introducing them to unfamiliar individuals. In order to maintain diverse gene pools in captive populations, zoo personnel must move individuals from one facility to another, where they are first exposed to a novel environment and later to unfamiliar individuals, either for breeding or exhibitry. In these cases, the individuals have lost a familiar territory and possibly a social network, losses which may cause animals to behave differently, particularly if the move to a new facility represents their first "dispersal." Dispersal is a sensitive time for captive and free-ranging wildlife, since they are in environments where there may be no familiar conspecifics, and they lack knowledge about the location of critical resources. In describing animals that are captured from the wild and brought into captivity, Hediger (1964) said that the animal must construct an entirely fresh "subjective world" while struggling with new and unfamiliar factors. Animals that move from one facility to another or even between social groups within a facility also must alter their subjective world, based on changes in their environment. Animal managers must work carefully to manage animals through this sensitive period.

In this chapter, I will set forth a framework for conducting successful introductions and socializations of captive mammals based on surveys of the literature, conversations with colleagues, and personal experience. I take a somewhat less mechanistic approach than had Kranz (1996) and Watts and Meder (1996) in the first edition of this book, but I strongly recommend reviewing their chapters when planning introductions. I consider physical introductions (e.g. admittance to exhibit spaces or holding areas) and social introductions (e.g. formation of social groups or breeding units) separately, although both processes have some similar characteristics. Within social introductions, I will only briefly discuss socialization processes for individuals that display some behavioral deficiency (e.g. hand-reared individuals or individuals showing inappropriate maternal care). Watts and Meder (1996) previously provided a good overview of the literature on socialization techniques for primates, and there is very little new literature since that time. For each class of introductions, the framework includes 4 general steps: identifying goals, considerations, preparation, and process. My goal is not to provide taxon-specific recommendations, but rather to provide a framework that can be applied to diverse taxa.

There is still relatively little published information on introduction and socialization techniques (Kranz 1996), especially for nonprimate mammals. A survey of the literature suggests that a few universal principles exist that should apply to introductions and socializations. These will be emphasized in this chapter. I encourage animal managers to share their experiences more widely (e.g. in journals, conference proceedings, husbandry manuals). A well-designed survey study would be a valuable tool for gathering the collective experience of professionals involved in animal introductions. The results of such a study could be published in professional journals and provide additional guidelines. Lindburg and Robinson's (1986) paper remains a valuable resource for planning social introductions of animals in captivity.

PHYSICAL INTRODUCTIONS

An introduction to a new physical space may or may not be accompanied by introduction to unfamiliar conspecifics. In this section, the focus is on planning the introduction of an individual or an intact social unit to a new physical space.

IDENTIFYING GOALS

First, it is useful to define both long- and short-term goals for the introduction to new physical space. Long-term goals identify the eventual outcome desired, while short-term goals help to clarify the steps to take along the way. The long-term goal of a physical introduction is generally to get animals comfortable with all the new living spaces and accustomed to new husbandry routines with minimal stress or injury. Short-term goals relevant here include acclimation to the holding facility, habituation to the husbandry routine and animal care personnel, easy transfer from one enclosure to another (including shifting on and off exhibit), familiarization with exhibit boundaries, and desensitization to certain stressors (e.g. visitor traffic, heavy machinery, and amusement rides), including animals in adjacent enclosures. For each goal, end points and criteria for determining whether the goal has been met should be developed, including criteria that outline when to halt an introduction due to presumed failure.

The animal care team should carefully review reasons for an introduction's failure and take actions to eliminate those obstacles. Knowledge of the animal's biology and individual history will be instructive in developing the criteria used to assess progress, success, and failure. To monitor animal progress during the introduction process, the animal care team should be sensitive to and record those behaviors known to indicate distress in the species; similarly, they should keep track of positive milestones (e.g. sleeping on exhibit, play, and foraging behavior). Everyone on the team should also understand the criteria that will determine when close monitoring can cease.

Goals may be developed by the animal manager or collectively by animal care staff. If only a subset of individuals develops the goals, all members of the animal care team (curators, supervisors, keepers) still should have a chance to comment on them. Since keepers will have the most in-depth knowledge of the *individual* animals at the facility, their input is critical to planning an introduction or socialization.

CONSIDERATIONS

A number of factors need to be considered when developing short- and long-term goals for an introduction, beginning with the species itself. First, what are the species' abilities in terms of locomotion, strength, agility, and intellect? Many of these will have already been taken into consideration during the design and construction of new and refurbished exhibits, but another review of these abilities may uncover problems. For example, when a species of monkey is put onto an island exhibit previously occupied by another primate species, zoo staff should reevaluate escape risks and hazards to the animals.

Ungulates may be moved between different paddocks. Containment developed for a large species may not be suitable for use with a smaller species and vice versa. Are the openings in the fencing small enough to prevent legs from getting caught and infants from escaping the enclosure?

Motivation can enhance an animal's abilities. An animal that feels threatened may jump farther or climb substrates that it never would under normal conditions (Hediger 1964). Under stress, an animal may take unexpected risks (e.g. jumping into moats and climbing over electrical wires). These worst-case scenarios must be considered when designing enclosures, and staff should be prepared to respond to these events.

Species behavioral characteristics, ecological niche, and temperament also need to be considered. Whether a species is a predator or prey or tends to be inquisitive or shy affects how it will adjust to new physical surroundings and sometimes more important, what its first reaction will be upon release into a new enclosure. For example, ungulates are generally more likely to flee, whereas many carnivores will look for hiding places. An understanding of niche will also aid in predicting what sorts of stimuli will be most stressful for the species (e.g. Grandin and Johnson 2005), and it will help predict where animals will go for shelter when they feel threatened. The species' propensity for territoriality can affect its adjustment to new spaces.

After reviewing the appropriate aspects of the species' biology, the history and temperament of each animal involved in the introduction needs consideration. Which animal in the group tends to be dominant? Are any individuals known to be especially "nervous"? Do any of the animals have a history of escape attempts? Are there important relevant experiences from the individual's developmental and rearing history? A group of female Przewalski's horses, *Equus caballus przewalskii*, at the Bronx Zoo was moved into a larger, forested enclosure that also included a rocky hillside. One concern was that the horses might choose to flee along this hillside during their early exposure to the new exhibit and possibly injure themselves. Our prior knowledge of the calm demeanor of these mares around people allowed us to use a line of animal care staff as a psychological barrier to traversing the hill on their first days in the exhibit rather than having to exclude the horses from the area by using a physical barrier.

When receiving animals from another facility, it is critical to ask the sending institution to provide details not only of the individual animals' histories, but also of the enclosures they lived in. For example, a zoo may receive animals that have not been exposed to glass barriers or electrical fencing ("hotwire"). Part of the introduction planning must then include measures to help animals identify, understand, and avoid these barriers.

Staff resources are important considerations. During introductions it is essential to have adequate staffing so that animals can be closely monitored during their early exposure to new exhibits. Animals may need to be watched for several hours or all day in some cases. Staff monitoring the animals should be familiar with the species' behavior so they can interpret the animal's movements and anticipate problems.

PREPARATION

Staff. While all the preceding steps will prepare the staff for conducting a physical introduction, there are a number of additional preparations that should take place immediately before the introduction. First, everyone must understand who the team leader is, i.e. who will decide to end a session or intervene in some other way. The team leader should ensure that everyone understands what the potential outcomes are of the introduction session, and must be sure that everyone on the team agrees on how to respond and intervene. For example, negative reinforcement (i.e. fire extinguishers, hoses, and tools for making noise) might be used to alter an animal's behavior. All team members should be comfortable using these techniques and trained in their use. If the animal has had a positive-reinforcement training program (see Mellen and MacPhee, chap. 26, this volume), the training may be helpful in keeping the animal calm during the introduction, but it should not be relied on solely to prevent the animal from injuring itself.

The goal of an introduction may be evaluated relative to the animals' behavior (e.g. calm or no excessive locomotion), to some time criterion (e.g. allow the animals to explore the exhibit for 30 minutes), or to another factor. Team members need to know when to end a session and/or how an introduction is progressing, even if they are not the individuals making the final decision. During one of the early Przewalski's horse introduction sessions mentioned above, the mares spent only about 10 minutes in the exhibit before moving back into the corral. The team leader decided to end the introduction session immediately, since the mares had shown no behavior indicative of stress and returned reliably to the holding facility. The mares were immediately fed in the holding area to reinforce the behavior of returning to holding.

The team leader should give one team member responsibility for collecting, recording, and summarizing basic data on the session (e.g. the length of the session, the animals' responses, the measures used to keep the animals calm) so that data can be shared with team members and available for future introductions.

Additional personnel. In addition to animal care staff, other zoo departments should be notified, depending on the situation. Veterinary personnel should be aware and perhaps present (in case immobilization is needed) when large or potentially dangerous animals are being introduced to exhibits. Veterinary staff should preferably remain out of view of the animals until needed, since many animals respond negatively to veterinarians. Although veterinary staff can contribute to planning an introduction, final decisions should rest with the animal managers. Individuals licensed in the use of appropriate firearms may also be present in case an animal escapes from the new enclosure. Zoo security staff may be helpful in restricting visitors from the introduction site. If exhibit areas are going to be closed to visitors during an introduction, admissions and public relations staff should be notified.

Introductions to new enclosures sometimes provide opportunities to observe rare or interesting behaviors. A photographer or videographer can be helpful in documenting the process and providing media that could be useful for public relations or marketing. Research staff can also document these behaviors and thus contribute to refining the next stages (e.g. Burks et al. 2004). However, for some animals, introduction to a new enclosure will be stressful and the presence of many people may be overwhelming; thus, animals should have been previously habituated to the visible staff. Additional support staff should be out of view during the procedure but be in contact (via radio).

Enclosure. The enclosure and holding facilities should be inspected very carefully by multiple individuals before introduction, especially if the enclosure was originally built for a different species. All barriers must be secure and intact and potential escape routes eliminated. Viewing areas for visitors may be seen as escape routes by animals, and the presence of visitors may be stressful at first. Visual access to animals in other exhibits might be stressful also. Kranz (1996) recommends that these areas be screened temporarily during acclimation to new enclosures.

Zoo exhibits often have electrified fencing, or "hotwire," as a form of secondary containment or for exclusion from certain areas. All hotwires should be tested and inspected daily by staff. Animals that are naïve to hotwire might benefit from having it clearly marked or having prior exposure to a hotwire panel while still in their old enclosure or their indoor holding area (e.g. Cowan 1998). This is not always necessary. Giant pandas, *Ailuropoda melanoleuca*, at the Smithsonian National Zoological Park in Washington, DC, learned to recognize and avoid exposed hotwire and naturalistic "hot vines" in their enclosures within the first week of occupancy, despite being naïve to hotwire of any kind (fig. 5.1). Animals can be trained to respect hotwire by luring them to it with food. If animals come in contact with hotwire, they must have an easy escape route. Exhibit features that will require complex hotwiring should be avoided when enclosures are designed. McKillop and Sibly (1988) provide a nice overview of the design of electrified fencing for wildlife and de-

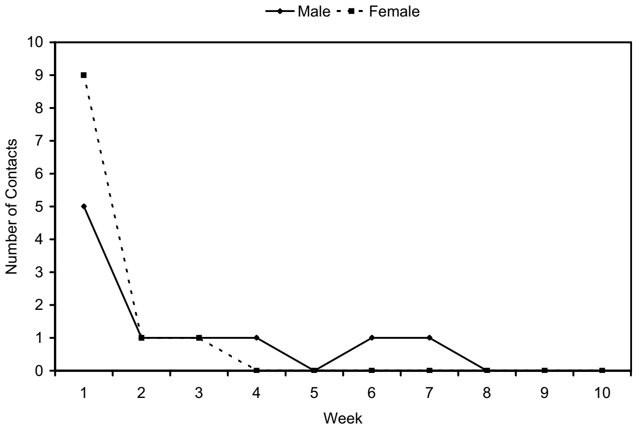

Fig. 5.1. A male and female giant panda at the Smithsonian National Zoological Park in Washington, DC, quickly learned to identify and avoid electrified wire in their enclosure, including wires disguised to look like vines. (Powell, D. M., Kleiman, D. G., and Beck, B. B., unpublished.)

scribe some procedures for training animals to recognize and avoid it.

In new enclosures, shifting mechanisms and locks should be functioning properly, and food and water delivery systems should be operational. Hardware used in construction should be secured (e.g. nuts and bolts welded) and foreign objects (e.g. glass, nails, and lumber) remaining after construction or renovation should be removed. Sensitive equipment (e.g. lights and surveillance cameras) needs adequate protection. Major horticultural or maintenance work should be completed before the introduction or postponed until after animals are acclimated.

Clearly identified exhibit boundaries are important. Ungulates tend to run into fences or moats when frightened (Farst et al. 1980; Kranz, Xanten, and Lumpkin 1984). Fences can be screened using burlap or shade cloth, or they may be marked at intervals with plastic flagging (fig. 5.2a-b). Moat edges should also be marked or flagged in some way. As described for the Przewalski's horse introduction, zoo staff can be used to discourage animals from approaching certain exhibit features that would be dangerous to traverse if in flight. Glass barriers can be made more obvious by covering them with paper, marking them with tape, or making them opaque using soap. Placement of these marking materials on the inside versus outside of the glass depends on the degree of visitor access to the glass and the likelihood of animals interacting with the marking materials (Kranz 1996). Papering the animal side of the exhibit glass may give new arrivals the ability to regulate their exposure to visitors in the early days of an introduction.

Before an introduction, environmental enrichment materials should be placed in the exhibit to help reduce anxiety and provide opportunities for distraction or displacement of stress-induced aggression. Critical resources such as nest boxes, areas of shade, perches, and feeding stations should be provided such that one is available for each animal. Transferring dung, urine, nest boxes, toys, or bedding from holding areas into exhibits can help make the exhibit seem familiar to the animal (Kranz 1996). Rewards or treats should be available to reward animals for calm behavior or returning to the holding area.

PROCESS

Timing. Some introductions proceed quickly and others may take many months; thus, introduction procedures must include adequate time for success. All construction, maintenance, and horticultural work should be completed before introduction to a new exhibit. Animals need at least one month to acclimate to new enclosures and routines. There is always pressure to open new exhibits as soon as possible; however, rushing an introduction can lead to animal injuries, animal management problems (e.g. getting the animal to shift in and out on time), and thus even longer delays. Zoo administration, public relations, development, and marketing departments must be aware of these constraints and plan accordingly when preparing press releases, promotions, and special donor events.

Outdoor introductions should take place when temperature extremes are unlikely so that animals do not overheat or become hypothermic. For many mammals, this means scheduling introductions during the warmer months and usually in the morning before the zoo opens to visitors. In the morning, there are also fewer external stressors such as visitors and noise from rides or attractions. Starting early provides more time for monitoring the introduction, allows managers to respond to unexpected events without public presence, and increases the likelihood that animals will return to holding areas before closing time.

Staffing. During an introduction, the right number and quality of staff need to be available. Keepers who have good relationships with the animals and the most knowledge of the particular individuals should be present, as well as personnel to monitor the animals for the duration of the first introduction session.

Monitoring. During the introduction, the animals should be observed from multiple locations, and someone must be available to operate shift doors immediately. Radio contact between observers is critical. Everyone present should be familiar with the behavior patterns of the animals, including signs of stress or abnormal behavior. Observers should be familiar with the exhibit and prepared to assist with interventions, including rescuing animals from water or other exhibit features. Any equipment needed for interventions (e.g. nets, ropes) should be readily available. Typically, newly introduced animals should be closely monitored during the first week, but this schedule can be reviewed and adjusted by team members.

Managing the animals and the environment. Some animal management guidelines are applicable to a wide variety of species during an introduction. First, animals should be allowed free access into and out of the holding facility. If the animals choose to spend only a few minutes in the new exhibit on the first day, they should not be forced back out, but rewarded for returning to holding, thus terminating the day's session. Second, while some food can be provided on exhibit, it is preferable to feed the majority of the diet off exhibit to encourage return to the holding facility. Third, introduction sessions should be ended long before the zoo closes to give the staff sufficient time to solve any problems that arise. Ending the session early also provides more opportunities to end the introduction positively. Finally, after animals are acclimated to the exhibit and the husbandry routine, they can be introduced to outside stressors. Only after our Przewalski's horse mares were acclimated to their new exhibit and routine did we allow the train that goes by their exhibit to operate.

Adjusting and evaluating the plan. The progress of the introduction should be discussed daily with team members and communicated to other departments when applicable. Team members should achieve consensus on how to proceed, solutions for problems, and appropriate levels of monitoring. Criteria and definitions for a "successful introduction" should be reviewed to see if they are still achievable; if problems arise, goals may have to be changed. Flexibility is important, and the plan should be adjusted when necessary. Lindburg and Robinson (1986) provide a sample data sheet

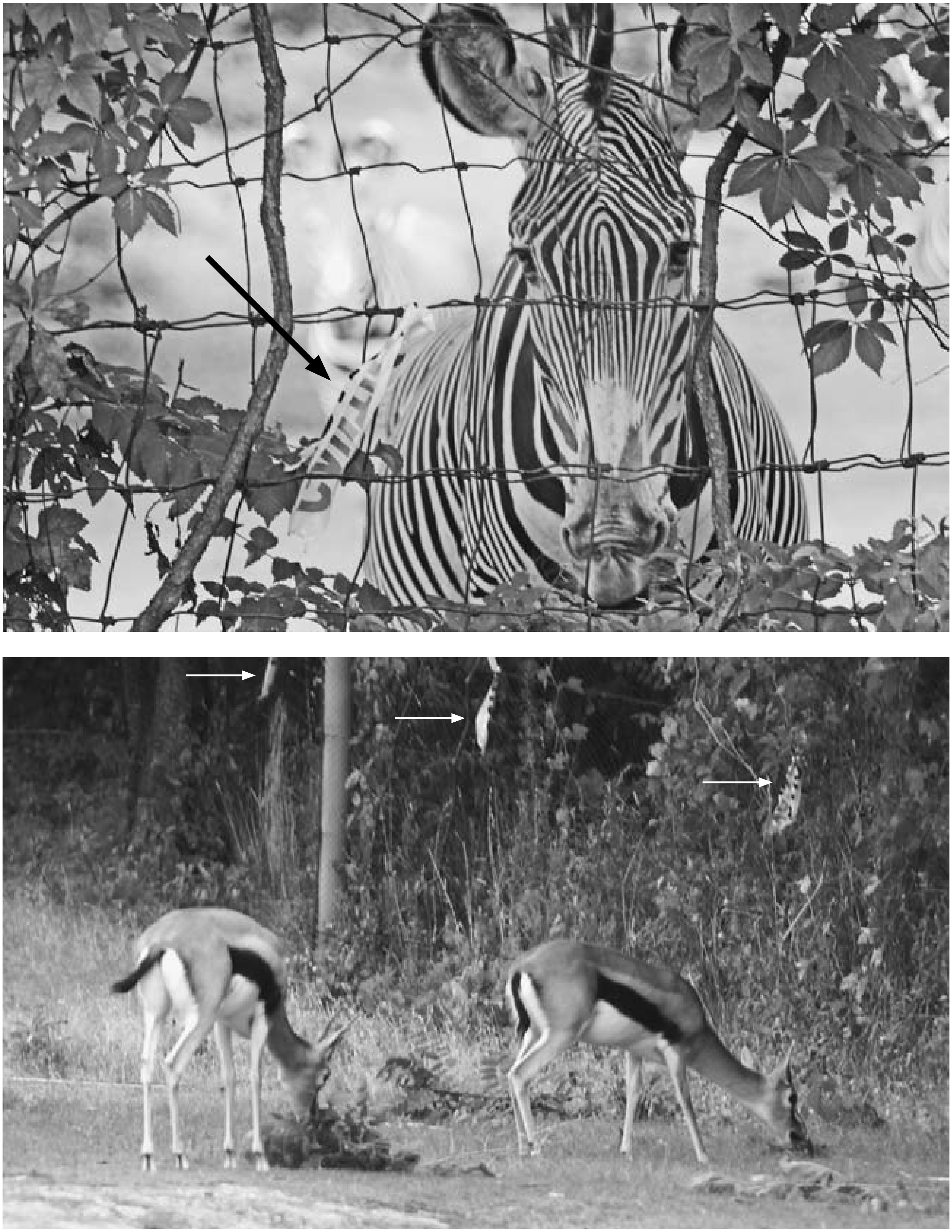

Fig. 5.2 (*A–B*). At the Bronx Zoo, New York, yellow plastic flagging is used to assist ungulates in identifying the boundaries of their enclosures. The flagging is usually removed after a couple of weeks. (Photography by Julie Larsen Maher. © Wildlife Conservation Society. Reprinted by permission.)

for recording data during introductions that can be used to adjust the plan.

SOCIAL INTRODUCTIONS AND SOCIALIZATION

Animals are introduced to one another for breeding, formation of new groups, addition to existing groups, and returning individuals to groups in which they lived previously. Socialization is a process whereby an animal learns appropriate social skills for the eventual purposes of breeding and rearing offspring, or simply living compatibly in a more natural social setting. In mammals, the mother-infant relationship plays a critical role in the development of normal adult social behavior. Removal of infants from their mothers should be avoided whenever possible (Watts and Meder 1996). Inappropriate socialization during development has a profound impact on the expression of normal maternal, reproductive, and social behavior throughout life (Harlow and Harlow 1962; Sackett 1965; Suomi, Harlow, and Kimball 1971).

Nonhuman primates, the focus of the vast majority of published literature on social introductions and socialization, exhibit some of the most complex social dynamics among mammals; thus, we can adapt and apply some of the principles and techniques learned from primates to other species.

IDENTIFYING GOALS

For any social introduction or socialization process, there should be both short- and long-term goals. For example, a long-term goal for a group of nonbreeding animals might be basic compatibility, good general health, and maintenance of body weight. In socializations, the short-term goal might be compatibility, while the long-term goals might include species-appropriate levels of social behavior, reproduction, and rearing of offspring. For females with poor maternal skills, while the long-term goal is to rear offspring properly, short-term goals might include showing appropriate maternal behavior toward a surrogate or allowing the infant to receive supplemental food from animal care staff.

While most physical introductions will eventually be successful, some social introductions will never succeed. Failure may simply be the result of mate choice or individual differences in behavior (e.g. excessive fearfulness or aggression, inappropriate socialization, "individual antipathies" [Hediger 1964]). At the Bronx Zoo, a new silverback gorilla, *Gorilla gorilla*, acquired for breeding was to be introduced to a group of 11 females. After approximately 7 months of introduction efforts, we succeeded in introducing him to 10 of the 11, but he was consistently aggressive to the one remaining female. We introduced the remaining female to another social group and left the silverback living compatibly with the 10 females.

CONSIDERATIONS

Many of the same factors that must be considered in physical introductions should be evaluated in a social introduction, beginning with a thorough understanding of the natural history, behavior, and ecology of the species. I suggest consulting with biologists familiar with the species' biology. When receiving a species with which they have no experience, animal care staff should visit facilities that have the species, and perhaps even the individual animals intended to come to their zoo, to learn their basic husbandry and behavior.

If breeding is a long-term goal for the animals, an understanding of the species' mating system and the specific group's social and dominance relations is crucial so that animal care personnel can predict which individuals might be sources of competition, aggression, and comfort for the new animal. Juveniles/subadults might have to be temporarily or permanently removed from their social group if they are viewed as competitors by a new breeding individual.

Social dominance may also dictate which sex can be successfully integrated into a social group. In some cases it is advantageous for the new individual to have an established ally when finally introduced to the larger social group. Since female Old World monkeys tend to be subordinate when they are introduced to new social groups, we typically introduce them to the male first so they have his support when they are introduced to the larger social group.

Regardless of sex, the specific histories of the group members will have an impact on which individuals will be an appropriate ally for a new social group member. A good choice for a new individual to meet first might be a social group member who has already experienced multiple introductions or has a calm temperament. If there are group members that are likely to be aggressive to a new individual, the new group member may need an ally before the introduction. These considerations apply when introducing new individuals of either sex.

When introducing a new silverback gorilla to an established group of females, we found that the temperament of the male could provide insight into which females to introduce first. With an aggressive male, it is preferable to introduce him first to the most dominant females, whereas if a new male is easily intimidated or timid, he should be introduced first to the most subordinate females. Knowledge of an individual's temperament is also useful in deciding where to do an introduction (see Process section below).

The timing of an introduction is also important, especially with respect to reproductive cycles. For example, Alford et al. (1995) introduced new female chimpanzees, *Pan troglodytes*, to males only when the new female was in estrus, while Bloomsmith, Lambeth, and Alford (1991) and McNary (1992) suggest that introducing females to one another when they are in estrus should be avoided, since estrous females are more likely to be aggressive or assertive. At the Bronx Zoo, introductions of male and female Matschie's tree kangaroos, *Dendrolagus matschiei*, have been most successful when they are timed to coincide with the female's estrus.

Territoriality is another consideration in social introductions. Both males and females may establish territories within their exhibits, consisting of preferred resting spots, perches, or den boxes, or the entire exhibit. When introducing individuals to a social group with an established territory, allowing the new individual(s) to explore the territory first without the established group present may be helpful. This technique will give the new individuals an opportunity to locate sources of food, water, and refuge with less harassment from animals in the established group. New individuals may also become familiar with the other animals through exposure to their sounds and odors in the physical space. Initial social introductions should preferably take place in a neutral environment (e.g. holding areas that are clean) so that territoriality is not a handicap to the new individual(s).

One factor that seems universal in mammalian introductions is that prior familiarity with space or other individuals increases the likelihood of success. Introduction of completely unfamiliar individuals may result in significant stress, fighting, injury, and sometimes death. In the vast majority of mammals, the first contact with an unfamiliar individual in nature takes place via scent or sound rather than in the animal's direct physical presence. Sex, age, reproductive condition, and even body size can be communicated by scent in some mammals (e.g. giant pandas: Swaisgood, Lindburg, and Zhou 1999; Swaisgood et al. 2000; Swaisgood, Lindburg, and Zhang 2002; White, Swaisgood, and Zhang 2002, 2003), so it is important to allow individuals to meet first in the most natural way possible.

In some species, individuals may be driven out from their social group (e.g. mongooses, *Helogale*, *Mungos*, *Crossarchus*, *Cynictis*, *Suricata* spp.: Rasa 1975; agouti, *Dasyprocta* spp.: Meritt 1978) whether they are newly introduced or established group members. These individuals can rarely be reintroduced to that group, which reinforces the need for a gradual introduction process and the monitoring of group dynamics. Craig (2007) describes a successful integration of a new male meerkat, *Suricata suricatta*, into an established group that had lost its breeding male.

PREPARATION

The preparations for a social introduction are similar to those suggested above for physical introductions. Some additional guidelines for preparing the staff, enclosure(s), and animals are outlined below.

Staff. Because social introductions can result in aggression, all staff must be aware of which behavior patterns are associated with different levels of aggression (e.g. body movements or postures, vocalizations) and especially the difference between normal and excessive aggression. Aggression may be reduced with positive-reinforcement training by asking animals to separate from one another or attempting to do short training sets with individuals during the introduction. Training has been used to moderate aggression during feeding in captive chimpanzees (Bloomsmith et al. 1994) and during social introductions of binturongs, *Arctictis binturong* (Goulart 2002). However, aversive methods (e.g. making noises or using a hose or a carbon dioxide fire extinguisher) may be necessary to distract animals or separate fighting individuals. All team members should know how to use these tools.

Physical intervention is also occasionally necessary; thus, staff members should have the appropriate tools and training to capture and restrain animals safely (see Christman, chap. 4, this volume), and a single team leader should have authority to give directions when excessive aggression occurs. Postintroduction evaluation sessions will permit the staff to determine whether changes could be made to improve the process.

Enclosure. Enclosures for conducting social introductions should be chosen on the basis of space availability and the ability to separate individuals quickly. Exhibit enclosures are often larger than off-exhibit spaces, but they are less desirable locations for introductions because intervening or separating animals may be more difficult. Courtship in some species (e.g. Indian rhinoceros, *Rhinoceros unicornis*) may be so aggressive and dangerous that animal managers may decide to restrict breeding introductions exclusively to off-exhibit areas for maximum animal control.

Indoor, off-exhibit enclosures tend to have multiple access doors, which make them a better choice for introductions. Multiple, interconnected cages should be made available to maximize space. All doors should be working properly. In some cases, the addition of visual barriers is helpful in reducing stress. Species that spend time in trees need multiple "arboreal" sites for sitting and should have multiple pathways to those sites. In some small mammal exhibits, where only one area may be available for introductions, a different introduction process is suggested (see Process section below).

Enclosures should be furnished with a variety of materials for enrichment and distraction (see Shepherdson, chap. 6, this volume; see Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume). If food is used, we recommend preventing competition by providing an excess of food, spreading it throughout the enclosure and, where appropriate, providing many smaller items mixed into straw, hay, and other substrates that encourage the animals to forage or search (e.g. seeds or nuts). Craig (2007) suggests that the provision of food during introductions of meerkats is beneficial in helping to establish social bonds, since animals were able to forage together. Plenty of bedding material should be available so that animals can make separate nests if they so choose (Wharton 1986).

During full-contact introductions, access to certain areas where animals might get trapped or injured (e.g. dens, nest boxes, and small corrals) should be prevented (McCaskill 1997; Law and Tatner 1998; Goulart 2002). By contrast, for some species a nest box may be a valuable refuge. The decision by animal care staff concerning whether or not to provide access to these areas depends on the possibility of intervening quickly and effectively, as is typically the case with small mammals when excessive aggression occurs in a confined space.

Animals. Before initiating an introduction or socialization process, all animals, both newly arrived and residents, should be determined to be in good health, because the stress of an introduction may result in the outbreak of a disease that was previously subclinical.

Pharmaceutical drugs have been used frequently during introductions of mammals, particularly primates and ungulates (e.g. chimpanzees and gorillas: Moran et al. 1993; ungulates: Ebedes and Raath 1999). The choice of drug depends on the desired effect. Some treatments will lower aggression, while others will reduce fear. The goal of temporary pharmaceutical use should be to facilitate the introduction by allowing animals to get accustomed to the new stimuli. Consultation with experts is recommended.

Before a social introduction, animal care staff may manipulate certain features of an animal's anatomy, e.g. antelopes' horns may be covered by rubber hose to decrease the likelihood of injury during the process. Colorful sexual skin in some species may communicate dominance. Gerald, Weiss, and Ayala (2006) found that increasing the contrast in sexual skin color using paint was effective at decreasing aggression between 2 unfamiliar male vervet monkeys, *Chlorocebus pygerythrus*, during an introduction.

PROCESS

Before full contact, at least 2 steps have been used in a wide variety of mammalian introductions: establishing sensory contact and limited tactile contact. Research by Burks et al. (2004) suggests that moving from nontactile sensory contact (i.e. animals could see, smell, and hear one another but not touch one another) to limited tactile contact (i.e. animals could touch one another through a barrier) to full contact was more effective at managing aggression and stress during a herd formation process in captive African elephants, *Loxodonta africana*, than using these steps in a more or less random sequence.

Thus, the first step is to establish familiarity through nontactile sensory contact (Andrews 1998), e.g. by giving individuals visual access to one another or rotating them through a common enclosure (e.g. Law and Tattner 1998). Scent can also be transferred from one enclosure to another by swapping dung, urine, scent-marked materials, or bedding between enclosures (e.g. Goulart 2002).

Once visual, olfactory, and auditory contact have been established, limited tactile contact across some kind of barrier (e.g. fencing or cage mesh) should be permitted. Access doors between exhibits can be fitted with mesh windows to allow this type of contact, with the size of the openings small enough to prevent injury from fighting through the mesh. Positive-reinforcement training can also be used at this stage to encourage individuals to sit adjacent to one another safely, a behavior that may be useful when full-contact introductions take place. For some species, the motivation for tactile contact may be so great that introduction windows are not only unnecessary, but in fact may contribute to greater stress. Our experience with the formation of breeding pairs of small-clawed otters, *Aonyx cinereus*, at the Bronx Zoo has been that the animals are so anxious for contact with one another that initial tactile introduction across a barrier causes them to become too excited. Similarly, when introducing a new male meerkat to an established group, Craig (2007) progressed to visual, olfactory, and limited tactile contact sooner than planned due to intense mutual interest between the new male and the group.

Many small mammal exhibits are glass fronted, with solid walls and little or no off-exhibit space, thus requiring partitioning with temporary barriers. During introductions of rodents at the Bronx Zoo, we have used cardboard to partition the enclosure, which provides initial olfactory and auditory contact and allows the animals to initiate tactile contact by chewing through the barrier. Protected tactile contact can also be achieved using a "cage within a cage" (often called a "howdy cage"): the new individual is placed in a small cage that is placed in the established individual's enclosure. This technique has been used successfully with many small mammals (e.g. striped grass mouse, *Lemniscomys striatus*: Wharton 1986; tiger quoll, *Dasyurus maculatus*: Conway 1988; agouti, *Dasyprocta* spp.: Meritt 1978). When forming an all-male group of Rodrigues fruit bats, *Pteropus rodricensis*, at the Bronx Zoo, we added successive individuals to the group by placing each new individual in a cage that hung in the free-flight area for 3–5 days.

Due to the design of some holding facilities, visual, olfactory, and limited tactile contact may have to be provided at the same time. Black rhinoceros, *Diceros bicornis*, have been prepared for full-contact breeding introductions in this way with success (McCaskill 1997). To introduce male maned wolves, *Chrysocyon brachyurus*, to their pups, the males and pups were given visual, olfactory, and limited tactile contact simultaneously. No aggression from the males was seen during this stage, and all the females remained calm (Bestelmeyer 1999).

Full-contact physical introductions should take place only after animals have stopped showing aggression or anxiety when housed next to each other with limited tactile contact (e.g. Rasa 1975). Some animal managers believe that affiliative or play behavior must first be observed through the barrier (e.g. Alford et al. 1995). However, serious aggression can still occur once animals have full access; thus, staff should monitor these introductions directly and be prepared to intervene. The number of staff monitoring the introduction should be restricted to only those needed to intervene effectively.

The full-contact stage of an introduction process is most variable in terms of its execution. For example, it may be advantageous to put all individuals into an exhibit at once without prior experience in the exhibit (Andrews 1998), since this can reduce the likelihood that any individual will claim the entire exhibit as its territory (Hediger 1964). Additionally, there may be less aggression if animals are exploring their surroundings rather than confronting one another. Finally, naïve individuals may seek contact with one another if they are put into a novel environment simultaneously.

If it is thought that a full-contact introduction and first exposure to a new enclosure will increase stress to unacceptable levels, the animals can first be introduced individually to the enclosure, and then to one another. When introducing timid or submissive individuals to new conspecifics, it is preferable for the introduction to take place in the timid animal's enclosure rather than the reverse. Among felids, males are more likely to be the aggressor during an introduction than females; thus, some zoo biologists suggest that physical introductions take place in the female's cage, thus giving her some advantage in dealing with the male (Andrews 1998).

When introducing individuals to established groups, the decision concerning whether to introduce the new animal to all group members simultaneously or first to individuals or subgroups will depend on the species and the situation. In many primate introductions, the latter method is generally chosen so that new individuals have the opportunity to establish affiliative bonds with at least some group members before meeting the entire group (e.g. McDonald 1994; Alford et al. 1995; Brent, Kessel, and Barrera 1997; Meshik 1999). In species characterized by strong dominance hierarchies or castes, introductions of subsets of individuals may not be possible without disrupting the hierarchy and unintentionally creating subgroups that cannot be re-formed (e.g. naked mole rats, *Heterocephalus glaber*).

The progress made by animals during the introduction process should guide the pace and timing of the introduction. Success may be achieved relatively quickly (days to weeks) or very slowly (months to years). Initial full-contact introductions should be short in duration, and zoo staff should attempt to end the session in a positive way (e.g. when the animals voluntarily separate themselves). Subsequent sessions can be longer based on the responses of the animals, but introduction sessions should happen consistently, as even short delays can set the process back (Andrews 1998). Animals should not be housed together overnight until there is consistently positive interaction between them during multiple all-day encounters, and all animals seem comfortable with one another and the environment. All individuals should be eating and resting normally before they are housed together overnight.

For some small mammal introductions, continuing with the introduction process is advisable, even on weekends when fewer staff are present, because stopping for even a couple of days may retard the process. At the Bronx Zoo, we reintroduced a hand-reared female Damaraland mole rat, *Cryptomys damarensis*, to her parents and 4 other offspring by confining her to a nest box that had a connected tube with metal mesh over its end and putting her into the enclosure with the colony for one week. During that week, feces from the female and the colony members were exchanged between enclosures. After a week, the female was released into the colony, but she was removed for the weekend when the senior keeper was off duty. When released again, the colony attacked her, and the process had to be restarted.

The timing of introductions is another issue, i.e. whether to do them during the day or at night. Most felids are nocturnal or crepuscular, and conspecific aggression tends to occur at night or in the dawn and dusk hours, when absent staff cannot witness interactions (Andrews 1998). Some institutions therefore separate animals at night. Introductions of clouded leopards, *Neofelis nebulosa*, for breeding are notoriously difficult, given that a male may kill or seriously injure its intended mate (Law 1991; Mellen 1991; Kitchener 1999). At the Glasgow Zoo, a clouded leopard male that had attacked a previous mate was successfully introduced at night to a female who had never accepted a mate, with keepers present through all stages of a gradual stepwise process (Law and Tatner 1998).

The timing of introductions in relation to feeding is another consideration. In some cases, hunger can be used to focus the animals' attention on feeding rather than aggression, but the food should not provoke competition. Alternatively, being satiated during an introduction may decrease the likelihood of aggression. In the clouded leopard introduction described above, the male was fed before the full-contact introduction in an attempt to suppress any hunting behavior he might direct toward the female (Law and Tatner 1998); he was also given catnip as a distraction. At the Bronx Zoo, we typically feed carnivores before any social introductions.

For some highly social species, staff may prefer to begin an introduction before the quarantine period has ended. If the medical record for the newly arrived individual is complete and concerns about disease transmission minimal, the benefits of having social contact may outweigh the disease risk to the collection and the stress caused by isolation.

The plans and processes for social introductions need ongoing monitoring, documentation, evaluation, and readjustment. The animals' comfort with one another should be the factor setting the pace for the process. Failure to take adequate time to progress from the various steps described above can result in more setbacks, a longer road to successful integration, long-term social instability, fighting, injury, and even death.

SOCIALIZATION

In this section, I will discuss the process of moving animals from living with humans or other surrogates to conspecifics. I will focus on adult mammals rather than infants or juveniles, since Watts and Meder (1996) provide detailed guidelines for the socialization of young mammals. Jendry (1996) also provides a good protocol for the use of surrogates to integrate hand-reared gorillas into social groups. When infants or juveniles must be removed from their mothers, animal care staff should provide opportunities for young mammals to have social stimulation and contact with conspecifics. I provide a list of references on socializing mammals in appendix 5.1 and also briefly discuss methods for eliciting appropriate maternal behavior from females that show behavioral deficiencies.

Socialization processes for adult great apes are well documented and often involve the same steps as those described above for social introductions (i.e. nontactile sensory contact, limited tactile contact, and then physical introduction), e.g. for chimpanzees (Fritz 1989; Bloomsmith et al. 1999). Zoo Atlanta successfully socialized 2 silverback gorillas, both of whom had lived in complete social isolation for nearly 30 years (Winslow, Ogden, and Maple 1992; Burks et al. 2001). Each introduction process used similar stages, but during the second socialization procedure, observers collected and then used formal behavioral data to evaluate when to proceed to the next stage rather than relying on subjective opinions of progress.

Socialization processes generally take more time than social introduction of behaviorally normal individuals, and only limited goals may be achievable. For instance, it may be possible to socialize individuals so that they can live with one another, but impossible to achieve complete social integration, reproduction, and rearing of offspring (Fritz 1989). Socialization programs require an even greater in-depth understanding of individual behavior so that the right choices are made for pairing individuals and moving on to more advanced stages of socialization. The likelihood of success in a socialization procedure is probably greater when there is a larger pool of known individuals of various ages and sexes that can be used for introduction to the behaviorally deficient individual. In chimpanzees, for example, socially normal individuals can serve as "teachers" for the compromised individual, and young individuals may be particularly useful in teaching older, compromised individuals how to play (ibid.). In rhesus monkeys, *Macaca mulatta*, using similar-aged, behaviorally normal individuals as "therapists" has been successful in reversing the effects of isolation rearing (Suomi, Harlow, and Novak 1974; Novak and Harlow 1975; Novak 1979).

To improve maternal skills in primate females, a remedial strategy involves housing deficient females with proficient females so that the former can learn from appropriate models (e.g. Hannah and Brotman 1990); however, in monogamous species this may not be possible, since 2 females may become aggressive to each other. Another strategy involves shaping and reinforcing good maternal behaviors (e.g. proper positioning of infants on the nipple) or training behaviors that allow caretakers to deliver food supplements to infants. The challenge is that the time available for training mothers is often very short, because infants need to nurse quickly and regularly. Fontaine (1979) and Thorpe (1988) describe training programs that were used with a female orangutan, *Pongo pygmaeus*, and gorilla, respectively, to permit supplemental feedings of infants. Zhang et al. (2000) report a method used to encourage maternal care in a female giant panda that initially displayed fear of her infant, necessitating hand rearing of the cub. Initially they exposed the mother regularly to 3 stimuli associated with infants (the mother's own milk, urine from the infant, and recordings of the infant's vocalizations) in association with a stuffed toy panda "surrogate." The urine cues elicited the strongest maternal behavior toward the surrogate. In the second phase, they slowly reintroduced the infant to the mother, first by allowing her to have limited tactile contact with the live cub through metal bars. Then a trusted caretaker entered the enclosure with the female and assisted the cub in nursing from the mother until she picked it up independently for nursing and grooming (an approach also used with a female orangutan in the Tama Zoo in Japan: Asano 1967). Animal care staff gradually reduced the human assistance, increased the infant's time with its mother, and provided the mother with rewards for allowing the cub to nurse. These studies highlight the importance of providing sensory stimuli from infants to females.

CONCLUSION

Introduction and socialization processes for captive mammals have always relied heavily on "the art of animal husbandry" and less so on science, in part due to the lack of published literature, particularly on nonprimate mammals. Most of the primate literature on this topic derives from laboratories, where housing and husbandry systems differ from zoos. More applied research on the topic of introduction and socialization processes for a wider range of mammals would be desirable, especially with the results communicated broadly within the zoo community. The introduction and socialization of mammals need significant planning and a systematic, stepwise process; thus, a more scientific analytical approach would be beneficial. Greater success will come from having well-designed facilities and an in-depth knowledge of the species' biology and individual history. Patience and flexibility are key features of successful programs.

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APPENDIX 5.1

References Related to Introduction and/or Socialization Processes for Taxonomic Orders of Mammals

General Reference
Kranz 1996

Marsupialia
Conway 1988

Artiodactyla
Addison and Baker 1982; Castillo 1990; Davidson 1974; Dittrich 1968; Dobroruka 1974; Ebedes and Raath 1999; Farst et al. 1980; Janecek 1971; Knowles and Oliver 1975; Kranz, Xanten, and Lumpkin 1984; Moreno 1990; Oeming 1965; Rahn 1978; Read 1982; Read and Frueh 1980; Stanley Price 1986; Sullivan 1967

Carnivora
Andrews 1998; Bestelmeyer 1999; Brambell 1974; Brand 1980; Craig 2007; Fitzgerald 1985; Frese 1981; Goulart 2002; Kempske and Cranfield 1987; Kinsey and Kreider 1990; Kitchener 1999; Law 1991; Law and Tatner 1998; Leslie 1971; Mellen 1991; Qiu 1990; Rasa 1975; Thomas et al. 1986; Weinheimer 1987; Wemmer and Fleming 1975; Yost 1976; Zhang et al. 2000

Cetacea
Griffin and Goldsberry 1968

Insectivora
Dryden 1975; Eisenberg 1975; Eisenberg and Gould 1967; Eisenberg and Maliniak 1974; Hoyt 1986; Martin 1975

Lagomorpha
Davison 1973, 1974

Perissodactyla
Atkinson and Blumer 1997; Barongi 1986; Boyd 1985; McCaskill 1997; Moreno 1990

Pholidota
Hoyt 1987

Primates
Alford et al. 1995; Anderson, Combette, and Roeder 1991; Asano 1967; Benton 1976; Bernstein 1969; Bernstein, Gordon, and Rose 1974; Bloomsmith et al. 1991, 1994, 1999; Bound, Shewman, and Sievert 1988; Bowen 1981; Brent, Kessel, and Barrera 1997; Burks et al. 2001; Caine and Short 1981; Coffman 1990; Cole et al. 1979; Cowan 1998; Doherty 1991; Dronzek et al. 1986; Fontaine 1979; Fritz 1989; Fritz and Fritz 1979; Gerald, Weiss, and Ayala 2006; Hannah and Brotman 1990; Haring and Wright 1989; Inglett et al. 1989; Jendry 1996; Johnstone-Scott 1988; Keiter 1983; Kennedy 1992; Lippold 1989; Mack and Kafka 1978; Margulis 1989; Martin 1975; McDonald 1994; Meder 1985; Mellen and Littlewood 1978; Meritt 1980; Me-

shik 1999; Meyer and Wilcox 1982; Moran et al. 1993; Nadler and Green 1975; Neugebauer 1980; Novak 1979; Novak and Harlow 1975; Puleo, Zucker, and Maple 1983; Ruedi 1981; Ryf 1990; Stevenson 1976; Suomi, Harlow, and Novak 1974; Thorpe 1988; Watts and Meder 1996; Williams and Abee 1988; Winslow, Ogden, and Maple 1992

Proboscidea
Burks et al. 2004; Young and Oelofse 1969

Rodentia
Blake and Gillett 1984; Meritt 1978; Richard 1975; Velte 1978; Wharton 1986

Xenarthra
Meritt 1975

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6

Principles of and Research on Environmental Enrichment for Mammals

David Shepherdson

INTRODUCTION

Environmental enrichment has matured over the last decade from a fringe activity with a few dedicated practitioners and advocates into a mainstream husbandry activity and productive area of zoo research. In many ways it has become the tool of choice for identifying and solving animal well-being issues in zoos. Environmental enrichment, while not a science per se, involves the application of many of the concepts and principles of the increasingly active scientific discipline of animal welfare. This link with science provides an objective foundation for enrichment activities and gives it its dynamic and intellectually interesting characteristics. A definition is a good place to start, particularly for a subject with such diverse roots and various applicants. An early definition was "Environmental enrichment is a principle of animal husbandry that enhances the quality of captive animals' lives by identifying and providing environmental stimuli necessary for optimal psychological and physiological well-being" (Shepherdson, Mellen, and Hutchins 1998). In an unpublished report in 1999, the Behavior Advisory Group of the American Zoo and Aquarium Association defined Environmental Enrichment thus:

> Environmental enrichment is a process for improving or enhancing zoo animal environments and care within the context of their inhabitant's behavioral biology and natural history. It is a dynamic process in which changes to structures and husbandry practices are made with the goal of increasing the behavioral choices available to animals and drawing out their species-appropriate behaviors and abilities, thus enhancing their welfare. As the term implies enrichment typically involves the identification and subsequent addition to the zoo environment of a specific stimulus or characteristic that the occupant/s needs but which was not previously present.

This latter definition succeeds (albeit somewhat clumsily) in encompassing the major goals and principles of enrichment. At its simplest, environmental enrichment is about making changes to an animal's environment that result in improved well-being as judged primarily by subsequent changes in behavior. It is an implicit assumption of environmental enrichment that it adds to the captive environment something that the animal was previously deprived of and which is necessary for its optimal well-being. This is an important semantic point, because otherwise the term can be seen to imply that environmental enrichment is something "extra" that is nice but not required (Burghardt 1996). As Mellen and MacPhee (2001, 214) have stated: "Enrichment needs to be more than a Band-Aid on abnormal behavior or inactivity; it should be a concerted plan of action for captive management with measurable goals and results."

Environmental enrichment activities cover a multitude of innovative, imaginative, and ingenious techniques, devices, and practices aimed at providing adequate social interaction, keeping captive animals occupied, allowing an increased range and diversity of behavioral opportunities, and providing more stimulating and responsive environments. Examples range from naturalistic foraging tasks such as tools for chimps (Celli et al. 2003), to objects introduced for manipulation, play, and exploration, to novelty and sensory stimulation such as scents for lions, *Panthera leo* (Powell 1995). Appropriate social stimulation (both inter- and intraspecies) and even training by humans are often described as environmental enrichment. Renovation of old and sterile exhibits and the construction of new exhibits with the design goal of providing enhanced opportunities for the expression of natural behavior patterns are also often considered as environmental enrichment. White et al. (2003) describe how moving animals between neighboring exhibits can be used to achieve more natural activity budgets and reduce stereotypic behavior.

The rest of this chapter will expand on concepts, principles, and goals of enrichment and describe some of the research findings on which they are based. Rather than a "how-to" guide to environmental enrichment (see Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume), this chapter is intended to be a strategic guide to thinking about enrichment and an essential starting point for developing effective environmental enrichment activities and programs as well as for designing future research. Given the broad nature of the topic, many other chapters in this volume also contain pertinent information (see chap. 15 by Cipreste, Schetini de Azevedo, and Young, chap. 25 by McPhee and Carlstead, chap. 26 by Mellen and MacPhee, chap. 5 by Powell, and chap. 27 by Swaisgood and Schulte; see also Young 2003).

CONCEPTUAL FRAMEWORK

Much has been written about the historical background of enrichment (Forthman-Quick 1984; Hutchins, Hancocks, and Crockett 1984; Mellen and MacPhee 2001; Shepherdson 2003) such that a detailed review here would be redundant. A brief overview, however, helps to set the stage. Markowitz (1982) is usually and appropriately credited with being the first to apply some of the ideas of zoo biologists such as Heini Hediger (Hediger 1964) and others along with his own, and integrate them with current ideas from experimental psychology, human psychology, and ethology to create "behavioral enrichment," the precursor to the activity now referred to by most as environmental enrichment. Much of this work was based on the concept of giving animals the opportunity of "working" (performing active behavior) for a food reward. The concepts of choice and control were also strong themes in this early work and continue to be so to this day. Research in the laboratory, on the farm, and in the zoo combined with practical experience and theoretical paradigms have resulted in the following commonly cited enrichment concepts.

MIMICKING NATURE

Mimicking nature is probably the most frequently cited rationale for enrichment and stems from publications such as those by Hediger (1950) and by Hutchins, Hancocks, and Crockett (1984). In a review of 25 published enrichment studies specifically aimed at reducing stereotypic behavior, Swaisgood and Shepherdson (2006) found that 76% of the papers cited this concept. As a scientific concept it is not well refined, and in many cases authors would probably do better to state their argument in terms of behavioral needs (see below). The argument is that animals have evolved over many generations to thrive in a specific set of natural environments; thus, by definition, in this environment (or a facsimile thereof) the animals' needs will be satisfactorily met. By extension, then, an animal that behaves in captivity the same way as it would in the wild is assumed to be in a good state of well-being. Veasey, Waran, and Young (1996) do a good job of outlining the major drawbacks of an overly simplistic application of this concept. Preeminent among these are the problems of defining "natural behavior" in a species with diverse habitats, the problem of deciding which behaviors and environmental stimuli are "good" (perhaps foraging opportunities) and which are "bad" (maybe predation events or poisoning), and the fact that most animals are capable of learning to adapt to novel environments and do this with novel behaviors. Nevertheless, the basic premise does have merit (Dawkins 1989), and in the absence of better information and if applied with discretion, this concept can and has resulted in some effective strategies for enrichment and exhibit design. That animals in captivity can have activity budgets that closely approximate those in the wild has certainly been documented (Melfi and Feistner 2002).

BEHAVIORAL NEEDS

Also described as ethological needs, this concept gained momentum when developed by Hughes and Duncan (1988). In the study by Swaisgood and Shepherdson (2006), this was the second most-cited concept in 64% of papers. Essentially, the argument is that animals have evolved complex patterns of behaviors, and that they have a "need" to perform these behaviors. If animals are reinforced not just by the functional consequences or end point of their behavior (e.g. for a predator, this might be eating its prey), but also by the performance of the behavior itself (such as exploring, digging, hunting), then the absence of either the ability to perform those behaviors or the stimuli needed to elicit them may result in frustration and ultimately stress. If this is the case, then it is not sufficient for us to simply anticipate our charges' needs and supply them; we must also allow for expression of the behaviors that are associated with satisfying those needs in the species' wild environment. Zoo research supports the validity of this concept. For example, Shepherdson et al. (1993) found that small cats given the opportunity to hunt for small food items displayed fewer stereotypic behaviors, became more active, and displayed a wider diversity of behaviors. Furthermore, these changes in behavior were not limited simply to the duration of interaction with the enrichment activity. In an exemplary study on giant pandas, *Ailuropoda melanoleuca*, Swaisgood et al. (2001) also found that the provision of complex foraging tasks as enrichment resulted in fewer stereotypic behaviors, increased activity, and greater diversity of behavior. Again, this effect was maintained even when the animals were not interacting with enrichment devices (an aspect that many studies fail to evaluate), and the authors concluded that the results were "consistent with the ethological needs model of motivation in that opportunities to perform more natural behavior appeared to improve motivational indices of well-being" (p. 447). Broadly similar results have been documented in elephants, *Loxodonta africana* (Stoinski, Daniel, and Maple 2000), large cats (McPhee 2002), and many others. Further credence has recently been given to this model in a study of carnivores by Clubb and Mason (2003) which found a correlation between range size in the wild and propensity to exhibit stereotypic locomotor behaviors (typically, "pacing") in captivity. Carnivores that range over larger areas in the wild also tend to be more prone to pacing in zoos, suggesting that they have a stronger motivation or "need" to perform locomotor behaviors in captivity that then presumably become stereotypic in nature due to restriction of space.

There are several practical problems associated with applying this concept. Presumably, some behaviors are more "necessary" than others, but how do we identify those behaviors? Some animals are so strongly motivated to perform specific behaviors that they will perform them in the absence of the usual eliciting stimuli (sometimes referred to as "vacuum activities"). Can we conclude for these animals that their needs are indeed being met?

INFORMATION PRIMACY

Animals will frequently "work" to obtain food in situations where "free" food is easily available. This is often referred to as "contra-freeloading" in the literature and also as an example of the "Neuringer effect" (Neuringer 1969). The behavioral needs concept described above is one way to explain these behaviors, but there is an interesting alternative. Inglis and Fergusson (1986) and Inglis et al. (2001) studied this phenomenon in captive starlings, *Sturnus vulgaris*, and argued that the purpose of this behavior was to gain knowledge about the quality and distribution of a food resource that might convey a fitness benefit in the future. They argue that for many (if not most) animals, information seeking is a primary motivation, and the information gained is used to construct cognitive models that provide a framework for the organization and prioritization of more goal-directed behaviors (Inglis 2000). Although Inglis et al. do not make the explicit connection between this information-seeking motivation and well-being, others have argued that frustrating this motivation (or perhaps preventing the construction of cognitive models that help an animal organize its actions) by providing environments lacking in biologically relevant "information" may indeed result in reduced well-being (Shepherdson et al. 1993; Swaisgood et al. 2001). As Mench (1998) points out, information seeking is likely to be important for a wide range of activities and not only for feeding-related activities. Enrichment activities based on this principle often include novel or manipulable objects in addition to food. General, but not exclusive, support for this concept is provided by many enrichment studies in which animals choose more energetic or behaviorally complex alternatives to obtain food when presented with a choice (Markowitz 1982; Coulton, Waran, and Young 1997).

CONTROL/BEHAVIORAL CONTINGENCY

Control can be defined as the probability that a certain outcome will occur in response to a given behavioral interaction. For example, an animal that is in control of its feeding can perform a behavior (foraging) and receive a food reward. An alternative definition is that there is a contingency between what the animal does and the response of the environment to this behavior. Traditional zoo husbandry typically conveys very little control to its charges. Theoretical models and research findings support the hypothesis that control is important to the well-being of captive animals (Joffe, Rawson, and Mulick 1973; Carlstead 1986; Carlstead, Brown, and Seidensticker 1993; Markowitz and Aday 1998). The concept of control can be applied to many aspects of an animal's life, including regulating body temperature, seeking shelter, and evading stress-inducing stimuli. For example, Carlstead, Brown, and Seidensticker (1993) demonstrated that leopard cats, *Felis bengalensis*, exhibited less stereotypic pacing when given places to hide from the sight of larger cats located in the same building. This concept is linked with that of information primacy in that both serve in different ways to increase predictability in the environment. Sambrook and Buchanan-Smith (1997) have developed this aspect further and suggest that it may in fact be the acquisition of control that is important rather than control per se. Although training is often cited as a form of enrichment through "cognitive stimulation," it might be useful to think of this also in terms of control. After all, training is about learning to control future events (e.g. obtaining a food reward) through carefully scripted behavioral interactions (with the trainer). It is worth emphasizing that the beneficial effects of training suggested by this concept really only apply to the training of new behaviors rather than the maintenance of behaviors that the animal already knows. Evidence of the beneficial effects of training on well-being are growing in the scientific literature (Kastelein and Wiepkema 1988; Laule 1993; Laule and Desmond 1998; Bloomsmith et al. 2003).

Understanding what motivates animals is the fundamental key to optimizing their well-being. These concepts help us to do that by providing good starting points for understanding how captive environments may be lacking and how enrichment may work to alleviate or improve zoo environments. Little is currently known about the relative utility of these concepts in enrichment. Although evidence exists to support each of them and these concepts are frequently cited in the literature, very few studies attempt to test them with competing hypotheses, as Swaisgood et al. (2001) did with giant pandas. It is hoped that researchers in the future will address this topic more rigorously.

In practice, most enrichment focuses on the more proximate goals of giving animals more choices, more complex environments, more "naturalistic" environments, and less "stressful" environments; providing more naturalistic behavioral opportunities; and reducing or eliminating abnormal or stress-related behaviors. As a practical interpretation of the concepts described, I would argue that this is a pragmatic and sensible approach and one that has proved successful. These proximate goals are also the only objective criteria that we have for measuring the effectiveness of enrichment.

HOW EFFECTIVE IS ENRICHMENT?

MEASURES OF EFFECTIVENESS

In order for the effectiveness of enrichment activities to be objectively evaluated, there must be a clear goal or hypothesis stated in terms of some measurable parameter, with a demonstrable or at least theoretical relationship to animal well-being. Clearly, it is not sufficient simply to document a behavioral change or interaction with an enrichment activity and assume that this is positive, although there is, unfortunately, a large literature on the topic that fits this description. In most cases hypotheses are based on behavioral changes because these are the easiest to observe in zoo animals, the underlying concepts (described above) predict certain specific changes in behavior, and behavior is often one of the most sensitive indicators of reduced well-being. Increasingly, however, physiological measures are being combined with behavior to increase the sophistication and reliability of studies.

The goals or hypotheses of most enrichment studies fall into one or more of the following categories.

Reducing abnormal behavior. Many of the abnormal behaviors seen in captive animals have been associated with reduced well-being (Mason and Latham 2004). By far the most commonly described abnormal behavior in zoo enrichment studies is stereotypic behavior (Clubb and Mason 2003). In a meta-analysis of 23 published enrichment studies with the stated goals of reducing stereotypic behavior, Swaisgood and Shepherdson (2006) found that on average stereotypies were reduced by over 50%. These effects were not transient and were not due to novelty effects, since longer-lasting enrichments had greater, not lesser, effects. In no cases was stereotypic behavior eliminated, but these reductions in stereotypic behavior are strong evidence of the effectiveness of enrichment at improving well-being. Good examples of these kinds of studies include the use of timed feeders for Amur tigers, *Panthera tigris altaica* (Jenny and Schmid 2002), more naturalistic enclosures for pandas (Liu et al. 2003), live fish and bones provided for lions and Sumatran tigers, *Panthera tigris sumatrae* (Bashaw et al. 2003), provision of live food and foraging opportunities to small cats (Shepherdson et al. 1993), and providing foraging tasks for 3 bear species (Forthman et al. 1992). The proven ability of environmental enrichment to reduce stereotypic behaviors remains one of the strongest indicators of its efficacy.

Increasing behavioral diversity. The behavioral diversity exhibited by captive animals is usually less than that of animals in the wild, and is also an indication of behavioral opportunities and degree of control. Increasing behavioral diversity is thus another mechanism for evaluating the effectiveness of enrichment. In studies where behavioral diversity has been assessed, enrichment has been shown to be effective at increasing it. For example, feeding live fish intermittently to a fishing cat, *Prionailurus viverrinus*, resulted in sustained increases in behavioral diversity (Shepherdson et al. 1993), as did novel object enrichment for giant pandas (Swaisgood et al. 2001) and lions (Powell 1995). Various mathematical indices have been developed in the field of ecology to quantify biological diversity (a product of total number of entities and the relative frequency of each entity in the population) which can be readily applied to the measurement of behavioral diversity. For example, the Shannon Diversity Index (Shannon and Weaver 1949) was used for this purpose by Shepherdson et al. (1993) to quantify changes in behavioral diversity in small cats. If behavioral diversity was measured more often, it would probably turn out to be a common consequence of enrichment.

Increasing duration or frequency of specific target behaviors. Many studies in the literature document the effectiveness of enrichment at increasing the frequency of "desirable" behaviors. The relationship between these kinds of studies and the "behavioral needs" or "mimicking nature" concepts are clear, but they can also support studies based on other concepts. For example, increases in exploratory behavior might be used to evaluate enrichment based on information primacy. The kinds of behaviors that are cited most frequently include foraging behaviors, exploration, and locomotion and play. For many years zoos have used various kinds of gum feeders to encourage specific gum foraging behaviors (McGrew, Brennan, and Russell 1986). A large literature documents the effectiveness of whole carcasses at stimulating a wide range of predatory-related behaviors; e.g. McPhee (2002) documented increased foraging behaviors (combined with reduced abnormal behaviors) when 3 different species of cat were fed whole carcasses. Bashaw et al. (2003) tested the effects of feeding live food (fish) and whole leg bones on behavior in Sumatran tigers and African lions, and again were able to document increases in both variety (live fish) and frequency of foraging behaviors (both). There are also clear health benefits to feeding large carnivores with whole carcasses, as Lindburg has argued (1988). Moving animals into new surroundings can be an effective way of producing quite long-lasting increases in exploratory and territorial behaviors (White et al. 2003). Chang, Forthman, and Maple (1999) documented increases in "natural" behavior patterns as a consequence of more naturalistic enclosures for mandrills, *Mandrillus sphinx*. Other studies have also been able to demonstrate the similarity between animal behavior in enriched captive environments and in nature (Melfi and Feistner 2002). Enrichment clearly can be an effective way of encouraging a wide range of behaviors considered beneficial, based on one or more of the concepts described above.

Increasing enclosure utilization. Many of the problems of captivity are a consequence of confinement or reduced space. If we define *space* in terms of the captive animal's use of available space, then it may be possible to increase perceived space without actually changing the physical size of the environment. Not many studies have taken this approach and compared indices of space use. However, those that have done this have been able to show that enrichment can increase the amount of space used by captive animals. Shepherdson et al. (1993) found this to be the case in an experiment with live prey for a fishing cat, as did Zucker, Deitchman, and Watts (1991) for a Diana monkey, *Cercopithecus diana*, and Forthman-Quick and Pappas (1986) for chamois, *Rupicapra rupicapra*. Mathematical indices such as the "spread of participation index" first used in this context by Traylor-Holzer and Fritz (1985) are useful for quantifying changes in space use. Sometimes the aim is not to increase space use but to encourage more "natural" space use, as in a study on orangutans, *Pongo pygmaeus*, by Hebert and Bard (2000). Use of space is an aspect of zoo animal behavior that could benefit from some creative thinking (see Coe and Dykstra, chap. 18, this volume).

Reducing physiological correlates of stress. Few zoo enrichment studies to date have evaluated physiological measures of well-being in zoo animals, although the technology is becoming more practical. Studies in laboratories (Van Loo et al. 2002) and on experimental farms (de Jong et al. 2000) increasingly use these measures. Potential physiological measures include direct and indirect measures of blood cortisol, immune function, and metabolic measures such as heart rate (Ruis et al. 2002). Analysis of pathology results also holds some potential for retroactive assessment of well-being, but most data recording systems are currently not standardized enough to make this realistic. Carlstead, Brown, and Seidensticker (1993) documented reductions in cortisol in leopard cats, *Felis bengalensis*, as a consequence of environmental enrichment involving novelty and visual barriers. Wielebnowski et al. (2002) also demonstrated convincingly that enrichment consisting of hiding places and climbing structures in modified clouded leopard, *Neofelis nebulosa*, enclosures resulted in lower fecal corticoid levels.

The studies cited above show that there is convincing scientific evidence that enrichment works, at least with respect to proximate goals. However, as in all animal welfare research, demonstrating a definitive link between achieving these goals (e.g. reduced stereotypic behavior) and improved well-being is more problematic, and future research needs to be more refined in this respect.

ENRICHMENT RESEARCH METHODOLOGY

A recent review of the enrichment literature with respect to stereotypic behavior (Swaisgood and Shepherdson 2005), while confirming the overall effectiveness of enrichment at reducing such behavior, revealed some consistent flaws in research methodology. A fundamental problem of most zoo studies is small sample size. One approach is to conduct multi-institutional studies with larger sample sizes. There are methodological problems with these also (e.g. large numbers of confounding variables), but they have produced useful results (Mellen 1991; Shepherdson, Carlstead, and Wielebnowski 2004).

Questionnaire studies are a valuable way of collecting information on large sample sizes at multiple institutions, but they are no substitute for direct observation (Bashaw et al. 2001). Experimental studies (preferably of an ABAB type of design) are the ideal, although correlative studies and "accidental experiments" are certainly useful. Probably owing to the small sample sizes inherent in these types of studies, data-pooling errors are common. A more acceptable alternative may be to report descriptive statistics for individuals or to conduct statistics on individuals. However, if this latter case study approach is taken, it must be made clear that the results cannot be generalized to the zoo population as a whole. Another approach to the sample size issue is to conduct meta-analyses of many small sample studies. In order for these to be productive, however, the treatments must be clearly described and the results described in full, rather than simply providing the results of statistical tests. Perhaps the biggest problem is that enrichment studies frequently combine many different types of enrichment in one study and fail to test multiple competing hypotheses.

CONCLUSION

While the relative importance of the various concepts underlying enrichment practiced on captive wild mammals is still a matter of debate, these concepts have been of great practical use in guiding the general direction of enrichment activities. While there are some problems with the research (more a comment on the challenging working environment perhaps than the research itself), the specified proximate goals of environmental enrichment are clearly being met on a regular basis, and there is good reason to believe that the increased enrichment activities of the last decade have resulted in improved well-being for captive wild mammals. Research will continue to refine the theoretical basis of enrichment and well-being, and it is hoped that this information will continue to translate into more effective strategies. In the meantime, great strides have been made in improving the programmatic effectiveness of enrichment in some of the ways suggested by Mellen and MacPhee (2001). Environmental enrichment continues to be an active and challenging field of endeavor at both the theoretical and the applied ends of the spectrum.

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7

Impact of Emerging and Zoonotic Diseases on Mammal Management

Dominic Travis and Robyn Barbiers

INTRODUCTION

Health risks must be actively assessed and managed in all kinds of captive situations. In addition, many strategies for health risk mitigation can be applied to programs that include long-term or transient captive management components. These programs include sanctuaries and some highly managed parks around the world that participate in wildlife translocations, reintroductions, rescues, and rehabilitations.

Disease can have a profound impact on captive wildlife facilities by affecting rates of death (mortality), disease (morbidity), and reproduction (fecundity). Even the mere threat of introduced pathogens can affect institutions through restrictions imposed on the kind of animals that can be kept (e.g. some species of rodents have been banned in the United States due to the recent introduction of monkey pox); how they are moved (e.g. there have been worldwide bans on the importation of small carnivores due to the threat of introducing severe acute respiratory disease [SARS], and bans on interstate movement of deer and elk in North America due to chronic wasting disease); the type and style of exhibits built (e.g. to prevent or control primate retroviruses); and the degree of public contact with animals (e.g. to avoid *E. coli* transmission in petting zoos). In turn, these changes affect breeding recommendations, species population management programs, education and reintroduction efforts, and the financial resources required for programs. In this chapter, our goal is to review the issue of emerging infectious disease ecology, to examine some of the ways that disease may be introduced into the captive environment, and to discuss the various courses of action available for disease prevention, control, and management. Although keepers of captive mammals are faced with this situation throughout the world, many of the examples herein refer to situations occurring in North American zoological institutions, since we are most familiar with these issues. In addition, we hope this discussion is useful to those managing the health of free- or semifree-ranging animals.

EMERGING DISEASE ECOLOGY: SHOULD MANAGERS BE CONCERNED?

Disease is a normal part of a healthy ecosystem, which it often helps to create. Fundamentally, the effects of disease are the result of the interaction between the host (plants, animals, or humans), the disease-causing agent (bacteria, virus, parasite, or fungus), and the environment, referred to as the "epidemiologic triad." As humans continue to manipulate their environment, disturbing the natural equilibrium established over long periods of time, both old and emerging disease agents find new ecological niches and naïve hosts to infect (Satcher 1995; Chomel, Belotto, and Meslin 2007). Naïve hosts do not have natural or acquired immunity to the new threat, and this often results in severe disease outbreaks (McMichael and Beaglehole 2000). For example, in 1999, West Nile virus (a disease agent) entered the United States (a new environment) and wreaked havoc in hundreds of nonimmune species of birds, ungulates, marine mammals, other small mammals, and even some reptiles housed in North America (naïve hosts) (Steele et al. 2000). Although outbreaks have been recorded in the Middle East and Europe, none have been of the same magnitude as in North America. Many experts assume that a new equilibrium will be reached among the virus, animals, and humans in the North American ecosystem, resulting in less mortality over time (Komar 2003). However, this can only occur if the virus does not mutate, immune systems remain competent, and new naïve species are not introduced. Unfortunately, it appears that the West Nile virus is already mutating. Extreme weather conditions, shipment, quarantine, and captivity itself can cause stress, which can adversely affect an animal's immune system; animal acquisitions bring immunologically naïve animals into new institutions all the time; and some collection animals are constantly exposed to wild animals in their environment. As responsible partners in conservation, we must assess the impact of our actions and minimize the introduction and spread of potential pathogens (Cleaveland et al. 2001).

Since the early 1990s (when the term *emerging disease* was popularized), both the usual suspects (rabies, tuberculosis, brucellosis, tularemia, avian influenza, and plague) and emerging diseases (Ebola hemorrhagic fever virus in great apes, SARS in civets, monkey pox in rodents, Nipah and Hendra virus in bats and flying foxes, and West Nile virus in hundreds of species) have dominated the popular and scientific literature (Levins et al. 1994; Daszak, Cunningham, and Hyatt 2001; Hansen et al. 2001; Murphy 2002; Huijbregts et al. 2003). The unique role of wildlife in the ecology of these diseases, combined with their importance to human health—either real or perceived—requires attention. As a result of the focus that international agencies, treaties, and regulatory authorities give to zoonotic diseases (those that can spread from animals to humans), managers of captive wildlife must assess the risk of disease in zoological and other captive environments. In addition, anthropozoonoses, diseases such as measles that spread from humans to animals, present a risk to animals and must also be considered. The terms *zoonotic* and *anthropozoonotic* are used synonymously throughout this text, since this is the current trend throughout the global epidemiological community.

How much do emerging diseases really matter? What is the likelihood that they will affect both animals and humans? In 2000, a team of researchers at the University of Edinburgh, led by Woolhouse et al., examined the relationship between emerging diseases and their zoonotic potential. They found that of approximately 1415 known diseases (viruses, bacteria, fungi, protozoa, and other parasites) of humans, 868 (61%) are zoonotic and 175 pathogenic diseases are considered "emerging." Of the emerging pathogens, 132 (75%) are known to be zoonotic (Taylor, Latham, and Woolhouse 2001). Assuming that we accept the premise that disease matters, and that we should think about the potential role of zoos in the ecology of emerging diseases, what is the potential that emerging or zoonotic diseases will be released from or introduced into captive mammal populations? A list of some emerging, reemerging, and/or zoonotic diseases affecting mammals as reported in North America and European literature shows that captive wildlife facilities and free-ranging populations are currently faced with a broad variety of these disease issues (table 7.1). While this list is certainly not exhaustive, it does establish that these issues occur regularly in the larger, well-funded institutions in Europe and North America. Those facilities in the tropics with fewer resources and a more conducive climate for disease introduction and spread are likely to be affected to a greater degree. In addition, the species categories listed in table 7.1 are only those investigated; a complete review of disease ecology must be conducted to assess adequately the risk of infection for other captive species.

HOW DO DISEASES ARRIVE?

The routine operational practices of most captive animal facilities provide ample opportunity for the introduction of disease, including emerging or zoonotic diseases. When assessing the risk of disease introduction, animal managers need to consider the source of introduction and the transmission route from carrier to host. Food, animals, and people are the 3 major sources of introduction. Transmission routes are different for every disease, and there may be multiple routes for any given disease. Common routes include direct contact between individuals, which includes spread through body fluids (including sexual transmission), and indirect transmission through the introduction of infectious fomites acting as biological (animals, people, mosquitoes) or mechanical (equipment, fly, soil, plants) vehicles of spread (vectors). Foodborne diseases can sometimes be difficult to categorize and are therefore usually treated differently. For example, Typhoid Mary received her nickname for spreading the bacteria *Salmonella typhi* from herself to other people via contaminated food in her job as a cook. In this case, she was the source but spread the disease indirectly through cross-contamination of food prepared using unsanitary practices. Therefore, she introduced the disease and spread it indirectly by a mechanical vector (food), although it is commonly referred to as a foodborne disease. The risk of foodborne diseases is potentially high in zoological institutions as a result of the large number of animals of differing species having various nutritional needs, with their meals being prepared in multiple kitchen facilities by many different individual nutritionists, keepers, or other staff. Incorporation of food safety principles (as outlined by the Hazard Analysis and Critical Control Point system) will help minimize risks associated with foodborne disease (Schmidt, Travis, and Williams 2006; see also Henry, Maslanka, and Slifka, chap. 10, this volume).

Captive mammals may be exposed to numerous types of wildlife that can introduce disease, including captive, free-ranging, rehabilitated, or confiscated wild animals of all taxa (Davidson and Nettles 1997; Friend and Franson 1999). Although collection animals recently shipped between institutions represent the most frequent opportunity for disease introduction, captive wildlife facilities should have preventive medical and preshipment protocols in place to minimize these risks. Many professional organizations, such as the Association of Zoos and Aquariums (AZA), the American Association of Zoo Veterinarians, the European Association of Zoos and Aquaria, and the European Association of Zoo and Wildlife Veterinarians, have written standards for the various taxa included in their collections (these are usually published on member-only Web sites, but most associations provide copies upon request). On the other hand, free-ranging wildlife are common in and around many captive facilities and are potentially an important source of disease introduction. For example, bats are the reservoir for many new lyssaviruses (Nipah and Hendra virus) in addition to rabies (McColl, Tordo, and Aquilar Setien 2000; Mohd Nor, Gan, and Ong 2000; Cliquet and Picard-Meyer 2004). They are also thought to be the primary host for the Ebola virus, although definitive evidence does not yet exist (Leroy et al. 2005). SARS was recently shown to have a bat/flying fox reservoir as well (Wang et al. 2005; Salazar-Bravo et al. 2006). Many species of rodents commonly carry leptospirosis, hantavirus, and plague (through hosting the flea reservoir) and played an important role in the recent introduction of monkey pox into the United States (Pattyn 2000; Higgins 2004; Enria and Levis 2004). Birds are the normal reservoir of West Nile virus, avian influenza, avian mycobacteriosis (which is increasingly important to immunocompromised people), and numerous types of zoonotic parasites and fungi; all cause disease in mammalian hosts as well. Free-ranging cervids have recently attracted at-

TABLE 7.1. Emerging and/or zoonotic diseases that have either recently affected, or may potentially affect, captive wildlife facilities

Disease agent or condition	Category	Reported in	Captive	Wild	Zoonotic
Coxiella burnetii (Q fever)	Bacteria	Marine mammals, ruminants	X	X	X
Erysipelothrix rhusiopathiae	Bacteria	Marine mammals	X		X
Eschericia coli (enteropathogenic)	Bacteria	Domestic mammals, ungulates, primates	X		X
Leptospira spp.	Bacteria	Mammals	X	X	X
Mycobacterium avium	Bacteria	birds, mammals	X	X	X
Mycobacterium bovis	Bacteria	Mammals	X	X	X
Mycobacterium kansasii	Bacteria	Ungulates	X		X
Mycobacterium paratuberculosis	Bacteria	Ungulates	X	X	X
Mycobacterium tuberculosis	Bacteria	Elephants, rhinoceroses, felids, goats	X		X
Shigella flexneri	Bacteria	Great apes	X		X
Tuleremia (*Francisella tularensis*)	Bacteria	Primates, rodents	X	X	X
Yersinia pestis (plague)	Bacteria	Ferrets, prairie dogs, felids, rodents	X	X	X
Yersinia pseudotuberculosis	Bacteria	Mammals, birds	X	X	X
Blastomyces dermatitidis	Fungus	Large carnivores, marine mammals	X		
Cryptococcus neoformans	Fungus	Small mammals, birds, ungulates	X	X	
Baylisascaris procyonis	Parasite	Birds, small mammals, primates	X	X	X
Trypanosomiasis (Chagas' disease)	Parasite	Hedgehog, rhinoceroses, rodents	X	X	
Bovine spongiform encephalopathy	Prion	Ungulates, felids, mink	X	X	X
Chronic wasting disease	Prion	Deer, elk	X	X	
Toxoplasmosis	Protozoan	Marsupials, primates, small and marine mammals	X	X	X
Avian influenza	Virus	Birds, felids	X	X	X
Contagious echthyma (orf)	Virus	Ungulates	X		X
Eastern equine encephalitis	Virus	Birds, ungulates	X	X	
Ebola virus (hemorrhagic fever)	Virus	Duikers, great apes, bats		X	X
Encephalomyocarditis virus	Virus	Ungulates, primates, elephants, felids	X	X	
Foot-and-mouth disease	Virus	Ungulates, many other mammals		X	
Hendra virus	Virus	Flying foxes		X	X
Herpesvirus	Virus	Elephants, marine mammals	X		
Herpes simiae (B)	Virus	Primates	X		X
Lymphocytic choriomeningitis virus	Virus	Primates, rodents	X		X
Lyssavirus (including rabies)	Virus	Bats, mammals	X	X	X
Malignant catarrhal fever	Virus	Sheep, wildebeest	X	X	
Morbillivirus	Virus	Primates, ungulates, canids, marine mammals	X	X	X
Nipah virus	Virus	Flying foxes, pigs	X	X	X
Orthopoxvirus	Virus	Giant anteater, canids, rodents	X	X	X
Rift Valley fever virus	Virus	Ungulates		X	X
Severe acute respiratory syndrome	Virus	Civets, felids	X	X	X
Simian foamy virus	Virus	Primates	X	X	X
Simian immunodeficiency virus	Virus	Primates	X	X	X
West Nile virus	Virus	Birds, mammals, reptiles	X	X	X

tention for their role in the ecology of brucellosis, tuberculosis, and chronic wasting disease; the former 2 are zoonotic and the latter is emerging (Mahy and Brown 2000; Travis and Miller 2003). Finally, wild/feral canids have been known to introduce leptospirosis, distemper, and rabies into captive mammal populations (Roelke-Parker et al. 1996).

The increasingly important role that zoos and wildlife rehabilitation centers play in providing assistance to free-ranging wildlife, abandoned exotic pets with unknown history, and both legally and illegally confiscated exotic animals adds an entirely new dimension to the risk of emerging disease introduction. For example, Ebola and monkey pox viruses were introduced into the United States via the laboratory animal and pet supply chains (CDC 1989; Guarner et al. 2004). Finally, although recent facility design requirements in the United States have greatly decreased direct interaction between people and captive animals, contact still occurs through animal caretakers, facility maintenance workers, researchers, and the general public in many different situations. Finally, the politics of today's world unfortunately requires that we also plan for the purposeful introduction of emerging or zoonotic disease agents.

DISEASE MANAGEMENT

The objectives of adequate disease management should be (1) prevention of disease introduction; (2) control of the spread of disease; and/or (3) eradication of an introduced disease. Although relying on prevention alone would be ideal, in reality control or eradication efforts are frequently necessary. A good disease management program must include the flexibility to address each objective, depending on which are most relevant or feasible in a given situation.

DISEASE PREVENTION

Design, implementation, and compliance with preventive medicine protocols are key factors in minimizing the risk of introducing disease into both captive and wild mammal populations. Although most protocols are primarily concerned with the individual animal, the impact of disease on the population must always be considered in the decision-making process.

The importance of preventive medicine in captive situations is widely recognized. For instance, AZA accreditation standards state that "The veterinary care program must emphasize disease prevention, implying that vaccination and preventive medicine programs must be in force for the entire collection and under the direction of qualified support staff," and that "an institution should adopt the guidelines for medical programs developed by the American Association of Zoo Veterinarians (AAZV)" (AZA 2006, 8). The AAZV guidelines state that "programs should include quarantine, parasite surveillance procedures and control, immunization, infectious disease screening (e.g. using serology and tuberculosis testing), dental prophylaxis, and periodic reviews of diets, husbandry techniques and vermin control" (Joslin et al. 1998, 9). Proper preventive medicine consists of numerous interlocking and integrated activities, including husbandry practices, occupational health considerations, and control of exposure to domestic and wild animals, as well as captive animal preshipment screening and proper quarantine procedures.

Good husbandry practices are an essential part of any preventive health program. In this light, many cooperative associations around the world continue to develop standardized care guidelines for managed species which address such issues as housing (size, complexity, temperature and humidity ranges, and light requirements), sanitation, social structure, reproduction, and nutrition, all of which can have an impact on stress, and therefore health. Mixed-species exhibits pose a unique challenge to managing disease risks for mammals. Two examples are (1) the risk of malignant catarrhal fever, an infectious disease common in African alcelaphins, which caused considerable mortality in the Asian cervid collections in mixed-species exhibits at several North American zoos (Heuschele, Swansen, and Fletcher 1983); and (2) the risk of herpesvirus transmission between Asian and African elephants if placed together, since herpes viruses endemic to one species can be fatal in the other (Richman et al. 1996, 1999).

Occupational health protocols need implementation to reduce disease transmission both from humans to animals and from animals to humans. At the most basic level, employees exhibiting symptoms of communicable diseases should avoid entering or working in areas where the risk of disease transmission is high or where there are susceptible species. Staff working directly with animals should employ personal protective equipment such as masks, gloves, and dedicated outerwear. Good hygiene practices (e.g. hand washing) are essential for all employees exposed directly or indirectly to animals. Precautions should be taken when staff works in more than one area; dedicated boots, outer clothing, and equipment for each animal area help reduce the likelihood of spreading disease between exhibits. Protocols should be implemented for specific diseases of concern. For example, tuberculosis screening of all staff/volunteers with direct animal contact is standard practice in many facilities. Protocols for cleaning animal areas should include safety measures aimed at protecting staff from aerosolization of potentially infectious fecal material—this is especially important in primate areas in which enteric bacteria and retroviruses may be present.

Although not always simple, controlling captive mammal exposure to free-ranging wildlife is an important aspect of any preventive medical protocol. Of highest concern with respect to emerging diseases are wild birds (i.e. feces containing bacteria, fungal spores, West Nile virus, and avian influenza), bats (lyssavirus and SARS), rodents (i.e. leptospirosis, monkey pox, tularemia, and fleas carrying plague), and other mammals potentially carrying distemper and rabies, and insect vectors such as mosquitoes and ticks. An integrated pest management (IPM) program using information on the life cycles of pests and their interaction with the environment to control them is essential to minimize the risk of disease introduction via species considered pests. Establishing an IPM program involves (1) setting an action threshold (the point at which pest populations or environmental conditions indicate that pest control actions should be taken), (2) identifying the pest and understanding its biology, (3) monitoring, (4) implementing prevention and control strategies, and (5) evaluating results. For instance, mosquito surveillance (trapping and species identification and testing) and control (breeding habitat reduction and application of larvicide and adulticide chemicals) is common practice in most North American zoos since the introduction of West Nile virus. Excluding wildlife from animal exhibits or enclosures that may provide them with food, water, and shelter minimizes the risk of attracting greater numbers of pests in the future and decreases the risk of spreading disease from wildlife to captive animals or their caretakers. This measure is more difficult to implement when managing risks associated with migratory bird populations such as those hypothesized to carry avian influenza and West Nile virus. Finally, conducting necropsies of wildlife found dead on zoo grounds provides a baseline measure of risk posed by local wildlife and should be part of the basic preventive medical protocol where feasible.

Quarantine is another essential aspect of minimizing disease risk in mammal management. Many zoological associations have set quarantine standards that their members must follow. The primary goal of quarantine is the prevention of disease introduction, but it also helps to "establish baseline health status of new arrivals" (Miller 1999, 14). Quarantine protocols must be reasonable and consider the welfare of the animal involved. For example, isolation of larger mammals, such as elephants or giraffes, may not be possible without endangering the health of the individual or the personnel involved. In these cases, preshipment testing, careful review of the medical history of both the individual and the source population, and strict sanitation protocols (such as dedicated equipment) may need to suffice. The risk to the animal of anesthesia to complete preshipment or quarantine testing must be weighed against the actual risk of disease. Complete isolation of social species for 30 or 60 days may cause behavioral or social problems. Providing a companion animal may help alleviate this, but animal managers need to assess the risk to the companion.

Preshipment testing is critical before any kind of animal transfer and is often conducted in conjunction with pre- or postshipment quarantine or isolation/quarantine. At a minimum, an in-depth observation of health and a basic clinical examination should be performed, ideally including sedation/immobilization, the collection of basic health parameters, and some diagnostic testing for diseases of concern. Diagnostic screening of the animal(s) to be moved may prevent the introduction of a new pathogen into a resident population. Conversely, the introduced animal must be prepared for any pathogens in its new environment; screening of the resident population is therefore an important aspect of preshipment testing for any animal transfer. Although more work needs to be done, recommended diagnostic panels for many specific species have been established; these may be influenced by factors such as the availability or validation of specific tests for a given species, known susceptibility of a species to a given disease, known geographic distribution of diseases, and regulatory requirements of the specific country.

In many countries, regulations focus on diseases of agricultural concern (e.g. tuberculosis or brucellosis) or "foreign" animal diseases of concern (e.g. in the United States, vesicular stomatitis, or foot-and-mouth disease, is considered foreign and has specific regulatory requirements). Animal shipments are rejected due to the perception that disease exposure could result in a negative impact on the population. Such perception-based individual animal decisions can also have a negative affect on cooperative population management planning. For instance, the AZA Old World Monkey Taxon Advisory Group (TAG) has had animal transfers based on breeding recommendations canceled because of positive foamy and simian immunodeficiency virus serology results (indicates an animal has been exposed during its life but not necessarily that it is currently infected and can spread the disease). Individual zoos have refused to accept the shipment of a positive animal, even though the receiving institutions had not screened their own populations to ensure the absence of preexisting disease. The TAG currently recommends that facilities know the viral status of their own collection so that informed decisions regarding risk can be made while planning animal transfers.

The lack of available data regarding the ecology of a disease and its vectors can adversely affect animal transfers (including translocations and reintroductions). Sometimes understanding the disease ecology and vectors can help managers minimize the risk of disease introduction/spread while allowing animal movements to continue. Several years ago, the AZA lion, *Panthera leo*, Species Survival Program (SSP) was attempting to import African lions from a captive facility in Africa to institutions in the United States in order to bolster the genetic diversity of the North American captive population. During preshipment testing, African ticks—possible vectors of important diseases such as babesiosis, African swine fever, and East coast fever—were discovered on the lions. After many discussions between federal regulatory agencies and the institutions involved, the importation was approved for facilities located in northern climates, since this species of tick would not survive the winter if it was introduced. Even though the southern facility could not accept the shipment (despite the inclusion of risk reduction measures such as the administration of acaracides), managing the risk based on understanding of the vector ecology allowed the managed population to benefit eventually from the import.

Many wild mammal conservation areas/programs are highly managed. Thus, many of the measures reviewed here are being implemented to reduce the threat of disease introduction or its impact once it occurs (Wolff and Seal 1993). For example, the staff of the Mountain Gorilla Veterinary Project (as well as numerous other wild primate conservation sites) monitors both the health of gorillas, *Gorilla beringei*, and people, including park employees, researchers, and tourists in parks in Uganda, Rwanda, and Democratic Republic of the Congo to reduce the threat of zoonotic disease transmission. The staff manages exposure of gorillas to potentially infected humans by limiting the number of people present, the amount of time they are in close proximity to the animals, and the distance between the people and the gorillas. Intervention is sometimes necessary when animal health is thought to be compromised by humans (e.g. injury due to snares or illness caused by exposure to a human infectious disease). In addition, programs aimed at managing disease spread between domestic and wild animals (e.g. the domestic dog rabies and distemper vaccination program around the Serengeti ecosystem in Tanzania) are becoming more common. Finally, some national parks (e.g. in South Africa) manage health risks to animals entering or leaving the population by implementing preventive protocols in special quarantine/isolation bomas, where animals are held before movement into or out of the park.

DISEASE CONTROL

Disease control involves manipulating the host, the disease agent, or the environment in order to decrease the likelihood of exposure and break the cycle of transmission and infection. Hosts may be both humans and animals. With respect to humans, animal managers must minimize disease spread in 2 directions: human-animal and animal-human. Since few effective human vaccines exist for emerging diseases, the use of proper personal protective equipment is the simplest and most effective measure to control both kinds of risk. However, no protocol is effective without proper compliance.

The interaction between the number of susceptible, infected, and recovered individuals in a population controls the dynamics of a disease; overall population density and an individual's likelihood of becoming a healthy carrier are other important factors. Wobeser (2006) lists 3 basic approaches to (animal host) population manipulation, which can help decrease disease transmission—all based on controlling exposure between these populations with respect to population density:

1. Reduce the density of the entire population
2. Reduce the proportion or density of infected individuals in the population
3. Reduce the proportion or density of susceptible individuals in the population

In managed programs in captivity, animal managers control the population size by spreading it over multiple institutions, thus reducing risk to much of the population at any given time. In rehabilitation or sanctuary settings, this is more difficult, since it involves building more enclosures or rejecting injured or orphaned individuals (which often goes against the mission of the facility). Some sanctuaries (e.g. members of the Pan African Sanctuary Alliance) are considering controlling population size by actively reintroducing animals according to the International Union for Conservation of Nature's Reintroduction Specialist Group guidelines (www.iucnsscrsg.org/downloads.html).

The impact of infected individuals, often identified while in quarantine, can be controlled through effective isolation, treatment, euthanasia, and sometimes birth control. Isolation of affected individuals until they no longer pose a threat to the population is sometimes the easiest method, but assumes full recovery at some point and has potential welfare implications. Specific treatment for emerging diseases is often unavailable, with only empirical or supportive care available. Treatment of a population is more difficult, but has been accomplished in small populations that are routinely monitored and relatively easy to medicate.

The goal of treatment may not be an actual cure but rather control of the disease or reduction of its adverse impacts, as in the case of various parasites. Euthanasia or culling can control many important emerging or regulatory diseases. Governmental agencies may use euthanasia as a tool to control disease. As this is usually not acceptable when managing endangered populations, captive facilities should form proactive partnerships with local regulatory authorities before an emerging/zoonotic disease outbreak. For wild populations that pose a risk to captive or human populations, reducing population density by birth control or culling may be unpalatable to the public and is usually only a short-term solution. Vaccination reduces the number of susceptible animals and is part of any preventive medicine program in captivity. It is not realistic for controlling emerging diseases, however, since vaccines have not generally been developed or validated.

Controlling a disease agent in captive facilities is generally done by attempting to limit risks within the environment. Treatment or vaccination of animals may reduce shedding of the organism from infected animals into the environment. Control of environmental contamination and reduction of exposure to sources of infectious agents are two of the most effective means of reducing disease problems in captive populations. Good husbandry practices minimize the disease-causing agents in the environment and reduce the risk of disease transmission. Pest and wildlife control is a major part of managing environmental disease risk. Disinfection of animals and/or the environment destroys many bacteria, viruses, or parasites and is fairly easily accomplished in most captive situations, but very difficult to implement in free-range settings.

DISEASE ERADICATION

Eradication is really an extreme form of control. The goal is to eliminate the disease in a certain species or geographic area in order to establish "freedom from disease." Due to the high costs of such eradication programs, they usually focus on diseases of agricultural (and hence economical) or human concern, and may affect wild animals (for better or worse). Captive mammals may fall under a regulatory eradication program, e.g. ungulate tuberculosis, foot-and-mouth disease, or bovine spongiform encephalopathy (mad cow disease). In these cases, special exemptions may be sought for captive cooperative breeding programs. In North America, the AZA has worked with the U.S. Department of Agriculture to develop zoo-specific outbreak response plans for foot-and-mouth disease, West Nile virus, and avian influenza. The goal of these plans is to minimize the risk of depopulating collection animals should a facility be included in a disease eradication zone. The success of these protocols depends on the facility's ability to show that it poses little or no risk for spreading an outbreak in the regulatory zone, which includes demonstrating the capability of having a very high level of biosecurity around susceptible species. Additionally, captive animal managers may have to demonstrate that they can manage separate areas of the zoo differently or accept euthanasia of some domestic (or other) species.

INFORMATION GAPS

We still have extremely limited knowledge of the ecology of diseases and how best to deal with these risks in exotic animals. We desperately need better diagnostic tools. The antemortem disease detection tools currently available are usually validated for domestic species or only a few exotic species that are intensely managed for agricultural purposes (i.e. cervids). We have limited information concerning the prevalence or incidence of various diseases both in captivity and in the wild (in any country) and therefore know very little about what to expect when assessing the risk of contact between these populations. A new record-keeping system (Zoological Information Management System) being developed by the International Species Information System for captive animal management should allow long-term tracking of medical and husbandry records and summarization of some disease information on a global scale. In the future, wild and captive animal managers need to integrate information management systems to complete the picture of wildlife disease ecology more holistically.

There are many resources readily available to animal managers that provide information on diseases. The World Animal Health Organization (www.oie.int) provides global and up-to-date news on reportable diseases. The World Health Organization (www.who.int) and, in the United States, the Centers for Disease Control and Prevention (www.cdc.gov/), provide information on many zoonotic diseases. The European Association of Zoo and Wildlife Veterinarians Infectious Disease Working Group has compiled a *Transmissible Diseases Handbook* (Kaandorp 2004), which provides standard information on infectious diseases such as causative organism, distribution, transmission, incubation, clinical symptoms, and diagnosis. This resource also goes beyond the standard information by addressing such issues as prevention and control in zoos, suggested disinfectants, legal issues, conditions for restoring disease-free status after an outbreak, and country-by-country information on reference laboratories. The Infectious Disease Committee of the American Association of Zoo Veterinarians is in the process of compiling a similar handbook for North America.

THE IMPLEMENTATION OF NEW MANAGEMENT STRATEGIES

Captive animal facilities are a lot like islands with respect to the threat of emerging and zoonotic disease introductions. For relatively isolated captive facilities that act alone or with very few partners, the creation of, and adherence to, strict disease prevention principles is crucial. In these cases, compliance is usually the limiting factor for success—vigilance is everything. For zoo associations (associations may be like archipelagoes) that depend on cooperative management, or individual facilities that are more "open" with respect to animal movements across their boundaries, risk management is more complicated. One benefit of joining more-organized associations is the ability to combine resources and infrastructure needed to cope with an emerging disease outbreak. Accreditation guidelines highlight preventive medicine programs, including quarantine protocols, and standards of husbandry and medical care. Unified in their approach, these associations have built-in communication mechanisms among members and have uniquely identified animals with standardized husbandry and medical records. Zookeepers are trained to monitor animal welfare and health; veterinarians investigate suspicious signs of disease; pathologists investigate mortalities; and endocrinologists, animal behaviorists, and nutritionists proactively address problems in their fields as they are discovered. Although all these characteristics are essential for proper disease outbreak investigation and response, more can be done.

The application of a few epidemiological principles on a broad scale can enhance the identification, response, and control of the introduction of an emerging disease into a captive facility. First, the implementation of a long-term, scientifically based health surveillance and monitoring system provides background information necessary for early identification of "abnormal" health signs; early identification of a potential problem provides an opportunity for proper investigation and response before it is too late (Munson and Cook 2003). Real-time descriptive summaries and analysis of data must be available for a timely response to be feasible. Second, animal health professionals and husbandry personnel must be equipped to conduct rigorous, methodical outbreak investigations when suspicious events occur. In order to do this, resources must be dedicated to the proper training of personnel, and animal managers must partner with local public and animal health officials for the benefit of the community. Finally, since emerging or zoonotic disease outbreaks may involve risk to the broader community, risk assessments must be conducted to set priorities for cost-effective management options. There is an emerging tool known as risk analysis for decision making in the face of the uncertainty that inherently surrounds emerging disease issues. This provides a framework for using existing data (such as those gathered from surveillance or outbreak investigations) to model and assess risk while testing management strategies and their costs (Leighton 2002; OIE 2004). Software exists for formulating genetic-based breeding recommendations (Spark Plug, Zoo Risk) and assessing extinction risk through population health viability analysis (Vortex). Tools for addressing disease risks are being developed through workshops conducted by the IUCN's Conservation Breeding Specialist Group among others (Armstrong, Jakob-Hoff, and Seal 2002). Many models already exist in the public and domestic animal health arenas. Captive wildlife facilities should be included in these efforts.

The realities of our world today make disease emergence and spread a real possibility. Although we have preventive measures in place, we must continue to improve our response to disease proactively through the use of new methodologies and technologies. Only by engaging our own community, and partnering with others both at home and abroad, can we hope to control, manage, and eliminate diseases.

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OTHER RESOURCES

www.eaza.net
www.wildlifeinformation.org
www.eazwv.org/php/
www.waza.org
www.iucn-vsg.org

8

Safety Considerations in a Zoological Park

Mark Rosenthal and William Xanten

INTRODUCTION

Working in a zoological setting carries its share of risks and dangers. While each organization's resources will be different, many of the basic philosophies are the same in dealing with safety issues. In every area in which animal keepers perform their duties, the aim of the organization should be to provide a work environment that is free from those identifiable safety hazards that might result in accidents and possible injury to the animal keeper or a member of the public.

Accidents usually occur on the job when employees are negligent and forgetful, do not follow established rules, or fail to keep equipment in excellent operational condition (Hartman 2007). Distractions and failure to concentrate on the job at hand are other causes of safety problems. Further, keepers may not receive sufficient training or plan ahead for emergencies, both of which can lead to an accident.

It is the zoo administration's responsibility to assess risks in the workplace. This assessment essentially is a thoughtful examination of what might cause harm to staff working directly with animals, and what precautions need to be put into place to prevent problems (e.g. accidents or ill health) from occurring. If a hazard is thought to be significant, the precautions taken should minimize the risk (AZA 2006).

The following steps are general rules for assessing risk in your organization:

1. Survey the facility and grounds to check for hazards. Members of the safety committee or supervisors in each section can do this.
2. Decide how a given hazard will potentially harm the keeper, other members of your staff, or visitors. Remember that not all individuals are at equal risk. At greater risk may be new staff members, trainees, or pregnant women; contractors and maintenance workers who might not be familiar with the physical layout of the zoo; and members of the public who visit the zoo.
3. Conduct an evaluation of the risk and decide if enough precautions are in place or if new ones are needed. If it is impossible to get rid of a hazard, how can you control it so that it is a low risk? To control the risk, a zoo may (a) issue personnel with proper protective gear and make sure they are used, (b) reduce exposure to the hazard, (c) provide facilities for removal of the risk (e.g. washing stations or eye-flushing stations), and (d) completely prevent access to the problem.
4. Record the findings in a document that is available to all employees in order to demonstrate that the zoo administration considered all the obvious hazards and all the individuals that might be involved.
5. Review the assessment periodically, and if necessary, revise the procedures. As the animal collection within the institution changes, evaluate whether there are new potential hazards needing documentation. It is good practice to review the written protocol annually.

HEALTH AND SAFETY

ROUTINE ANIMAL HUSBANDRY

In typical zoos and aquariums, animal keepers are probably injured more often by cutting themselves with a knife while preparing food or hurting their back when improperly lifting heavy objects than by animal bites and scratches. Keepers need to think about their regular daily activities and have protocols for dealing with them. Performing a job safety analysis (Lincoln Park Zoo 2003b) as a daily routine may help define the hazards and the equipment needed to do a job safely. The analysis can be broken down into the task, potential hazards, and recommended action or procedure.

Many zoos and aquariums now have a dedicated safety officer who is responsible for formulating, carrying out, and monitoring a safety program. In the absence of a safety officer, a safety committee composed of senior staff, supervisors, and animal keepers should be responsible for the zoo's safety program, including the investigation of accidents and recommendations for methods and protocols to prevent future accidents. The section supervisor needs to check daily that safety equipment is available for employees, and that employees know how to use the equipment properly and do so. Supervisors are responsible for inspecting equipment and ensuring that repairs are made in a timely fashion.

Personal protective equipment is vital for keepers who are performing routine animal husbandry functions in potentially dangerous conditions. The use of steel-capped boots will protect toes from being crushed. Safety glasses or face shields should always be worn when keepers are working in an area where there is a risk of damage to their eyes. Stations for flushing irritants from the eyes should be easily accessible. Having keepers wear specialized gloves while cutting food may prevent serious injuries from a knife. Lifting food containers, boxes with fresh produce, or animal crates can cause back injuries unless done properly. When lifting a heavy object, the back should be straight and the knees slightly bent, so that the lifting uses the leg muscles rather than the back muscles (www.back.com). A keeper should never attempt to lift very heavy objects alone, but should enlist the help of others to divide the load.

All cleaning chemicals and other potentially hazardous materials that keepers work with daily should be labeled and housed in unbreakable containers. Material Safety Data Sheets for all materials should be maintained in a central area with easy access for all staff.

When staff members need to handle individual animals manually, general protection can include a mask, gloves, long sleeves, and a heavy jacket (Karsten 1974; San Antonio Zoo 2002; see also Christman, chap. 4, this volume). Animal keepers also are susceptible to acquiring zoonotic diseases in their daily activities (see Travis and Barbiers, chap. 7, this volume), and these risks can be reduced by correct hygiene (e.g. using proper hand-washing techniques after handling animals) as well as preventing improper exposure to animals in the first place.

Duty assignments need to consider special physical conditions such as pregnancy in keepers. Toxoplasmosis is widespread in people and other warm-blooded animals. Although it usually has no impact, it may have adverse consequences for human fetuses/infants and people whose immune system is compromised. Wild felids are hosts of the parasite *Toxoplasma gondii* and excrete *T. gondii* oocysts in their feces. Pregnant keepers should avoid dealing with cat feces and probably not be assigned to a felid area during their pregnancy.

Several mammal species can be infected by rabies, and the virus in the saliva can be transmitted to humans by bites (Hinshaw, Armand, and Tinkelman 1996). If it becomes necessary to restrain bats, raccoons, foxes, and skunks, personal protection equipment in the form of heavy gloves and jackets should be employed. Protection of employees against zoonotics and protection of the animal collection from staff-transmitted disease need to be addressed separately in each institution (see also Travis and Barbiers, chap. 7, this volume).

ANIMAL KEEPERS (OR PUBLIC) IN THE ANIMALS' ENCLOSURES

A classic problem is that keepers think they have secured or locked a dangerous animal into a behind-the-scenes location, which permits them to enter the animal's exhibit safely to clean or to deliver food or enrichment materials. Once in the exhibit, they discover, too late, that they did not really contain the animal properly, and they are faced with serious danger (Herrmann 2005; Sweeney and Donovan 2005).

How does one guard against this form of "keeper error"? There is no easy answer except to have strong safety policies and review them with staff on a regular basis. Also, having additional safeguards that might prevent an accident or at least assist a keeper caught in such a potentially deadly situation may be helpful. It is easy to become lax when performing the same routine each day; thus, before keepers enter an area that houses dangerous animals, they need to double-check that the number of animals originally in the exhibit are now safely housed in a secure back area. All the animals must be accounted for before entry into the exhibit, and before leaving an area, all locks must be checked to ensure they are locked. Animal locks need to be inspected regularly to ensure maximum security.

Keepers working with dangerous animals should have radios for sending a distress call in an emergency, and there should always be 2 keepers working in such areas—with both carrying radios. Staff in every area of a zoo should be able to send and receive radio messages, so that even someone working in a lion or tiger moat will have a radio that functions. When shifting animals between enclosures, only one keeper should be responsible for the operation of doors and gates. Keepers should always be aware of the locations of other staff when doing this task.

In zoos today, animal keepers manage elephants either in a free contact situation, where they interact with the elephants directly, or in protected contact, where the keeper and elephant are separated via some type of barrier. Each of these forms of elephant management has its pros and cons (Roocroft and Zoll 1994), but each still brings the keeper in close association with a large, potentially dangerous animal. In either case, certain basic safety considerations need implementation. More than one keeper should always be present, so that in the event of a problem there is someone available to seek help. Above all, the zoo should have an emergency plan developed so that staff understands how to respond to an attack (Kauffman 1983; AZA Accreditation 2006). Although a keeper's first impulse might be to attempt rescuing a keeper being attacked, the first response should actually be to summon help after quickly assessing the situation. Radios or alarms that can bring help quickly should be easily accessible.

If the use of pepper spray is legal in your zoo, keepers should carry it. Pepper spray can be a powerful tool to protect a keeper threatened by a dangerous animal. Alternatively, spray cans or fire extinguishers can be placed in strategic locations, so that in an emergency keepers can easily find something for their defense.

Millions of people visit zoos each year, and most come to enjoy themselves and view the animals in a peaceful manner. Some visitors, however, are mentally ill (Hediger, 1969) or just reckless, and feel that they can enter an animal exhibit without harm. Visitors may put their hands through a barrier in the hopes of touching a special animal if they cannot enter an exhibit. Even careful parents may not pay enough attention to their small children, who could slip under a fence (O'Brien 1996) and approach dangerous animals. Zoos have a legal responsibility to reduce these hazards by providing effective public barriers. To prevent people from approaching an exhibit too closely, horticultural staff can plant hedges that are difficult to penetrate or have sharp thorns, but are attractive to the eye.

With any emergency, good communication, a rapid staff response, and the use of common sense can avert a disaster. Using a high-pressure hose to direct water into an exhibit may separate a dangerous animal from a foolhardy guest and give staff time to react to the emergency.

Many zoos provide public access to animals via walk-through exhibits that may house domesticated animals, small mammals (including primates), or exotic birds. In some exhibits visitors can pet or feed selected animals, while for others the goal is the experience of viewing animals without barriers. Zoo personnel need to monitor these exhibits to prevent visitors from feeding unauthorized food items or being too rough with the animals. Also, if the zoo encourages contact with the animals, then hand-washing stations should be easy to access as people leave the exhibit (Ryan 1998).

SHIPPING OR RECEIVING ANIMALS

In planning for any animal transfer, the biology of the animal must be considered (Hediger 1969; see also Christman, chap. 4, this volume). When excited, normally docile animals can be incredibly powerful and can destroy a poorly constructed shipping crate. Trying to force an animal into or out of a shipping container presents safety hazards to both the keepers involved in the operation and the animal itself. Many animals can reach out of crates, if given the opportunity, and grab or claw a keeper. Larger species can rock or move a crate; thus, keepers should always be aware of where they are positioned relative to the animal. For example, standing between a wall and a crate containing a rhinoceros is potentially dangerous if the animal's movement shifts the crate.

Crates or shipping containers approved by the International Air Transport Association should be used for all shipments (www.iata.org). Its Live Animals Regulations are the basic guidelines for the construction of all types of animal shipping crates.

When loading or unloading any animal, the following checklist should be considered:

- the number of keepers, veterinarians, and tradespeople needed for the operation
- the role of each person on the team
- the individual who will be in charge of the operation
- the equipment, transportation, or tools that will be needed
- the mechanism of transport of the crate to its final destination
- a backup plan, if there are problems

Usually, one person should direct the crating of the animal and its transport. You invite problems and potential injuries if multiple individuals give orders simultaneously or disagree with a command. Each individual involved in the crating or transfer of an animal should know exactly what his or her role is. Have backup plans, and know what those plans are before you start.

EMERGENCY PLANNING

ANIMAL ESCAPES

Occasionally, an animal may escape from its exhibit (Hediger 1964; Vansickle 2006; *Hindu* 2006a, 2006b). Poorly designed exhibits, keeper error, or natural events (e.g. lightning striking a tree which destroys part of a fence, thus allowing an escape) are all potential causes of escapes. All zoos should have an emergency plan to handle escapes where animals are free either on zoo grounds or inside a building. A yearly survey of all fencing and animal barriers will help to assess risks and document and correct any weak areas.

The key is to have in place a written escape plan that deals with dangerous and nondangerous animals (San Francisco Zoo 2003; Hanna 2005), and to practice that plan regularly. A written animal escape protocol may look great, but will not be effective if the keeper staff has never practiced it. Zoos should have unannounced escape drills at least 2 to 3 times per year. The main ingredients for any escape plan are clarity and simplicity. More complicated plans provide more potential for things to go wrong or for individuals to forget their roles and responsibilities. All plans must consider the safety of the public, the safety of zoo staff, and the recapture of the escaped animal (Flanagan and Tsipis 1996; Poppen 2007).

Communication plays a vital role in any emergency plan. Emergencies occur not only during the day but at night, when the majority of the zoo staff is absent; thus, methods to communicate with key people quickly are necessary. Emergency plans need to include all possible scenarios and how to respond to them, e.g. if the zoo is permitting an outside group to have a black-tie event on the grounds during the evening. Usually when an animal escapes during the day, a member of the public will see it before a staff member, and the first person to hear of it will likely be a volunteer, staff from a zoo restaurant or shop, or a facilities person. All these people need to be well acquainted with the overall emergency plan as well as their role in that plan. If possible, zoos should develop a training film that can easily and regularly be shown to all staff and especially new staff members.

In case of an animal escape, one of the first lines of defense is the zoo's veterinary team, since it will likely be handling the tranquilizer equipment. If allowed by law, however, zoos should consider having all senior staff trained in the use of tranquilizing drugs and the weapons that deliver them, such as pistols, blowpipes, and rifles, since a veterinarian may not always be available. All drugs and equipment should be in one or two secure locations that all senior staff (or the appropriate designated individual) can access quickly. Preparedness to respond instantly to emergencies is vitally important.

There is always the possibility that an escaped animal will have to be killed. To that end the zoo should have an emergency weapons team made up of animal keepers and senior staff (Baker 1999; Beetem 2006), who should be thoroughly drilled in the use of the zoo's weapons. This team needs frequent practice sessions during the year and clear requirements for continued participation (Good 2003). Again, only people on the team should have access to guns, which should be maintained in high-security areas.

Some zoos have security forces or police on their staff; they will probably be responsible for handling weapons and responding at any hour to a situation involving a dangerous animal. As stated earlier, communication is essential so that these individuals know their role and are aware of who is in charge of the situation.

The zoo staff also needs to communicate with local law enforcement agencies to ensure that in the event of a dangerous situation, police officers arriving on zoo grounds are clearly aware of the zoo's emergency protocols (Menzer 2005), and zoo staff knows exactly how the police will respond. Police often respond with deadly weapons to a dangerous animal escape. Zoos must realize that public safety is their first priority (Murphy 2005).

How do you get the word out to everyone and in a quick and efficient manner? Many zoos use the term *red* before the name of an animal to alert all staff members, over a loudspeaker or via radio, of a dangerous-animal emergency.

Some zoos (Lincoln Park Zoo 2003a) place large boxes or trunks at key locations on the grounds; these contain all the materials that staff potentially needs in an emergency, e.g. bullhorns, plastic tape to close off a section to the public, rope, nets, duct tape, hammer, nails, a sharp knife, and a quick-release lasso. The boxes can be on wheels so that they can be moved quickly to any area of the zoo. As with all equipment, the section supervisor is responsible for checking and maintaining the equipment monthly.

When an animal is inside a building but out of its exhibit, the tactics for its recovery are slightly different than if the animal is outside on the grounds. By containing the animal within the building, the staff has more time to plan and act, knowing that the animal cannot go farther. If the animal is outside, setting up a barrier may contain it. However, once an animal has left the zoo grounds, local police may automatically take over.

Essentially, an animal escape is broken down into 6 parts:

1. The animal escapes; a visitor or a zoo employee sees it.
2. The escape is reported to a staff person, who relays the information via radio or phone to a central predesignated location.
3. The alert goes out via radio and the public address system.
4. Keeper staff and veterinarians, along with special teams, arrive at the escape area.
5. The zoo grounds are evacuated or the visitors are closed into buildings.
6. Police and fire services are alerted.

There are, of course, variations on these steps, but in general an escape plan should cover these vital areas.

DISASTER PLANS

In case of a natural or man-made disaster, e.g. fire, hurricane, earthquake, tornado, bomb threat, terrorism, loss of power, or very severe weather, a disaster plan provides the template for staff to know what is expected of them (Baker and Hainley 1999). As with animal escapes, making the staff aware of the plan and putting it into practice are key to a successful response. Drills are an effective method for staff to understand what could happen and to respond in a real disaster scenario. Key local agencies such as the fire department and police should be invited to consult with zoo staff and to become familiar with the zoo's infrastructure and the location of the animals in the collection.

The plan must include all the correct phone numbers of key people and agencies, both inside and outside the zoo, and should address each possible disaster separately with specific recommendations for action by specific staff members. Such a disaster plan, like any emergency plan, will be a fluid document, needing an annual update by all staff members who will be involved in its implementation.

One disaster that is common to all zoos regardless of their geographic location is fire (Hall 2007). Any plan that is conceived should emphasize that safety of the public and staff is a primary concern. Staff members, especially keepers, need to be brought into discussions about what to do with the collection in the event of fire inside a building. Staff needs to be told in no uncertain terms that their first responsibility is to the public and to themselves. Once all people have vacated the affected building, the collection's safety and rescue become the responsibility of the fire department. Meetings need to be held with the local fire officials, and they need to have current plans of the buildings as well as which animals are in the outdoor enclosures. If the keepers are not clear on this procedure and attempt to stay in the building to capture or release animals into outdoor enclosures, they run the serious risk of getting trapped inside. All buildings should have fire detectors to help alert staff and to summon the local fire authorities automatically at any time of the day or night. Fire extinguishers should be placed at key locations in all areas, and annual inspections to refill or replace units should be regularly scheduled. In certain situations staff may use carbon dioxide (CO_2) fire extinguishers to aid in animal-related control. The units used for these events must be separate from the ones earmarked for fire prevention. Carrying out annual fire drills with staff, so that all roles and responsibilities are clearly defined, is an excellent proactive activity.

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Part Three

Nutrition

Introduction

Charlotte Kirk Baer

This new volume presents "a new chapter" in our knowledge of nutrition and goals for feeding wild mammals. When the first edition of this book was published, zoo animal nutrition was a new and relatively unexplored field. The goals of captive animal feeding programs were "to provide nutritional support for all stages of life, including gestation, lactation, and early postnatal growth." The focus at that time was to elucidate the value of nutritionally complete diets, to argue the dangers of "traditional zoo diets," and to dispel the myth of exotic animal "nutritional wisdom."

Today, the focus of wild mammal nutrition is centered not only on maintaining animals at various life stages, but, just as important, on maintaining and enhancing animal well-being, health, and longevity, and sustaining reproductively active populations that will allow for continuation of species that are, or will be, extinct in the wild. Mammals in captivity are increasingly fed with consideration of their natural feeding behaviors, digestive physiology, social needs, growth and reproductive status, and genetic background. In the first chapter in this section, Kirk Baer et al. address these important aspects of animal nutrition and provide their recommendations on various issues.

In addition to the contemporary goals of wild mammal nutrition, we are now feeding animals in a global regulatory environment and a rapidly changing marketplace that presents numerous challenges, as attested by Henry,

A bat roosts at the Smithsonian's National Zoological Park, Washington, DC. Photography by Jessie Cohen, Smithsonian's National Zoological Park. Reprinted by permission.

Maslanka, and Slifka in their chapter. Recent advances in food-safety knowledge and food-handling requirements necessitate a new way of implementing captive animal feeding programs, as described in this section of the book. Science-based nutritional management of mammals in captivity has become a multifaceted endeavor.

In an effort to ensure the most meaningful contributions to this volume, the authors of this section chose to base their discussions and recommendations on sound scientific evidence drawn primarily from peer-reviewed literature. The availability of, and easy access to, numerous scholarly works representing the latest original research in the field are luxuries that authors of the previous edition did not have.

Nutrition is a key component of animal management; however, the science of animal nutrition is often not viewed as the priority it should be, especially in the zoological community. We have not only an opportunity but an obligation to assure that animal diets promote health, well-being, and longevity. When the first edition of this book was published in 1996, only 6 zoos in North America employed trained nutritionists, and a handful of others engaged nutritional consultants. Today, with the printing of this new edition, the number of full-time trained animal nutritionists in North American zoos has more than doubled—yet only approximately 10% of zoos (20 zoos out of more than 200 institutions) employ nutritionists. These statistics point to the fact that roughly 90% of the organizations responsible for maintaining wild animals in captivity are managing animals without formal and skilled expertise in animal nutrition.

I challenge every reader of this volume to heed the words of the world-renowned biologist and environmentalist Peter Raven, given in his 2002 presidential address to the American Association for the Advancement of Science: “Many of the world’s life-support systems are deteriorating rapidly and visibly, and it is clear that in the future our planet will be less diverse, less resilient, and less interesting than it is now; in the face of these trends, the most important truth is that the actual dimensions of that world will depend on what we do with our many institutions, and with the spiritual dimensions of our own dedication.” As institutions and as individuals responsible for animals in our care, let’s move forward together to implement basic conditions of change for the good of the animals in our charge and ultimately for the good of the world. This change must come from each individual and each institution in the form of responsible decisions and wise allocation of resources that translate into sometimes small, but significant, steps toward the sustainability of our children’s future.

9

Contemporary Topics in Wild Mammal Nutrition

Charlotte Kirk Baer, Duane E. Ullrey, Michael L. Schlegel, Govindasamy Agoramoorthy, and David J. Baer

INTRODUCTION

Feeding wild mammals successfully in captivity requires knowledge of basic nutritional concepts, an understanding of different animal types and digestive physiologies, an appreciation for natural feeding behaviors, a familiarity with appropriate food sources, and an awareness of potential diet-related diseases. This chapter presents an overview of major classes of wild mammals organized by feeding strategy, with accompanying descriptions of typical dietary components and feeding considerations as well as diseases that are dietary in origin or impacted by nutrition. This chapter is not intended to be a comprehensive treatise on animal nutrition; rather it is meant to provide contemporary views on principal aspects of wild mammal feeding and nutrition.

NATURAL FEEDING BEHAVIOR

Despite the fact that mammals exploit many types of food, a single species usually consumes a limited selection of foods that it is structurally, physiologically, and behaviorally competent of utilizing efficiently. Ingesting food involves 2 main acts: manipulating the food and reducing it to particles small enough to swallow. The act of biting, tearing, and chewing the food may vary from one type of mammal to the other depending on their dentition; the swallow reflex is considered uniform for the order Mammalia (Eisenberg 1981). A foraging mammal may have a variety of potential foods available in its natural environment. Some may be easier to find, handle, and digest, while some may have a higher nutritional value than others. So the mammal has to decide what to choose from the available courses of action, and the one whose benefit outweighs its costs by the greatest margin will be favored by natural selection. According to the optimal foraging theory, individuals that forage optimally are likely to be fitter to leave more offspring than those that do not (MacArthur and Pianka 1966). However, the link between reproductive fitness and optimal foraging is difficult to verify, because fitness is measured as a lifetime reproductive success, and foraging success is usually measured in proximate terms. Nonetheless, scientific studies have suggested a correlation between foraging success and fitness (Sherman 1994).

Although a variety of mammals has been maintained in captivity for centuries and commercial diets are available in the market to keep them alive, providing appropriate food is challenging and crucial to successfully maintain mainly sensitive species in good physical and psychological health.

NATURAL FOOD RESOURCES OF MAMMALS

Plants and insects are the most common food items for mammals in the terrestrial ecosystem, and the predominant mammalian orders, namely Rodentia and Chiroptera, depend mainly on these food resources. Members of the orders such as Pholidota and Tubulidentata are primarily insect eaters, while members of the orders of Marsupialia, Lagomorpha, Proboscidea, Hyracoidea, Sirenia, Perissodactyla, and most Artiodactyls, Primates, and Rodentia are herbivores. Although many herbivores are selective in their feeding, a wide range of food items is generally consumed, and seasonal variations in feeding habits are found in temperate-zone species.

INSECTS

Insects apparently have been a major source of food for mammals for over 180 million years and have had remarkable influence on patterns of mammalian evolution. The Early Tertiary adaptive radiation of the highly successful microchiropteran bats might have been due to the abundance of nocturnal insects (Fenton 1992). In tropical forests, termites are of significant importance to mammals even today. At least some members of 10 out of 19 mammalian orders commonly eat termites, and species of anteaters, pangolins, and aardvark as well as some insectivores are specialized termite eaters.

PLANTS

Herbivory has been common among mammals, since plants have been the most abundant source of food in the terrestrial ecosystem for at least 65 million years. Many plant tissues are difficult to digest; they often hold low levels of protein. They are protected by defensive chemicals known as secondary compounds, which affect the diets and feeding strategies of mammals. Because defensive chemicals in plants are broad occurrences, they have forced herbivores to evolve countermeasures (McArthur, Hagerman, and Robbins 1992). One such measure is microbial breakdown in the large intestine or rumen for mammals such as rabbits, rodents, pigs, horses, and some ruminant artiodactyls; they are known to degrade oxalates by microbial action (Allison and Cook 1981). A second measure is selective foraging, the ability to discriminate among individual plants and feed only on those with relatively low levels of defensive chemicals. An interesting example is the leaf-eating howler monkey, *Alouatta palliata*, in Costa Rica—a species forced to be selective by defensive chemicals in the leaves of trees (Glander 1977). A third way in which mammals avoid the effects of defensive chemicals is by having a diverse diet of various plants, to keep the levels of chemicals ingested low enough to be tolerated.

DIGESTIVE IMPLICATIONS OF FIBER FORMS AND CARBOHYDRATE FRACTIONS

Carbohydrates are defined based on the analytical procedures used to quantify them. They are classified by their size (monosaccharides, disaccharides, oligosaccharides, and polysaccharides) and availability to animals consuming them, differing among monogastrics and ruminants. The primary roles of dietary carbohydrate are (1) to provide energy and (2) to maintain the health of the gastrointestinal tract. Different forages have different carbohydrate characteristics (fiber and nonfiber carbohydrate fractions) that can impact health and that can complement one another when used together in herbivore diets. Few data are available on the effect of plant carbohydrates and fiber on food intake, nutrient utilization, and growth of many captive mammalian herbivores; however, abundant data exist on carbohydrate nutrition and fiber digestion in domestic species, which can be applied to similar or related wild species (NRC 1996, 1998, 2001; National Academies 2003).

The ability to utilize dietary fiber differs among captive wild mammals. Ruminants and some primates with extensive pregastric fermentation (e.g. Colobinae) are able to utilize, and in fact require, high concentrations of fiber in the diet.

Several human studies have indicated a generally positive relationship between a high-fiber diet and good health, although it has been difficult to separate the effects of fiber from other dietary and lifestyle factors that may play a role. Some of this information can be useful when considering captive mammal diets. A high-fiber diet appears to reduce disease risk by (1) increasing fecal bulk, (2) decreasing the transit time of food through the gastrointestinal tract, (3) reducing blood cholesterol levels, and (4) helping control blood sugar levels. With their distinct physical characteristics, insoluble and soluble fibers work differently to produce these results.

Insoluble fiber (cellulose, hemicellulose, and lignin) increases fecal bulk (Stephen 1985). Cardiovascular disease and colon cancer risk may be reduced with increased dietary fiber intake (Hill and Fernandez 1990; Lanza 1990). Soluble fiber in the diet may help control the rise in blood sugar following a meal, modulating the postprandial glycemic and insulinemic responses (Trowell 1990). In addition, increasing total dietary fiber intake decreases digestion and absorption of both fat and protein, which could be a weight-control benefit in some species (Baer et al. 1997).

PLANT AND ANIMAL MATTER

Mammals that eat a wide range of plant and animal matters are found among the orders of Marsupialia, Insectivora, Primates, Rodentia, Carnivora, and Artiodactyla. These omnivores are less specialized in structure than those mammals adapted to a narrower diet, and among some orders such as the rodents, their mode of life has been very successful.

HIGHER VERTEBRATES

Several species of mammals also prey on higher vertebrates including reptiles, birds, and other mammals, and these carnivores occur in the orders Marsupialia, Insectivora, Chiroptera, Cetacea, and Carnivora. Most carnivores are specialized structurally and behaviorally for killing and consuming their prey, so the learning of proficient hunting methods is crucial to the survival of carnivores.

SUMMARY

The natural food resources described above correlate with feeding strategies of groups of mammals, which can be classified as herbivores, carnivores, and omnivores. Subsequent discussion of nutritional needs, appropriate foods, and nutrition-related diseases in this chapter are broken out by these animal groups.

HERBIVORE NUTRITION

Mammalian herbivores are animals that have evolved to eat primarily plant matter. Lacking the endogenous enzymes required for digestion of fibrous plant material, mammalian herbivores rely on anaerobic fermentation of dietary fiber by symbiotic microorganisms that live in the gut. Herbivorous mammals can be classified into 2 subgroups defined by the location of the major fermentation region in the digestive tract: pregastric fermenters and postgastric fermenters.

PREGASTRIC FERMENTERS

Ruminants comprise the majority of pregastric fermenters and include cattle, sheep, deer, antelope, giraffe, and duiker, among many others. The basic anatomy of the ruminant digestive system is especially designed to digest feeds high in plant fiber (particularly cellulose and hemicellulose). The stomach is divided into 4 main parts: reticulum, rumen (reticulo-rumen), omasum, and abomasum (gastric, acid-secreting chamber) (Van Soest 1994). It is in the reticulo-rumen where food is retained for microbial fermentation.

The increased retention time allows for more extensive digestion of fiber and might be important in detoxification of secondary plant compounds. Some plant components such as cellulose are of greater nutritive value to the animal if they remain in the rumen over an extended period, where they are degraded to absorbable end products (e.g. volatile fatty acids), or else their fermentation contributes to the formation of other substances (such as microbial cells) that are subsequently digested. Otherwise, such components are destined to provide minimal nutrient yield from colonic/cecal fermentation or be excreted. A unique feature of the ruminant is its ability to regurgitate food boluses from the fermentation vat for further mastication (rumination, or chewing of the cud). There are 4 steps to the rumination process: regurgitation, remastication, resalivation, and reswallowing.

A distinction of ruminants, as it relates to their ability to use forage, stems from 3 characteristics unique to this group of animals. First, a pregastric fermentation chamber allows ruminants to utilize structural carbohydrates (neutral detergent fiber, or NDF) more effectively than either nonruminants or postgastric fermenters of comparable size. Second, whereas nonruminants depend largely on preformed amino acids and vitamins in their diet, ruminants are comparatively free of these requirements. Symbiotic microorganisms synthesize B-complex vitamins, and simple forms of dietary or endogenous nitrogen can be used by ruminants in the microbial synthesis of protein, which is subsequently digested. This adaptation is enhanced by the ruminant's ability to recycle urea via salivary and ruminal mucosal secretions. Microbial protein generally fulfills the minimal amino acid requirements of ruminants. Finally, dietary overlap of sympatric animal species can be very high or low depending on forage diversity and availability, environmental conditions, and management. The net effect of these physiological and behavioral characteristics is that ruminants, as a group, are well adapted to forage-based diets.

Nonruminant pregastric fermenters have a compartmentalized stomach where microbial digestion occurs, but they do not ruminate. Examples of mammals that are primarily herbivorous nonruminant pregastric fermenters include hippopotamuses, kangaroos, and the leaf-eating colobus and langur primates.

POSTGASTRIC FERMENTERS

Fermentation takes place in the large cecum and colon of herbivorous postgastric fermenters. Examples of postgastric fermenting mammals include capybaras, rabbits, rats, horses, rhinoceroses, elephants, sloths, and apes. Coprophagy, or the eating of dung or excrement that is normal behavior among many insects, birds, and mammals, is important for many hind-gut fermenters. They are able to recycle microbially derived nutrients such as vitamins by practicing coprophagy.

FOODS AND FEEDING CONSIDERATIONS FOR CAPTIVE MAMMALIAN HERBIVORES

TABLE 9.1. Nutrient substrates for herbivores and their symbiotic digestive microbes

	Herbivore type		
Nutrient	Nonruminant	Ruminant	Digestive microbes
		Substrate	
Energy	Sugars, starches, volatile fatty acids, organic acids	Volatile fatty acids, glucose, organic acids amino acids	Complex carbohydrates, sugars, starches
Protein	Amino acids (microbial protein)	Microbial protein, amino acids	Ammonia, amino acids, peptides
Minerals	Diet	Diet (bacterial modification)	Diet
Vitamins	Diet, bacterial synthesis	Bacterial, diet	Diet, synthesized

Depending on their digestive physiology, mammalian herbivores obtain specific nutrients from various sources (see table 9.1). Because microbial fermentation is an important part of herbivore digestion, it is important that the microbes—in addition to their herbivore host—receive adequate and appropriate food substrates from which to derive energy and nutrient needs.

HAY

Hays—forages that are harvested and dried—are important sources of nutrients for herbivores and often provide a major portion of dry-matter intake for captive mammalian herbivores. Hays are especially valuable as a source of fiber in support of normal microbial fermentation and normal feeding behavior. In the wild, herbivores may spend many hours each day acquiring and consuming food. In captivity, animals fed relatively concentrated diets can consume them in minutes rather than hours and may develop behavioral vices, such as chewing on exhibit or stall materials and obsessive licking, grooming, or other stereotypic behaviors. Because consumption of hay requires prolonged periods of chewing, its use may help prevent these vices.

Proper drying and curing of freshly cut forage is a critical step in producing high-quality hay (Church and Pond 1988; Van Soest 1994). Once cut, hay must be dried before baling. If hay is too wet when it is baled, bacteria and mold can begin to grow. These microorganisms can reduce feed intake and may produce toxins that adversely affect animal health. If hay is baled when it is too dry, however, leaves may fracture and fall off the stems, reducing nutritional value. When overdried hay is offered to herbivores, feed intake also may be adversely affected. The time required for drying depends to a large extent on local weather conditions and the method of drying. Most commonly, hay is left in the field to be dried by the sun (sun curing). Minimum dry-matter content of hay should be 85%. If too dry, >93% dry matter, hay may be subject to excessive leaf fracture.

Some other nutritional changes occur during the curing process. Sun-curing hay in the field generally increases its vitamin D_2 content. This increase is a result of phytochemical conversion of vitamin D_2 precursors to vitamin D_2 (Morrison 1956). However, there is a concomitant loss in vitamin

A activity of the hay resulting from oxidative destruction of carotenes, some of which are precursors of vitamin A. During excessive drying, the losses of carotenes can be substantial (ibid.). Once cured to the proper dry-matter content, hay that is stored under dry conditions will remain relatively stable in its nutritional value (Church 1988).

Hays are commonly made from grasses and/or legumes. Taxonomically, grass hays include plants in the family Poaceae (Graminae), whereas legume hays include plants in the family Fabaceae (Leguminosae). Examples of grass hays include timothy, *Phleum pratense*; orchardgrass, *Dactylis glomerata* L.; Bermudagrass, *Cynodon dactylon*; fescue, *Festuca* spp.; bluegrass, *Poa* spp.; reed canarygrass, *Phalaris arundinacea* L.; and Sudangrass, *Sorghum sudanense* Stapf. The most commonly used legume is alfalfa, *Medicago sativa*, called lucerne in Europe and Australasia. Other legume hays include clovers, *Trifolium* spp.; lespedeza, *Lespedeza* spp.; birdsfoot trefoil, *Lotus corniculatus* L.; and vetches, *Vicia* spp.

Hay producers often grow mixtures of legume and grasses. Feeding mixed legume-grass hay has benefits and challenges. Mixed hay generally provides crude protein and calcium concentrations appropriate to need. Legume hay alone may have more protein and calcium than needed by many herbivores, and grass hay, depending on species and maturity, may be lower in protein and calcium than required. In addition, purchasing supplies of mixed legume-grass hay with consistent proportions of legume and grass may be difficult.

The important nutritional similarities and differences among legume and grass hays are shown in table 9.2. In general, legume hays are higher in crude protein, calcium, magnesium, and sulfur than grass hays. Grass hays are generally higher in manganese and zinc (Church and Pond 1988). Differences in fiber levels between legumes and grasses are also important and can influence voluntary feed intake. Legumes are generally higher in lignin and lower in NDF and hemicellulose than grasses (Van Soest 1994). In ruminants, voluntary feed intake is negatively correlated with NDF content (Mertens 1973). Because legumes are frequently lower in NDF than grasses, voluntary intake of legumes can be higher than that of grasses (ibid. 1973; Van Soest 1994).

Some of these nutritional differences are dependent on geological origins of soil, soil pH, amounts and types of fertilizer used, climatic region, and local growing conditions. The mineral and crude protein content of hays can be affected by soil fertilization and by adjustments of soil pH (Church and Pond 1988; Van Soest 1994). The more common nutrients in fertilizers include nitrogen, phosphorus, potassium, calcium, and magnesium. Sulfur fertilization may be used on some crops. Nitrogen fertilization is especially important for increasing protein concentration of grass hays. Fertilization

TABLE 9.2. Composition of sun-cured legume and grass hays at various stages of maturity[1]

		Fiber fraction					
Hay	Crude protein, %	Neutral detergent fiber, %	Acid detergent fiber, %	Lignin, %	Ca, %	P, %	Ca:P
Legumes							
Alfalfa							
Early bloom	19.9	39.3	31.9	7.86	1.63	0.21	7.8
Midbloom	18.7	47.1	36.7	10.71	1.37	0.22	6.2
Full bloom	17.0	48.8	38.7	11.18	1.19	0.24	5.0
Birdsfoot trefoil	15.9	47.5	36.0	9.10	1.70	0.23	7.4
Red clover	15.0	46.9	36.0	8.38	1.38	0.24	5.8
Grasses							
Coastal Bermuda grass							
15–28 days' growth	12.0	73.0	34.0	—	0.40	0.27	1.5
29–42 days' growth	12.0	75.0	36.2	—	0.32	0.20	1.6
43–56 days' growth	7.8	76.6	38.3	—	0.26	0.18	1.4
Orchardgrass				—			
Early bloom	12.8	59.6	33.8	4.59	0.27	0.34	0.8
Late bloom	8.4	65.0	37.8	7.41	0.26	0.30	0.9
Ryegrass, perennial	8.6	41.0	30.0	2.0	0.65	0.32	2.0
Smooth bromegrass							
Midbloom	14.4	57.7	36.8	3.50	0.29	0.28	1.0
Mature	6.0	70.5	44.8	7.95	0.26	0.22	1.2
Sudangrass	9.4	64.8	40.0	6.0	0.54	0.20	2.7
Timothy							
Early bloom	10.8	61.4	35.2	4.03	0.51	0.29	1.8
Full bloom	8.1	64.2	37.5	5.66	0.43	0.20	2.2

Source: Adapted from NRC 1989b (table 6-1), 1996 (tables 11-1 and 1-A), and 2001 (table 15-1).

[1] Dry-matter basis.

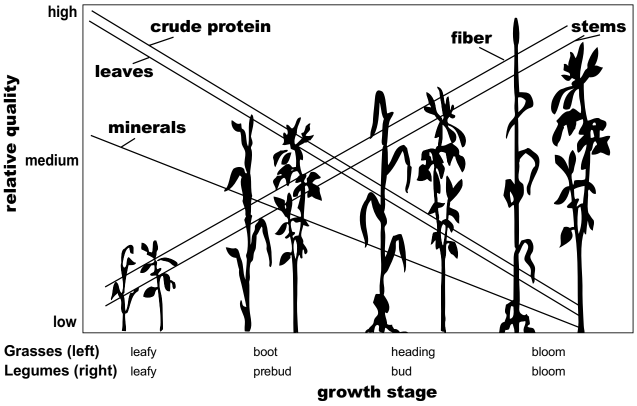

Fig. 9.1. Effect of plant maturity of forage on proportions of plant components and nutrient content. Adapted from Blaser et al. (1986).

with nitrogen and phosphorus may also improve hay palatability (Rhykerd and Noller 1973). Soil testing and the advice of local agricultural extension agents are important components of a sound hay-producing program.

Regional variations among hays, especially in minerals, should be considered when purchasing them for feed (Underwood 1981). The mineral content of hay is often related to soil mineral levels and availability. Available soil concentrations of nutritionally important minerals, such as cobalt, molybdenum, iodine, iron, and selenium, vary greatly across geographic regions.

An important factor influencing the nutritional value of both legumes and grass hays is the stage of maturity at cutting (Morrison 1956; Van Soest 1994), and this stage is an important criterion in establishing hay grades. As plants mature, there is usually a decrease in the relative amount of leaf and an increase in the amount of stem. Also, with the onset of flowering, nutrients are diverted from the vegetative portion (leaf) to the reproductive portion (flower buds). These changes may result in decreased concentrations of crude protein and soluble carbohydrates in the vegetative portion and an increase in lignin content (fig. 9.1). Levels of certain minerals such as calcium, potassium, and phosphorus may also decline. The net result is a decrease in hay palatability, digestibility, and nutritional value as maturity at cutting advances (Van Soest 1994).

In addition to plant species and maturity, harvesting and storage factors can influence hay quality. The ideal weather for hay making is low humidity and no rain. If hay is rained on before baling, soluble proteins and carbohydrates may be leached out, decreasing hay quality (Kellems and Church 1998). After the hay is cut, plant enzymes remain active (and may lower available nutrient levels) until moisture levels decrease to 40%. Table 9.3 demonstrates that when hay is rained on, nutrient losses of 9.6 to 54.5% can occur. If hay is baled wet at moisture levels above 25%, it spontaneously heats and becomes moldy, and protein may complex with carbohydrates, reducing its availability (ibid. 1998).

Hay is sometimes treated with ammonia, which might improve hay quality for several reasons. First, ammoniation breaks cell wall linkages and increases digestibility. Second, ammoniation requires that hay be covered, indirectly providing a good storage environment. Third, ammoniation may reduce danger from toxins (see section on tall fescue toxicosis below). Ammonia can reduce the undesirable effects of endophyte toxins, and in grain crops it has a comparable impact on aflatoxins.

TABLE 9.3. Effect of rain on leaf loss, leaching and enzyme metabolism in alfalfa hay harvested at the bud stage of maturity

	Amount of rain, centimeters			
Loss	0	2.5	4.2	6.35
Leaf loss	7.6%	13.6%	16.6%	17.5%
Leaching and enzyme metabolism	2.0%	6.6%	30.1%	36.9%
Total	9.6%	20.2%	46.6%	54.5%

Source: Adapted from Kellems and Church 1998.

Each shipment of hay should be examined prior to acceptance. Hay quality can be evaluated initially by sight and smell upon arrival (Morrison 1956). The hay should contain minimal weed contamination and should not appear excessively bleached; bleaching may indicate improper field drying. Hays, especially alfalfa hay, should appear leafy, and the leaves should not readily fall off the stems when a bale is opened. The amount of leaf may indicate the stage of growth at the time of cutting, but excessive leaf fall may also indicate that the hay is too dry. A number of flowers on legume hay and well-developed heads on grass hay may indicate late cutting (Rohweder 1987). Stems should feel pliable; stems that feel brittle or snap when they are bent may indicate that the hay is too dry or that the hay was too mature at the time of cutting. Excessive dustiness, a musty smell, or a choking sensation when smelled closely suggest that mold growth may be a problem.

Even if hay is harvested and baled properly, improper storage can have a significant impact on nutritional value. If hay is exposed to moisture during storage, sufficient to cause deterioration, 30%–35% of the dry matter could be lost (Kellems and Church 1998). If possible, hay should be stored in a building. General recommendations include ensuring that hay storage areas have adequate drainage, natural or fan ventilation, protection from precipitation and soil moisture, and protection from contamination by wild animals (birds, rodents, and deer). If hay is stored outdoors, it should be kept off the ground by placing it on pallets or other similar devices to stop movement of soil moisture into the stored bales. The hay should be covered with a tarp or plastic that is weighted to prevent the cover blowing off.

Hay can be purchased in multiple bale shapes and sizes. Small rectangular bales are easily stored and transported around most zoos. Large square bales and compressed pelletized bales also are available. Additionally, large round bales can be purchased and are an efficient way to feed large groups of herbivores, but storage and handling may require special equipment.

If the zoo has land available, it may be advantageous for it to produce its own hay. Before proceeding, the local agricultural cooperative extension agent should be contacted to assist with selecting appropriate plant species, fertilization and pest management strategies, and proper harvesting techniques, and estimating costs of production.

BROWSE

Browse is used as a foraging food in many institutions. It is defined as small bushes, twigs, sprouts, herbaceous plants, small trees, and other vegetation—including buds, twigs, leaves, fruit, and flowers of woody plants—fed on by wildlife. Browse used at zoos varies in type, quality, and nutrient composition. Because some browse species contain toxins or have characteristics that may lead to formation of indigestible phytobezoars in the consumer, they must be selected and used with care (Ensley et al. 1982; Fowler 1986; Knapka et al. 1995). Examples of the nutrient composition of some browse species commonly used to feed captive wild mammals are provided in table 9.4.

Providing adequate browse from late fall to early spring can be difficult in areas where temperatures fall below freezing. Drying, freezing, or ensiling can be used to provide browse during months of low availability.

MANUFACTURED DIETS

A wide range of manufactured diets is available for feeding captive wild herbivores. The most common form of commercial herbivore diet is a pellet.

Pelleted diets. Pelleted diets are manufactured from ground ingredients that are compressed into cylinder-shaped particles. These diets differ from extruded products in the following ways: they may be composed of recognizable ingredient particles, they are more dense, they are not cooked as much, they tend to have slightly more moisture (mold inhibitors are frequently used), their starch tends to be less digestible, and they can be less palatable than extruded particles for carnivores and omnivores.

MANAGING HERBIVORES IN LARGE ENCLOSURES

Managing captive wild herbivores in large enclosures presents several important feeding husbandry challenges. Some are highlighted below.

Pasture species selection and management. Pastures in zoo exhibits are used as an enclosure substrate, for aesthetics purposes, and as potential food. As a substrate, choice of plant species will depend on whether the pastures can be rotated or will be continually grazed. If the pastures will be continually grazed, plant species such as Kentucky bluegrass, *Poa pratensis* L., or Bermuda grass are more appropriate choices, because they will withstand the grazing pressure. Plant species such as orchardgrass, smooth bromegrass, *Bromerus inermis*, and red clover, *Trifolium pretense* L., cannot tolerate continual grazing pressure. In addition, certain plant species are more tolerant of cold or hot temperatures and humid or arid conditions.

In most cases, animals maintained on pasture will graze in preference to consuming hay. Depending on animal species and exhibit size, pasture plants may contribute a significant proportion of dry-matter, energy, and nutrient intake, even though pasture may not have been intended as all or part of the diet.

Water sources. Adequate water sources in large exhibits are essential. Water troughs, natural streams, or ponds may be utilized as sources of water, although the latter should be fenced off to prevent erosion and contamination with fecal material. Some animal species can meet water needs from consumption of fresh vegetation and will not consume liquid water. Care must be taken during periods of drought or limited irrigation to ensure that all animals are properly hydrated.

Feeding locations and access to feed. Feed troughs and hay and browse feeders should be placed throughout exhibits in

TABLE 9.4. Nutrient composition of some browse used to feed mammals in captivity (dry-matter basis)

	Dry matter (as fed) (%)	Crude protein (%)	Crude fat (%)	Ash (%)	Neutral detergent fiber (%)	Acid detergent fiber (%)	Acid lignin (%)
Acacia leaves (*Acacia longifolia*)	57.9	11.3	4.6	8.1	39.8	33.6	32.6
Alder leaves, sun cured (*Alnus* spp.)	85	22	6.0	5.9	—	21.0	—
Bamboo, arrow leaves (*Psuedosasa japonica*)	24.1	12.7	2.7	9.1	76.8	48.9	8.4
Beech (*Fagus* spp.)	86	12.2	2.5	4.8	64.7	47.6	16.8
Broad-leaf ficus leaves (*Ficus microcarpa* var. "nitida")	33.3	12.9	4.1	14.9	66.0	26.8	10.0
Broad-leaf ficus leaves (*Ficus microcarpa* var. "nitida")	37.8	8.8	3.8	16.3	30.3	26.2	8.8
Cape plumbago leaves (*Plumbago auriculata*)	24.2	22.2	2.3	8.4	16.5	8.6	4.0
Curly leaf ficus leaves (*Ficus benjamina*)	35.9	9.7	4.1	15.3	56.7	31.4	12.1
Mulberry, fresh (*Morus* spp.)	40	18.1	5.7	15.0	—	—	—
Waxy bush leaves (*Xylosma congestum*)	33.0	8.0	3.6	11.7	34.0	25.0	10.1
Willow, fresh (*Salix* spp.)	41	9.8	4.9	7.4	—	—	—

Source: Adapted from National Academies 2003 and Baer and Associates, LLC (unpublished data).

a manner that accommodates the feeding behavior of species herds and individuals within those herds. Mixed-species exhibits may require a minimal distance between feeding stations for individual herds. While some species readily mix during feeding, others may segregate. In addition, feeder space should allow individuals within a herd to feed without excessive competition.

Feeding animals with different nutrient requirements in a single enclosure may require control of animal access to feeders. When feeding specific diets or medicated feeds to single animals or groups of animals within a large mixed-species enclosure, elevated feeders, exclusion feeders, and creep feeders can be used. Training groups of animals to enter a separate feeding area is also possible.

Key concerns. Adequate nutrient intake is the primary feeding husbandry concern with herbivores in large enclosures. In most cases, pasture alone will be inadequate to meet nutrient requirements of every life stage. Nutrient inadequacies can be compounded by local soil containing overly high or low mineral concentrations. Ideally, a supplemental nutrient source, such as a pelleted feed, should be formulated to complement the pasture.

Some species preferentially graze pasture and consume very little, if any, pelleted feed. If local soil conditions provide appropriate mineral nutrition, then the pasture may be nutritionally adequate, but in many instances this will not be true. These situations pose a considerable challenge. For example, blesbok are notorious for not consuming pellets when pasture is available. At 2 institutions, blesbok housed in large, multispecies enclosures exhibited signs of copper deficiency, which was attributed to a combination of low pellet consumption, low copper concentration in the pasture, and excessive molybdenum, iron, or sulfur content in the pasture and/or water. Correcting this deficiency may require a multifactorial approach and can involve changing pasture plant species, identifying a more palatable pellet or mineral supplement, dosing each individual with a copper bolus, or removing the species from the multispecies enclosure.

Where adequate mineral intake is a concern, mineral blocks formulated to provide essential salt and a balanced supplement of trace minerals can be used. Blocks and bricks can be obtained that are weather resistant for free-choice feeding. Caution is urged when using mineral blocks in mixed-species exhibits, because mineral requirements vary with species and some animals are more susceptible to certain mineral toxicities than others (e.g. copper toxicity in sheep).

NUTRITION-RELATED DISEASES

Bloat. Bloat is a digestive disorder characterized by an accumulation of gas in the first 2 compartments of a ruminant's stomach (reticulo-rumen). Production of gas (primarily carbon dioxide and methane) is a normal result of fermentation processes. The gas is usually discharged by belching (eructation), but if the animal is unable to remove the excess gas, pressure builds up in the reticulo-rumen, exerting pressure on the diaphragm and restricting breathing. The most common type of bloat is frothy bloat, where gas builds up in a foam or froth above the rumen contents, and normal belching is inhibited.

Animals can bloat due to a variety of factors. However, a common cause is production of gas by microorganisms in the digestive tract. Normally, cattle are able to belch to release the gas that is produced. Bloat is caused not by increased gas production but rather the inability to release gas via the belching process. Finely ground feeds promote foaming or frothiness in the rumen, increasing the incidence of bloat because the gases are trapped in the foam and belching is prevented. High-grain diets encourage the growth of certain rumen bacteria that create an environment that traps gasses. Acidic conditions in the rumen tend to stabilize the foam. Saliva contains antifoaming agents, but saliva production is greatly reduced on high-grain diets. All these factors contribute to the occurrence of bloat.

Bloat also can occur on forages that are low in fiber and high in protein but is most common on immature legume pastures, which may contain foam-stabilizing saponins. Bloat has been observed on alfalfa, white-clover, and red-clover pastures. It seldom occurs on grasses (or pastures with at least 50% grass), coarser pastures, or hay. Bloat usually follows a heavy feeding or grazing period. Animals that are hungry or greedy feeders are most susceptible. Frost, dew, or rain on the pasture may increase the likelihood of bloat. Bloat incidence is likely to be increased during periods of rapid plant growth, especially in the spring. When bloat is observed, animals should be offered dry hay. Walking bloated animals is also helpful. Bloat can cause death in as little as one hour and is believed to be caused by asphyxiation; the rumen becomes so distended that the animal can no longer breathe.

Rumenitis. Rumenitis is an inflammation resulting from irritation of the rumen wall. It is typically a consequence of rapid ruminal fermentation of dietary carbohydrate with subsequent production of lactic acid and increased acidity of the ruminal fluid, along with lack of physical stimulation or abrasion of the rumen tissue. Diets with high levels of carbohydrate can be a primary cause, but the texture of the feed and method of feeding can be contributing factors. Increasing the amount of fiber in the diet, or feeding roughage, provides what some term a "scratch factor," to keep the tissue healthy. Like acidosis, a low level of rumenitis is typical when concentrate diets are fed. When rumenitis becomes severe, the tissue lining the rumen wall becomes ulcerated and is no longer effective in absorbing nutrients. When ulcers develop in the rumen wall, ruminal bacteria pass through to the blood, travel to the liver, and form abscesses. Rumenitis has been observed with increased frequency in a herd of white-tailed deer, *Odocoileus virginianus*, maintained on a high-carbohydrate supplemental ration (Woolf and Kradel 1977).

It has been suggested that rumenitis (and acidosis) may be associated with heat stress (Wren 2003). Clinical signs of heat stress include salivation with open-mouth breathing. During heat stress, ruminants continue to salivate but they do not swallow, because they would have to close their mouth and stop breathing; heat exchange occurs through respiration.

Magnesium deficiency (hypomagnesemia). Magnesium (Mg) is a major intracellular cation and serves as a cofactor in over

300 metabolic reactions (Shils 1999). It is involved in the regulation of muscle and nerve function and influences the metabolism of carbohydrate, protein, fat, and nucleic acids. The combination of Mg adenosine triphosphate (ATP) and adenylate cyclase forms cyclic adenosine monophosphate (cAMP), which influences the secretion of parathormone and may explain why magnesium deficiency sometimes results in hypocalcemia as well as hypomagnesemia.

Magnesium deficiency occurs more often in ruminants than nonruminants, particularly when grazing. Lush growing pastures tend to be low in magnesium and relatively high in protein, potassium, and organic acids, all of which serve as antagonists that interfere with magnesium transport across the rumen wall, the major site of magnesium absorption (Martens and Schweigel 2000). Nonruminants absorb most of their magnesium from the small intestine. Although adult ruminants also absorb magnesium from the small intestine, magnesium absorption in this area is generally exceeded by magnesium secretion (Greene, Webb, and Fontenot 1983).

Signs of magnesium deficiency include hyperexcitability, muscle fasciculations, convulsions, respiratory distress, collapse, and death. Plasma magnesium concentrations in deficient animals are often <1.5 mg/dL (<0.65 mmol/L). Miller et al. (2003) observed some of these signs in captive kudu, *Tragelaphus strepsiceros*, eland, *Taurotragus oryx*, and nyala, *Tragelaphus angasii*, and speculated that, in these cases, inappropriate concentrate feeding may have induced rumen acidosis/chronic rumenitis and affected calcium-to-phosphorus ratios and magnesium absorption.

Vitamin E deficiency. Vitamin E is a collective term used for 8 compounds synthesized by plants and found principally as free alcohols in lipid-containing fractions of green leaves and seeds (Sokol 1996; Chow 2000). Four are designated α-, β-, γ-, and δ-tocopherols (or tocols), and 4 are designated α-, β-, γ-, and δ-tocotrienols. Of the various isomers, *RRR*-α-tocopherol (formerly D-α-tocopherol) has the highest biological activity in preventing fetal resorption in rats. The biological ranking of the tocopherols and tocotrienols as antioxidants is based on their ability to scavenge peroxyl radicals. Selenium (Se) also fulfills an antioxidant role, particularly as a component of glutathione peroxidases (GSHPx). Selenium and vitamin E each have unique metabolic roles, and the factors that alter the oxidative state of an animal may differentially affect their dietary needs.

Grains are generally low in *RRR*-α-tocopherol, and when stored for extensive periods much is lost, particularly from high-moisture or acid-treated grains (Mahan 2000). Although some seed oils have a relatively high tocopherol concentration, much of that in corn and soybean oils is γ-tocopherol. Young growing forages have relatively high α-tocopherol concentrations, but this declines with maturity, cutting and curing for hay, and during storage.

A deficiency of vitamin E may result in necrotizing myopathy of skeletal and cardiac muscle, placental blood vessel pathology with fetal death and resorption, degeneration of testicular epithelium, gastric ulceration, cataracts, retinal degeneration, encephalomalacia, erythrocyte hemolysis, and impaired immune function. Captive white-tailed deer, *Odocoileus virginianus*, were protected against white muscle disease, and mortality of fawns was reduced when diets containing about 5 mg α-tocopherol/kg were supplemented with 45 mg all-*rac*-α-tocopheryl acetate/kg (Brady et al. 1978). Muscular dystrophy in wild Hunter's hartebeest, *Beatragus hunteri*, following capture was indistinguishable from white muscle disease in vitamin E–deficient cattle (Jarrett et al. 1964), and so-called capture myopathy has been observed in gemsbok, *Oryx gazella* (see Ebedes 1969), hartebeest, *Alcelaphus buselaphus* (see Young 1966), and other African animals (Basson et al. 1971). Reproducing cattle exhibit an increased incidence of retained placentas and mastitis, and reproducing swine frequently exhibit mastitis, metritis, and agalactia (Mahan 2000; NRC 2001). Because α-tocopherol does not effectively cross the maternal-fetal barrier, the neonate has low tissue tocopherol levels; therefore, consumption of relatively tocopherol-rich colostrum is important for postnatal welfare (Mahan 2000).

Certain toxins, high dietary levels of polyunsaturated fatty acids, large excesses of dietary iron, extremes in environmental temperature, intense physical activity, and infectious diseases tend to increase oxidant stress. Collectively or individually, these factors influence the accumulation of reactive oxygen species and increase the dietary requirement for vitamin E (Surai 2002).

Sources of vitamin E. The principal commercial dietary vitamin E sources are the acetate or hydrogen succinate esters of all-*rac*-α-tocopherol (formerly D, L-α-tocopherol) or of *RRR*-α-tocopherol. These compounds are more stable in mixed feeds than free tocopherol (Mahan 2000).

RRR-α-tocopheryl polyethylene glycol 1000 succinate (TPGS) is a waxy solid that is water miscible. Because it has both hydrophilic and lipophilic characteristics, its absorption from the gut does not require bile salts. Thus, it has been proposed that humans with cholestasis, and perhaps some animal species, may be better able to derive their vitamin E needs from this source than from fat-soluble tocopherols or tocopheryl esters. Papas et al. (1990) reported major differences between species in serum or plasma concentrations of α-tocopherol following equimolar oral administration of various vitamin E forms, with TPGS producing the greatest short-term responses in Asian and African elephants and black rhinoceroses. TPGS produced no greater long-term plasma α-tocopherol concentration in horses than did *RRR*-α-tocopheryl acetate. Howard et al. (1990) made the same observation in horses, and found oral TPGS resulted in much lower plasma α-tocopherol concentrations than did *RRR*-α-tocopheryl acetate in white-tailed deer.

Tall fescue toxicosis. Fescue is a pasture forage that is sometimes used to feed captive wild herbivores. It is insect and nematode resistant, is soil and weather tolerant, and has a long growing season. Despite its advantages, some tall fescue cultivars can be infected with a fungal endophyte, *Neotyphodium coenophialum* (formerly called *Acremonium coenophialum*), that is toxic to animals. Toxins that are produced by the endophyte create a number of problems for herbivores. Animals do not gain and can lose body weight despite constant grazing. They also experience reproductive problems such as low conception rates and poor offspring survival. In addition, cattle grazing infected tall fescue have elevated body temperatures and declines in blood flow to the extremities, causing "fescue foot" and other signs. Potential problems also have been reported in exotic ruminants such as Thomson's gazelles and impala grazing on fescue (Ballance et al. 2005).

Presently there is no cure for tall fescue toxicosis. Although endophyte-free tall fescue cultivars are available, it might not be feasible or cost effective to use them. There are several other management options aimed at limiting the amount of toxin ingested by animals to reduce potential for toxicosis. Rotation of grazing animals to other pastures will reduce exposure. Other options involve management of toxic tall fescue pastures by interseeding other forages that can dilute the toxins, such as red clover, lespedeza, or alfalfa. Supplementing animal diets with alternative sources of fiber or carbohydrate at rates that do not impact fiber digestion can reduce toxic effects of endophyte on ruminants. Finally, ammoniation of hay can reduce effects of endophyte toxins. Ammoniation of toxic fescue has been reported to increase daily gains and prolactin levels in cattle by at least 50%.

Enterolithiasis. Enteroliths are stones, concretions, or calculi that are formed in the intestine and result in a condition called enterolithiasis (Hassel, Schiffman, and Snyder 2001). Concerns arise when enteroliths cause a blockage, resulting in colic and potentially death. Enteroliths are common in domestic horses (Hassel, Schiffman, and Snyder 2001), and have been observed in Przewalski's horses (Gaffney, Bray, and Edwards 1999), zebras (McDuffee et al. 1994), eastern kiangs (Gaffney, Bray, and Edwards 1999), Somali wild asses, and tapirs (Murphy et al. 1997). Among domestic horses, Arabian and Arabian-cross horses and quarter horses appear to be the breeds most commonly affected (Hassel et al. 1999).

Factors that result in a large-intestine environment with increased mineral content, alkaline pH (>7), and exposure to a nidus (foreign material) contribute to enterolith formation (Hassel et al. 1999). Although struvite crystals (magnesium ammonium phosphate $[Mg(NH_4)(PO_4)\cdot 6H_2O]$) are the most commonly found enteroliths in equids, vivianite ($Fe_3[PO_4]_2\cdot 8H_2O$) and newberyite ($MgH[PO_4]\cdot 3H_2$) containing enteroliths were found in tapirs (Murphy et al. 1997).

Dietary factors that contribute to struvite enterolith formation include an excessive amount of free ammonia as a result of digestion of high-protein feeds and high dietary concentrations of magnesium and phosphorus (Hassel, Schiffman, and Snyder 2001). Alfalfa hay is a dietary concern, because 99% of horses with enteroliths were offered diets of at least 50% alfalfa hay (on a dry-matter basis) in a retrospective study of cases in California (Hassel et al. 1999). In the southwestern United States and other areas of North America, alfalfa hay is a source of high protein and high magnesium due to high soil magnesium concentrations (ibid.). The excess free ammonia combines with phosphorus and magnesium and binds to a nidus (foreign material), which initiates enterolith formation (Hassel, Schiffman, and Snyder 2001). Feeding wheat bran has also been implicated in promotion of enterolith formation in domestic equids due to its high magnesium and phosphorus content (Hassel et al. 1999). Although phosphorus is a component of struvite enteroliths, excess dietary phosphorus does not appear to be a contributing factor (Lloyd et al. 1987). Water mineral content and pH also may play a role in enterolith formation (Hassel et al. 1999). Gaffney, Bray, and Edwards (1999) found an increased incidence of enteroliths in exotic equids maintained in exhibits that had alkaline water ($pH > 7.5$).

Some preventive measures to reduce the potential for enterolith formation include reducing dietary protein and magnesium concentrations and ensuring that sources of water are not high in pH or magnesium. In addition, some evidence suggests that the addition of apple cider vinegar to the diet might decrease the pH of the large intestine, making the environment unfavorable for enterolith formation (Hintz et al. 1989).

Urolithiasis. Urolithiasis is a general term for the presence of aggregates of mineral crystals that have precipitated from urine and formed macroscopically visible uroliths (calculi or stones) within the urinary tract. They generally have an organic matrix, constituting less than 10% of total dry mass, with the remainder composed of mineral matter. The urolith minerals identified in various animal species include struvite (magnesium ammonium phosphate hexahydrate), whewellite (calcium oxalate monohydrate), weddellite (calcium oxalate dihydrate), hydroxyl apatite, urate, ammonium urate, sodium urate, cystine, silica, and xanthine. More than one crystal type can be found in some uroliths, with the core corresponding to the urinary conditions prevailing when the urolith was first formed, and the outer layers corresponding to more recent conditions favoring further growth. Solute concentrations, urine pH, urinary tract infections, urine volume, frequency of urination, genetics, and other factors may influence urolith development. Clinical signs are seldom seen until the crystalline aggregates are large enough to interfere with urine flow or irritate the urinary tract mucosa. Subsequently, dysuria, hematuria, flank or renal pain, and other signs may be seen, depending on species and the location and degree of obstruction (Kahn and Line 2005).

Urolithiasis in domestic ruminants is considered primarily a nutritional disease, seen most often in young animals castrated at an early age and fed high-grain diets that either have an approximate 1:1 calcium-to-phosphorus ratio or are high in magnesium. Those fed high-grain diets with low calcium-to-phosphorus ratios are most likely to develop struvite uroliths, whereas those grazing silica-rich forages are predisposed to silica uroliths. Ruminants grazing plants high in calcium relative to phosphorus may develop calcium carbonate uroliths, whereas oxalate-rich forages may lead to calcium oxalate uroliths. Calcium carbonate and calcium oxalate uroliths have been reported in cervids (Reynolds 1982). Calcium oxalate uroliths also have been reported in 4 species of macropods (*Macropus rufus*, *Macropus fuliginosus*, *Macropus rufogriseus banksianus*, and *Macropus giganteus giganteus*) (Bryant and Rose 2003). Uroliths in a young llama, *Lama glama*, were found to be 90% hydroxyl apatite and 10% struvite (Kock and Fowler 1982). Limited water supplies are predisposing.

Uroliths in equids are not common but are seen most often in adults and in males rather than females. Calcium carbonate uroliths are most frequent; struvite uroliths are seen occasionally. Equine urine tends to be alkaline and has high mineral and mucoprotein concentrations, favoring urolith formation. Rabbit urine is similar, and calcium carbonate and triple-phosphate crystals may precipitate and obstruct the urinary tract when high-calcium diets are fed and water intake is limited.

Obstructive urolithiasis has been reported in a 12-year-old male reticulated giraffe, *Giraffa camelopardalis reticulata*, by Wolfe, Sladky, and Loomis (2000). The urolith was determined to have a core of magnesium calcium phosphate with a shell of struvite. The reported diet included a commercial pelleted diet (marketed for browsers), free-choice alfalfa hay, and a mineral block of uncharacterized composition. The "concentrate" (presumably the pellet) was said to contain 1.07% calcium and 0.74% phosphorus. A further report by Wolfe (2003) stated that uroliths found in other captive giraffes appeared to be composed primarily of calcium phosphate and struvite. Although an attempt was made to identify dietary features that might lead to this problem, the conclusions were largely speculative.

CARNIVORE NUTRITION

Carnivores are defined by the fact that they eat other animals or animal products. They represent a relatively small portion of the animal kingdom and are animals with body sizes spanning 3 orders of magnitude. Carnivores have specialized features (dentition and claws) to secure and eat prey. They also have digestive enzymes that break down protein into amino acids, which can then be absorbed through the intestinal wall. Unlike herbivores, carnivores have no need for special gut development that allows for fermentation. It is important to note that many animals considered carnivores are not truly carnivorous. Examples are the maned wolf and many bear species, which consume a diet more distinctive of omnivores.

The majority of terrestrial carnivores feed on invertebrates and small vertebrates or on large vertebrates (Carbone et al. 1999). Small carnivores feed predominantly on invertebrates, and intake rates of invertebrate feeders are low (about one-tenth of those of vertebrate feeders). Small carnivores can subsist on this diet because of low absolute energy requirements; however, invertebrate feeding appears to be inadequate for larger carnivores.

Many carnivores are obligate carnivores, which means they obtain nutrients from animal matter because they cannot obtain the nutrients that they need from plants and bacteria. Obligate carnivores such as cats lack the enzyme needed to metabolize carotene, obtained from plants, into vitamin A. These animals obtain their vitamin A from the liver of their prey. Obligate carnivores are also unable to synthesize some fatty acids.

Strict carnivores like cats cannot handle a varied diet like omnivores and herbivores. For example, the inability to synthesize sufficient vitamin A from carotene, ornithine from glutamic acid, arachidonate from linoleate, and taurine from cysteine is a result of complete deletion or severe limitation of the enzyme or pathway that makes each nutrient (MacDonald, Rogers, and Morris 1984). The cat's requirement for niacin and its relatively high dietary protein requirement appear to result from its high enzymatic activity and because it cannot change the quantities or activities of enzymes involved in the metabolic pathways. This evolutionary development has resulted in more-stringent nutrient requirements for cats than for omnivores. This pattern may also be common among other strict carnivores (ibid.).

FOODS AND FEEDING CONSIDERATIONS FOR CAPTIVE MAMMALIAN CARNIVORES

The form of diet is an important consideration for carnivores, because it can affect acceptability. Various forms of carnivore diets are available commercially. Each has its advantages and disadvantages.

Meat-based diets. Meat-based diets are commonly fed to captive mammalian carnivores. A primary ingredient in this type of diet is muscle. In and of itself, muscle is not properly balanced to meet the nutrient requirements of carnivores, and there have been many reports of diseases (e.g. rickets) associated with the use of muscle as the sole dietary component. In general, muscle is deficient in calcium and not appropriately balanced in several other essential nutrients.

In order to correct the inherent nutrient deficiencies of muscle when used as a food for mammalian carnivores, it is possible to supplement muscle with appropriate vitamins and minerals to achieve a nutritionally complete diet. This approach has been used successfully for many years. In some cases, it may not be practical to provide a nutritionally complete diet. In these cases, muscle meat supplemented with a multivitamin and mineral product is sufficient.

It is common practice to skip a day of feeding for large cats. This historical practice is presumably based on the observation that these large carnivores are sporadic eaters in their wild habitat. There are no reported data on the nutritional consequences of this practice in captivity.

Issues relating to safety and handling of meat-based diets are discussed later in the text (see Hancocks, chap. 11, this volume).

Manufactured meat-based diets. Manufactured meat-based diets comprise a variety of raw animal components (usually muscle, organs, and fat) supplemented with various other ingredients, such as vitamins and minerals (Lintzenich et al. 2006). Raw meat–based diets are highly perishable, which is why most of these diets are frozen. Proper handling—at the time of manufacture, during storage and thawing, and before feeding the thawed product—is critical to minimize the degree of microbial contamination.

It is not uncommon to find inconsistencies in the nutrient composition of manufactured meat-based diets. Variations in the amounts of muscle and organ tissue used in the mixes and their inherent variability in composition can lead to significant differences in nutrient profile. Diets that contain appreciable quantities of organ tissue tend to have greater nutrient variability than diets that contain large quantities of muscle.

While manufactured (e.g. extruded) diets are readily available for dogs and cats, these products have been used for larger carnivores (e.g. bears, large cats) with limited success.

While these diets may be palatable for smaller animals, acceptability by large cats generally has been poor.

Nutritionally complete, meat-based diets have been reported to exacerbate oral health problems of large carnivores. These products tend to be soft and sticky, adhere to the teeth, and promote accumulation of plaque and calculus. Multiplication of pathogenic oral bacteria in this medium favors development of gum disease (gingivitis). Offering knucklebones at least twice weekly is efficacious in reducing plaque and calculus buildup. It is important that the bones contain enough attached meat to stimulate their use.

Gel diets. Gel diets are high-moisture products formed with either a protein or a carbohydrate gel matrix containing a fixed set of nutrients. These diets have the advantages of nutritional flexibility and palatability. Gels have the same disadvantages as do other wet diets; they are highly perishable. Gel diets have been used for bears and may be particularly useful as treats or to provide medication.

Whole prey. Whole-prey animals that are properly managed before being fed can be acceptable and complete sources of nutrients for carnivores that eat prey as part or all of their diet. Rodents, lagomorphs, poultry, and fish are the most common whole vertebrate prey, although lizards, snakes, and invertebrates also are fed. Unlike invertebrates, vertebrate prey composition is similar across species and more commonly reflects the nutrient needs of the consumer. Nevertheless, both vertebrates and invertebrates must be appropriately handled to maintain their nutritional integrity.

Mice and rats of various ages are suitable food for many mammalian carnivores. When properly handled, these prey items can meet the nutrient needs of the predator. In general, body composition changes over time, with younger animals (pinkies and pups) having a greater proportion of water and protein than older animals (table 9.5). As animals age, there is a reduction in the lean body mass and a concomitant increase in body fat.

Fish. As with other vertebrate prey items, fish can be a nutritionally complete source of food for many piscivorous captive mammals. Animals fed diets that are solely or primarily fish are typically provided dead fish that have been frozen. Providing fish can lead to logistical and nutritional challenges. Generally, diets that consist of a single species of fish are unlikely to provide appropriate composition and levels of all nutrients. Similarly, a single diet will not serve all piscivorous mammals' needs. Proper storage and handling of fish are particularly important in maintaining quality. Storage and thawing of frozen fish should be monitored carefully to reduce deterioration of their nutritional value through oxidation of amino acids and unsaturated lipids. A detailed discussion of quality standards is provided in a subsequent chapter (see Henry, Maslanka, and Slifka, chap. 10, this volume).

TABLE 9.5. Average nutrient composition of pinkie mice (dry-matter basis)

Nutrient	Pinkie mouse
Dry matter (%)	24.2
Crude protein (%)	60.8
Crude fat (%)	22.4
Total carbohydrate (%)	6.7
Ash (%)	10.0
Calcium (%)	2.98
Phosphorus (%)	1.68
Sodium (%)	0.48
Magnesium (%)	0.10
Potassium (%)	1.01
Iron (ppm)	387
Copper (ppm)	24.0
Zinc (ppm)	85

Source: Baer and Associates, LLC (unpublished data).

Insects. Feeding invertebrates to mammals in captivity creates a common and interesting nutritional problem, which can be easy to correct. The exoskeleton of invertebrates that are generally fed to captive mammals is much different from the endoskeleton of mammals. A major mineral constituent of the mammalian endoskeleton is calcium. Dietary calcium is essential for proper bone formation in mammals as well as for many other physiological functions. The exoskeleton of insects contains a very low concentration of calcium, as does the whole insect body (table 9.6). Thus, when insects are fed to mammals, the amount of calcium (and other nutrients) is too low to meet nutritional requirements. Bone abnormalities (e.g. osteomalacia and rickets) are a common consequence of feeding insects to mammals. Dusting insects with calcium salts (e.g. calcium carbonate) has been one approach used to increase their calcium content. However, this approach is not the most efficacious. Gut-loading calcium is more consistently effective. Gut-loading is accomplished by adding a relatively high concentration of calcium (and other nutrients) to the diet of the insect. After 2 to 3 days of feeding this diet to the insects, the nutrients in their gastrointestinal tract are of a sufficient concentration to correct the inherent deficiency of the insect body. Thus, a nutritionally complete and appropriately balanced nutrient "package" is available for consumption.

One notable exception among commonly used invertebrates is the earthworm. In circumstances where earthworms are consuming calcium-rich soils, the calcium content of the

TABLE 9.6. Nutrient composition of crickets and crickets fed a complete insect diet (dry-matter) basis

	Dry matter (%)	Crude protein (%)	Crude fat (%)	Total carbohydrate (%)	Ash (%)	Calcium (%)	Phosphorus (%)
Crickets	31.0	64.9	13.8	15.6	5.7	0.14	0.99
Crickets, complete diet	30.3	65.2	12.6	12.4	9.8	0.90	0.92

Source: Baer and Associates, LLC (unpublished data).

whole earthworm may be sufficient to meet the calcium requirement of mammalian species.

Another notable variation in insect composition is that of fat. The fat content of several commonly used invertebrates differs widely. Waxworms tend to contain the greatest amount of fat, whereas crickets tend to contain the least amount. If managing the body weight or condition of a mammalian species is a goal, then altering the type of invertebrate used for feeding may be helpful in achieving a desirable body weight.

NUTRITION-RELATED DISEASES

Urolithiasis. Urolithiasis is described earlier in this chapter (see under the "Nutrition-Related Diseases" heading of the Herbivore Nutrition section). The most common uroliths in domestic canids are struvite, calcium oxalate, and urate; cystine, silica, calcium phosphate, and xanthine are less common. Prevention of struvite uroliths requires control of urinary infections, and reduction of urinary magnesium, phosphate, and pH (struvite is more soluble at ≤ pH 6.5) with diet. Several breeds of dogs show a genetic predisposition to calcium oxalate stones, and diets that are lower than average in oxalate, protein, and sodium and that maintain urine pH at 6.5–7.5 appear to be helpful. The incidence of ammonium urate stones in dogs with this predisposition is reduced by feeding lower-protein, lower-purine diets, thus decreasing urinary ammonium and urate output to levels unlikely to induce flocculation. Cystine uroliths form in dogs that have a defect in renal tubular reabsorption of cystine and certain other basic amino acids. The poor solubility of cystine in acidic urine leads to cystine crystalluria and urolithiasis. This appears to be an inherited problem in some breeds of dogs, with clinical signs primarily in males. Prevention involves dietary protein reductions and urinary alkalinization. (See also the discussion of cystinuria in maned wolves below, under the Cystinuria heading of the Omnivore Nutrition section.) Silica stones are occasionally seen in older dogs of many breeds, although the role of diet is unclear. Since plants often contain abundant concentrations of silica, prevention involves reduction of plant protein sources, induction of diuresis, and treatment of urinary tract infections, if present.

The most common uroliths in domestic felids are calcium oxalate and struvite. Magnesium may inhibit calcium oxalate formation; thus, the reduction of magnesium in urine-acidifying diets used to prevent struvite urolithiasis may result in some increase in calcium oxalate uroliths. Struvite uroliths tend to be one of 3 types: amorphous uroliths with unusually large amounts of organic matrix, sterile uroliths associated with dietary ingredients that tend to be urine alkalizing, and uroliths associated with urinary tract infections by urease-producing bacteria.

Urolithiasis has been reported in several species of mustelids (Petrini et al. 1996). Struvite is the most common type in mink and ferrets, and a narrow or slightly inverse dietary-calcium-to-phosphorus ratio may be helpful in prevention (Edfors, Ullrey, and Aulerich 1989). Uroliths reported in Asian small-clawed otters, *Aonyx cinerea*, are primarily calcium oxalate or urates (Calle 1987; Petrini et al. 1996). Bilateral uric acid nephrolithiasis has been reported in a free-ranging river otter, *Lontra canadensis*, from the Skagit River of western Washington (Grove et al. 2003).

Taurine deficiency. Taurine is involved in fetal development, growth, reproduction, neuromodulation, sight, hearing, cardiac function, osmoregulation, disease resistance, and excretion of bile acids (Huxtable 1992). This amino acid is found in liberal quantities in the tissues of fish, birds, and small rodents but is rare in plants. The domestic cat has been shown to require taurine in its diet (Hayes, Carey, and Schmidt 1975), as has the fox (Moise et al. 1991). Deficiency signs appear when taurine is not supplied in adequate amounts. Most domestic dogs appear to be able to synthesize taurine from sulfur amino acids, assuming dietary concentrations are sufficient and bioavailable (Backus et al. 2003). There are breed differences in this regard, and some breeds of dogs have exhibited clinical signs of taurine deficiency, including dilated cardiomyopathy, bilaterally symmetrical hyperreflective retinal lesions (similar to feline central retinal degeneration), and poor reproduction (NRC 2006).

Dilated cardiomyopathy with clinical signs of progressive exercise intolerance and dyspnea, apparently associated with taurine deficiency, also has been reported in giant anteaters, *Myrmecophaga tridactyla*, fed a commercial dog diet (Wilson et al. 2003). Maned wolves, *Chrysocyon brachyurus*, fed diets limited in protein and sulfur-amino acids exhibited plasma taurine levels more than 20 times less than the normal canine reference range (60–120 nmol/ml) (Childs-Sanford and Angel 2004). Taurine deficiency has not been confirmed in bears, but necropsy reports on captive animals include some signs generally consistent with such a deficiency (Griner 1983).

Because dog diets are commonly fed to omnivorous bears, inadequate concentrations of taurine and/or biologically available sulfur amino acids may limit reproductive success, lessen disease resistance, impair visual and auditory acuity, and damage the heart. If individuals within the single dog species differ in their ability to synthesize taurine, it is possible that such differences might exist among species of bears. The hepatic enzymes required to metabolically convert sulfur amino acids to taurine are cysteine dioxygenase and cysteine sulfinic acid decarboxylase. It is presumed that this metabolic ability is unnecessary or largely has been lost in the cat and polar bear because dietary supplies of preformed taurine in wild prey are adequate. The more omnivorous diet of the dog and diets of omnivorous and herbivorous bears are likely to be limiting in taurine; thus, the ability to synthesize this compound from an adequate supply of dietary precursors may be critical, or alternatively, taurine may be required in the diet.

Thiamin deficiency. Lions, *Panthera leo*, fed diets of beef muscle supplemented only with calcium may exhibit signs of thiamin deficiency (Tanwar and Mittal 1984; DiGesualdo, Hoover, and Lorenz 2005). These include anorexia, along with episodic ataxia, weakness, recumbency, tonic-clonic movements of the front limbs, and convulsions. A lion exhibiting these signs had a measured whole blood thiamin concentration of 11 nmol/L, compared with a reference range of 59–226 nmol/L for domestic cats and a mean ± standard deviation of 249 ± 43.5 (range 160–350) nmol/L for 22 adult African lions fed presumably adequate diets in 10 North American zoos (Hoover and DiGesualdo 2005). The clinical signs resolved completely after 9 days on a nutritionally complete diet and administration of an oral thiamin supplement (3 mg/kg body weight/day).

Vitamin D and metabolic bone diseases. Solar irradiation may be responsible for the presence of vitamin D in forms of life from phytoplankton to humans (Holick 1989). Provitamin D_2, ergosterol, in molds, yeasts, senescent lower leaves of growing plants, and sun-dried cut forage is converted to vitamin D_2 by UVB irradiation. Provitamin D_3, 7-dehydrocholesterol, in the malpighian layer of the epidermis of human skin is converted to previtamin D_3 by UV irradiation in the range of 290–315 nm, with maximum conversion at 297 ± 3 nm (Holick et al. 1982).

Vitamin D_3, formed in the skin, is bound to D-binding protein (DBP), enters the circulation, and is transported to the liver, where it is converted to 25-hydroxycholecalciferol (25[OH]D_3; calcidiol). From there, 25[OH]D_3 is transported to the kidney, where it is converted to the principal active form, 1α,25-dihydroxycholecalciferol (1,25[OH]$_2D_3$; calcitriol), or to 24,25-dihydroxycholecalciferol (24,25[OH]$_2D_3$). If vitamin D_2 or vitamin D_3 are present in the diet, absorption has been shown to occur in the small intestine of rats, chicks, and certain primates, and is stimulated by bile acids and fat. Most of the absorbed vitamin D is associated with chylomicrons in the lymph, is transferred to DBP in the blood, and enters the metabolic pathways described above. Absorbed vitamin D_3 is ultimately converted to 1,25[OH]$_2D_3$, whereas absorbed vitamin D_2 is converted to 1α,25-dihydroxyergocalciferol (1,25[OH]$_2D_3$; ercalcitriol) or to 24,25-dihydroxyergocalciferol (24,25[OH]$_2D_3$). However, there are species differences in the absorption and metabolism of vitamins D_2 and D_3, and some species may not easily absorb orally presented vitamin D in either form.

Nutritional and metabolic bone diseases are common problems in many zoo animals, but identification of their cause may be quite difficult. When carnivores are fed muscle meat without bone, calcium intakes will be deficient, calcium-to-phosphorus ratios will be markedly inverse (approximately 1:20), and nutritional secondary hyperparathyroidism may result. Excessive vitamin A intakes from the consumption of liver may interfere with vitamin D metabolism, exaggerate bone remodeling, and increase the severity of skeletal changes.

There is developing evidence that some carnivores may have limited ability to use UVB light for cutaneous biogenesis of vitamin D. Skin from domestic dogs and cats had low concentrations of 7-dehydrocholesterol (10% that of rat skin), and UVB irradiation produced no cutaneous increases in vitamin D_3 concentration, compared with a 40-fold increase in rat skin (How, Hazewinkel, and Mol 1994). This and previous studies with intact dogs indicate that, unlike herbivores and omnivores, dogs and cats are unable to synthesize sufficient vitamin D in the skin and are dependent on a dietary source. Thus, for these species and perhaps some of their relatives, vitamin D fulfills the traditional definition of an essential nutrient rather than that of a hormone.

Oral disease. Large felines use their oral structures (mouth, teeth, tongue) to obtain and consume food in the wild much differently from the way they use them as they are fed and consume food in captivity. Although zoos cannot re-create a completely natural existence, there are points at which nature's ways can guide management in improving the quality of life for zoo animals (Lindburg 1988). Providing an adequate diet with appropriate nutrients can sometimes lead to a diet that ignores nonnutritive requirements to maintain oral health. Substitute activities, oral health in relation to food texture, and the psychological aspects of feeding have been reviewed (ibid.).

OMNIVORE NUTRITION

Omnivores are species whose teeth and digestive system are designed to eat a relatively concentrated diet of plant and animal matter, since unlike herbivores, they have no large sac or chamber for the fermentation of fibrous material. They are able to chew and digest meat; however, they do not have an absolute requirement for it unless there is no other practical source of vitamin B_{12} (cobalamin). Examples of omnivorous mammals include swine, skunks, coatimundis, raccoons, hedgehogs, many primates, and many bears. The lifestyle of many of these animals in their natural habitat necessitates a diet that is seasonally dependent. For example, animal dietary components are consumed certain times of the year, while plant components are consumed during other parts of the year, depending on when the food is plentiful.

FOODS AND FEEDING CONSIDERATIONS FOR CAPTIVE MAMMALIAN OMNIVORES

Manufactured diets. As with carnivore diets, there is a wide variety of diets manufactured for omnivores. Most of the commercially manufactured diets are delivered in an extruded form. In addition to commercial diets, domestic produce and browse are often used to augment captive omnivore diets.

Extruded diets. Extruded diets are manufactured using a technology that employs steam, compression, and friction to quickly pressure-cook the food. Most commercial pet foods are extruded products. Extruded diets are available in various sizes and shapes. They are typically less than 11% moisture, which allows for an extended shelf life.

Produce. Some of the highest food expenditures for institutions that maintain wild mammals are for produce (fruit and vegetables). These expenditures reflect the fact that fruit and vegetables have evolved to be a major dietary ingredient for many small mammal and primate diets.

The most commonly fed domestic produce items in zoos throughout the world are fruit, including apples and bananas, and vegetables, including potatoes, carrots, and leafy greens. Annual apple use alone can be greater than 9900 kg per year in a single institution. In 2002, the annual budget for apples in U.S. institutions holding captive wild animals reportedly ranged from $4000 to $11,000 (Crissey 2002).

An important point to consider when feeding produce is that the domestic varieties fed in zoos and other institutions

TABLE 9.7. Fiber composition of wild and domestic fruit consumed by mammals in their natural habitat and in captivity

Species	Fiber (NDF) content of wild fruit consumed (% dry matter)	Domestic fruit typically fed inU.S. facilities	Fiber (NDF) content of fruit (% of dry matter)
Alouatta palliata	50.8	Banana	5.4
Alouatta seniculus	53.8	Orange	18.1
Macaca fuscata	41.8	Apple	12.6
Papio anubis	37.2	Grape	8.5
Procolobus badius	62.2	Strawberry	22.5
Gorilla gorilla	33.7–64.6	—	—
Average	49.2	—	13.4

Source: USDA National Nutrient Database for Standard Reference, Release 22; and Baer and Associates, LLC (unpublished data).
Note: NDF denotes neutral detergent fiber.

are very different in nutrient composition from the fruit and vegetables eaten in the wild (table 9.7). Although the intent is to mimic wild diets and feeding behavior, feeding cultivated fruit to captive mammals bears little similarity to the natural diet and in many instances, if not used appropriately, can introduce nutrient imbalances. Comprehensive analytical data on nutrient composition of cultivated fruit are maintained by the U.S. Department of Agriculture and can be accessed through the Agricultural Research Service's USDA National Nutrient Database for Standard Reference, Release 22, Nutrient Data Laboratory Home Page, www.ars.usda.gov/ba/bhnrc/ndl.

Browse. Food and foraging for food are important for the psychological well-being of captive wild mammals. Food and nonfood items can be used in ways that stimulate natural feeding behaviors, extend feeding activity, and inhibit stereotypy (Knapka et al. 1995). Foraging enrichment can be used to disperse animals, occupy their time, and reduce tension and aggressive interactions (Boccia 1989) (see the detailed discussion of browse in the Herbivore Nutrition section above).

NUTRITION-RELATED DISEASES

Cardiovascular disease. Cardiovascular disease has been reported extensively in captive mammalian omnivores, is a general concern in captive primates, and has been identified as a significant cause of death in captive gorillas specifically (Allchurch 1993; Schulman et al. 1995; Miller et al. 1999). Hypertension, which can be related to diet, has been suspected in many deaths related to cardiovascular disease. While many dietary, behavioral, and genetic factors may initiate or influence the progression of cardiovascular disease, hypercholesterolemia is a major factor, as is the amount and/or character of fat in the diet. Primates on long-term hypercholesterolemic diets will develop coronary artery atherosclerosis. Many species of nonhuman primates have a diet-related susceptibility to atherosclerosis (National Academies 2003).

As with humans, the central obesity that occurs spontaneously in rhesus monkeys appears to confer increased cardiovascular-disease risk. Plasma cholesterol, triglycerides, and lipoproteins also play a role in cardiovascular disease. In obese insulin-resistant rhesus monkeys, an increase in plasma concentration of very-low-density lipoprotein cholesterol and triglycerides and a decrease in high-density lipoprotein cholesterol increase the risk of coronary heart disease (Hannah et al. 1991).

Converse to the contributions that obesity makes to cardiovascular disease, dietary restriction (undernutrition without malnutrition) appears to decrease risk of heart disease. In addition, dietary restriction has been shown to increase longevity (Lane et al. 1995a, 1995b).

Diabetes. Captive omnivores, specifically apes, can develop diabetes. Many primates (e.g. orangutans, and rhesus and Diana monkeys) have a propensity to become obese and to develop diabetes (Gresl, Baum, and Kemnitz 2000). In some instances, dietary intervention can be a useful means to control blood sugar, especially for type 2 diabetes (previously referred to as non–insulin-dependent diabetes mellitus or adult-onset diabetes). In type 2 diabetes, the body produces insulin (and sometimes in very high concentrations), but the cells are resistant to the insulin's intended action (to move sugar from the blood into the cells); consequently, the sugar concentrates in the blood. Sugar is lost through the urine, which is the clinical basis for the diagnosis of diabetes, when blood sugar becomes sufficiently high. In addition, the high blood-sugar concentration can have serious effects on many physiological functions and systems, particularly those related to the cardiovascular system, renal system, and eyes.

Historically, avoidance of sugar and foods high in sugar (including fruit) was the recommended approach to control diabetics. More recently, a goal to control diabetes has shifted away from avoiding sugar to eating foods that minimize the insulin response, known as the glycemic index. A method related to glycemic index for evaluating foods is the glycemic load. Some foods, including fruit, have relatively low glycemic indexes (or loads). For example, apples, oranges, and pears have glycemic indexes of about 30. Bananas have a glycemic index of about 46. Potatoes (including sweet potatoes) have a glycemic index ranging from the mid-40s to 100. Dried fruit such as raisins and dates have high glycemic indices. Thus, some fruit, such as apples and oranges, may have less of an impact on blood-sugar concentration than potatoes.

Another dietary component that can improve blood-sugar control is soluble fiber. Soluble fibers are also termed beta-glucans, and can be found in certain whole grains such a barley and oats. Other sources of soluble fiber include commercially available products, which are odorless, tasteless, and highly soluble in aqueous solutions.

Immunodeficiencies. Nutrition has a major influence on immunological function (Klasing 2005). Several key nutrients affect cell-mediated (humoral) and T-cell-mediated (cellular) immune functions. Even the interaction of the immune systems can be influenced by deficiencies or excesses of dietary constituents. In experimental systems where it is possible to control precisely the influence of specific nutriments, development and expression of autoimmune diseases and the associated immunodeficiencies of aging can be delayed by restrictions of dietary protein, protein and calories, fat, zinc, or even essential fatty acids (Hansen 1982). Tumor immunities also can be affected by restriction of protein, calories, or protein and calories, an influence associated with delays in development of experimental cancers. T-cell-mediated immunodeficiencies associated with protein or protein-calorie malnutrition are often attributable not to a protein or energy deficiency, but rather to the accompanying zinc deficiency, which reflects the vital role of zinc in many immunological functions. Dietary zinc deficiency appears to be responsible, at least in part, for a whole host of immunodeficiencies. Many other nutrients are important in maintaining proper immune system function; selenium, vitamin D, vitamin E, and the B vitamins all play roles in preventing immunodeficiencies.

Iron-storage disease (hepatic iron overload). Although iron is an essential nutrient and a requirement for normal cellular physiology, excessive intestinal absorption of iron—as seen in hemochromatosis—leads to its deposition in parenchymal cells of various organs such as the liver, heart, and pancreas, resulting in cellular toxicity, tissue injury, and organ fibrosis. Cellular injury is induced by iron-generated oxyradicals and peroxidation of lipid membranes. In the liver, lipid peroxidation results in damage to hepatocellular organelles, such as mitochondria and lysosomes, which is thought to contribute to hepatocyte necrosis and apoptosis, and ultimately lead to the development of hepatic fibrogenesis (Brunt 2005). Hepatic stellate cells are central to the development of hepatic fibrosis, as they can be transformed into collagen-producing myofibroblasts. Numerous potential stimuli associated with hepatic iron overload and iron-induced hepatocellular injury have been assessed in an attempt to explain stellate cell transformation in hemochromatosis. Stellate cell activation and fibrosis appear to be regulated by a series of events involving cellular interactions between resident and nonresident cells of the liver, the sequestration of free iron versus the transport and storage of mobilizable iron, and extracellular matrix remodeling, as well as intracellular signaling events associated with inflammatory and fibrogenic cytokines.

Iron storage disease in lemurs was reported as early as the 1960s, and in the 1980s was demonstrated to be a consistent finding in postmortem exams of captive lemurs. Following preclinical screening, the preventive effects of dietary intervention on iron absorption were quantified in 23 individual lemurs of 4 species, using the transferrin saturation test (%TS). Dietary iron and vitamin C levels were reduced, and dietary levels of iron-chelating tannins and/or phytates were increased. After retesting, a matched-pair comparison of %TS values before and after the diet change revealed significantly ($P = 0.038$, $n = 7$) lower %TS values afterward. All species averages were in the human hyperabsorption range on conventional zoo diets ($n = 21$). No species averages were in that range after the dietary change ($n = 18$).

The role of liver biopsy in all chronic liver diseases continues to evolve with the emergence of new laboratory and imaging tests. However, the value of histologic examination for fibrosis, parenchymal architectural remodeling, and possible concurrent disease remains relatively unchallenged, including in human patients with suspected iron overload. In addition, only histologic evaluation allows detailed analysis of cellular and acinar localization of iron. Routine use of an iron stain for all liver biopsy analyses enables detection of iron when not otherwise suspected. The broad classifications of iron overload include parenchymal ("primary") or reticuloendothelial ("secondary"), and mixed. These classifications, however, serve only as guidelines to differential diagnoses.

Vitamin D deficiency and metabolic bone disease. A general overview of vitamin D is provided in the Nutrition-Related Disease heading under the Carnivore Nutrition section above. With regard to omnivores, some research on vitamin D deficiency and numerous practical observations of metabolic bone disease have been documented in primates. Primates in captivity have exhibited rickets or osteomalacia on numerous occasions (Vickers 1968; Miller 1971; Ullrey 1986; Allen, Oftedal, and Horst 1995; Morrisey et al. 1995). Terms used for the syndrome include "simian bone disease," "woolly monkey disease," and "cage paralysis." It has been reported more often in young primates than in mature animals, and in platyrrhines (New World primates) more often than in catarrhines (Old World primates). Some have proposed that this difference is a consequence of a higher vitamin D requirement in New World primates or of a limited ability to use vitamin D_2 (Hunt, Garcia, and Hegsted 1966); however, the suggestion that it is a failure of conversion of vitamin D_2 to vitamin D_3 is not consistent with known metabolic pathways.

Relatively few of the extant New World and Old World primate species have been studied; however, evidence that vitamin D_2 is less active than vitamin D_3 for the studied New World primates is convincing. For example, Lehner et al. (1967) found that growing squirrel monkeys, *Saimiri sciureus*, fed no vitamin D or vitamin D_2 at 1250, 2500, 5000, or 10,000 IU/kg diet grew poorly and showed evidence of rickets. In contrast, squirrel monkeys fed vitamin D_3 at 1250, 2500, 5000, or 10,000 IU/kg diet grew equally well and did not show evidence of rickets. Suggestions that New World primates, as a group, have unusually high dietary vitamin D_3 requirements are not supported by published research. Until controlled studies demonstrate elevated requirements in individual primate species or groups of species, the narrow margin of safety of vitamin D in diets for humans (NRC 1989a) and many other species (NRC 1987) argues against excessive use.

An attempt has been made to establish serum norms for 25[OH]D in cotton-top tamarins so that incipient vitamin D deficiency might be detected before the appearance of clinical pathology (Power et al. 1997). Blood was collected from 18 wild cotton-top tamarins in Colombia, South America, and the mean serum concentration of 25[OH]D was 76 ng/ml with a range of 25–120 ng/ml. Power et al. (1997) suggested that their data and those of Shinki et al. (1983) and Yamaguchi et al. (1986) infer a high probability of acute bone problems in captive common marmosets when serum 25[OH]D concentrations are below 20 ng/ml.

The range of serum 25[OH]D values reported by others in captive callitrichids is very wide, with a concentration as high as 600 ng/ml in a common marmoset (Yamaguchi et al. 1986). Fivefold higher plasma 1,25$[OH]_2D_3$ concentrations have been reported in a New World species than in an Old World species, and an end-organ resistance to this hormone has been inferred (Adams et al. 1985; Shinki et al. 1983).

It is common for captive New World primates to be fed much higher dietary vitamin D_3 levels than are Old World primates. Marmosets and tamarins are often fed commercial diets containing 7000–22000 IU vitamin D_3/kg dry matter. Whether such high values are necessary needs to be established. High vitamin D levels may produce signs of hypervitaminosis D in Old World primates (Knapka et al. 1995) and frank toxicity in pacas, *Cuniculus paca*, and agoutis, *Dasyprocta leporina*, that consume primate diets dropped on the floor of multispecies exhibits containing New World primates (Kenny et al. 1993).

Cystinuria. Cystinuria is a disorder caused by a defect in the transport of the amino acid cystine in the kidney tubules. Normally, cystine that is filtered in the kidney is reabsorbed within the tubules, resulting in only a small amount of cystine in the urine. Animals with cystinuria do not properly reabsorb cystine (and a few other amino acids) in the kidney tubules, causing the urine to contain abnormally high levels of cystine. Because cystine is insoluble in acidic urine, excess urinary cystine results in formation of cystine crystals, which in turn can lead to formation of cystine calculi (stones) in the kidney and/or bladder.

Cystinuria appears to be an inherited defect in several breeds of domestic dogs (e.g. Newfoundlands, Labrador retrievers, Australian cattle dogs, English bulldogs, Scottish deerhounds, dachshunds, Tibetan spaniels, and basset hounds) (Case et al. 1992). Normal dogs reabsorb about 97% of filtered cystine, but affected dogs reabsorb much less and may even exhibit net cystine excretion. A urine cystine concentration of .75 mg/g creatinine is likely to lead to cystine urolithiasis. Cystine solubility increases with increasing urine pH; dogs fed meat-based diets tend to excrete acidic urine, leading to urine cystine supersaturation (Kahn and Line 2005).

Cystinuria has been reported in the maned wolf, *Chrysocyon brachyurus* (Bovee et al. 1981). In the wild, the diets of maned wolves vary appreciably in proportions of vegetable and animal matter, depending on location, but include small rodents, birds, armadillos, invertebrates, fruit (particularly *Solanum lycocarpum*), herbs, and grass (Nowak 1999). The proportions of vegetable matter tend to be considerably greater than in the diets of true wolves, such as *Canis lupus*.

In U.S. zoos, maned wolves have been historically fed diets consisting of red meat. European and Australian zoos exhibiting maned wolves have usually fed a diet more suitable for omnivorous canids. These zoos do not report morbidity from urinary tract obstruction as do U.S. zoos. Muscle meat has high concentrations of sulfur-containing amino acids that tend to result in low urinary pH concentrations (Kahn and Line 2005) which inhibit cystine solubilization.

Because of concern for cystinuria and cystine urolith formation, attempts have been made to limit cystine excretion by controlling sulfur amino acid intakes, using less animal protein, or restricting dietary protein concentration. However, when cystinuric dogs were fed diets that were protein restricted but containing sulfur amino acid concentrations recommended by American Association of Feed Control Officials (but no added taurine), taurine deficiency was observed (Sanderson et al. 2001). In addition, modifications of maned wolf diets to incorporate more plant protein sources have been associated with poor stool consistency. Loose, watery stools may predispose to soiling in the perineal area, dehydration, and poor nutrient absorption.

To limit the opportunity for cystine urolith formation, maintain normal taurine and iron status, and improve fecal consistency and palatability of diets fed to maned wolves, a revised dietary formulation has been tested with young adult beagles (Allen et al. 2004). This diet had good palatability, maintained body weight, produced normal stools, and supported normal metabolism in dogs while resulting in urine with a pH (6.98–7.37) favorable to the solubility of cystine.

Cystinuria is not a disease limited to canids. Cystinuria and cystine uroliths also have been reported in felids, including the caracal lynx, *Caracal caracal* (see Jackson and Jones 1979), and serval, *Leptailurus serval* (see Moresco, Van Hoeven, and Giger 2004).

CONCLUSIONS

Diets fed to wild animals in captivity should meet the nutrient needs of the animals and should take into account variability in digestive physiology and natural feeding behavior. That animals may select items from a broad array of foods in the wild should not be taken to mean that they must be offered a similar array of foods in captivity.

Given the differences in nutrient composition between domestic produce and plants eaten in the wild and those between farm-raised and wild prey items, together with our limited understanding of the factors affecting food choice in the wild, it is difficult if not impossible to replicate the natural diet. A more practical approach is to provide a diet that will meet estimated nutrient requirements.

Providing appropriate quantities and quality of required nutrients is critical to avoid nutrition-related diseases. Many diseases observed in captive wildlife are the result of dietary nutrient deficiencies; the animal's inability to synthesize, transport, or metabolize specific nutrients; and excessive dietary intake or absorption of nutrients. With careful consideration of nutrient needs and potential impacts of dietary nutrients and their interactions, appropriate diets and feeding regimes can be used successfully to maintain wild animals in captivity.

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10

Quality Control Aspects of Feeding Wild Mammals in Captivity

Barbara Henry, Michael Maslanka, and Kerri A. Slifka

INTRODUCTION

All facilities involved in the feeding of wild mammals in captivity should strive to ensure that the food fed to their animals is safe and of the highest quality possible. This chapter deals with those elements that are essential to providing high-quality, safe food. Addressing food safety through a Hazard Analysis Critical Control Point (HACCP) program is an effective method, which we outline here. We address physical, chemical, and biological food-related hazards and offer as guidance quality-control standards for meat, fish, whole prey, hay, pelleted and extruded feeds, produce, and canned foods. This chapter also covers proper food- and feed-handling practices from the producer to the consumer. Finally, we provide suggestions for appropriate product specifications, analysis, evaluation, and follow-up that provide checks and balances for a successful and safe food system.

FOOD SAFETY

Food safety involves controlling all aspects of physical, chemical, and biological hazards. The HACCP system is a preventive measure that assists in identifying food-safety hazards and establishes monitoring procedures. The principles of HACCP apply to all aspects of food production and presentation. An HACCP program provides the outline and approaches to follow for proper handling of all foods.

GENERAL HANDLING PRACTICES

The following guidelines, among others, are tools in the proper handling of foods used in captive animal facilities: *Handling Fish Fed to Fish-Eating Animals: A Manual of Standard Operating Procedures* (Crissey 1998), *Handling Frozen/Thawed Meat and Prey Items Fed to Captive Exotic Animals* (Crissey, Shumway, and Spencer 2001), *Considerations for Meat Diets Fed to Zoo Animals* (Lintzenich, Slifka, and Ward 2004), *Microbiological and Temperature Evaluation as Part of a Comprehensive Raw Meat Quality Control Program* (Maslanka and Ward 2005), *Guidelines for Creating Food Safety HACCP Programs in Zoos and Aquaria* (Schmidt, Travis, and Williams 2006).

HAZARD ANALYSIS AND CRITICAL CONTROL POINT SYSTEMS AS A GUIDE FOR FOOD QUALITY CONTROL

HACCP programs help ensure that food items are handled appropriately, from the point of harvest or collection through consumption. HACCP requires that producers, manufacturers, and handlers identify and control for hazards within their food-handling process. HACCP programs monitor the entire process in a stepwise fashion in order to (1) detect potential hazards or risks within the system (what are the hazards?), (2) identify critical control points (CCPs) in the process (where are the hazards?), (3) establish critical limits (at what point do the hazards become health risks?), (4) establish CCP monitoring procedures and protocols, (5) establish methods of record keeping, and (6) find ways to verify the methods of monitoring. The HACCP program is used to maintain adequate food service sanitation in human food preparation operations, and is readily adaptable to any and all food-handling operations. An example of the logical flow of key CCPs within a system is shown in figure 10.1.

Facilities feeding captive wild animals should establish and maintain their own HACCP programs as well as ask their vendors/suppliers to share the HACCP programs they have in place for the food items they distribute to captive animal facilities (Maslanka et al. 2003). HACCP programs that are in place from the initial step in handling the food item through the time the item is offered to the animal help ensure the maintenance of the best-quality ingredients throughout the entire process, thus yielding the best-quality diets. Table 10.1 provides some of the questions to be considered in developing a HACCP system. Additional considerations, specific to food types included in captive mammal diets, will be included in the following sections.

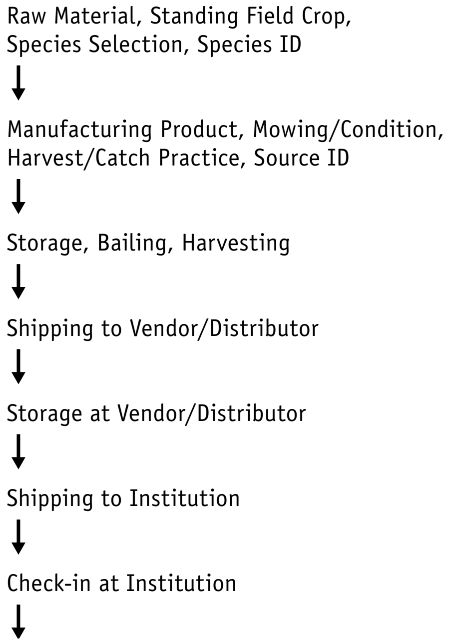

Fig. 10.1. Critical control points flow chart.

NUTRIENT ANALYSES, EVALUATION, AND FEEDBACK

Nutrient analyses are an integral part of a quality control program designed to ensure the nutritional value and monitor the nutrient composition of food items offered to all animals in captivity (Bernard and Dempsey 1999). A critical part of the quality control program should be to establish which food items should be analyzed, thorough evaluation of the analysis, and feedback on the product. Bernard and Dempsey (ibid.) outlined general guidelines for quality control of feedstuffs used in zoos, which can be applied to other types of animal holding facilities. The authors discuss identifying feeds for analysis, choosing analyses to be performed, selecting a representative sample, protocols for the sampling of different food items, and choosing a laboratory.

FOOD-RELATED HAZARDS

Food-related hazards can be physical, biological, or chemical. Each type of hazard represents unique challenges.

PHYSICAL HAZARDS

Physical hazards are foreign bodies in the food. They can be introduced into the feed at manufacture or harvest (e.g. objects in hay, manufacturing parts in a bagged feed, plastic), or they can be introduced at the preparation or feeding point (e.g. glass from a broken lightbulb, peeling paint, plastic bag). These items can injure the mouth or gastrointestinal tract or cause a blockage. Food should always be examined for foreign bodies during preparation and before feeding.

BIOLOGICAL HAZARDS

Biological hazards include any of the microorganisms that commonly cause foodborne illness, which captive animals may be exposed to through contaminated food or water (Fowler 1986). Foodborne illnesses are most commonly recognized as diseases that are caused by bacterial infections such as *E. coli*, *Salmonella*, *Streptococcus*, *Listeria*, and *Campylobacter*, or by a group of viruses called calicivirus (e.g. Norwalk virus). Diarrhea and vomiting are common results, which may or may not be identified as a foodborne illness. Most can be avoided with proper food-handling practices. Most *E. coli* infections result in vomiting and diarrhea (possibly bloody). *Salmonella*, commonly found in raw poultry products, can result in gastroenteritis, septicemia, and death (Quinn et al. 1994). Lewis, Bemis, and Ramsay (2002) showed a reduction in *Salmonella* shed in the feces of captive felids when fed a diet that contained minimal salmonella contamination. Neonatal mortality was reduced dramatically when improved slaughter, transport, and handling measures were instituted in a captive population of South African cheetah, *Acinonyx jubatus* (Venter et al. 2003). *Streptococcus zooepidemicus* is found in the mucous membranes of most animals and in high numbers on skin, and in the oral cavity and respiratory tract of equids. *Streptococcus* can cause disease ranging from localized to general infection and death and is frequently reported in animals which are fed uncooked horsemeat, but are not members of the order Carnivora. *Listeria*, in its most serious form, can cause meningitis and septicemia, and in pregnant women can lead to abortion, stillbirth, or delivery of an acutely ill infant. *Campylobacter* can cause severe diarrhea as well as central nervous system infections.

Some common diseases are occasionally foodborne, even though they are usually transmitted by other routes. These include infections caused by *Shigella*, hepatitis A, and the parasites *Giardia lamblia* and *Cryptosporidia*.

Some foodborne diseases are caused by the presence of a toxin that is produced by a microbe in the food. For example, the bacterium *Staphylococcus aureus* can produce a toxin that causes intense vomiting. Botulism occurs when the bacterium *Clostridium botulinum* produces a powerful paralytic toxin in foods. These toxins can produce illness even if the microbes that produced them are no longer present in the food. Proper manufacturing, thawing, and handling will reduce the potential for foodborne disease.

THE CHANGING NATURE OF FOODBORNE ILLNESS

The spectrum of foodborne diseases has changed over the years. It continues to change as a result of our food production and handling practices, transport and importation of a wider variety of foods, and the range of potentially disease-susceptible mammals that we maintain in captivity. Once common foodborne illnesses, tuberculosis and cholera, have almost been eliminated through improvements in food safety, such as pasteurization of milk, canning, and disinfection of water supplies. Today other foodborne infections have taken their place, including some that have only recently been recognized as serious threats, such as bovine spongiform encephalopathy (BSE).

TABLE 10.1. Examples of questions to be considered when conducting a hazard analysis

Developing a hazard analysis system requires asking a series of questions that are appropriate to the process under consideration. The purpose of the questions is to assist in identifying potential hazards.

A. Ingredients

1. Does the food contain any sensitive ingredients that may present microbiological hazards (e.g. *Salmonella, Staphylococcus aureus*); chemical hazards (e.g. aflatoxin, antibiotic, or pesticide residues); or physical hazards (e.g. stones, glass, metal)?
2. Are potable water, ice, and steam used in formulating or in handling the food?
3. What are the sources (e.g. geographic region, specific supplier)?

B. Intrinsic factors: Physical characteristics and composition (e.g. pH, fermentable carbohydrate, water activity, preservatives) of the food during and after processing

1. What hazards may result if the food composition is not controlled?
2. Does the type of food allow for survival or multiplication of pathogens and/or toxin formation in the food during processing?
3. Will the food permit survival or multiplication of pathogens and/or toxin formation during subsequent steps in the food chain?
4. Are there other similar products in the marketplace? What has been the safety record for these products? What hazards have been associated with the products?

C. Procedures used for processing

1. Does the process include a controllable step that destroys pathogens? If so, which pathogens?
2. If the product is subject to recontamination between processing (e.g. cooking, pasteurizing) and packaging, which biological, chemical, or physical hazards are likely to occur?

D. Microbial content of the food

1. What is the normal microbial content of the food?
2. Does the microbial population change during the normal time the food is stored before consumption?
3. Does the subsequent change in microbial population alter the safety of the food?
4. Do the answers to the above questions indicate a high likelihood of certain biological hazards?

E. Facility design

1. Does the layout of the facility provide an adequate separation of raw materials from ready-to-eat foods like fruits and vegetables?
2. Is the traffic pattern for people and moving equipment a significant source of contamination?

F. Equipment design and use

1. Will the equipment provide the time-temperature control that is necessary for safe food?
2. Is the equipment properly sized for the volume of food that will be processed or stored?
3. Can the equipment be sufficiently controlled so that the variation in performance will be within the tolerances required to produce a safe food?
4. Is the equipment reliable or is it prone to frequent breakdowns?
5. Is the equipment designed so that it can be easily cleaned and sanitized?
6. Is there a chance for product contamination with hazardous substances; (e.g. glass, chemicals)?
7. Are any product safety devices used to enhance consumer safety?
   - metal detectors
   - magnets
   - sifters
   - filters
   - screens
   - thermometers
   - bone removal devices
8. To what degree will normal equipment wear affect the likely occurrence of a physical hazard (e.g. metal) in the product?
9. Are allergen protocols needed in using equipment for different products?

G. Packaging

1. Does the method of packaging affect the multiplication of microbial pathogens and/or the formation of toxins?
2. Is the package clearly labeled Keep Refrigerated or Keep Frozen if this is required for safety?
3. Does the package include instructions for the safe handling and preparation of the food by the end user?
4. Is the packaging material resistant to damage, thereby preventing the entrance of microbial contamination?
5. Are tamper-evident packaging features used?
6. Is each package and case legibly and accurately coded with date of manufacture?
7. Does each package contain the proper label?
8. Are potential allergens in the ingredients included in the list of ingredients on the label?

TABLE 10.1. continued

H. Sanitation
  1. Can sanitation have an impact on the safety of the food that is being processed?
  2. Can the facility and equipment be easily cleaned and sanitized to permit the safe handling of food?
  3. Is it possible to provide sanitary conditions consistently and adequately to assure safe foods?

I. Employee health, hygiene, and education
  1. Can employee health or personal hygiene practices have an impact on the safety of the food being processed?
  2. Do the employees understand the process and the factors they must control to assure the preparation of safe foods?
  3. Will the employees inform management of a problem that could have an impact on the safety of food?

J. Conditions of storage between packaging and the end user
  1. What is the likelihood that the food will be stored at the wrong temperature?
  2. Would improper storage lead to a microbiologically unsafe food?

K. Intended use
  1. Will the food be manipulated, washed, or further processed by the keeper staff? By the animal?
  2. Are the amounts offered adequate? Will there likely be waste?

L. Intended consumer
  1. Is the food intended for mixed-species exhibits?
  2. Is the food intended for consumption by a population with increased susceptibility to illness (e.g. the young, the aged, and the infirm, immunocompromised individuals)?
  3. Is the food to be used for feeding off or on exhibit where exposure to environmental elements might be a factor?

Source: Adapted from U.S. Department of Health and Human Services Food and Drug Administration and U.S. Department of Agriculture. 1997. Hazard Analysis and Critical Control Point Principles and Application Guidelines Adopted August 14, 1997. National Advisory Committee on Microbiological Criteria for Foods.

Irradiation, while not a replacement for appropriate handling practices, has been utilized in both the human and pet food industries for the reduction of *E. coli*, *Salmonella*, and other foodborne pathogens. Pork, spices, fruit, and vegetables were approved by the U.S. Food and Drug Administration (FDA) for irradiation in 1986, followed by poultry in 1992, and most recently animal feed and feed ingredients (FDA 2001). Crissey et al. (2001) found that irradiation doses of 0.5–3.9 kilograys reduced most microbial populations in raw-horsemeat-based diets without affecting feed consumption or fecal consistency of captive exotic felids. While not commonly used in the zoo industry, irradiation provides another potential method for manufacturers to reduce microbial contamination in the food supply as well as extend shelf life.

CHEMICAL HAZARDS

Chemical hazards can result from residues due to improper or insufficient rinsing of sanitizers, cleaners used on surfaces that touch food, or chemicals stored above food preparation or storage areas (USDA 1999a). Improper labeling of containers, especially vitamins or minerals, can result in a chemical hazard because of toxicity from improper dosage or use of the wrong product. All items should remain in their original labeled container; however, if this is not possible, the container should be labeled with the full name of the product, including supplier/manufacturer, dosage/strength of the item, and expiration date. Pesticides and pesticide residues as well as environmental contaminants such as heavy metals may contaminate raw foods (e.g. produce, fish) or materials utilized in feed manufacture (e.g. grains). Regular testing is helpful in detecting these chemical hazards.

CONTAMINANTS, TOXIC AGENTS, AND ANTIBIOTIC RESIDUES

A variety of nonfood agents can affect the safety of the food supply. These include environmental contaminants, naturally occurring and synthetic toxic agents, and antibiotic residues. These 3 categories pose food safety risks.

Environmental contaminants. A variety of compounds, both organic and inorganic, can be found in feedstuffs, including industrial pollutants, pesticides, heavy metals, and radionuclides (van Barneveld 1999). Dioxins and polychlorinated biphenyls (PCBs) are examples of industrial contaminants. In the Netherlands in 2004, clay used in the potato-sorting process was the source of dioxin contamination in animal feed made with potato by-products, which affected 200 livestock farms in the Netherlands, Belgium, France, Spain, and Germany (Elliot 2004). Similar incidences occurred in Belgium in 1999 which affected poultry and eggs, and in the southern United States in 1997 which affected chicken, eggs, and catfish. Pesticide residues known to contaminate feeds include organochlorines, organophosphates, and pyrethroid compounds (van Barneveld 1999). Heavy metal (e.g. mercury, cadmium, lead) contamination can arise from the use of fishmeal in feeds, fertilizer application, or industrial pollution. The Chernobyl incident in 1986, an example of radionuclide pollution, caused the release of caesium-134 and caesium-137. Pastures and forages were contaminated, resulting in restriction on milk and sheep products (MAFF 1994). Environmental contaminants have an impact on both human and animal health by contaminating feed ingredients, which are then either consumed by the end user or consumed by livestock, where they enter the food chain.

Mycotoxins. Mycotoxins are secondary metabolites of fungi that can have a negative impact on animal health and productivity (D'Mello and Macdonald 1998). Contamination can occur in the field, during processing, and/or storage if conditions are right for spoilage. *Fusarium* mycotoxins can cause diseases of cereal crops (e.g. wheat, barley, corn) in the field, thus contaminating the feed produced with these grains. Aflatoxins are mycotoxins that can result from high moisture and temperature conditions during storage. Common feed ingredients affected include corn and corn products, peanuts, peanut products, tree nuts, and cottonseed products. In 2005, pet food manufactured in the eastern United States was contaminated with aflatoxins, prompting recalls in 23 states (www.diamondpetrecall.net). In most cases, regular testing of feed ingredients by manufacturers minimizes contamination from mycotoxins.

Plant toxins. Many plants contain compounds in their seeds or foliage that can have adverse effects on animals. Lectins, proteinase inhibitors, and cyanogens are sensitive to heat processing, while tannins, alkaloids, antigenic proteins, gossypol, saponins, and phytoestrogens are not. Their impact on animal health and productivity can range from reduced nutrient absorption and immune function to dysfunction of a variety of organ systems.

Antibiotic residues. Antimicrobials have been used at subtherapeutic doses by the meat industry as growth promoters and to enhance feed efficiency. In July 1998, the U.S. National Academy of Sciences, in a report prepared at the request of the U.S. Department of Agriculture (USDA) and the FDA, concluded that there is a link between the use of antibiotics in food animals, the development of bacterial resistance to these drugs, and human disease (NRC 1998). Resistant bacteria have been cultured from a variety of meats, including poultry, beef, and pork (White et al. 2001; Hayes et al. 2005), as well as from captive wild animals (Marrow et al. 2005). The American Medical Association adopted a resolution opposing nontherapeutic use of antimicrobials in animal agriculture (AMA 2001). In 2003, the FDA released a new guidance document (Guidance for Industry [GFI] #152, "Evaluating the Safety of Antimicrobial New Animal Drugs with Regard to Their Microbiological Effects on Bacteria of Human Health Concern") that outlines a comprehensive, evidence-based approach to preventing antimicrobial resistance which may result from the use of antimicrobial drugs in animals. Microbial resistance through food sources has the potential to have a serious impact on the health of captive wild animals.

Allergens. Reactions to ingested food can affect the body in many ways, including clinical signs of the skin, digestive system, respiratory system, and central nervous system (Wills 1992). True food allergies elicit an immunological response, while food intolerances are generally nonimmunological. Food intolerance is rare in domestic cats, but is the second most important cause of allergic dermatitis (ibid.; Guaguere 1996). More than 50% of the cases are caused by reactions to the proteins in beef, cow's milk, and fish; however, reactions to commercially prepared foods are regularly reported as well (Guaguere 1996). Fungal contaminants and chemicals in water have been cited as causes of food intolerances in dogs (Wills 1992).

Manufactured diets that contain cereal grains are standard diet ingredients for many captive mammals. Some animals may develop gluten-sensitive enteropathy (GSE) in response to proteins in cereals. Gliadin is the potentially toxic agent in gluten. Irish setter dogs exposed to cereal before one year of age were susceptible to damaging effects of gluten, while those maintained on cereal-free diets from weaning to adulthood did not develop GSE from later gluten exposure (Hall and Batt 1991). Medically significant levels of IgA-gliadin antibodies can be found in marmosets and tamarins whose diet contained cereal grain proteins (Schroeder et al. 1999; Gore et al. 2001). Effective January 1, 2006, the FDA required human food labels to state clearly if food products contain any ingredients with protein derived from the eight major allergenic foods. As a result of the U.S. Food Allergen Labeling and Consumer Protection Act of 2004, manufacturers must identify in plain English the presence of ingredients that contain protein derived from milk, eggs, fish, crustacean shellfish, tree nuts, peanuts, wheat, or soybeans in the list of ingredients or say "contains" followed by name of the source of the food allergen after or adjacent to the list of ingredients (www.fda.gov). There have been few studies of allergens conducted with captive wild mammals.

REGULATORY AUTHORITY

Recent developments in biosecurity in food and agriculture worldwide require integration and cooperation across different areas, including the government and private sectors. The U.S. government, for example, has implemented rigorous federal agency standards and voluntary industry guidelines that have improved food safety measures over the past 2 decades. The 3 branches of U.S. government—legislative, executive, and judicial—all have roles to ensure food and feed safety in the nation. Congress enacts statutes designed to ensure the safety of the food supply and that establish the nation's level of protection. The executive branch departments and agencies are responsible for implementation, and may do so by promulgating regulations. The judicial branch is responsible for enforcement of the standards. Additional details about U.S. regulations are included in appendix 10.1.

The European Parliament established the European Food Safety Authority in 2002 in order to increase consumer confidence in the food supply after a series of food scares in the 1990s (BSE, dioxins, etc). The European Union works with a number of organizations to ensure the overall safety of the food supply: World Trade Organization/Agreement on Sanitary and Phytosanitary Measures, Codex Alimentarius Commission, and the Convention on Biological Diversity and its Cartagena Protocol on Biosafety (FAO 2002). Within the EU, the Food and Veterinary Office is responsible for ensuring that legislation on food safety, animal health, plant health, and animal welfare is properly implemented and enforced.

PRIMARY CONCERNS ABOUT FOODS COMMONLY USED IN ZOOS AND AQUARIUMS

Food-handling practices. Proper food-handling practices are a complex interaction among people, places, and things. Some important aspects of acceptable food-handling practices include product tracking, food inspection, proper storage and preparation, and cross-contamination avoidance. Attention to the details involved in each of these aspects will ensure the best-quality products, from receipt through consumption by the target animal. Many of these practices are common among food groups, whereas others are food type specific.

Tracking products. Purchased products need to be tracked from the point of origin, whether from the grower (for produce) or from the raw ingredients (for a bagged food item; fig. 10.1). An outline for all the steps through receipt of the product could be (1) producer, grower, manufacturer, (2) shipper, hauler, transporter, (3) receiving and handling, (4) storage, (5) actual processing and preparation at the institution, (6) storage after processing and preparation at the institution, and (7) delivery and storage before feeding to animal. When dealing with any product, consistency in proper handling methods at each step is imperative. Outlining expectations and protocols, and sharing those with vendors, are good practices to ensure procurement of the best-quality product. We recommend a visit to the manufacturer to observe actual product, if feasible. At the very least, the manufacturer, vendor, or producer should be asked to delineate each step of the handling process.

Delivery and inspection. Delivery of a product should always be during business hours. Once the product arrives at the facility, the delivery vehicle should be examined for overall condition, cleanliness, and smell. Temperature records, if applicable (in the case of frozen foods), should be examined. Handling protocols and product specifications should be shared with the transport company so it can take an active role in maintaining product quality. Truck inspection guidelines should be established and a check sheet followed for each inspection. If the product is unacceptable, reject it. Once the product has been accepted, store it appropriately. The product should be stored to maintain a "first in, first out" rotation system. Labeling the products with the date received is the best practice to ensure adequate rotation.

Critical temperatures for storage. Standards for optimal storage temperatures are designed to help minimize nutrient loss and quality degradation of products during storage and processing (table 10.2). In the case of frozen storage, recommended temperatures of −30 to −18°C (Geraci 1978; Stoskopf 1986; Crissey, Allen, and Baer 1987; Shinaburger 1992; IDPH 1993; USDA 1999b 9 CFR 3.105) help to minimize oxidation and thiaminase activity. Derosier (1978) indicated that in the United States the commercial frozen storage temperature is −18°C, but lower temperatures may be better for prolonged storage. Refrigeration should be used for thawing or storing already thawed items for short periods only (USDA 1999b 9 CFR 3.105). Proper thawing technique includes maintaining the item(s) in a closed and sealed container at refrigeration temperatures. Refrigeration should be the only method used for thawing, as incorrect thawing may result in nutritive losses, lipid peroxidation (rancidity), microbial buildup, and loss of palatability. If more rapid thawing is needed, running cold water over an item in a closed and sealed container is acceptable. Food items should never be thawed at room temperatures. It is important to remember the temperature danger zone of 5–60°C (National Restaurant Association Education Foundation 1985), where bacterial growth rate is greatest, and strive to avoid this range of temperatures when handling diet items. According to the USDA, animal food and human food should be stored in separate refrigerators and freezers to avoid cross-contamination. Maintaining daily logs of both refrigerator and freezer temperatures is a good practice.

Food preparation. In general, safe food-handling practices include (1) washing hands before handling food, (2) using gloves when handling food, (3) washing gloves/hands between meat/fish and other food items, and (4) using clean and sanitized utensils. Cleaning and sanitizing are sequential steps, and cannot be achieved in a single step or in reverse order. *Cleaning* is defined as removal of gross visible filth from the surface of an item. *Sanitizing* is defined as the application of a chemical or manual agent designed to reduce or minimize surface bacteria to an acceptable level. A handling procedure outline should be established for diet items before, during, and after processing/preparation through to offering to and consumption by the animal. Equipment, including all utensils, cutting boards, food containers, and work surfaces, can harbor pathogens and should be cleaned and sanitized after use (Stoskopf 1986). The USDA states specifically for marine mammals that containers and utensils used for holding, thawing, or preparing food must be cleaned and sanitized after each feeding or at least once daily (USDA 1999b 9 CFR 3.105). It further states that all kitchens or other food-handling areas must be cleaned at least once daily and sani-

TABLE 10.2. Temperature guidelines for storage and processing of food items used in captive mammal diets

Product	Area	Temperature	Humidity
Meat/fish/prey	Freezer	−30 to −18°C	—
Produce	Refrigerator	7.2°C	—
Pelleted feeds	Dry storage	10°C	50%-60%
Canned foods	Dry storage	10 to 21°C	50%-60%

Note: Prolonged storage temperature guideline is −23°C. Optimal recommended refrigeration temperature range is 4 to 6°C.
— No guideline.

tized at least once weekly, a practice that should be followed in all food-handling areas. In addition, a safe practice is to treat any vehicles, carts, or transport containers in a similar fashion to food surfaces.

Cross-contamination. Cross-contamination is the transfer of harmful microorganisms from one food to another by means of a nonfood surface. Some examples of cross-contamination are (1) meat to cutting board to other food, (2) fish to hands to other food, and (3) meat to knife to other food. Cross-contamination may cause significant microorganisms to build up on unlikely surfaces before it becomes apparent. The best sanitizing step is use of a high-heat dishwasher (temperature above 71.2°C). However, there are guidelines for manual sanitation using chemicals. As outlined in the National Restaurant Association Education Foundation (1985), a sanitizing step may include one of the following: (1) 100 ppm (parts per million) chlorine solution for 20 seconds or 50 ppm for one minute, (2) an iodine solution 25 ppm for one minute, (3) 200 ppm quaternary ammonia for one minute, or (4) a detergent solution followed by disinfectant, following the correct contact time. After any sanitizing step, dishes should be either rinsed or allowed to air dry according to the specific application (heat or chemical). Dishes and utensils should not be towel dried.

Meat and whole prey: Purchasing, handling, and storage for quality. Dogs fed commercially available raw meat diets and the humans who prepare the diets are at a greater risk of foodborne illness (Strohmeyer et al. 2006). Generally, it is recognized that raw meat may be contaminated with microbes. Contamination is typically associated with handling and processing. Regulations are established for products manufactured for human consumption but not for pets or zoo animals; however, guidelines for products manufactured as raw meat foods for companion and captive noncompanion carnivores and omnivores are available from the FDA. This is only guidance; in the United States, no regulatory authority oversees bacterial contamination in such products.

The freshness and wholesomeness of the meat, the source of the prey item, and the history of processing should be determined when purchasing meat and prey to feed zoo animals. Any supplier used for meat products should have an effective quality assurance program, including. agreed-on specifications, auditing of suppliers, and Certificate of Analysis. Additionally, raw material or finished product specifications should include details of the identity of the manufacturer, a description of the raw materials, ingredients breakdown, absence of hazardous organisms, analytical/microbial sampling plan, labeling, storage/distribution conditions, safe handling/use instructions, and description of package type/size/quantity. Ideally, an inspection-site visit to the manufacturer to see handling and processing methods would ensure the best possible product. Since a visit to the manufacturer is not always possible, products should be inspected upon arrival to the institutions. The products should be delivered during business hours, inspected quickly, and stored immediately in the freezer. At minimum, open and examine at least 10% or a minimum of 3 packages in the front, middle, and end of the load. Look for evidence that the product may have been frozen, thawed, and refrozen. Evidence could include water or ice buildup on the boxes or floor and/or wrappings that are moist, slimy, or discolored. Inspection upon arrival also should include the truck in which the product is delivered. The truck should not include nonfood items, and the temperature in the truck should indicate frozen conditions.

Some institutions use meat that has not been frozen. These products should be handled similarly to thawed products. Thawed products should be kept iced or refrigerated until the time of feeding. A quality inspection should occur while handling thawed product before feeding, as quickly as possible to minimize contamination and microbial buildup. Utensils and surfaces used while preparing the product should be cleaned and sanitized following established and approved protocols.

Processes and procedures used with meat products should be validated and reviewed periodically. Sampling of the meat products should be done once a year at the minimum for nutritional analysis and microbial loads, although it would be ideal to have every shipment tested. A wide variety of lab facilities perform nutritional and microbiological analyses. It is critical to select a reputable lab facility to analyze samples (Bernard and Dempsey 1999).

Fish: Purchasing, handling, and storage for quality. Since daily food availability is crucial to any captive zoo program, most fish purchases are made in bulk, which requires the items to be frozen and stored until use. Given the perishable nature of fish, appropriate food-handling procedures are crucial to the nutritive quality of the food and consequently to the successful management and welfare of the animals (see also Joseph and Antrim, chap. 16, this volume).

The term *fish* is used throughout this chapter to mean all fish, including freshwater and saltwater fish, and other seafood items that may be fed to fish-eating animals. Types of fish selected for use by an institution are chosen for specific nutrient content, quality, availability, price, and animal preference. The nutrient value of fish varies considerably due to several factors: species differences, and individual differences due to season of capture, age, and sex (Stoskopf 1986).

Nutritional requirements of the animal and the quality of the fish must be considered major factors in fish selection. Food for captive marine animals must be of the highest quality. USDA regulations state that "food for marine mammals shall be wholesome, palatable, and free from contamination, and shall be of sufficient quality and nutritive value to maintain all of the marine mammals in a state of good health" (USDA 1999b 9 CFR 3.105).

Geraci (1978) emphasizes the need to feed more than one food type, including high- and low-fat fish, in order to help ensure a balanced diet. Uncertainties in the future availability of fish stocks, reliance on farmed fish, and the development of technologies such as a fish substitute for marine mammal diets make selection of appropriate fish and their handling of utmost importance. Such uncertainties and possibilities require an awareness and evaluation of the diets' nutritional content and quality.

To determine the freshness and wholesomeness of fish, the history of the catch should be ascertained and should include knowledge of precapture conditions. Epidemiological data such as local and periodic occurrences of pesticide and heavy metal pollution also are useful (Stoskopf 1986). The broker or fishery can be contacted for this information. Also, for information about current fish supplies, status, or contamination problems, newspapers and fisheries reports may be helpful. Additionally, request that a catch date be recorded on the boxes received to provide an indication of freshness of fish. The date can provide a link between the catch and environmental events that may have affected it. As conservation-minded institutions, zoos and related facilities should, to the best of their ability, base the selection of fish species used in animal diets on the status and sustainability of the species' wild populations.

In order to provide the best quality of food possible, all fish should be of the same quality as that intended for human use (USDA 1999b 9 CFR 3.105). Therefore, fish fed to animals should be supplied from fisheries that have caught, processed, and stored the fish as if they were intended for humans. The primary difference between fish for human use and those for captive fish-eating animals is that whole fish are usually fed to animals. Therefore, the product need not be deboned and cleaned of internal organs. The packaging of fish by a processor can play a significant role in fish quality. Fish must be packaged in plastic-lined boxes or plastic-impregnated boxes, with date of catch printed on the box. Fish may be block frozen, individually quick frozen (IQF), or in a shatter pack. The optimal size for packages should be 10 kg–20 kg, to allow for proper thawing. Stoskopf (1986) suggests that package size provide one day's supply without leftovers. The type and usage of fish also determines package size. Those fish used in smaller quantities should be purchased in smaller packages or should be prepared in a manner that allows for easy access to smaller quantities (by using IQF or shatter pack). Ideally, to ensure that fresh fish are handled appropriately throughout processing by the fisheries, the fisheries should be visited during processing and the fish inspected at that time. Since this may be impractical for most institutions, they should concentrate on a thorough inspection when the product arrives at the storage facility.

Inspection should occur at the place of receipt (storage site) before or possibly during unloading of the shipment, and a representative number of boxes examined. Inspectors should be one of the institution's employees familiar with proper inspection techniques and fish quality. A thorough inspection should include looking for signs of pests around and inside containers, maintenance of proper temperatures during shipment, and signs of thawing and refreezing (Crissey, Allen, and Baer 1987). Every lot or shipment of fish must be inspected before paperwork is signed to receive the shipment officially from the supplier.

When thawed, fresh fish have bright-red gills, prominent clear eyes, and firm and elastic flesh. Old or thawed and refrozen fish are dull in appearance, have cloudy and red-bordered eyes and soft flesh, and finger impressions are made easily and remain (U.S. Navy 1965). If the quality is questionable, it is wise to thaw a few fish from several packages to determine better their state. Again, try to do this before officially accepting the shipment. If the order is acceptable, a sample of fish should be taken for nutrient analyses at this time. If the fish have been found to be unsatisfactory for any reason, refuse to take receipt, even if that means reloading the vehicle. The shipper should take the load back. If there is any disagreement as to the quality of the product or what the shipper is to do with it, contact the supplier. Bad fish are unusable, unpalatable, and a health hazard, and may cause a significant economic loss due to illness or death of the animals that consume it.

Once a fish shipment is accepted, it should be placed immediately in the institution's storage facility. This facility should adequately protect supplies from deterioration or contamination. It is crucial that the length (not more than one year) and conditions of storage minimize contamination and ensure that the product retains its nutritive value and wholesome quality. Before storing a new shipment, inspect the storage freezer to ensure that it is in good working order. There should be no potential for contamination by chemicals or other items that may also be stored in the freezer. Any older stock remaining in the freezer should be placed so that it will be used before the new stocks, on a "first in, first out" basis.

When transporting fish from bulk freezer storage to a location used for storing smaller quantities and subsequent thawing and processing (kitchen preparation area), it is important that the fish are kept solidly frozen in a cooled or insulated vehicle. If this is not possible, the load can be covered or insulated while in transit, depending on outside environmental conditions. The length of transportation time necessary to move stock from storage to the appropriate short-term storage or preparation area should be minimized. The temperature of fish in transit can be monitored by placing a maximum/minimum thermometer or another temperature-sensing or recording device in one or more of the boxes during transport. Temperatures that are monitored should be documented. Any boxes thawed or partially thawed during transport should be used immediately and not refrozen.

Fish should be handled similarly to other thawed products. Thawed products should be kept iced or refrigerated until the time of feeding. Inspect thawed product quickly (to minimize contamination and microbial buildup) for quality while handling it before feeding.

Processes and procedures used with fish should be validated and reviewed periodically. Sampling of the fish should be done once a year at the minimum for nutrient analysis and microbial loads. Ideally, each delivery of fish of different catch date should be sampled.

PRODUCE

Beuchat and Ryu (1997) state that treatment of produce with chlorinated water reduces populations of pathogenic and other microorganisms on fresh produce, but cannot eliminate them. They state that reduction of risk for human illness associated with raw produce can be better achieved through controlling points of potential contamination in the field, during harvest, during transit, and during processing rather than dipping.

Quality produce results from careful attention paid at each CCP, from field to consumption. Zoos can provide a protocol outlining its expectations to the produce vendor. In the fall of 1998, the U.S. FDA issued a new, wide-ranging guide (not regulation) to minimize microbial food safety hazards for fresh fruit and vegetables (FDA/CFSAN 1998). The guide addresses food safety hazards due to microbial contamination, and good agricultural and management practices common to the growing, harvesting, washing, sorting, packing, and transporting of most fruit and vegetables sold to consumers in an unprocessed or minimally raw form. The document outlines the basic principles and practices associated with minimizing microbial food safety hazards, from the field to the distribution of fresh fruits and vegetables. It then outlines the different aspects of the guide, with sections on water, manure/municipal biosolids, worker health/hygiene, sanitary facilities, field sanitation, packing facility sanitation, transportation of product, and tracing of product. In October of 2004, the FDA outlined a plan (Produce safety from production to consumption: 2004 plan) to minimize foodborne illness associated with fresh produce consumption (FDA 2004). This plan has 4 objectives: (1) prevent contamination, (2) minimize impact when contamination occurs, (3) improve communication for producers, preparers, and consumers, and (4) facilitate and support research relevant to fresh produce. In March 2006, the FDA issued draft guidance for the safe production of fresh-cut fruit and vegetables (FDA/CFSAN 2006) in order to minimize microbial food-safety hazards common to the processing of most fresh-cut fruit and vegetables sold in a ready-to-eat form. The guidance discusses the production and harvest of fresh produce and provides recommendations for processing in terms of personal health/hygiene, training, building/equipment, sanitation operations, and fresh-cut production/processing controls, from product specification to packaging, storage, and transport. The plan encourages the adoption of safe practices for all parts of the supply chain.

There are potential hazards with all steps before and after the produce is received at the institution. If possible, obtain a copy of the HACCP plan from the grower and distributor of the produce to make sure they are following procedures you would have outlined. Discussion points for the grower could include the fertilization regime, pesticide application, including the preharvest interval and application rate, presence of vertebrate and/or invertebrate pests, and irrigation. How the produce is handled can be just as important as the selection of the product. Physiology of fruit maturation may be an important consideration. If a produce item needs to be placed under certain conditions after harvest for ripening, it is important to monitor those steps and the condition of that location. Ask the produce distributor for a site visit or records of temperature logs. During all steps in the handling of the produce before it is received, consider places for possible bacterial contamination. Upon delivery of the produce, monitor the truck for other items besides produce. During the check-in process, look for signs of spoilage, pests (vertebrate and invertebrate), and any environmental damage to the produce. It is good to have more than one person conduct inspections. If there are signs of unsatisfactory produce, it should be rejected. Developing standards for each type of produce purchased will help all employees and vendors understand the outlined criteria. After produce is accepted and before it is stored in the cooler, it should be labeled with date of receipt. Storage in the cooler should follow the same guidelines that it was under during transit. The cooler should be pest free, and all items should be stored off the ground on shelves or pallets.

PELLETED AND EXTRUDED DRY FEED

Investigation of the pelleted and extruded dry-feed products should begin with the raw materials gathered to make the product and end with consumption by the animal. Since pelleted and extruded dry-feed products are made from many different sources, ask the manufacturer for a HACCP plan for the raw ingredients, processing, and plant. This will help monitor products before they arrive from the distributor. Things to consider for inspection of raw materials would be positive identification of the ingredients, source of the ingredients, geographic location of the materials purchased, and presence of vertebrates or invertebrates. After the product is manufactured, make sure there is enough time to cool the product so it will not mold from the heat of pelleting/extruding. The plant should be free of pests. Upon arrival at the institution, check bags for pests, tears/slashes, date code, and lot number. When receiving the product, compare the packing slip of the received order with that of the original order. It is a good practice to date the bags upon arrival. Store in a dry, well-ventilated area. The storage area needs to have an outlined pest control program, regardless of whether pests are routinely observed. Upon opening the bags, check for pests, foreign materials, mold, dust, color, and smell. Additionally, when transferring the product to a container, label and date the new container. Once the product is offered to the animals, monitor for palatability and consumption. Quality control nutrient analyses should be performed shortly after product arrival to assure quality and nutrient composition as per specifications. Three black rhinoceros (*Diceros bicornis*) died of suspected vitamin D toxicosis after consuming a pelleted grain product (Fleming and Citino 2003). Subsequent testing of the product showed high levels of vitamin D in the feed.

HAY AND OTHER FORAGES

Forage (hay) quality depends on numerous factors throughout the entire handling process, from the management of the standing crop all the way through to the methods of storage and delivery. The grower and/or handler, not the customer, controls most of the steps in the process. Standing crop quality depends on the species of grasses or legumes planted, weed species management, fertilization, irrigation, soil type, growing season, and prevailing climate patterns during growth. During harvest, quality is influenced by maturity at harvest, prevailing climate conditions at that time, and equipment used to harvest the hay. For example, the physical nature of alfalfa hay changes considerably whether it is cut at the late bud/early bloom stage or at full bloom stage (Holland and Kezar 1990). Rain or high humidity at the time of cutting can lengthen drying time, which can increase the chances of molding and nutrient loss (Rayburn 2002). Drying time is influenced by whether the alfalfa is crimped at the time of mowing (crimping opens more air to the stem); in uncrimped hay, prolonged drying time to reach a desired overall moisture content can lead to poor leaf retention and loss of nutrients during baling (Collins 1999). Conversely, crimping alfalfa from a field that is infested with blister beetles ensures that the blister beetles will remain in the cut crop and be included in the bale (rather than escape once the hay is cut without crimping), which may lead to cantharidin poisoning (Ward 2001). Baling hay that is too wet or too dry can cause molding issues or loss of nutrients via leaf shatter, respectively; thus, attention to moisture content of the cut crop is imperative before baling. Weeds, rocks, and soil from the field, and other foreign objects can get into the hay during baling, and are sometimes undetectable when the hay is first examined. Once baled, hay should be stored in a covered facility, out of the sun and moisture (dew or rain), but with adequate ventilation. Mild bleaching by the sun can yellow the outside of the bales while doing minimal damage to the inside of the bale or the nutrient content. Prolonged sun exposure or exposure to rain or dew can cause nutrient loss or improper moisture (too much or too little) to maintain the stability of the hay. Excessive heat during storage can cause nutrient losses (see Ullrey 1997 for details of hay evaluation). Zoos can avoid problems by having a positive working relationship with the hay supplier and visiting as much of the operation as possible to see how the hay is handled until its receipt. In this way, the CCPs can be identified, discussed, and managed through the entire process to ensure best quality of the final product.

CANNED GOODS

In the early 1970s, several botulism outbreaks occurred in the United States as a result of inadequate thermal processing of commercially prepared, low-acid foods packaged in hermetically sealed containers, and improper acidification of commercially prepared acidified foods. Therefore, special regulations were established for the manufacture of heat–processed, low-acid canned foods and acidified foods (USDA 21 CFR 108, 113, and 114). These guidelines were first adopted in the United States in 1973, with a revision in 1979 (ibid.). The purpose of the regulations is to ensure safety from harmful bacteria and their toxins, especially *Clostridium botulinum*. These guidelines outline proper methods for processing controls and appropriate processing methods, including proper temperatures and sufficient time for cooking, adequately acidifying the food, and controlling the water activity. Additionally, all foods canned and/or sold in the United States must have labeling that complies with regulations (USDA 21 CFR 101 1998). In most cases we do not know the ingredients and how the product was processed; however, protocols and questions can be discussed with vendors. Ask the manufacturer to share its HACCP plan and describe its ingredient tracing and recall plan. When the product arrives, examine it for dents, swelling, leakage, and rust. Note the date code and lot number of the product. Some manufacturers have special codes outlining the manufacturing information. If the code is not obvious, instructions to understand the code should be obtained and kept on file. Once the product is opened, it should be placed in refrigeration and used within 3 days. Additionally when the product is opened, examine for foreign bodies, odor, color, and texture. Finally, with so many items offered to animals, it is important to track palatability and consumption.

NUTRIENT SPECIFICATIONS, NUTRITIONAL ANALYSIS, AND ASSESSMENT OF FEEDS

ESTABLISHING SPECIFICATIONS FOR FEEDS

It is critical to establish specifications for all the food items used to feed captive wildlife. This better allows assessment of quality control measures, budget planning, and consistent nutrient content of formulated diets. Specifications should be clearly written for the product(s) in question, discussed with the vendor or supplier, and agreed on ahead of time. If the specifications as written and discussed are too stringent for the vendor, they should be evaluated as potentially too rigorous overall, or as a method to eliminate certain suppliers who cannot meet the standards of the institution. Criteria should be met consistently, and if they are not, the vendor/supplier must be held accountable. Specifications for food items may include the period that the specifications are valid, purchase amounts, purchase price, ordering and delivery details, payment details, sampling schedule for quality control and nutrient content (financial responsibility, laboratory details), labeling and/or descriptive details on product, size, specific ingredients (pelleted feeds, meat mixes), sources of minerals and vitamins (chelated versus nonchelated forms of minerals), and minimum and maximum nutrient concentrations (meat example, Allen, Ullrey, and Edwards 1999; hay example, table 10.3).

Pelleted or extruded dry diets. Specifications for pelleted or extruded dry diets not only revolve around the nutrient content of those items, but can be as detailed as indicating the specific ingredients used in the formulations, and even the forms of minerals and vitamins chosen. Specifications should include the product's packaging (weight, size, shape, lined or unlined bags, weight, and square footage of pallets) and mode of transport for delivery. In addition, a plan for product recovery, if product is deemed unacceptable at the site of receipt, also should be incorporated.

Meat. Several publications provide detailed descriptions of meat specifications (Allen, Ullrey, and Edwards 1999; Crissey, Shumway, and Spencer 2001), including the types of ingredients used in the product (what can and cannot be used), microorganism thresholds, and nutrient concentrations. In addition, specifications are important for how the product is handled, from initial processing through freezing and delivery to the animal facility (maintained at temperatures that minimize bacterial growth, solidly frozen in a short amount of time, and delivered to the site frozen solid on a freezer truck).

Fish. Several publications address the evaluation and handling of frozen fish (Crissey 1998; Crissey, Allen, and Baer 1987; Oftedal and Boness 1983). Specifications should include how the fish is packed, dates and lot numbers on boxes, size of boxes (for adequate thaw), handling guidelines (i.e. to remain frozen, stacked squarely), male versus female, nutrient content, specified product recovery plan, history of the catch (fisheries reports, epidemiological data), and freezing method.

Hay. Specifications for hay can be established across all species (i.e. lacking weather damage, stored appropriately, containing

TABLE 10.3. Example alfalfa specifications in terms of agreement

1. The supplier will hold X tons of satisfactory alfalfa (*Medicago* spp.) hay (see condition 3 for definition of satisfactory hay) cut in 2006 for the institution. The price quote should include delivery, unloading, and stacking per ton of hay.
2. The hay must be free from pests (blister beetle or other harmful insects) and harvested from documented pest-free areas. This information is provided via state and local Cooperative Extension Services.
3. The hay will be stored by the supplier and delivered to the institution upon request of the institution. Deliveries must arrive between 8 and 10 AM, and trucks will be occupied in the park for approximately 3 hours. Suppliers should be able to provide hay with at least one week's notice from the zoo.
4. The alfalfa hay to be purchased by the institution must meet the following specifications in order to be deemed satisfactory:
    a. Minimum of 18% crude protein (dry-matter basis)
    b. Maximum of 35% acid detergent fiber (dry-matter basis)
    c. Grade 1, 2, or 3 alfalfa hay based on market hay grades established by the Hay Market Task Force
    d. At least 85% alfalfa (*Medicago* spp)
    e. Free of mold, musty odor, and dust
    f. Free of toxic or noxious weeds and hardware
    g. Must not be stained, badly weathered, heat damaged, smoke damaged, or wet
    h. Maximum of 18% moisture
    i. Bales must be rectangular, held together by nylon and/or wire binding, and maintain their integrity during handling and stacking
    j. Bale weights must not exceed 45 kg (please specify average bale weights).

    Crude protein, acid detergent fiber, and moisture analyses will be performed on core samples taken by the institution. The supplier should know the nutrient content of the hay it provides to the institution.
5. The zoo must be compensated for hay that molds in storage at institution due to excessive moisture and improper curing. Compensation must be in the form of a cash reimbursement at the original purchase price for moldy hay, or replacement of the moldy hay with an equal amount of satisfactory hay at no additional cost to the institution.
6. The institution will reserve the right to reject hay that it considers unsatisfactory. The institution will not pay freight charges on rejected hay.

minimal percentage of weeds or foreign species, having appropriate bale size and shape) or for individual species (baled at appropriate moisture, having adequate leaf retention, color, nutrient content). In addition, specifications can be made for whether the product is picked up from the farm/distributor, delivered to the facility, or delivered and unloaded. Hay quality standards have been developed by the Hay Market Taskforce of the American Forage and Grassland Council, and additional details can be found in Ullrey (1997). An example of comprehensive alfalfa specifications is provided (table 10.3). Note that the specifications include not only nutrient content guidelines, but also guides for exactly what type of binding materials are used and the weight of the bales.

Produce. Specifications for produce can incorporate case sizes and weights (certain counts and item sizes), packing needs (wrapped in plastic, packed in waxed boxes, inserted dividers to protect from bruising, etc.), and vendor handling (how delivered). Produce vendors should understand the evaluation process and criteria used for checking in their products.

Prices can change significantly throughout the year for numerous items used in captive wildlife diets, based on overall availability (issues caused by drought, fuel costs). For this reason, it may be fiscally responsible to contract prices for specific items. When contracting for prices, terms rarely exceed one year, and often incorporate the volatility of the market and projections of future supplies. For this reason, contract prices may be higher than what normally would be daily or weekly costs for items. On the other hand, contracts will ensure a consistent supply of product, and recourse if specifications or supplies are not provided as detailed. Any product that does not meet specifications should be consistently rejected.

SAMPLING

Products included in feeding programs need to be sampled on a specified and regular basis. We strongly recommend that feeds for analysis, number of samples (based on a set schedule), and types of analysis be considered a routine part of the annual budgeting process. Samples can be collected for overall assessment of product quality, nutrient content, and/or microbiological/toxin analysis. Samples can always be banked for troubleshooting or retrospective examinations, especially if funds and time are not available as the sample is collected. The goal when sampling any product is to ensure that a homogeneous specimen is obtained that is identical to the bulk of the lot from which it was taken. The frequency of sampling is based on the variation in the parameter in the feed in question—the more variable (or the greater likelihood of an issue), the more frequent the sampling. Sampling protocols and guidelines, schedules, and laboratory selection/evaluation are described in detail in Bernard and Dempsey (1999).

ENSURING COMPLIANCE

Regularly sampling food items allows managers to incorporate the best information available into their diets. It also allows for vendors/suppliers/producers to be held accountable for the quality of their products. Designing specifications and contracting for specified food items helps ensure quality, quantity, and price consistency in the products used in captive animal diets. It is important to ensure that the suppliers of the food items comply with the specified parameters for each feed.

Clear indication of nutrient content, physical form, packing, and other requirements will help ensure compliance. In addition, clearly communicating what is not acceptable (physical, chemical, microbiological hazards) will help maintain standards. As food items are sampled and results obtained, zoo staff should share not only situations where products fail to comply with the specifications (and receive adequate resolution to these issues), but also results that meet specifications as they are obtained. Open and clear communication with suppliers helps maintain good working relationships, which benefit collection management efforts in the long term.

CONCLUSIONS

Using the various recommendations outlined in this chapter will facilitate efforts to feed the highest-quality food to captive mammals. Development of a HACCP program will address food safety issues. Surveillance and detection of food-related hazards, including physical, chemical, and biological contaminants, will prevent potential illnesses and death. Based on location, international, federal, state, and local agencies have authority over facilities that maintain captive mammals, and thus it is prudent to be aware of the policies, responsibilities, and guidance of each. Whereas many captive-animal care facilities are held to specific standards, the suppliers of the food items included in their animal diets are, in many cases, not bound by such regulations. Quality control standards and proper handling practices for meat, fish, whole prey, hay, pelleted and extruded dry feeds, produce, and canned foods are essential elements of a diet management system. Establishing appropriate product specifications, conducting routine analysis and evaluation of raw and commercial products, and following up on identified issues will help ensure quality in nutrition and feeding programs.

APPENDIX 10.1

Government Oversight of Animal Food Processing and Handling in the United States

A number of U.S. government agencies regulate food safety. Principal federal executive-level organizations are the Department of Health and Human Services' (DHHS) Food and Drug Administration (FDA), the U.S. Department of Agriculture's (USDA) Food Safety and Inspection Service (FSIS) and Animal and Plant Health Inspection Service (APHIS), and the Environmental Protection Agency (EPA).

U.S. Department of Health and Human Services

The Food and Drug Administration (FDA) of the Department of Health and Human Services (DHHS) oversees food safety in all domestic and imported food sold in interstate commerce, including shell eggs, but not meat and poultry, bottled water, and wine beverages with less than 7% alcohol. It enforces food safety laws governing domestic and imported food, except meat and poultry, by

- inspecting food production establishments and food warehouses, and collecting and analyzing samples for physical, chemical, and microbial contamination
- reviewing safety of food and color additives before marketing
- reviewing animal drugs for safety to animals that receive them and humans who eat food produced from the animals
- monitoring safety of animal feeds
- developing model codes and ordinances, guidelines, and interpretations, and working with states to implement them in regulating milk and shellfish as well as retail food establishments, such as restaurants and grocery stores.
- establishing good food-manufacturing practices and other production standards, such as plant sanitation, packaging requirements, and HACCP programs
- working with foreign governments to ensure safety of certain imported food products
- requesting manufacturers to recall unsafe food products and monitoring those recalls
- taking appropriate enforcement actions

The 2 centers within the FDA that specifically contribute to animal food safety or have authority to regulate animal feed are the Center for Veterinary Medicine (CVM) and the Center for Food Safety and Nutrition (CFSAN). The CVM regulates the manufacture and distribution of food additives and drugs that will be given to animals. CFSAN has responsibility for inspection and enforcement of game meats and for in-plant inspection of all domestic and imported foods (except meat and poultry products) for sale or distribution in interstate commerce.

U.S. Department of Agriculture

The U.S. Department of Agriculture's (USDA) Food Safety and Inspection Service (FSIS) oversees domestic and imported meat and poultry and related products, and processed egg products (generally liquid, frozen, or dried pasteurized egg products). It is a regulatory agency that enforces food safety laws governing domestic and imported meat and poultry products by

- inspecting food animals for diseases before and after slaughter
- inspecting meat and poultry slaughter and processing plants
- with USDA's Agricultural Marketing Service, monitoring and inspecting processed egg products
- collecting and analyzing samples of food products for microbial and chemical contaminants and infectious and toxic agents
- establishing production standards for use of food additives and other ingredients in preparing and packaging meat and poultry products, thermal processing and other processes, and overall plant sanitation
- making sure all foreign meat and poultry processing plants exporting to the United States meet U.S. standards
- seeking voluntary recalls by meat and poultry processors of unsafe products

The USDA's Animal and Plant Health Inspection Service (APHIS) carries out U.S. border quarantine activities to detect and eliminate animal health problems and exotic organisms, many of which pose potential food safety threats. It also enforces the Animal Welfare Act, including inspections of animal facilities. Under its regulatory discretion, APHIS inspections include aspects of food handling, storage, and feeding.

U.S. Department of Commerce

The National Marine Fisheries Service (NMFS) of the Department of Commerce's National Oceanic and Atmospheric Administration oversees fish and seafood products. Through its fee-for-service Seafood Inspection Program, it inspects and certifies fishing vessels, seafood processing plants, and retail facilities for federal sanitation standards.

U.S. Environmental Protection Agency

The U.S. Environmental Protection Agency (EPA) establishes safe drinking water standards, regulates toxic substances and wastes to prevent their entry into the environment and food chain, assists states in monitoring quality of drinking water, determines safety of new pesticides, sets tolerance levels for pesticide residues in foods, publishes directions on safe use of pesticides, regulates sanitizers on eggs and in meat and poultry facilities, and regulates labeling of detergents, antimicrobials, and cleaning agents.

Other U.S. Agencies

Many other federal agencies and offices have food safety missions within their research, education, prevention, surveillance, standard-setting, and/or outbreak response activities, including Department of Health and Human Services' Centers for Disease Control and Prevention (CDC) and National Institutes of Health (NIH); USDA's Agricultural Research Service (ARS); Cooperative State Research, Education, and Extension Service (CSREES); Agricultural Marketing Service (AMS); Economic Research Service (ERS); Grain Inspection, Packers and Stockyard Administration (GIPSA); and the U.S. Codex office.

State and Local Governments

State and local governments oversee all foods within their jurisdictions. They work with the FDA and other federal agencies to implement food safety standards for fish, seafood, milk, and other foods produced within state borders. They inspect restaurants, grocery stores, and other retail food establishments, as well as dairy farms and milk processing plants, grain mills, and food manufacturing plants within local jurisdictions. State and local authorities can embargo unsafe food products made or distributed within state borders.

Associations

The Association of American Feed Control Officials (AAFCO) is a private nongovernmental association; its membership is drawn from government, academe, and industry. It provides a forum to discuss issues related to development and enforcement of standards and laws as well as definition of feed ingredients. The association offers guidance and advice to federal and state regulatory bodies. In addition, it produces a publication that contains proceedings from AAFCO meetings, listings of the association's committees, feed terms and ingredients definitions, laboratory contacts, sample forms, and model bills (e.g. AAFCO has created a model feed bill that states can adopt in their own laws). The AAFCO publication is updated annually and is available in English and Spanish (Association of American Feed Control Officials, Incorporated. 2006. Official Publication. ISBN 1-878341-17-0).

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Part Four

Exhibitry

Introduction

Devra G. Kleiman

Zoo exhibitry has transcended the "stamp collection" menageries of the past. Through creative exhibit design, zoos now strive to educate visitors about biology, ecology, and the grave threats to our planet's biodiversity. We know that zoo visitors, whether actively or passively, come away with distinct feelings, beliefs, and views after visiting our zoos, and it is our responsibility to try to change not only attitudes, but also behavior. This part summarizes modern approaches to exhibit design, both philosophical and practical, and provides a glimpse of the future of zoo exhibitry. It also emphasizes the essential role that zoo education programs now have in the development of new exhibits. Many of the chapters integrate highly practical advice on the technical aspects of exhibit design with philosophical and value considerations.

Hancocks begins by providing a history of zoo exhibitry, and emphasizes the importance of the recent development of the landscape immersion concept and its objective of replicating the essence of the wild and conveying to the visitor the experience of discovering an animal in a wild place. By exhibiting animals in their natural contexts, zoos can reinforce the message of the interdependency of animals and their ecosystems. Both he and other authors in this section focus on the need for zoos to be sustainable environmentally and for visitors to be exposed to the programs, operations, and exhibits as one intertwined whole so that shops, education programs, exhibits, and restaurants all have a single unifying message. Hancocks ends his chapter with "Rules for Exhibiting Mammals in Zoos" and "Zoo Exhibit Design Principles."

A giant panda pair interacts at the Smithsonian's National Zoological Park, Washington, DC. Photography by Jessie Cohen, Smithsonian's National Zoological Park. Reprinted by permission.

Routman, Ogden, and Winsten present the recent evolution of zoo visitor education programs, which derives from the understanding that zoos and aquariums have the opportunity and responsibility to shape public values and behavior. Education is now an essential element of the zoo conservation strategy, and for the first time is being tested and explored explicitly by multi-institutional research programs that study how to achieve attitudinal and behavioral changes in adults and children. The goal is to make visitors better stewards of their environment.

Veasey and Hammer summarize the costs and benefits of mixed-species exhibits. Benefits include enrichment, a more effective use of resources, and a benefit to the visitor, since animals in mixed-species exhibits are often more active. However, there are potential risks in that individual animals may exhibit undesirable behavior (e.g. aggression), some animals may be overly stressed under such conditions, and management of species with different dietary requirements might be more difficult than with a single-species exhibit. Veasey and Hammer provide guidance in establishing mixed-species exhibits, and review the impact of taxonomy, sex, reproductive status, age, and body size on the success of such exhibits.

Rosenthal and Xanten review the basic structural issues to be considered when designing new exhibits, including among other topics the utilities, floors, fencing, walls, doors, and ceilings. They emphasize the need for sufficient off-exhibit space and flexibility to isolate individuals or transfer animals between enclosures. Additionally, they highlight the importance of the proper location and size of the keeper service areas for safety and functionality.

Cipreste, Schetini de Azevedo, and Young provide guidelines for establishing an enrichment program in a zoo, including establishing the team, setting priorities (how many species; how many animals), developing a budget, and ensuring that enrichment efforts are evaluated to determine their efficacy. They focus on the need to make enrichment an integral part of the zoo's programs and to ensure that all new and renovated exhibits incorporate enrichment.

Joseph and Antrim concentrate on the special issues that need consideration when designing exhibits for marine mammals. Most important for managing marine mammals in zoo exhibits are the maintenance of natural behaviors, proper nutrition, and medical management. Marine mammals can pollute their environment to an amazing degree; thus, maintaining water quality is a major issue. Joseph and Antrim provide a summary of the types of water handling and treatment systems and the importance of testing water for pH, salinity, coliforms, and so on. The design and construction of appropriate marine mammal habitats need to focus on the natural history and behavior of the species to be maintained so that individuals can perform most, if not all, of their natural behaviors.

Although the use of plants in and around zoo exhibits has greatly increased in recent years, the result, all too often, has been a haphazard mixture of plant and animal life that lacks a coherent ecological message. Moore and Peterkin argue for the importance of the zoo horticulturalist in participating in the development of new exhibits, especially those that intend to present natural habitats. They provide nuts-and-bolts advice for dealing with contractors, choosing species, and protecting existing vegetation during construction. They argue that plant selection is as important as choosing animal species and that the actual acquisition may be as complex as animal transport. Moore and Peterkin point out that zoo horticulturalists can play a leadership role in zoo education programs and especially in demonstrating the organization's commitment to a sustainable world (e.g. through the efficient use of water and composting).

In the last chapter of this section, Coe and Dykstra summarize and integrate much of the preceding chapters, but also present what they believe is the future trajectory for zoos and zoo exhibits. The chapter is organized to review issues of husbandry, animal well-being, education, and entertainment. Among the new trends in exhibitry are immersion exhibits that include cultural considerations; exhibits that provide mammals with more enrichment and choice; rotation exhibits; the use of minitheaters or story-based displays to present information; behind-the-scenes tours; and night safaris. Finally, they discuss the new trend to develop "green" exhibits that are environmentally sustainable.

11

The History and Principles of Zoo Exhibition

David Hancocks

INTRODUCTION

The idea of taking wild animals and putting them on public display in zoological parks in small enclosures might be seen as truly audacious if it wasn't so commonplace throughout human history, and now enshrined as one of the hallmarks of a modern city. A universal and unthinking acceptance of what could be regarded as a quirky human trait prevents critical analysis of the extent of its success. There are 2 decisive measures for zoo exhibits: the degree to which they meet the animal's biological requirements—their psychological, physiological, behavioral, social, and emotional needs and wants; and the degree to which they inspire and enthuse human visitors to develop a more caring and compassionate view of wild animals. These goals are rarely examined objectively. Yet, despite the spin of modern zoo marketing, zoo exhibits often fail on most if not all accounts. The polar bear exhibit at Taman Safari Zoo, Indonesia (fig. 11.1), is one typical example. It stands in stark contrast with the wonder of seeing the power and dignity of a polar bear in its natural habitat (fig. 11.2).

The origins of this peculiar custom have deep roots. Almost since the first settled human communities, ownership of wild animals (especially big or rare ones) has been an important emblem of prestige: a mark of social distinction, and an illustration of the apparently inherent fascination that humans have for other animals. The first zoo appeared 4300 years ago in the city of Ur, in southern Iraq, only about 1000 years after the world's first farming villages, in southern Mesopotamia. Since then, zoos have evolved in all developed societies, and their growth or decline has tracked the swelling and collapsing of civilizations across the centuries.

The stupendously wealthy Egyptian pharaohs maintained collections of wild animal species that grew to thousands of animals, as symbols of kingly status and national pride. At the beginning of China's classical age over 3000 years ago, Wen-Wang, founder of the Zhou dynasty, assembled a zoological collection as part of a vast "Park of Knowledge" in Henan Province. As other kingdoms spread across Asia, court palaces often served as repositories of experience of the known world, typically including such features as libraries, museums, botanical gardens, and zoos. The ancient Greeks, too, formed collections of animals and plants, for curiosity and for show. Twenty-four centuries ago, most Greek city-states maintained zoos, and visits were part of the education for young scholars (Fisher 1966; Kisling 2001).

In ancient Rome, the wealthy elite built the world's first private zoos; but as the Roman Empire fell apart such institutions as private libraries, lavish gardens, and zoos eroded and then all but disappeared for the next thousand years of Europe's history. With the exception of the extraordinary Charlemagne, who maintained 3 royal zoos in the eighth century, no European court or government had sufficient wealth or urbanized population to support such complex developments. It is worth noting that most of Charlemagne's animals were gifts from the Caliph of Baghdad and the Emir of Cairo. During the approximately 1000 years of Europe's Dark Ages, a time when scholarly and artistic pursuits there were constrained by the punitive strictures of Christianity, much of what was being lost or suppressed was held safe in Islamic cultures. Arabic scholars expanded on the works of the ancient Greeks and, like them, studied the wonders of nature in zoological and botanical enclaves that flourished under princely patronage, until their work in turn was subdued by the narrow confines of religious orthodoxy.

It was not until the late or High Middle Ages, with increased stability, gradual reurbanization, and the growth of literacy and learning, that zoos began to emerge once again in Europe as symbols of regal power. The thirteenth-century Holy Roman Emperor Frederick II, founder of the University of Naples, was the first in several hundred years to assemble a major zoological collection in Europe, at his court in Palermo (Fisher 1966). There were, however, major zoos of considerable size in other regions of the world. Marco Polo recorded vast numbers of wild animals on display at the thirteenth-century court of Kublai Khan, in Cambaluc (now Beijing);

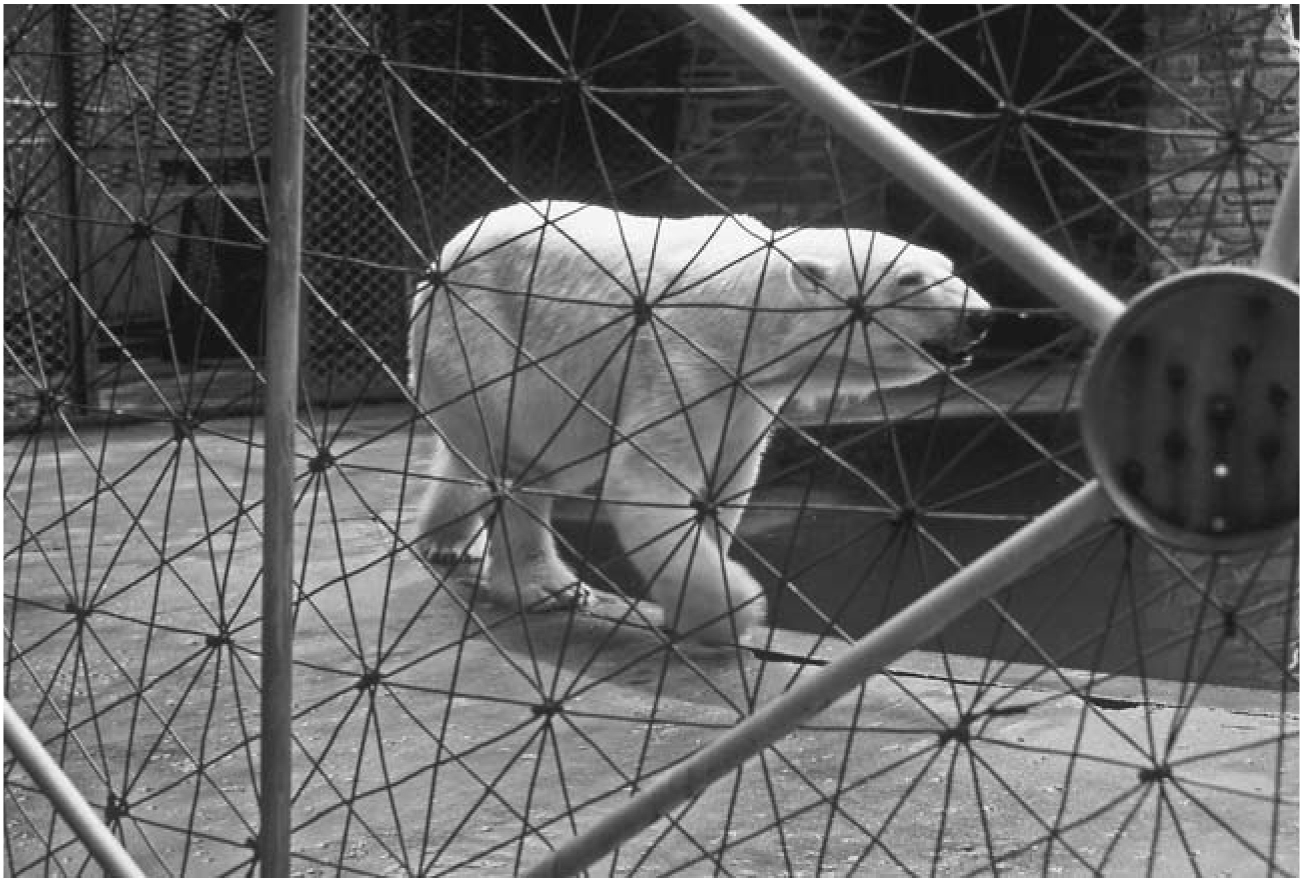

Fig. 11.1. Taman Safari Zoo, Indonesia, promotes itself as a "real window to nature." The environment this zoo provides for polar bears echoes most zoo bear exhibits worldwide. (Photography by Rob Laidlaw. Reprinted by permission.)

and the Chinese mariner Zheng He shipped giraffe and zebra from Africa to the Ming imperial zoo in the early fifteenth century. In Tenochtitlán (now Mexico City), Hernando Cortés in 1519 discovered the staggeringly immense animal collections of Montezuma II. Before Cortés destroyed it by fire, this zoo had a staff of 600 keepers and a team of nursing staff for sick animals: an extraordinary level of care in a society that was based on ritual murder and steeped in gore (Loisel 1912; Schjeldahl 2004). Four hundred years ago, Jelal-ed-din-Mohammed, the Mogul emperor of India known as Akbar the Great, established several zoos in various Indian cities. His progressive court was a center for arts, letters, and learning, and his zoos reflected his tolerance and compassion. They were open to the public, and at the entrance to each he posted a message: "Meet your brothers. Take them to your hearts, and respect them." It was a long time before such sentiments gained support elsewhere.

The Renaissance in Europe rode a wave of commercial expansion and colonization. It brought new ways of thinking and seeing, and a renewed interest in the arts and science. One reflection of these changes was that private zoos and gardens came into vogue. By the late sixteenth century, many wealthy princes and merchants owned aviaries or menageries and competed enthusiastically for animal collections. Until this time, zoo exhibits had been designed principally as containment devices, with greatest emphasis on effective enclosure. But now attention was also being given to elegance of design, and the French pattern of formal symmetry became the dominant fashion for zoo planning. The most stylish menagerie of the era, created by Louis XIV at Versailles in the late 1600s, was a perfect example of the French academic approach. Its radial symmetry and mathematically precise ornamentation was a conscious rejection of the disorder and chaos of nature; it made manifest the superiority of human and especially aristocratic control (Hancocks 1971; Robbins 2002). The zoo at Schönbrunn, in Vienna's suburbs, is the best-known remaining example of this style. Designed for Empress Maria Theresa in 1752, one of its main purposes, as at Versailles, was to exaggerate the elegant refinement of the court in contrast with the comic or brute appeal of wild nature.

Zoos throughout history had traditionally been created for the benefit of the social elite. However, humans from all walks of life are fascinated with wild animals, and in the eighteenth century traveling menageries began appearing across western Europe as showmen started to take advantage of the increasingly rapid influx of exotic creatures from distant lands. Many an impresario made a living from displaying strange wild creatures to the curious gaze of country folk. Gilbert Pidcock seems to have been the first to assemble a collection of any significant size and take it on the road, in England in 1708. By the close of the century a Mr. Pidcock

Fig. 11.2. A polar bear in the wild, as a comparison. (Photography by Lynn Rogers. Reprinted by permission.)

(presumably a descendant of Gilbert's) was at first wintering and eventually permanently displaying a menagerie of wild animals in London at, curiously, a commercial building for milliners and drapers, named the Exeter 'Change (Hancocks 1971). A lion, a tiger, various primates, even an elephant were on show in cages so small the occupants could barely turn around in them. The conditions would appall most modern visitors, but in those days the displays were regarded as educational. The poets Wordsworth and Byron and the sculptor Sir Edwin Landseer visited the 'Change and found it a source of inspiration. It suited the needs of the time: people were curious only to know what exotic animals looked like. Operated over time by various showmen, the Exeter 'Change was demolished in 1829, and what had become known as the Royal Menagerie was closed (Weinreb and Hibbert 1993). Just one year before this, however, the Zoological Society of London had opened its Zoological Gardens in Regent's Park. This was to prove, perhaps, the most consequential moment in modern zoo history.

A comprehensive mix of social, intellectual, and economic shifts in England over almost 2 centuries led to the emergence of the modern zoo concept. There was a new and increasingly affluent middle class with an intense interest in natural history; a keen recognition of the value of scientific studies; an expanding concern for animal care; a passion for wild and distant places, and a strong interest in adventure stories about the expanding British Empire; a desire for wholesome, outdoor family entertainment; and a devout belief in education and enlightenment as the mark of a progressive and civilized society (Hancocks 2001). Set in a newly fashionable part of the world's premier metropolis, in spacious and attractive gardens, with the layout of its collection planned on the newly developed principles of taxonomy, London Zoo quickly established itself as a progressive, stylish, and highly approved place to be seen. With admission restricted to fee-paying members, visitors delighted in dressing in their finery to parade among their peers and other quaint creatures. The first zoo to be based on scientific principles, its taxonomic approach inevitably led it to introduce the first reptile house, in 1849; the first public aquarium, in 1853; and the first insect house, in 1881 (Guillery 1993). The first to be called by the name *zoo*, it has had greater impact on zoos worldwide than any other—which made its unremitting decline in exhibition standards during the latter part of the twentieth century especially frustrating.

The enormous and early success of London Zoo encouraged other facilities. Many new zoos were soon being built, with great enthusiasm and often with massive financial investments, first from the 1830s to the 1850s in British provincial cities and in the port cities of the colonial nations in western Europe. A wave of zoo building then spread across the rest of Europe during the latter half of the nineteenth century, with considerable activity and fervent rivalry in the German-speaking world, where 17 major zoos were developed in a period of 55 years. It became almost essential for any self-respecting world city to have a zoological park, starting in Melbourne, Australia, in 1872, then to Philadelphia and other U.S. cities westward, and to Calcutta, Tokyo, Cairo, and Pretoria. The great swell of nineteenth-century zoo building climaxed with the opening of the Bronx Zoo in New York City, in November 1899.

Despite the nineteenth century's prolonged surge of zoo development, there was very little gain in information about the wild animals or their habits. Hence the main stimuli for zoo exhibit designs were architectural copybooks and fragments of exotic mythologies. Reproductions of religious buildings were commonplace. Cologne Zoo's ostrich house resembled a Hindu place of prayer. Buildings styled as Egyptian and Greek temples were highly approved additions to the new zoos. Moorish birdhouses, an antelope house with minarets, an Eastern Palace for monkeys, and a sumptuous elephant house in the style of a Burmese temple decorated the grounds of Berlin Zoo, where the architects Ende and Böckmann, in particular, produced exhibition buildings of extraordinary grandeur that bespoke power and respectability with great authority and immense confidence. Designers also employed their imagination in fanciful romanticism, with zoo buildings that replicated fantastical castles, rustic cottages, alpine chalets, Renaissance pavilions, and whimsical ruins and other follies (Hancocks 1971, 1996). Briefed only to hold the animals on public display, the designers produced hundreds of new exhibition spaces, none of them much improved from those in the old menageries in terms of animal welfare. This problem persists even today in far too many modern zoological parks (see Kagan and Veasey, chap. 2, this volume).

After so much fanciful and ornate exhibit building throughout the nineteenth century, a few zoos, mainly in Europe, experimented with the bold and simple styles of modernism. Copenhagen Zoo's ape house, designed by Fritz Schlegels and opened in 1928, is maybe the earliest example. G. F. van Laarhoven designed a modernistic abstract monkey island for Amsterdam's Artis Zoo in the 1960s, replacing a more functional naturalistic design of greater character. Sir Hugh Casson's marvelously expressionistic elephant house for London Zoo in 1965 had much influence on the design world, but was never suitable for the housing of living elephants. Zoo exhibits are unusual fare for architects, and they tend to approach the problem like an Expo pavilion, with buildings of self-consciously unique and memorable form. Sir Norman Foster's 2003 design for an elephant exhibit at Copenhagen Zoo is a notable and prominent example, aiming to satisfy visiting architectural critics more than the resident elephants.

The most numerous as well as the most eminent examples of zoo modernism are the works of Berthold Lubetkin, principal with the design firm Tecton, who designed many projects for English zoos in Dudley, London, and Whipsnade in the 1930s (Hancocks 1971; Allan 2002). Tecton's work was simple and elegant in form, with swirling concrete planes in clever articulations. They were precocious examples of international modernism in Britain, radical in form and structure, but not progressive in regard to animal needs. Lubetkin's daughter, Louise Kehoe, likens the controlling world of London Zoo's Penguin Pool to the way its designer saw nature: "He liked the contrast between the perfect man-made symmetry . . . and the wobbling idiocy of the animals. The penguins are just instruments to display man's ability to control nature" (Walter 1996, 9). Kehoe's analysis throws light on an aspect of zoo exhibit design that has unfortunately been commonplace in zoo exhibit design history. Heritage architects adore Lubetkin's works and plead for their renovation, but one must hope that wild animals never again have to endure any of them. The sterile plainness of the buildings so loved by architects who paid only lip service to the notion that "Form follows Function" was never suitable for living creatures.

Most zoos, however, have usually stayed well away from anything radical or intellectual. For most of their history they have mainly preferred to expend their energy by competing against one another with large collections of rare specimens or consciously grand buildings. But 2 valuable new directions in zoo design did occur in the twentieth century: one in Hamburg, Germany, in its opening decade; the other in Seattle, Washington, in the 1970s, the decade increasingly recognized as the century's premature close (Wheen 2004). Both of them, interestingly, pivot on naturalism, and on the design treatment of barriers.

The zoological park that Carl Hagenbeck opened in 1907 in Hamburg was the first to combine naturalistic exhibition landscapes, barless enclosures, and regional groups of mixed species (Reichenbach 1996). Comprising African and Arctic panoramas, the exhibits were of a scale and naturalistic grandeur never before attempted. Key to Hagenbeck's grand panoramas, other than their impressively bold size, was his successful adaptation and expansion of the ha-ha—a device from eighteenth-century English landscape gardening whereby a ditch kept animals out of cultivated garden areas but allowed uninterrupted views to the open countryside. He was keen to "give the animals the maximum of liberty . . . with no bars to obstruct the view and serve as a reminder of captivity" (Hagenbeck 1910, 113). Dry-moat barriers or ha-has separated people and animals, but more cleverly, and most significant in the history of zoo exhibit design, also kept animal species, notably predators and their prey, separated. Enclosures could thus be treated like theater stages, each one at the back of and slightly higher than the other, creating a totality of scenic landscape. These gigantic and dramatic exhibits, with a diversity of animals from one type of habitat all apparently living together, and with surprisingly realistic rock formations designed and built by the Swiss sculptor Urs Eggenschwyler, were immediately and hugely popular.

Before Hagenbeck, zoo designers had never looked to nature as a source of inspiration. Zoo architects would have considered it unsavory if not ridiculous to examine the wild homes or to consider the wild habits of the animals. They preferred to construct ornate and exotically flavored buildings, which guaranteed praise from the socially elite and awards from their peers. The sheer scale of what Hagenbeck had achieved, however, could not be ignored, and it was clearly appreciated by the public. But it did not receive approval from conservative zoo professionals. Ludwig Heck, director of Berlin Zoo, irately claimed that Hagenbeck's style of presentation threatened the scientific taxonomic approach (Baetens 1995). The Bronx Zoo's William Hornaday scorned it as "a fad," grumbling that people were too distant from the animals and that the approach was not only inadequate but also too costly (Bridges 1974).

America's early zoos modeled themselves on Europe's traditional designs. Philadelphia Zoo was based firmly on the style of London Zoo. Cincinnati in the mid-1800s had planned a zoo on mainly German styles. When William Hornaday was hired as the first director of the Bronx Zoo, he sailed straightway to Europe and examined 15 of its zoos (Bridges 1974). Thus, the Bronx Zoo's lion and reptile houses were modeled on London's, the elephant house on Antwerp's, and the antelope house on Frankfurt's. The National Zoo in

Washington, DC, initially built romanticized versions of log-and-stone buildings of the American West for its essentially American collection, but soon moved toward a traditional zoo collection: when Albert Harris was contracted to develop its new exhibition houses, he made a study tour of European zoos and drew up his plans on the ship home (Ewing 1993; Horowitz 1996).

Despite Hornaday's and Heck's criticisms of Hagenbeck's work, some zoos sought to copy his style. But they rarely understood his logic, and failed to adopt the same sense of assurance or of scale. The 1914 Mappin Terraces exhibit at London Zoo was an early example that failed to capture the conviction of Hamburg's grand panoramas. Hagenbeck's creation of high visual drama as well as Eggenschwyler's attention to realism was perpetually reduced as zoos merely parroted each other's design mannerisms. Soon, many zoos were producing grottoes and cliffs and islands of fake rock formations devoid of any geological awareness. Today, artificial rockwork is omnipresent in every type of exhibit, regardless of habitat type, and oftentimes in degraded caricature that mocks the beauty and fascination of natural formations. If one zoo designer had patented the notion of a smooth vertical wall with an overhanging lip, he or she would now be able to own a professional basketball team.

Convincingly realistic rockwork is highly unusual: examples such as those created for Tucson's Arizona-Sonora Desert Museum exhibits, first under Merv Larson in the 1960s and more recently and with even greater geological realism under the guidance of the landscape architect Ken Stockton; or for the Bronx Zoo under the direction of landscape architect John Gwynne, are rare exceptions. Yet at one time American zoos, especially, did know how to build artificial rock formations of compelling veracity and strong aesthetic appeal. Denver Zoo's mountain habitat, built in 1918, surpassed even Eggenschwyler's level of geological accuracy, taking plaster molds from local mountain ranges. Saint Louis Zoo's 1921 bear exhibits were inspired by careful attention to the stratification and form of natural limestone bluffs. San Antonio Zoo also produced bear and monkey exhibits in the 1920s with high levels of authenticity in their rockwork (Hancocks 2001).

Artificial rockwork is now the preferred solution of choice for many zoo designers to almost every zoo design problem. It dominates much exhibit design, but is usually a mere pastiche of the real thing, typically looks insubstantial—resembling crumpled cardboard or poured mounds of concrete—and indiscriminately pops out of the ground like mushrooms. In Europe, instead of making artificial rockwork, many zoos tend to pile individual rocks on top of each other, and then praise themselves for using real rock, as if it guaranteed naturalness. Real rocks, however, especially those of good size, do provide some benefits for the animals. They retain heat longer and are slower to lose it than thin-walled artificial rocks that are devoid of any insulation value, and thus can provide some comfort on cool or hot days.

In the mid-twentieth century, some very important publications were produced that should have led to far-reaching changes in zoo exhibit design. The Bronx Zoo director William Conway published a paper in the journal *Curator*, "How to Exhibit a Bullfrog" (Conway 1968), that argued in lively prose why exhibits should focus on habitats and not just on animal forms or individual species. It was many years before the challenges in that paper were met, most effectively by Conway himself, in the Bronx Zoo's Congo exhibit. Before that paper, however, Heini Hediger, director of first the Basel and then the Zürich Zoo, published 2 books (Hediger 1950, 1955) in which he argued for a biological approach to zoo exhibit design. Hediger explained the concepts of territory, the phenomenon of flight distance, the importance of play for animals, and the need for animals to interact with natural elements of the environment. He made it clear that designers should concentrate on the contents and the quality of the space. But his ideas fell largely on barren ground. Zoo managers and zoo designers continued to develop exhibits insufficient for living creatures. Arboreal animals survived in empty cages. Burrowing animals lived on concrete floors. Social animals endured solitary confinement. Predators were denied distant views. Animals were fed monotonous diets at regulated feeding times, devoid of contact with natural vegetation or, often, of natural weather. Zoo exhibits through almost the entire twentieth century were typically sterile spaces, designed more for convenient scrubbing and sluicing rather than for the comfort or well-being of wild animals.

Partly, this was because zoo directors and curators either demonstrated their own lack of design ability by planning exhibits themselves, or depended on the services of an architect. Most architects are in their profession because they like making buildings, and many of them tend to focus on what the buildings look like above all else. They rarely see beyond the structure to notice what effect it has on the inhabitants, and generally dislike living beings spoiling the purity of their designed environments. Zoo directors spent many decades repeating the old joke about an architect being the most dangerous animal in the zoo—yet persisted in employing them. Architects, trained to produce architectonic solutions, pay close attention to hard materials and the aesthetics of built forms. They are usually not the best people to design spaces for wild animals or to employ the vocabulary of a design palette that embraces living plants, soils, natural drainages, and landforms, which are of course the design elements of *landscape* architects, who have quite different training and aims.

The works and the roles of landscape architects have hardly been a secret. English landscape gardeners such as William Kent, Lancelot "Capability" Brown, and Humphrey Repton had in the seventeenth and eighteenth centuries created graceful landscapes with strongly romantic allusions to nature (Hoskins 1970). Frederick Law Olmsted's 1858 design for Manhattan's Central Park, as well as the many other parks, parkways, and neighborhoods that he created across the United States, had spoken eloquently of the benefits to be gained from intelligent application of landscape design in urban life (Olmsted 1971, Ewing 1996), and he was initially employed for the first—but aborted—concept plans for the National Zoo in Washington. Yet landscape architects were not actively engaged in zoo design until the mid-1970s, when the new firm of Jones & Jones was hired to produce a master plan for Seattle's Woodland Park Zoo. The firm introduced a different approach to zoo planning, diagramming the site's shade and sun patterns, slopes, drainage, soils, and vegetation to arrive at the best locations for replicating different habitats, and developing a matrix to assess these against an ecological system of life zones (Jones, Coe, and Paulson 1976). Its master plan included designs for new exhibits that used natural landscapes as a guide rather than works from other zoos: indeed, as director I made a deliberate decision that the design team should *not* take the traditional international zoo tour when they obtained the Woodland Park Zoo contract.

The needs of the animals, in particular, were considered a priority, and resulted in their being given places to hide from view if they wished; natural vegetation to interact with; landscapes that were complex and sufficiently challenging to invite exploration; and, for interior spaces, close attention to comfortable and variable lighting and to soft acoustic treatments. The outdoor spaces were designed to reflect as closely as possible the visual mood and quality of the animals' natural habitats.

Further, and significantly, this natural habitat landscape was expanded to encompass the public areas, with special emphasis on embedding visitors in the landscape before they encountered the animals on display. The intent was to give visitors the opportunity to engage their senses in a rich natural environment and, since habitat loss is the greatest threat to wildlife, for them to gain an appreciation—if only subconsciously—of the link between specific animals and specific types of habitat. Grant Jones coined the term *landscape immersion* for this approach (Hancocks 2001). It was critical, in this philosophy, that there be no sense of barrier between humans and animals and landscape. Thus, instead of copying ideas of barriers from other zoos, the zoo staff and the design team gathered examples of scenes from nature that could be employed as barriers, such as fallen trees, earth slippages, washouts, mud banks, streams, and grass-edged ponds. The essential goal of the design was to replicate the sense of exploring a wilderness.

Jones & Jones sought ways to incorporate artificial structures into the landscape, burying buildings under sod roofs, for instance. It was the antithesis of an architectural approach. Housing structures were necessary at Woodland Park Zoo, as they are in most zoos, to accommodate animals from climes quite different from the local weather patterns. When zoos display large animals from a climate similar to their own location, or, better, from within their own regional biome, they do not need to build big, climate-controlled structures for shelter. At the Arizona-Sonora Desert Museum, for example, species from the region require minimal shelter, and the exhibits often incorporate the surrounding desert terrain. The 1998 coyote exhibit ensures the animals a quality and quantity of space that could never be achieved architecturally (fig. 11.3).

Exhibits of this quality are not achieved simply by fencing off a section of land. The siting of the rock in this scene was carefully considered, to create distant views for the animal—all predators seem to benefit from elevated viewing sites—and thereby encourage it to be in good public view. Every detail of the exhibit was considered, to create an experience equal to an authentic wildlife encounter. The enclosing lightweight mesh fence of very thin and knotted cables, now marketed as Invisinet, is so skillfully designed as to be practically invisible. It required significant amounts of Stockton's ingenuity and time to conceive and to test this design—a situation unsupportable by consultant designers working under the conditions imposed by competitive contract bids, and another example of the benefits obtained from having talented designers on staff.

Initially, the landscape immersion concept introduced at Woodland Park Zoo in the 1970s evoked a mainly hostile reaction from most other zoos, especially from professionals in established zoos who intensely disliked its unkempt appearance. San Diego Zoo set the accepted standard of the time: its zookeepers, with obligatorily clean-shaven faces, were also required to mow the grass in their exhibits. Many zoo directors and curators thought the additional landscaping for public areas was a waste of money, that the dedication to naturalism was unnecessary since animals only judged their enclosures on practicality, and that efforts to make the exhibits look like wild places only made it difficult to see the animals. Some deigned to take notice of the new approach. Wichita's Sedgwick County Zoo director, Ronald Blakely, writing on significant zoo design for a national survey (1985), thought only the new developments in his own zoo and at the zoos in Louisville and Columbia, South Carolina, were noteworthy. He considered them "paradises."

Within a couple of decades, however, zoos across the United States had adopted landscape immersion as the essential exhibition design technique. Today, landscape architects who once worked in Jones & Jones's office are principals in the majority of American zoo design firms, and Seattle is "considered the global center of zoo design" (Chozick 2009). It is a tragic irony, then, that the fundamental principles of landscape immersion exhibits are now rarely practiced. The demands of commercialism in today's corporatized zoo mean that animal needs are not paramount, but are always at risk of being compromised in favor of what the paying visitor wants. Attention to the fine details of realism is rarely considered worthwhile for any intrinsic value. A prolific combination of fence posts, drain covers, stainless steel dishes, concrete edges to water bodies, dead trees with sawn-off limbs, paved surfaces, even artificial grass, is common in most zoo exhibits. Because the exhibits are typically impoverished, keepers routinely add a jumble of artificial objects for animal activity. It all defeats the justifications for the exhibit's existence, and reverts to the menageries' base purpose of showing people the shape, size, and color of wild animals.

Zoo professionals usually dismiss such criticism as simply elitist aestheticism. But the physical environment in which people view wild animals has a direct influence on their attitudes. The Yale psychologist Stephen Kellert (Kellert and Dunlap 1989) measured zoo visitor opinions and noted that zoos displaying animals in naturalistic environments had positive impacts on their visitors: the more authentic in appearance, the more positive the response. Animals presented in ugly and unnatural environments increased visitors' negative attitudes toward wildlife, and generated fear and dislike. A study by the psychologist Ted Finlay (Finlay, James, and Maple 1988) on people's perceptions of animals in various zoo environments and in wild habitats also demonstrated that the context in which an animal is viewed influences how and what people think of the animal. Wild animals evolved in specific types of wild habitats: they are inevitably seen out of context when viewed in anything other than their natural

Fig. 11.3. The coyote exhibit at the Arizona-Sonora Desert Museum, Tucson, designed by staff landscape architect Kenneth Stockton. (Photography by Kenneth Stockton. Reprinted by permission.)

environment. Every detail that heads away from a natural scene is therefore a move toward artificiality, and failure.

Many zoo managers apparently do not know what the words *natural habitat* mean. They routinely use the expression to describe exhibits of exceedingly poor design that bear no visual or practical resemblance to wild places. There are hundreds of examples, ranging from some recent ones at Chester Zoo, England, to many in China's zoos.

Each time that zoos present wild animals in environments clumsily constructed of artificial components, they insult their visitors' intelligence and, worse, ignore their responsibilities to the animals in their care and their justification for having them in captivity. When an architect designs a monument to his or her own ego, or a keeper places a clear-sawn limb off a dead tree in plain view, or a wall is formed of concrete blocks or stained planks, or a stainless steel dish is openly displayed on a shelf or ledge, or yet another piece of crudely fake rock is accepted by a curator, or a floor is formed of asphalt, or a metal or timber fence is visible, or a metal gate faces the viewing area, or a lampshade is dangled over an animal's resting spot, or drain covers are exposed to view, or neatly milled fence posts are allowed into the scene, or the edge of a pond is lined with artificial curbing, or ropes and chains dangle in view, there is another step away from the natural. And when a number of these awful details accumulate in one exhibit, as they frequently do, then the result becomes meaningless. Zoo managers are often blind to all this, perhaps because it is difficult to see one's daily surroundings with a fresh eye and to note incremental degradation, but also because they typically are not trained to analyze the quality of a designed environment. Sadly, too, they often fixate only on *the animal* rather than on *the animal within its environment*. Most British and many European zoos specialize in degrading the inherent beauty or dignity of a wild animal with inappropriate exhibit designs. A new zoo in the Netherlands, called Gaia Park, displays animals in exhibits so lacking in either naturalness or visual quality that it manages to debase both the animals and the Gaia hypothesis whose name it has hijacked.

Zoos would therefore benefit from adding formal design skills to their mix of professional staff abilities. It was once unusual to have veterinarians or educators on staff. Zoo fundraisers and marketing staff were unheard of until quite recent times. Employment of zoo design staff is overdue. In-house designers are needed to plan new small exhibits, to handle

Fig. 11.4. This giant panda exhibit at Ocean Park, Aberdeen, Hong Kong Island, is but one example of zoo doublespeak: a strange and obviously artificial assembly by Taoho Architects that the zoo nevertheless describes as “simulating a wild highland.” This sort of false labeling is commonplace in zoos around the world. It is a disservice to the zoo’s visitors, and to the complexity and beauty inherent in real wildlife habitats.

modifications of existing exhibits, to coordinate consultants for large exhibits, and to be a voice and a translator of design jargon for the zoo operational staff. In addition, design teams would benefit specifically from injecting the occasional expertise of ecologists and geologists into exhibit designs. And special advancement would be achieved if every zoo design team also nominated at least one staff member as a delegated spokesperson for the animals. The need for this cannot be overstated.

One of the main reasons the Bronx Zoo produced consistently high-quality exhibits during the long tenure of director William Conway was the existence of a resident design team, and because it comprised designers from a variety of arts and design backgrounds, and was never led by an architect. Between 1982 and 2009, the staff landscape architect (and ornithologist) John Gwynne led a team that produced exhibits of grand scale, superb quality, and impressive creativity. Simple but effective design techniques created the sense of vast distance that characterizes the natural habitat of Gelada baboons and Nubian ibex (fig. 11.5), an exhibit that is an extraordinarily convincing replication of a wild habitat inspired by close study of the real thing. Exquisite attention is given to the visual mood and topographic scale of the landscape, to the quality of the appearance of the exhibit, and to the diverse needs of the visitors and the animals. Gwynne always seems concerned about meeting the needs of the animals.

If animal needs were at the highest levels of priority for zoo exhibit design, there would be instant and important improvements. Given a voice, animals would not choose to sleep on concrete, be locked inside for days and even weeks, breathe stale air, wake to sudden bright lights, or suffer loud noises ricocheting off walls. They would not ask for cramped spaces where they could not carry out natural behaviors. They would instead prefer environments rich with possibility, big and complex enough to explore. Some would choose large, stable groups; others would prefer only their own company. They would ask for interactions with different types of water bodies, with different types of soils and other substrates, and with a variety of different types of natural vegetation. They would appreciate maximum opportunities for natural browsing or grazing, and insist on facilities for digging or swimming or climbing and all their other natural behaviors. They would request protection from stress or boredom, and shelter to suit their immediate desires at any time they chose.

Developing and operating a zoological park is a challenging and complex task. Indeed, it would be difficult to find another institution so multifaceted. Zoos must continuously balance a very wide array of disciplines that are sometimes conflicting: science, recreation, education, commerce, conser-

Fig. 11.5. The Baboon Reserve at the Bronx Zoo, New York, opened in 1990, was designed by the staff landscape architect John Gwynne and the exhibits design team of the Wildlife Conservation Society. (Photograph © Wildlife Conservation Society. Reprinted by permission.)

vation, animal husbandry, ethics, media relations, breeding, philosophy, horticulture, health care, entertainment, welfare, food services, financial strategizing, strategic and physical planning, and exhibit design. But because they must attract visitors, and aim to encourage respect for wildlife and shape public attitudes, zoos need to pay extra attention to the way they present animals, and to the quality of their designed environments. Unforgivably, spaces for the animals are often deficient. John Seidensticker, former curator of mammals at the Smithsonian's National Zoo, once was hired to advise a "well known zoological park" on a new exhibit for jaguars (Seidensticker and Doherty 1996, 181). The zoo's designers wanted to create an image of a jaguar lying in the sun by a body of water in the tropics, as if they were assembling a static diorama. For this they had allocated less than 28 m^2—equivalent to about 3 automobile parking spaces. Seidensticker knew from studies that this limited space would engender "excessive stereotypic behavior in the jaguar," and that visitors would take home "a negative message" (ibid.). The designers, however, insisted that the allocated space was adequate, and that design work had proceeded too far to allow changes. (In other words, their fees would be negatively affected if they needed to produce more design work.) Similarly mean-spirited attitudes and inadequate spaces are prevalent in zoos. The multimillion-dollar Lied Jungle that opened at Henry Doorly Zoo, Omaha, Nebraska, in 1994, one of the world's largest zoo rain-forest exhibits, provides pitifully small spaces (formed principally of concrete) for its animals, both on and off exhibit.

The zoo design specialist Jon Coe has said that he judges the effectiveness of a zoo exhibit by "the pulse rate of the zoo-goer" (Greene 1987, 62). He talks of the need to design exhibits that will make the hair stand on the back of a viewer's neck. It is the same sensation one can experience upon encountering an animal in the wild: a mix of admiration, respect, awe, and a touch of fear, and is a combination only achieved in the theatrical milieu of a wild landscape. Attempts to convince zoos of the need to reach visitors at this emotional level have often been derided as romanticism. Yet if zoos are to help in creating an informed and aware citizenry that is sympathetic to the increasingly urgent plight of wildlife, they need to be much more effective than they have been in the past. They need to remind their urban visitors of the *wildness* of wild animals. This cannot be stressed too highly. Rather than displaying wild animals as aberrant beings, or cute exotic pets, or creatures clearly in captive conditions, zoos have to find ways to convince people of the splendor, the beauty, the ruggedness, the realism of the wild. A central component of the answer to this problem lies in design, and in finding more convincing ways of presenting animals to the urban and suburban zoo audiences that are increasingly divorced from any contact with nature.

The origins and history of zoos reveal the best and worst of humans. Our reverence for nature is matched by our continuous attempts to control and smother its wildness. Zoos have repeatedly been assembled as mere symbols of status, and have frequently been sources of anguish and misery for the animals in their care. The reason for zoos' existence today, however, is urgent and critical, most especially to serve as an advocate for wildlife and as a venue for respectful human contact with wild animals. This is why zoo design requires the most superb and exquisite care.

WHERE NEXT?

Stunningly impressive exhibits were developed in zoos in the latter part of the twentieth century. Tacoma, Washington's Point Defiance Zoo built especially fine immersion exhibits in the 1980s, the first to follow Seattle's examples. Under the directorship of William Conway, the Wildlife Conservation Society produced an extraordinarily large number of highly competent exhibits at its several New York zoo sites. The Congo and the Baboon Reserve exhibits at the Bronx Zoo are some of the finest emotional and educational experiences for zoo visitors ever created. These 2 complex exhibits are based on intellectually sound approaches, are dedicated to and supported by remarkably strong conservation ethics, and demonstrate a consistent commitment to the highest design standards. The "Ring of Fire" Arctic exhibits at Detroit Zoo, designed by Jones & Jones, are similarly noteworthy, as is that firm's work at San Diego's Wild Animal Park. Disney's Animal Kingdom in Bay Lake, Florida, has a vast African savanna landscape of forceful realism, also designed by Jones & Jones. Kenneth Stockton at the Arizona-Sonora Desert Museum has produced perhaps the most compellingly realistic immersion experiences, following a naturalistic design tradition at the Desert Museum that was established by Merv Larson in the 1960s; but he takes the concept much further by also paying as much attention to the behavioral and psychological needs of the captive animals as to the physical components that create the sense of realism for visitors.

The effectiveness of exhibits at the Desert Museum is greatly enhanced by their being surrounded by the natural habitat they seek to interpret. Yet, notwithstanding polar bears at Singapore Zoo and elephants at any number of cold-weather sites, a logical argument can sometimes be made for zoos to display life-forms far removed from their own climate, such as many of the exhibits for small animals that demonstrate the excellent conservation work with exotic island species at the Durrell Wildlife Conservation Trust, on the isle of Jersey in the English Channel. At Zoo Zürich, Switzerland, visitors can escape from cold, bleak days and enter a world of lush green vegetation and warm humidity within the very large space of the Masoala Rainforest Hall designed by the architects Gautschi Storres and the landscape architects Vogt AG (fig. 11.6). Here they can explore a habitat that skillfully

Fig. 11.6. Built to high environmental standards, the Masoala Rainforest Hall at Zoo Zürich, Switzerland, employs the best available technology to reduce energy consumption. (Photography by Edi Day, courtesy of Zoo Zürich. Reprinted by permission.)

Fig. 11.7. The Platypusary at Healesville Sanctuary, Victoria, Australia. According to its architect, Catherine Fahey, it is "intended to imply the dream world these small animals occupy" (Norman Day, "Healesville Platypusary," *Age*, August 23, 2005). To what purpose is not apparent to the author. (Photography by David Hancocks. Reprinted by permission.)

replicates features of Madagascar's Masoala National Park. A diverse range of small animals lives within this exhibit, which focuses on habitat complexity, gives equal attention to plants and animals, and minimizes attention to the designers' hand. Masoala Rainforest Hall is the public face of the zoo's strong conservation partnership in Madagascar, and could be considered worthy for just this fact. But it also offers visitors a landscape of impressive authenticity, equal to other exhibits developed at this zoo under Alex Rübel's direction (such as the 1995 spectacled bear exhibit by the landscape architect Walter Vetsch), which celebrate not only good works in conservation but also sensitive and intelligent design.

These examples are all gorgeous exhibits: beautiful in concept and in visual detail. They contain a fundamental lesson for zoo exhibit design teams. It is rather like the guiding ethic for medical practitioners—*First, do no harm*. Zoo exhibit designers and caretakers should insert nothing that will detract from the inherent beauty of the animal, or diminish the inherent splendor of the habitat in which the animal evolved and is an integral being.

When zoos employ architects to design new exhibits, they assume a responsibility to ensure that they are especially attentive to this aspect of zoo design. It takes greater heroism, and is a more noble aspiration, for architects to subsume their professional tendency to make bold statements with built structures when attention needs to be diverted to the animals. Not only are the zoo's animals its primary clients; they also need to be viewed and understood by visitors within the context of their natural habitats—not as isolated species, and not as natural objects within a high-design environment. The contemporary trend in architecture toward visual extravagance, as Witold Rybczynski, one of America's most prominent writers on architecture, has noted, is an aberration (Rybczynski 2001) and an especially regrettable one in zoos. Part of the problem is a common failure for architects to understand what style is. The modernists consciously rejected "style" (the Swiss-French architect Le Corbusier, for example, declared that style was nothing more than "a feather in a woman's hat"), but it is in fact an essential aspect of architectural design, its lexicon. Rather than embracing fashion and rejecting style, architects tackling zoo projects would better note Gabrielle Chanel's observation: "Fashion passes, style endures." And in terms of zoo design, the dominant and enduring style is that of *nature*. It is what must be prominent in the architect's design vocabulary.

In the 1990s, Healesville Sanctuary, Australia, built a platypus exhibit by the architect Greg Burgess and the landscape architect Kevin Taylor that blended into its forested habitat with a pleasing subtlety. But an additional Platypusary built at this zoo in 2005 pursues a very different philosophy. This exhibit (fig. 11.7), by the architect Catherine Fahey, clamors for attention to itself rather than attempting to focus on nature. It screams loudly that architectural design is more important than either the platypuses or their freshwater habitats. The structure is flamboyantly clad in day-glow pink panels—of a hue that the sanctuary's then director, Matt Vincent, proudly claimed to have selected himself, though it seems unlikely the architect would have allowed such a thing—affixed to a shiny, golden metal structure, with orange and lime-green graphics and flooring of glistening glass marbles set in concrete.

The foundation of the landscape immersion concept for zoo exhibits was that it should aim to convey the essential experiences of discovering an animal in a wild place. The fact that this is difficult to achieve, and requires exquisite attention to place and to detail, is no excuse for zoos to make only a half-hearted attempt at it. Moreover, and critically, the problem must not be restricted to the appearance of the exhibit. Satisfying only the superficial aspect of the problem has resulted in too many zoo exhibits which look vaguely realistic, but are clearly ersatz places, and which fail to meet any of the behavioral requirements of the animal inhabitants. Creating the illusion of a wild place is not the same as creating the illusion of *a wild encounter in a wild place*. Both the animals and the human visitors need to have that sense of a natural experience with a natural environment.

The aim of replicating the essence of the wild must always remain a basic goal for zoo exhibit design. It may create frustrations for designers and operators, and easily swept concrete floors or wire mesh barriers may be much more appealing to budget managers, but no milieu other than their wilderness home is appropriate for wild animals. Wild habitat exhibits are timeless in style, and can never go out of fashion. Most important, they are also the basis for understanding any wild animal: its appearance, its behaviors, its adaptations, its very being are all the product of evolving within and adapting to a certain type of environment. If zoos are willing to display animals in any other type of setting, or in some tame and tawdry version of a natural habitat, they are undermining the justification for their existence.

The very difficult challenge for zoo exhibit designers is to find ways in which they can create exhibit landscapes that look and feel and sound and smell like the real thing, and that not only are thus very convincing but also can be effectively and economically managed and maintained for wild animal interaction. It is not an easy task, but it is an imperative goal.

Design of an exhibit is only one component of its success (or failure). Maintenance and management are equally important, and must be considered in the design. Access for cranes to remove and introduce very large objects is required, so that the exhibit space can be enlivened periodically. Introducing large trees is especially beneficial for a wide range of species. When the concept of landscape immersion was introduced, at Woodland Park Zoo in the mid-1970s, a principal and inherent objective in its philosophy was that not only zoo visitors but also zoo animals should be within a simulation of the animal's natural habitat that was as accurate as possible. This was not just for educational and aesthetic reasons, but also for direct benefit of the animals, to allow them direct interaction with living vegetation. It was soon apparent that the animals greatly enjoy such interaction, but to such an extent that, in the small spaces of zoo exhibits, they killed the vegetation. Two very important lessons emerged: provide live vegetation for animal and public benefits, but provide, too, for its easy replacement.

Trees and shrubs newly introduced into an exhibition space require temporary protection. Unfortunately, zoos have invariably chosen to avoid the inconvenience and cost of periodically replacing live vegetation, preferring instead to erect permanent protection devices to prevent animal contact. It is a cheaper and easier strategy, but it is the antithesis of the landscape immersion philosophy. As compensation, and usually at the behest of zookeepers aware of the boredom of the animals in their daily care, zoos then clutter the exhibit space with a variety of extraneous artificial objects to "enrich" the animal's life, further removing the exhibits from landscape immersion principles.

Interaction with living vegetation is an immensely satisfying and natural activity for many mammals—from primates to carnivores, from big ungulates to almost all small mammals—and observing these activities adds greatly to visitor enjoyment of exhibits. When a new exhibit space for gorillas was opened at Melbourne Zoo in 1990, these benefits were clearly in evidence (fig. 11.8). The curator of horticulture, Michael de Oliviera, was closely involved with the design and planning, and was intent on replacing vegetation often enough to meet both animals' and visitors' needs. Today, however, such an approach has long disappeared. As is the norm at most zoos, electrified wires now permanently deny the gorillas contact with live vegetation. To the casual public eye, the animals appear to be in lushly planted environments, but in reality their world consists only of quarantined spaces; impoverished corridors of heavily trampled grass and dirt. This problem is intensified by the fact that most zoos also persist in locking up their animals after public hours, confining the animals in night quarters that are as sterile and noisy and inappropriate as the cages of the old menageries of past days. In far too many instances of zoo exhibit design and management, fundamental aspects of the nineteenth-century approach to zoo exhibit/cage design still prevail beneath a modern veneer of naturalism. The obsession with designing spaces that keep the animals on public view at all times is driven so hard by marketing directors (and, equally often, by zoo board members) that it prevents essential progress in zoo exhibit design.

Fig. 11.8. The gorilla exhibit at Melbourne Zoo, Australia, in 1990 (design concept by David Hancocks, landscape architecture by Stuart Green, horticulture development by curator Michael de Oliviera), before the introduction of electric wires to prevent animals interacting with live vegetation. (Photograph courtesy of Zoos Victoria Photographic Collection. Reprinted by permission.)

Zoo exhibits of the future will also need to employ more persuasive techniques for effective interpretation. In days past, zoos were accepted as nothing more than a place where people could observe an animal's size, shape, and color. Inevitably, amidst such an ethos, many generations of zoo animals passed lives of great boredom in empty enclosures. Millions of zoo visitors, at the same time, had no opportunity for any activity other than gawking, and eating junk food.

A favorable marriage of presentation and interpretive techniques must be the mainstay of future zoo exhibits. In the early 2000s, through the efforts of Jackie Ogden, conservation director at Disney's Animal Kingdom, the Association of Zoos and Aquariums (AZA) at last began the process of objectively assessing the educational effectiveness and the degree of conservation awareness that zoo visits may or may not generate.

At the time of writing this chapter, the AZA was engaged in a flurry of activity on behalf of several of its member institutions who were being criticized about standards of care and environmental quality for their elephants. On several occasions the AZA directorate distributed media releases, claiming, "as ambassadors for their species [zoo elephants] inspire people to protect them" (e.g. Vehrs 2006, B7). There is no evidence that this is true. Inspiring zoo visitors to protect wildlife can be presented as a laudable goal, but is not a fact achieved. Indeed, even before such media releases were distributed, the AZA, prompted by Ogden, had funded a review of the literature about what visitors learn in zoos. This review, by the Institute for Learning Innovation, had confirmed that "little to no systematic research on the impact of visits to zoos and aquariums on visitor conservation knowledge, awareness, affect, or behavior has been conducted" (Dierking et al. 2002, 19).

A close examination of the impact of zoo visits on visitor behavior (Smith, Broad, and Weiler 2008, 545) determined that "despite the rhetoric . . . there is little evidence" that zoo visits influence behavior. It reviewed many studies that examined the role of zoos in influencing visitor behavior and determined that "there is little long-term impact from a single experience at a zoo," and that any increased commitment to conservation after a zoo visit soon reverted to previsit levels.

Zoos enthusiastically promote themselves as conservation organizations, and routinely claim that their exhibits promote conservation ideals. There is much distance, however, between the ambition and the result. Much of the problem lies in lack of integration and of focus.

The programs, the operations, and the exhibits that zoos create serve as one intertwined whole. The goods that zoos choose to purchase for their own use, the content of the education programs they offer, the products for sale in the gift shop, the type of food in the restaurant, and the ways in which animals are presented in the exhibit spaces are each equally important components of the purpose and justification for the zoo, and in concert they determine what people learn. In their own way they are all, in effect, zoo exhibits. No animal exhibit alone can convey all the messages and carry the degrees of understanding that visitors need to acquire to ensure a valuable result from a zoo visit.

Interpretation is thus a critical component that deserves far more careful attention: the exhibit itself serves most usefully as a stage for telling the stories, not as the only source of the interpretation. At present the typical zoo exhibit is designed to meet several criteria—most especially preventing animal escape, ensuring animal visibility, and, sometimes, even providing drains that work. It is then usually turned over to the education staff to develop some stories for presentation on graphics panels. The best design solutions, however, come from an inversion of this system, when an interpretive message is determined as a fundamental guide for the designers. And the best interpretive solution surely does not emanate from the ubiquitous graphics panel. There is no evidence that this interpretation tool has benefits that match even slightly the high cost of its production and visual intrusion on the landscape.

There are 2 nontraditional examples that seem to carry the possibility of greater effectiveness. At the Arizona-Sonora Desert Museum, very highly trained (and highly dedicated) docents stationed around the grounds employ a wide range of artifacts, including many types of small life-forms in portable habitat display tanks. The docents engage visitors in direct and personal story-telling experiences that are automatically custom-tailored to the visitors' levels of apparent interest and comprehension. The docents, including a cadre of junior docents for communicating with young visitors, are not *tour* guides; they position themselves at set stations, often with stories and artifacts relative to adjacent specific landscape elements or thematic exhibits. They are also not intended to be substitutes for static interpretive displays, for different types of visitors have different learning strategies. But a wealth of surveys over many years makes the museum believe that this method of interpretation, based as it is on personal contact with generalists who have graduated from a remarkably thorough training program, has a profound effect on the perceived value of the visit. There is also much anecdotal evidence that these docents have often shifted visitors' attitudes and values. Assessing the long-term general effectiveness of this docent system would be immensely useful.

Another method of interpretation worthy of close consideration by zoo designers and educators is the use of high-technology equipment that was employed at Wildwalk, in Bristol, England—the city that is the world's center of wildlife filmmaking. Moving images via various media were integrated with exhibition habitats containing live animals. This mix encourages animal *watching*, which is a potentially far more valuable way to gain people's interest and support for animal welfare and conservation than they might have from just animal *looking*. However, for most visitors most of the time at most zoo exhibits, looking at an animal that is doing little or nothing of interest is the only option.

Animals are not constantly engaged in interesting activities: many of their most fascinating behaviors are usually ephemeral or seasonal and thus rarely witnessed. Moving images, however, can show behaviors that people would normally never see—sometimes even once-in-a-lifetime events. Nonetheless, projected images have their own limitations, and living animals have an attraction that is far greater than film alone. The cleverness of Wildwalk, a grand experiment conceived and created by the filmmaker Christopher Parsons, former head of the BBC television natural history unit, was its combination of living animals *and* moving images of their behaviors. Wildwalk, which closed March 2007, focused on very small life-forms, and placed more emphasis on film presentation than on live animals. Even so, this integration of film and reality contained important lessons that zoos could very usefully consider and that creative exhibit designers should carefully review. The BBC—most notably with David Attenborough's programs that have examined the lives of plants and animals in a vast array of habitats and times, from life underground and in the sea, to time across seasons and in milliseconds—has developed examples of technological wizardry that could surely benefit zoo exhibits. One simple and obvious example at Wildwalk was the integration of moving images into the interpretive graphics.

Wildwalk, like several modern zoos, was deeply engaged in wildlife conservation. Such institutions recognize that the manner in which animals are presented to visitors is a critical component in forming opinions and establishing values. The stakes for zoos and for public support of wildlife conservation programs are high in this regard. Zoos attract huge numbers of mainly urban visitors: people who in large part are disconnected from contact with or understanding of the natural world.

Terry Maple, former university professor, AZA president, and director and builder of Zoo Atlanta, is trained as a scientist. He has argued that although AZA members voted in 1980 to establish *conservation* as the association's first priority, it may have been preferable to put *animal welfare* at the top of the list (Maple 2003). He has addressed the beneficial impacts this could have on collection planning, and it is well worth designers' considering the benefits it could bring to exhibit design. *Conservation*, in zoo parlance, usually means "breeding," and the criteria for successfully managed breeding programs are increasingly the basis for exhibit design briefs. Zoos first and foremost are needed as places to engage with the public on matters and issues that will shift their values and attitudes. I support Maple's notion that welfare would better serve as the principal priority for zoos, and I would place education as the close second item on the list. The AZA's Species Survival Plan is, however, officially regarded as the dominant justification and guide for modern zoos. The program is commonly referred to as the SSP, which could be more accurately defined as an acronym for a Self-Sustaining Program for zoos. It is less about guaranteeing the survival of wild animals than it is about ensuring the perpetuation of species *in zoos*. The zoo curators' breeding programs are vital, but they are better served in large tracts of land away from public zoo visitors; zoo exhibits can then concentrate on public education and attitudinal goals, unimpeded by other demands. This may be rather an oversimplification of the situation, but is presented here to serve the point that zoo exhibits are principally for *exhibition*. If Maple's admonition about the priority of welfare could be adopted, we would find beneficial changes both subtle and deep in the design approach to zoo exhibits. Once again, as was originally intended with the landscape immersion philosophy, the animal would be the principal client.

AZA likes to boast that attendance at its member zoos exceeds that at all U.S. professional sporting events combined. Surely, if these millions of zoo visitors were in fact gaining new understandings, new insights, and new enthusiasms for the protection and care of wildlife, we would not be facing the extreme situations that are decimating wild animals and their habitats all over the globe. Despite almost 200 years of professionally operated public zoos in the West, a large percentage of the citizenry is alarmingly ignorant about wild habitat desecration, and is biologically and ecologically illiterate to a disturbing degree. Whatever the future ambitions and direction for zoos and their exhibits, one thing is clear: we need to do much better.

RULES FOR EXHIBITING MAMMALS IN ZOOS

Philosophies and methods of approach are 2 vital keys to progress and improvement, but it can nonetheless be useful to review basic rules from time to time. A set of rules first drafted at Woodland Park Zoo in the 1970s, but surely still relevant, is presented here:

- Create discrete viewing places with overlapping lines of sight. This will encourage a sense of intimacy with the exhibit; prevent a feeling of being in a crowd; and, critically, prevent the distraction of cross views to other people. (Few things attract our attention more than other human beings.)
- Place animals at or above eye level: they look more impressive that way. Also, the animals then have wider and more distant views, will feel less stressed and crowded, and won't have objects dropped into their space.
- Provide places of safe retreat for the animals to use at their own discretion.
- Create as much variety as possible within the animals' spaces, and allow them to select their own options and individual preferences.
- Provide every possible important element from the animals' natural habitats, and in abundance. Make special effort to include natural features that stimulate useful activity, such as shrubs and herbs, live trees and rotting tree trunks, mud wallows, streams, various soil types, digging areas, etc. Importantly, plan for their periodic replacement.
- Replicate exhibition habitats that are typical and true to the characteristics of the animals' natural environments.
- Don't relegate plants to the role of merely being background fill-in greenery.
- Place viewers in the same replicated landscape as the animals.
- Make it difficult to determine what separates animals and people, so that visitors gain a greater sense of being part of the animals' world.
- Don't position food or retail outlets so they compete with the animal exhibit for attention.
- Design for natural-sized animal groupings.
- Ensure that adjacent exhibits relate to each other logically and form a complex whole.
- For best visual effect, combine as many species from the same habitat as sensibly possible, integrating mammals, birds, reptiles, amphibians, and invertebrates. (The curatorial frustrations with mixed-species exhibits as a conflict to their breeding programs highlight the need to recognize that the primary purpose of a public zoo is to display wildlife to visitors. Off-display areas are required for conservation breeding programs. On-display areas are required for making emotional and intellectual connections with visitors, and should thus be visually effective and highly realistic.)
- Pay close attention to every visual detail, and compare it to what one would find in the natural world.

Any of these rules can be broken, for a reason. But they should always at least be considered before rejection. The following principles, however, are essential for all zoo exhibits.

ZOO EXHIBIT DESIGN PRINCIPLES

1. ANIMAL REQUIREMENTS

Treat the animals as the principal clients. When evaluating their needs—psychological, social, emotional, practical, physiological, behavioral—compared to those of keeper staff and of visitors, place the animals at least first among equals. Carefully consider the quality of *all* their spaces, on and off exhibit. Above all, aim to provide the animals, if at all possible, with everything they would wish for themselves, in every detail. To this end, include one staff person on every design team to act as spokesperson for the animal client.

Fig. 11.9. Giraffes and zebras at the Werribee Open Range Zoo, Victoria, Australia, where they gallop, wander, and explore a 36-ha savanna habitat exhibit. (Photography by Max Deliopoulos. Photograph courtesy of Zoos Victoria Photographic Collection. Reprinted by permission.)

2. SPACE AND TIME

Allow a generous period for the research phase of the exhibit design, so that all aspects of the zoo site and of the natural habitat can be analyzed and close examination made of the natural lifestyles of the animals. Set construction schedules that allow time for plants to establish themselves before opening day. (Ideally, don't even set a grand opening day. The exhibit is never ready or at its best on opening day.) Design the exhibit to allow for future change: it is not a permanent set piece.

3. VISITOR AND STAFF NEEDS

Exhibition spaces must do more than just put animals on show. They should aim to satisfy the aesthetic, educational, experiential, intellectual, and emotional needs of human visitors, and provide a good functional working environment for zoo staff. Treat the visitors as guests: make the place look nice. Treat the staff as family: make the place safe and comfortable.

4. NEW WAYS OF DOING THINGS

Be perfectly clear about the exhibit's purpose: exactly why is it being developed? Exhibits that set out simply to show a particular animal species are unpleasantly close to the inadequate goals of the archaic menageries.

Note that if zoo visitors walking the site did not know just what they were expected to encounter or when, as happens in wilderness trekking experiences, they would approach the zoo with a different mindset: so, too, would zoo exhibit designers.

5. BASIC ESSENTIALS

Always argue for more and better space for the animals. We almost never provide enough (figs. 11.9 and 11.10).

Intense accuracy in visual replication is extremely important for good exhibit design, and *quality* of space is essential. But the amount of space is equally vital. *Quantity* of space is an integral component of the formula for assessing exhibit requirements of both the visitors and the animals. Big animals in particular need big spaces, especially those that are active and vigorous by nature.

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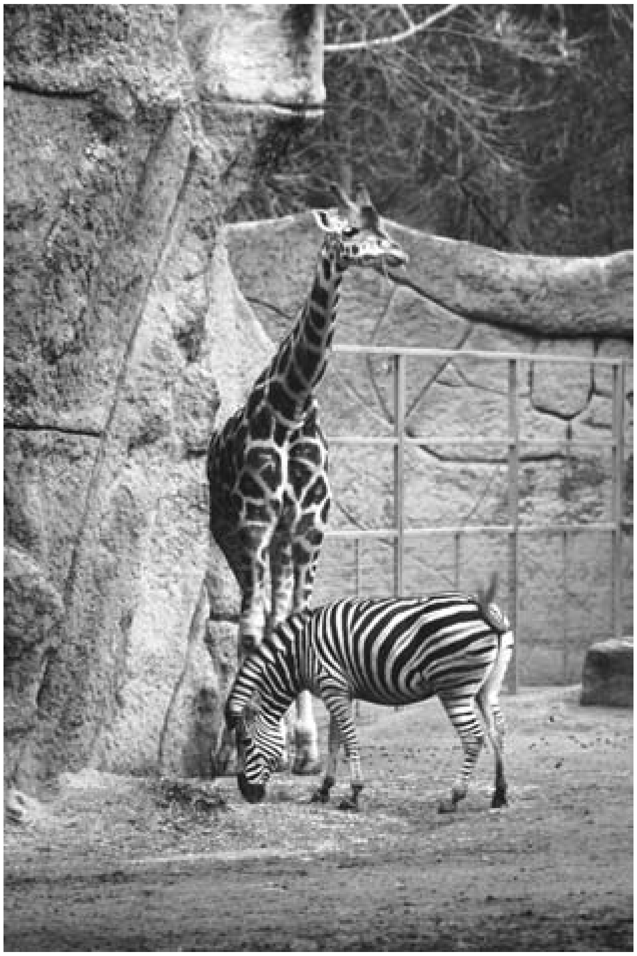

Fig. 11.10. Giraffe and zebra in a cramped enclosure at their nearby sister institution, Melbourne Zoo. (Photography by David Hannah. Photograph courtesy of Zoos Victoria Photographic Collection. Reprinted by permission.)

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12

Visitors, Conservation Learning, and the Design of Zoo and Aquarium Experiences

Emily Routman, Jackie Ogden, and Keith Winsten

INTRODUCTION

Many chapters in this volume describe how zoos have changed philosophically, operationally, and physically in recent decades. Responsible, professionally managed zoos and aquariums such as those accredited by the Association of Zoos and Aquariums (AZA) of North America, the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA), the European Association of Zoos and Aquaria (EAZA), and other regional associations have become conservation centers, dedicated to promoting the survival of the wild species we care for and the natural environment as a whole (Dierking and Saunders 2004; Rabb 2004). What sets zoos and aquariums apart from other conservation organizations is our quintessential feature: the opportunities we offer the public to get close to wildlife from around the world.

In 2004, annual attendance at AZA institutions was close to 140 million people; worldwide, zoo and aquarium attendance exceeded 600 million (AZA 2007). In the United States, more people visit zoos and aquariums than attend all major professional sports combined. The fact that so much of the public comes to our institutions seeking wildlife experiences puts us in a unique position among conservation organizations. The defining conservation role for zoos and aquariums today is to leverage these connections between our visitors and wildlife as a means to move the general public toward a more caring and sustainable relationship with nature.

The AZA captures that purpose in its vision statement: "We envision a world where all people respect, value and conserve animals and nature" (AZA 2007). The EAZA Web site states that education is central to the organization's mission, because "if conservation is to succeed, people need to be inspired to care about and understand animals and the threats they face in the wild" (EAZA 2007). Similarly, ARAZPA's education policy reads: "To provide exemplary learning opportunities that connect people with nature . . . [and] enable the community to better understand and contribute to a future where humans live in balance with the natural world" (ARAZPA 2003, 1).

The understanding that zoos and aquariums have the opportunity and responsibility to shape public values and behavior has inspired the recent evolution of visitor education. Although it always has been part of the purpose of zoos, only recently has education become such an essential element of the zoo conservation strategy, and for the first time is being tested and explored explicitly. This transformation has unfolded primarily over the past 3 decades, engaging a broad cross-section of the zoo professional community. It has been informed by knowledge from other fields, such as educational psychology, social psychology, and public health, and from institutions like children's museums and science centers. At the same time, it has benefited from our own field's progress in understanding visitor motivation and satisfaction, and new animal husbandry practices that have led to more active, visible animals—both of which make the zoo experience more enjoyable and more conducive to learning.

As the challenges to the world's biodiversity intensify, it is ever more critical to understand how zoos and aquariums can have the greatest positive influence on visitors' conservation-related attitudes and behavior. In this chapter we examine how visitor education and the design of zoos and aquarium experiences have changed through time: how far we have come, where we are today, and where we are going.

THE EVOLUTION OF VISITOR EDUCATION IN ZOO EXHIBITS

THE CHANGING ROLE OF ZOOS AND AQUARIUMS IN PUBLIC EDUCATION

The earliest zoos were fundamentally menageries (Hancocks 2001, Hancocks, chap. 11, this volume), often exhibiting collections of animals maintained by members of royalty. These institutions served to reinforce the social order. Just as the aristocracy had dominion over their people, so, too, did zoos demonstrate their dominion over animals. This changed dramatically in the French Revolution, when the gates of the king's menagerie, the Jardin de Plantes, were thrown open to the public. Under this new world order, zoos, along with museums and other public exhibitions, served as "public universities," providing a forum for learning about taxonomy and natural history (Hargrove 1996). This early form of visitor education was driven not by trained educators, but by scientists and architects. Animals usually were displayed in taxonomic groups, with signs providing scientific names. The hope was that visitors would create "accurate" mental models of the natural world that reflected the latest thinking on Linnean organization. In the early twentieth century, zoo designers such as Carl Hagenbeck began creating environments that simulated natural habitats or immersed the visitor in the animals' world. Although not explicitly recognized at the time as having an educational purpose, the intent behind such designs was to foster an awareness and visceral appreciation for wildlife in their natural habitats, an experiential goal that has become a central tenet of modern zoo design (see Coe and Dykstra, chap. 18, this volume).

The role of zoos in public education shifted dramatically during Hagenbeck's time. As information became more readily available to the public through books, radio, and other media, zoos and museums began to introduce organized educational programs. In the United States, the Bronx Zoo in New York City was one of the first to establish informative classes for schools and the general public. Today, most zoos and aquariums have active education departments.

As valuable as these formal education programs may be, the comparatively small numbers of people they reach limits their impact. This drawback became especially conspicuous during the rise of the environmental movement in the 1960s and 1970s. As people began to worry about clean water, land, and air, they became concerned for wildlife as well, and began to question whether keeping animals in zoos was justified. For some, neither the educational benefit of programs that reached only a small number of students nor the public entertainment provided by the zoo experience justified keeping animal collections. And with the advent of nature programming on television, zoos and aquariums were no longer the primary source of natural history information for the masses of guests who passed through our gates. What role could the zoo play? Zoos and aquariums began to focus their efforts on saving the natural world one species at a time, through the breeding of endangered species. The "Noah's Ark" paradigm was born.

This paradigm served us well through the 1970s, but by the 1980s the flaw in our thinking was apparent: saving species without preserving habitats ultimately would be futile. Consequently, zoos and aquariums began to support and implement habitat and community-based conservation projects. Although many of these important initiatives were successful, this investment, too, represented only a small portion of our institutions' operating budgets. Slowly, zoo and aquarium professionals came to realize that our most significant conservation assets were not only our animals, but also the millions of people coming through our gates, and that our greatest potential in conservation was as an agent of change—influencing the knowledge, attitudes, and behavior of our loyal audiences. By the 1990s, zoos and aquariums had come full circle, focusing once again on the educational impact of the visit, but now with conservation as the goal. Most recently, zoo professionals have become cognizant of the need to stop *assuming* that we influence visitors and instead are now *measuring* our impact and applying what we learn, thus increasing both our confidence and our competence as agents of change.

DESIGNING FOR LEARNING

Over time, zoo professionals came to recognize the need to capitalize on the essential zoo experience, encounters with wildlife, as "teachable moments." Reasoning that if visitors knew more about animals they also would appreciate them and care about them more, educators took out their reference books and began to create content that went beyond scientific names and species ranges. They tried to set a context by talking about habitat and causes of endangerment. But the resulting signage tended to be heavy on text and low on appeal. Perhaps even worse, any conservation messages were typically of the "doom-and-gloom" variety and generally failed to prove inspirational.

As education became accepted as a mission-critical function, zoos and aquariums increased their investment in reaching visitors. The field of visitor research began expanding from the museum environment into our zoos and aquariums, revealing, for example, how graphics could be made more effective (Rand 1985; Bitgood et al. 1986; Serrell 1996). At the same time, educators began to understand that even well-crafted graphics were not always the best way to reach all visitors. Educators and designers began to work together to apply principles of learning known to formal educators and educational psychologists, and to integrate techniques that other informal learning centers, such as science centers and children's museums, had begun using to great effect. Staff and volunteers began interacting with general visitors, pointing out animal adaptations and presenting wildlife biofacts such as skulls and fur. Educational concepts such as multiple intelligences and learning styles became part of the zoo and aquarium exhibit-planning vocabulary. Zoos and aquariums came to recognize the value of creating diverse opportunities for multisensory, experiential learning (White 1983; Brong 1989; Leiweke and Waterhouse 1990; Mayes et al. 1990; Wineman, Piper, and Maple 1996).

THE ADVENT OF VISITOR LEARNING CENTERS

As educators and designers began to adopt these new interpretive methods from other informal learning settings, highly interactive, media-rich learning centers began to appear in zoos and aquariums. As early as 1972, the noted herpetologist Carl Gans consulted with the Antwerp Zoo in Belgium to help it create a reptile exhibit that included reptile behavior videos controlled by visitors and innovative ideas like "cricket guns," which periodically stimulated feeding behavior. Later that decade, the Toledo Zoo opened the Diversity of Life gallery, which combined hands-on learning experiences with living animal exhibits. Visitors could crank a device that demonstrated different quadruped gaits, examine natural history specimens under a microscope, and balance a giant penguin egg on their feet. The Smithsonian National Zoological Park's HerpLab in Washington, DC, offered a variety of tabletop learning activities, including examining small, living reptiles and amphibians in specially-designed observation boxes (White 1983). In Philadelphia Zoo's Treehouse, children could climb on, hear, smell, and interact with magnified animals and animal homes such as a 7.5-m-high milkweed plant adorned with giant monarch butterfly life stages and a sweet-smelling honeycomb complete with child-sized bees. Brookfield (Illinois) Zoo's Be a Bird engaged visitors in full-body and multimedia activities that gave them the empathetic experience of living an avian lifestyle.

In keeping with the evolution of exhibit media in museums and science centers, zoos and aquariums eventually began to experiment with more high-tech exhibits. Toledo Zoo added a fanciful animatronic (animated robotic) creature that talked to visitors about animal adaptations. Saint Louis Zoo opened The Living World, which displayed over 150 species of animals in a dense installation with animatronics (including a robotic Charles Darwin), interactive computer stations, natural object displays, videos, prehistoric animal models, video microscopes, holograms, and more. Adventure Island, the Los Angeles Zoo's children's zoo, opened with a large number of technology-based elements alongside living animals and low-tech interactive devices. Two animal habitats had video effects that caused an image of an actor to appear in the exhibit with the animal. At a lizard exhibit, visitors could use remote thermal sensors to measure temperature in the enclosure, or delve into reptile adaptations for desert living at an adjacent interactive computer station.

Evaluations demonstrated that visitors enjoyed these kinds of facilities and learned from them (Birney 1990, 1991; Routman and Korn 1993), but the interactive exhibits generally were expensive to produce and to maintain, and the overall experience did not always make the best use of the unique asset of zoos and aquariums—the living collection. As a result of visitor satisfaction surveys (Normandia 1990) and problems maintaining the technology, Adventure Island eventually added more animals and opportunities for animal contact, and reduced the amount of technology. Most of the low-tech interactive devices, including stepping stones with animal sounds and viewers simulating animal vision, were retained, along with the popular animal exhibits. The Saint Louis Zoo's studies of The Living World showed that the computer-interactive devices effectively captured visitors' interest and conveyed information, while the live animals evoked wonder and appreciation. But in the denser of the 2 galleries, visitor attention was spread so thin that most of the exhibit elements were attended to only briefly—indicating that much of the money spent on creating and maintaining the exhibits was wasted, and visitor attention to the animals was diluted (Routman and Korn 1993).

While not without their challenges, these ambitious facilities helped the field as a whole learn about diverse types of media. Institutions that tried new approaches expanded the zoo and aquarium educators' tool kit for reaching visitors. Using interactive components, audiovisual media, and other educational strategies to increase visitor learning became the convention in zoological exhibit design. However, while clearly representing an improvement over static signage alone, these exhibits had yet to see the advent of storylines (or themes) to help visitors create meaning from experiences; nor was there much overt attention to creating inspiring experiences.

EMOTIONAL LEARNING: RECOGNIZING THE VALUE OF AFFECT

These new strategies for educating visitors were geared mostly toward cognitive learning, i.e. increasing factual knowledge. The hope was that increased knowledge would make visitors better stewards of the natural world. Unfortunately, new evidence was revealing a lack of correlation between increased knowledge and changes in behavior (Monroe 2003). Eventually, our profession began awakening to the significance of learning in the affective domain—feelings and attitudes. Based on the belief that if people cared about wildlife they would protect it, zoos and aquariums began to focus on fostering feelings of personal connection, appreciation, and caring.

Affective learning went from being regarded as *one* important dimension of learning, to being considered by some as the *most* important dimension. Certainly, researchers had documented affective learning through visits to zoos and aquariums; e.g. Marcellini and Jenssen (1988) found that a visit to HerpLab had significantly greater impact on attitudes toward animals than on knowledge. As zoos and aquariums began accepting the importance of the affective realm, they began to use more of a storyline approach to exhibit design, with interpretive elements and animal viewing experiences woven together into an educational whole designed to convey a unifying concept, such as the benefits to humans of a healthy ecosystem.

Recent exhibits strongly promote this focus on caring. Some use media rather than live animals. Detroit Zoo, for example, introduced a wildlife art gallery at the zoo entrance, live theater programs, and an animal adventure-themed simulator ride. Disney's Animal Kingdom Theme Park, Orlando, Florida, features a 3-D animated experience focused on fostering positive feelings toward invertebrates, called "It's Tough to Be a Bug"; and The Living Seas at Walt Disney World's Epcot Theme Park offers an interactive animated theater experience, starring the sea turtle "Crush" from the movie *Finding Nemo*, that promotes caring for marine life.

Other exhibits engage visitors in behaviors believed to foster an affinity for nature. At Brookfield Zoo's Hamill Family Play Zoo, facilitators known as "Play Partners" guide kids and their parents in a variety of role-playing and nature play activities: planting a garden, giving veterinary care to plush toy animals, searching for bugs, touching live animals, and building animal homes (Mikenas 2001). At the San Francisco Zoo's Meerkats and Prairie Dogs exhibit, kids dig, burrow, and cooperate like the animals in the exhibit, discovering similarities between the animals and themselves (Routman 2000).

Some exhibits are designed to increase the feeling of connection between visitors and wildlife. Many zoos and aquariums provide opportunities for visitors to get close to charismatic megavertebrates such as bears, gorillas, lions, and tigers. The PECO Primate Reserve at the Philadelphia Zoo, designed to provide a "strong, emotion-based experience" by reducing the sense of separation from the animals, uses

Fig. 12.1. Giraffe feeding at Brevard Zoo, Melbourne, Florida. Giraffe feeding is just one of a myriad of new, humane techniques that zoos and aquariums are using to connect guests to wildlife. (Photograph courtesy of Brevard Zoo. Reprinted by permission.)

"howdy" crates that appear to pass through the glass barrier (Baker 1999, 207). Inviting to both apes and people, they offer intimate spaces for close animal-visitor encounters. In the Bronx Zoo's Congo exhibit, animals and people seem to share the same naturalistic habitat, separated only by nearly invisible glass barriers. The Monterey Bay Aquarium in Monterey, California, not relying on the intrinsic charisma of large mammals to elicit appreciation, immerses visitors in the graceful beauty of a swaying kelp forest in its towering Kelp Forest exhibit, and surrounds visitors with delicate, drifting jellyfish in Jellies: Living Art.

Finally, more zoos and aquariums are allowing—even encouraging—direct interactions between guests and animals, ranging from touching animals during keeper demonstrations, to feeding browse to giraffes, to swimming with dolphins. Walk-through animal habitats like the lemur exhibit at the Berlin Zoo are becoming more common, and in some, like the many butterfly aviaries around the world and even a pelican aviary at the Hanover Zoo in Germany, visitors can touch the animals. At the Taronga Zoo, Sydney, Australia, and other ARAZPA zoos, visitors have long been able to feed giraffes, and the Brevard Zoo in Melbourne, Florida, Cheyenne Mountain Zoo in Colorado Springs, Colorado, and San Diego Zoo are among the growing number of U.S. zoos to follow suit (fig. 12.1). The San Francisco Zoo lets visitors offer fresh browse and food treats to lemurs with the assistance of a keeper.

FOCUSING ON BEHAVIOR CHANGE

At the same time that this emphasis on affective transformation was developing, zoo professionals realized that if the goal was to inspire conservation action, the design of visitor experiences might need to focus more explicitly on influencing visitor's behavior. Research was showing that although the connection between affect and conservation action was stronger than that between knowledge and behavior, sustained changes in behavior on a measurable scale required educational efforts that explicitly targeted behavior change (see next section). Building on their previous efforts to advance cognitive and affective learning, zoos and aquariums began to introduce more messages and activities aimed specifically at influencing personal conservation action.

For example, many zoos and aquariums began encouraging accessible actions that people could take to help wildlife locally or regionally. Brookfield Zoo's Swamp exhibit describes simple actions that visitors can take to help promote healthy wetlands. The National Aquarium in Baltimore links new exhibits, education programs, and field conservation activities to the conservation of nearby Chesapeake Bay. Aquarium visitors can enter their name in a computer database and receive information about local conservation initiatives in which they can become involved.

In other cases, zoos and aquariums are striving to make creative links between behaviors at home and conservation in the more distant wild. Visitors to the Monterey Bay Aquarium can take home a Seafood Watch Pocket Guide, an easy-to-read reference listing seafood purchases that do not harm marine wildlife populations. Many zoos and aquariums now distribute these, or similar, wallet cards. An exhibit at the Bristol Zoo Gardens in the United Kingdom shows visitors how they can help protect wildlife and their habitats by recycling. Other environmentally responsible purchasing practices promoted in zoos and aquariums include buying shade-grown coffee, purchasing certified sustainably harvested wood products, and choosing nontoxic lawn care products. A number of aquariums around the world distribute the Citizen of the Ocean Passport created by The World Ocean Network, which is headquartered at Nausicaä French National Sea Experience in Boulogne, France. Available in adult and child versions, it offers a customizable guide to individual actions and a way for visitors to gain official recognition for their commitments from participating organizations.

Zoos and aquariums now commonly encourage donations to support field conservation projects. At Disney's Animal Kingdom Theme Park and Epcot's The Seas, both at Walt Disney World in Orlando, Florida, guests are encouraged to "add a dollar" to their merchandise purchase to support conservation projects around the world. Bronx Zoo's Congo exhibit gives visitors a chance to learn about several conservation projects relating to the species they encountered in the exhibit, and to earmark their exhibit admission fee to the project of their choice. Denver Zoo's Primate Panorama offers a similar choice, with visitors using an ATM-like machine to make a donation with cash, a credit card, or an ATM card. The Vancouver (Canada) Aquarium's Beluga Encounter experience concludes with opportunities to contribute to ocean conservation organizations. And many facilities use interactive donation devices such as the Conservation Parking Meter developed by the Center for Ecosystem Survival, which channels contributions toward the purchase of acreage of tropical rainforest.

JUST ONE POINT IN TIME

The current state of the art is just one phase in our development. Most recently, zoo and aquarium educators have begun to look to other fields, such as social marketing (McKenzie-Mohr and Smith 1999) and the emerging discipline of conservation psychology (Saunders 2003), for more insights into how to create learning experiences that lead to changes in behavior. What we are learning is driving the ongoing evolution in zoo and aquarium visitor education.

This overview has described trends in visitor education over time, drawing primarily on North American examples. In reality, of course, the change has not been linear. Different institutions, educators, and designers discovered and began to apply these principles and approaches at different times. Ultimately, the field as a whole has converged on the understanding that we must become explicit about our desired educational outcomes for visitors if we wish to live up to our goal as conservation organizations, and that we must explore new avenues for reaching our audiences and inspiring conservation stewardship.

WHAT WE KNOW ABOUT VISITOR EDUCATION

WHAT HAVE WE LEARNED ABOUT HOW BEST TO REACH OUR VISITORS?

Our approach to education within zoos and aquariums has changed, in part, due to a better understanding of how to influence conservation-related knowledge, affect, and behavior. This learning has come largely from increased research and evaluation within our facilities as we have become more outcome based. We also have gained insights from academic disciplines such as environmental education, cognitive psychology, public health, and child development, as well as organizations such as science centers and children's museums. Below, we summarize some of these key learnings, emphasizing the applications to zoo and aquarium visitor education.

Key Learning no. 1: Know our audience. We know that visitors come to our zoos and aquariums with widely varying perspectives regarding animals and conservation. To maximize our impact, it is necessary to understand these points of view (Falk and Adelman 2003; Falk and Storksdieck 2005). A study by the environmental communications organization The Biodiversity Project found that the public relates to environmental protection primarily in terms of 3 ideas: preserving the natural environment for the next generation; being stewards of God's creation; and wanting their family to live in a healthy environment (Belden and Russonello Research and Communications 1996; Belden, Russonello, and Stewart 2002). Of these themes, zoo and aquarium exhibits tend to be most closely aligned with the first. We rarely tie our experiences to either religious values or general health. This research suggests a direction we could take to link our experiences more closely to values that most resonate with our visitors. Similarly, Schultz (2001) and Schultz et al. (2004) demonstrated that how people think of themselves in relation to nature has a direct relationship to how they behave in nature—thus, considering how individuals relate to nature may be critical to understanding how to influence their conservation-related affect and behavior.

Second, research shows that our guests are generally more knowledgeable and more concerned about conservation issues than the general public, although this knowledge and concern remains fairly superficial (Adelman, Falk, and James 2000; Dierking et al. 2004; Falk et al. 2007). Knowing what our visitors already know—and continually studying this—allows us to focus our educational energies appropriately. For example, visitors that are already aware of conservation issues seem to value more explicit direction in how to become responsible stewards of the environment (Doering 1992; Hayward 1998).

Finally, to match the changing demographics of our society, zoos and aquariums are seeking to attract more diverse audiences. Different cultures perceive the relationship between animals and people in very different ways, and each culture attributes to animals and nature a unique role specific to its own beliefs and lifestyles (e.g. Floyd 1999; Brown 2002). Furthermore, people from different cultures may actually process information differently, and thus may differ in how they experience animal exhibits (Nisbett et al. 2001). Finally, the type of social group in which people visit our facilities affects their experience, e.g. family groups learn more when exhibits have interactive components, are accessible for multiple users and users of different ages, and are designed to appeal to multiple learning styles and levels of knowledge (Borun et al. 1998; Wagner 1999).

Key Learning no. 2: Teaching about conservation must be age specific. The literature on child development indicates that people process information differently at different ages. Recently, researchers such as David Sobel have demonstrated the relevance of these developmental stages to conservation education. Sobel (1995) described studies showing that doom-and-gloom environmental messages caused young children to be less interested in protecting the environment than children who were provided with no information at all. He concluded that hearing negative conservation stories—particularly those related to exotic species that live far away from most of our young visitors—can cause children to feel disempowered and worried, and as a result to disassociate from nature. Clearly, relaying conservation problems such as the bushmeat or extinction crisis to children younger than 10 years is not a good approach to early environmental education. There is strong face validity in this concept: most of us instinctively would shy away from presenting graphic details of a murder to a young child.

This does not mean that zoos and aquariums should not try to introduce young children to conservation. Early conservation education, before the fourth grade, should aim to foster interest and empathy. As Sobel (1995, 10) said, "What's important is that children have an opportunity to bond with the natural world, to learn to love it and feel comfortable in it, before being asked to heal its wounds." The feeling of connection to nature creates the intrinsic motivation for later action. Calls to action should emphasize situations where children can actually make a difference, such as litter in a neighborhood stream, and species that children can find locally, e.g. turtles in their backyards. More complex, remote challenges should be reserved for teens and adults, with the caveat that the disempowering effect of frightening, gloomy messages does not apply only to young children. To inspire action rather than apathy when presenting distant and serious conservation problems, it is necessary to include empowering messages pointing to solutions (Ruiter, Abraham, and Kok 2001) (see table 12.1).

TABLE 12.1. Brookfield Zoo's recommendations for age-appropriate environmental education, based on studies of children's responses to different kinds of conservation messages apply to both programs and exhibits

Ages	Appropriate topics	Inappropriate topics
Birth to 3	Animals are cool	Ecosystems (*too abstract*)
	Sensory experiences	Life cycles (birth, death, etc.)
	Animals that are close to home	Endangered species
	Families (moms, dads, babies)	Environmental problems/issues
4 to 7	Animal homes	Ecosystems (*too abstract*)
	Farm/domestic animals	Endangered species
	Predators/prey	Environmental problems/issues
	Compare/contrast animals to self	Consequences of not using good environmental manners (habitat loss, pollution, endangered species, etc.)
	Animal groups	
	Life cycles (birth, death, etc.)	
	Good environmental manners (recycling, reusing, turning off lights, etc.)	
8 to 11	All of the above	Dire consequences of not using good environmental manners (habitat loss, pollution, endangered species, etc.)
	Good environmental manners (recycling, reusing, turning off lights, etc.)	
	Ecosystems	
	Physical adaptations	
	Animal habitats and needs	
	Site-specific investigations	
	Cycles (life, water, etc.)	
	Introduce direct, simple (not overwhelming) consequences of *not* using good environmental manners, such as "If we don't recycle, we will need more landfill space."	
12 and up	All of the above (*older kids like to learn fun stuff about animals, too!*)	*Most topics are appropriate if presented in a sensitive manner*
	Behavioral adaptations	*Focus on those issues that students have some hope of influencing (whether or not the U.S. should drill for oil in the Arctic National Wildlife Refuge)*
	Consequences of not using good environmental manners	*Consider avoiding topics children can do nothing about (affecting the bushmeat crisis in Africa)*
	Ecosystem investigation with concrete experiences	
	Endangered species	

Source: Used with permission from the Chicago Zoological Society, www.brookfieldzoo.com. Copyright 2001. All rights reserved.

Key Learning no. 3: Interactive experiences are better than passive experiences, and people are better than signs. Interactive experiences are, almost without exception, more powerful than passive experiences. Signs, while appealing to a certain type of learner, are generally not as effective as more interactive forms of media (Bielick and Karns 1998; Ogden, Lehnhardt, and Savage 2000; Lehnhardt et al. 2004). But even signage can be improved through strategic placement and careful design (Bitgood et al. 1986; Serrell 1996) and by increasing the level of interactivity (Derwin and Piper 1988). Similarly, video and computer experiences are most effective when they have a high degree of interactivity. A temporary exhibit about dolphins at the New York Aquarium in New York City using interactive video, role playing, and interactive computer simulations of dolphin behavior increased visitors' appreciation and empathy for dolphins as well as their understanding of dolphin intelligence (Sickler et al. 2006). At the Saint Louis Zoo's Living World exhibit, the best-designed interactive computer programs were second only to live animals in their popularity, had the longest holding power of any medium in the exhibit, and were successful in achieving communication goals (Routman 1994).

But the most effective form of interpretation may be that provided by people (Adelman et al. 2001b; Lehnhardt et al. 2004; Meluch and Routman 2004a, 2004b). This can range from theater—increasingly applied in zoos and aquariums—to single-person presentations, which may be just as effective (Lehnhardt et al. 2004). In a study at the Goldau Animal Park in Switzerland, Lindemann-Matthies and Kamer (2006) found that visitors who stopped at a touch cart with biofacts learned more about biology, ecology, and conservation of bearded vultures than visitors who just saw graphics. Meluch and Routman (2004a, 2004b) demonstrated that visitors who saw a keeper presentation at the Lemur Forest in the San Francisco Zoo showed a greater increase in caring about lemur conservation than those who had seen the exhibit without a keeper talk; and Lehnhardt and her colleagues found that the presentations had the same effect on concern about the bushmeat trade at Disney's Animal Kingdom (Lehnhardt et al. 2004). Swanagan (2000) found that viewing an elephant demonstration and biofact cart increased the likelihood that visitors would send a postcard opposing the ivory trade. At the Atlanta Zoo, visitors who had attended a theatrical presentation using actors and live animals were significantly more aware that wild animals do not make good pets and somewhat more inclined toward conservation action, compared to visitors who had not attended the presentation (Davison et al. 1993).

Key Learning no. 4: Animals are our key differentiator. Animals are the key differentiator of zoos and aquariums—they are what set us apart from other conservation organizations, and from most museums and science centers. The attraction that people feel toward animals appears to have a biological basis (Wilson 1984; Kellert and Wilson 1993; Louv 2005). Real, live animals have greater educational value than models or images (Morgan and Gramann 1989), and animal demonstrations and up-close interactions with animals have been shown to be especially powerful in affecting visitor emotions, attitudes, and even behavior (Heinrich and Birney 1992; Yerke and Burns 1991; Gates and Ellis 1999; Swanagan 2000; Povey and Rios 2003).

Large mammals, as representatives of that special class of animal often referred to as charismatic megavertebrates, are perfectly positioned to attract attention and to elicit an emotional response. Larger animals generally attract more attention and longer viewing times, as do more active animals (Bitgood, Patterson, and Benefield 1998). Further, people are more likely to have positive feelings and feelings of affiliation with mammals than with, e.g., reptiles or invertebrates. Being our closest relatives may give mammals an edge in eliciting positive emotional responses, since they often bear greater obvious similarity to humans (Myers, Saunders, and Birjulin 2004).

Researchers describe the power of animal-related peak experiences in nature, specifically those involving up-close interaction, animals approaching the person, and eye contact with the animal (DeMares and Krycka 1999; Schanzel and McIntosh 2000). Although these particular studies focused on interactions with wild cetaceans and penguins, such peak experiences in zoos and aquariums may have a similar impact. Recent pilot work in a "butterfly house" appears to support this conclusion (L. Pennisi, personal communication). In studies of the Congo Gorilla Forest at the Bronx Zoo, which demonstrated significant success in increasing visitors' conservation understanding and concern, visitors cited seeing gorillas up close as the most enjoyable and memorable part of their experience (Hayward and Rothenberg 2004). In this case, the animal experiences were complemented by a naturalistic exhibit environment and interpretive media, both of which also contributed substantially to visitors' enjoyment and learning (fig. 12.2).

There is no question that our core resource, our animal collection, evokes strong emotional responses from our visitors. This response appears to be strongest when an animal experience is combined with a talk by an animal expert—combining Key Learnings 3 and 4 (see figure 12.3) (Anderson et al. 2003; Povey and Rios 2003; Lehnhardt et al. 2004; Meluch and Routman 2004a, 2004b).

Key Learning no. 5: Well-informed, thoughtful anthropomorphism is okay. Zoo and aquarium professionals traditionally have been adamant about avoiding anthropomorphism, but there may be a more moderate approach. Anthropomorphism is defined as "the attribution of a human form, human characteristics, or human behavior to nonhuman things" (Encarta 2005), and often refers to inappropriate attribution of emotions or thoughts to nonhuman animals (e.g. "Isn't that pacing bear sad?"). However, it also includes making valid comparisons between animals and visitors based on real similarities, like the many comparisons drawn between dolphins and humans in the New York Aquarium exhibit. From that perspective, anthropomorphism can be an effective and appropriate technique for connecting people to animals, rather than something to avoid at all times. The similarities between human and animal behavior provide a powerful teaching tool and a basis for reinforcing empathy and understanding (Burghardt 1997; Mitchell, Thompson, and Miles 1997; Sickler et. al. 2006). This does not suggest that we should depict animals as cute fuzzy critters that think just like people, but instead is an endorsement for well-informed anthropomor-

Fig. 12.2. Congo Gorilla Forest at the Bronx Zoo, New York. Visitors to this exhibit described seeing gorillas up close as the most enjoyable and memorable part of their experience. (Photography by D. DeMello © Wildlife Conservation Society. Reprinted by permission.)

Fig. 12.3. Keeper presentation at the San Francisco Zoo. There is a growing body of evidence demonstrating the impact of animal demonstrations and up-close interactions with live animals on visitors' emotions, attitudes, and behavior. (Photography by Emily Routman. Reprinted by permission.)

phism, where real similarities help demonstrate the connections between human and nonhuman animals.

Key Learning no. 6: Natural environments provide strong positive effects. As described in Coe and Dykstra (chap. 18, this volume), learning in a zoo or aquarium is affected not only by the kinds of experiences we offer, but also by the character of the environments we create. Animals viewed in more natural environments (versus obviously caged environments) are viewed for longer periods and may be perceived in a more positive way (Rhoades and Goldsworthy 1979; Ogden, Carpanzano, and Maple 1994; Price, Ashmore, and McGivern 1994). Such immersion exhibits also seem to be tied to increased learning and to more positive affective responses (Ford and Burton 1991; Ogden, Carpanzano, and Maple 1994), particularly when the exhibits are both functionally and aesthetically naturalistic (see figure 12.4). However, if animals are not visible in the environment, visitors may find the experience unsatisfactory (Spruce and Esson 2005).

A number of studies link nature experiences to conservation attitudes and action (see Louv 2005). Adults active in conservation are generally those who had much free time to play in nature as children and had a significant adult in their life who taught respect for nature (e.g. Chawla 1998). Siemer and Brown (1997) found that providing nature experiences for families made them more receptive to conservation messages. Kals, Schumacher, and Montada (1999) demonstrated that people who had spent time in nature were more likely to feel an emotional affinity toward nature and to demonstrate conservation-related behavior. It is unclear whether the kinds of experiences with wildlife that zoos and aquariums typically provide can fill this "nature niche" in the same way, but it is intriguing to consider that they may. Recent investigations by AZA indicate that a visit to a zoo or aquarium does lead to increased feelings of connection with nature (Falk et al. 2007). The importance of connecting to nature further indicates that zoos and aquariums should provide more true nature play experiences, especially for kids. Brookfield Zoo's Hamill Family Play Zoo provides spaces and materials for real nature play. Nature Exchange at the Dallas Zoo encourages exploration of nature beyond the zoo by rewarding children for bringing in interesting natural objects. The increasing role that zoos and aquariums are taking in *in situ* conservation provides opportunities to link our on-site education programs with local conservation efforts—thus providing participants with more direct "in nature" time. Such experiences are even more critical given the increased urbanization of our world.

Key Learning no. 7: Certain activities make behavior change more likely. We are beginning to understand some of the key experiences associated with inspiring conservation action. As described earlier, we now know that increases in conservation-related awareness do *not* directly lead to environmentally responsible behavior (McKenzie-Mohr and Smith 1999; Kollmuss and Agyeman 2002; Monroe 2003). Some types of knowledge do appear to be important, however. One of the findings of The Biodiversity Project's research was that most U.S. citizens want to protect habitats and wildlife, but do not know how. They want to know specifically how they can help, and they need these actions to be very manageable (Beldon and Rusonello Communications and Research 1996). The Monterey Bay Aquarium's Seafood Watch Pocket Guide, which provides just such guidance, has been found to change significantly the seafood-buying habits of 80% of visitors who take one home (Quadra Planning Consultants and Galiano Institute 2004).

Fig. 12.4. Kilimanjaro Safari at Disney's Animal Kingdom Theme Park, Orlando, Florida, where guests are immersed in an African savanna habitat. Immersion exhibits seem to be tied to increased learning and more positive affective responses. (Photograph courtesy Disney's Animal Kingdom Theme Park. Reprinted by permission.)

As mentioned, the relationship between attitudes/affect and behavior may be stronger than that between knowledge and behavior. Although attitudes in general only weakly predict behavior change (Wicker 1969), establishment of a connection between people and nature (i.e. affective transformation) appears to assist in the development of a conservation ethic, which in turn correlates to more environmentally responsible behavior (Hungerford and Volk 1990; Chawla 1998; Kals, Schumacher, and Montada 1999; Mayer and Frantz 2004; Monroe 2003).

We also are beginning to learn some things that make behavior change more likely. Influencing people's behaviors may be viewed from 2 perspectives: the long-term developmental approach, with a focus on values, informed decision making, and critical thinking (i.e. environmental education); and the more short-term approach of social marketing, with a focus on changing specific behaviors (Monroe 2003). The developmental approach aims to foster a general environmental ethic, while social marketing promotes highly specific behaviors for targeted audiences. Although some studies indicate that environmental education can be effective in promoting environmentally responsible behaviors over the long term (ibid.), the data regarding social marketing are arguably more compelling, perhaps in part due to a greater ease in studying short-term effects (McKenzie-Mohr and Smith 1999; Monroe 2003).

Several factors have been shown to increase the likelihood of behavior change in the short term. Within the field of public health, 2 factors that appear to promote behavior change most strongly are incentives and social support (Webb and Sheeran 2006). Another key to changing behavior is that practice makes perfect. Having any sort of conservation action experience seems to increase the likelihood of future action (Finger 1993). This suggests that we should encourage our visitors to participate actively in conservation behaviors, either on our grounds or in community events. Establishing personal relevance regarding the benefits of an action also has value; e.g. sports fishermen may more easily see the value of cleaning up a local river where they fish than a remote location (Robinson and Glanznig 2003). Social marketing research also has shown that making a public promise or statement of intent (e.g. signing a petition or utilizing a pledge board) increases the likelihood of behavior change, as do clear, specific prompts (e.g. clear instructions about recycling placed directly on the recycling container) (McKenzie-Mohr and Smith 1999; Monroe 2003). Using a respected and trusted messenger helps inspire behavior change, as does demonstrating, or modeling, the desired behavior (McKenzie-Mohr and Smith 1999; Monroe 2003; Webb and Sheeran 2006). In many cases it is necessary to address barriers to specific behaviors, e.g. sustainable seafood wallet cards eliminate the barrier of lack of knowledge.

Finally, it is easier to change behaviors if the changes are simple, understandable, concrete, and have no negative social stigmas attached to them (Monroe 2003; Webb and Sheeran 2006). This last finding is one that our field should pay particular attention to, as conservation action is frequently complex and at times may have negative public opinion associated with it. In such cases, the establishment of related social norms is especially important (Fishbein and Ajzen 1975), suggesting the critical importance of zoos and aquariums working together to support the establishment of these in the realm of conservation.

These lessons from the field of behavior change have the potential to advance significantly the efforts of zoos and aquariums to affect behavior change. Work that is currently ongoing in zoo and aquarium education, such as AZA's Multi-Institutional Research Program: Why Zoos and Aquariums Matter (described below), is geared toward integrating these recent findings into a more focused and successful approach to behavior change.

OUR COLLECTIVE IMPACT

Public opinion polls have established that zoos are a trusted source of conservation information, behind only National Geographic and Jacques Cousteau (Favel 2003). In a poll conducted in the United States in 2004, respondents overwhelmingly felt that visiting zoos and aquariums helps people to appreciate animals, and also that such visits encourage people to support conservation (AZA 2007).

Of critical importance, however, is assessing the actual impact of a visit to our facilities. In 1999, the AZA began an educational research initiative called the Multi-Institutional Research Program: Why Zoos and Aquariums Matter (MIRP). A comprehensive literature review funded by the AZA Conservation Endowment Fund found that at that time there had been little systematic research on the overall impact of our facilities on visitor conservation knowledge, affect, or behavior (Dierking et al. 2000). However, a number of independent studies—some looking at an entire visit, and others looking at key exhibits—did indicate that zoo and aquarium visits can have a significant impact. Further, recent years have seen increased attention to this important question (see Doering 1992; Adelman et al. 2001a, 2001b; Ramburg, Rand, and Romulanis 2002; Dierking et al. 2004; Hayward and Rothenberg 2004).

Collectively, existing studies indicate that zoo and aquarium exhibits can promote awareness and understanding of conservation messages (Hayward 1997, 1998; Roper Starch Worldwide 1998; Adelman et al. 2001b). Experiences in zoos and aquariums have been demonstrated to both broaden and deepen understanding of conservation issues, both short- and long-term (Doering 1992; Bielick and Karns 1998; Swanagan 2000; Adelman et al. 2001a, 2001b; Dierking et al. 2004; Hayward and Rothenberg 2004), although Dunlap and Kellert (1989) found little knowledge gain in one study.

Creating positive affective responses toward animals, i.e. instilling caring for animals and nature, is something for which zoos and aquariums seem particularly well suited. Certainly, many conservation professionals have described their childhood zoo experiences as formative. The research results are mixed, but generally point to a positive impact. Visitors at 4 different aquariums expressed increased concern for marine conservation (Roper Starch Worldwide 1998). Marcellini and Jenssen (1988) saw greater changes in attitudes than knowledge resulting from HerpLab experiences. Post-visit surveys of visitors to San Francisco Zoo's Lemur Forest showed an increase in the use of positive affective terms in describing lemurs and in the level of concern expressed about lemur conservation (Meluch and Routman 2004a, 2004b). Similarly, visitors to both Disney's Animal Kingdom and the National Aquarium of Baltimore came away with an increased concern regarding wildlife which, unfortunately, declined over time (Adelman et al. 2001a, 2001b; Dierking et al. 2004). Alternatively, Hayward (1997) found that while a particular exhibit did have an impact on understanding of conservation, the impact on attitudes was less clear.

Zoo and aquarium experiences have been shown to increase visitors' intentions toward conservation actions (Roper Starch Worldwide 1998), even up to 6 months later (Saunders and Stuart-Perry 1997; Dotzour et al. 2002; Dierking et al. 2004). However, not all intentions translate into action over time (Dierking et al. 2004). A recent meta-analysis of behavior change research in the public health field has helped clarify the relationship between intention to change behavior and actual behavior change. Behavioral intention was found to lead to behavior change only when the behavioral intent was quite strong, and even then, the resulting behavior change was less overall than the intent (Webb and Sheeran 2006).

The work on measuring our impact and improving our effectiveness continues. Following the 2000 literature review, the AZA, in partnership with the Institute for Learning Innovation and the Monterey Bay Aquarium, received a grant from the National Science Foundation to launch the research phase of the MIRP, starting with a study of visitor motivation and learning. The study, which involved more than 5,500 visitors and 12 AZA-accredited institutions, found that a zoo or aquarium visit raised visitors' awareness of their personal role in conservation and reinforced beliefs about stewardship, conservation, and love of animals. This effect was still measurable after several months. A summary of the study is available on the AZA Website, www.aza.org/ConEd/MIRP/ (Falk et al. 2007).

AZA institutions have implemented a broad array of initiatives that complement or are part of the MIRP research, focusing on understanding and enhancing our effect on conservation-related affect and behavior. These have included workshops at the San Francisco Zoo, Brookfield Zoo, and Disney's Animal Kingdom as well as extensive research programs at a number of zoos and aquariums, including Brookfield Zoo; Disney's Animal Kingdom; The Living Seas, Orlando, Florida; the Philadelphia Zoo; the Point Defiance Zoo, Tacoma, Washington; the Wildlife Conservation Society, New York, New York; and the Woodland Park Zoo, Seattle, Washington (see Ogden et al. 2004).

The zoo and aquarium community as a whole has now begun to increase attention to working collectively on particular conservation actions. EAZA led the way in developing associationwide campaigns focused on specific conservation issues, from bushmeat to turtles to rhinoceroses (EAZA 2007). ARAZPA initiated its far-reaching Frog Focus in 2000. AZA is following in ARAZPA's footsteps, working to align member facilities in campaigns to promote specific actions. As part of MIRP, AZA is developing and evaluating national behavior change programs, including a campaign to promote "wildlife-friendly families" through member institutions, encouraging accessible, local actions such as building homes for backyard wildlife. In a related project, AZA and the Environmental Education and Training Partnership are developing a professional training workshop designed to integrate and advance our understanding of effective practices in changing conservation-related attitudes and behavior.

CONCLUSION

The role of education in zoos has in many ways gone full circle. Early zoos focused on meeting the needs of the multitudes of guests who entered their gates every day. Today's responsible zoos and aquariums do so as well, putting valuable resources into public education and influence—but with many changes.

In the past, public zoos gave guests opportunities to get close to the animals, providing unforgettable, personal animal experiences such as feeding marshmallows to a polar bear or riding an elephant. Although memorable, these experiences had unfortunate implications for both the animals' well-being and the messages visitors received. Today, zoo professionals constantly strive to create the humane, message-appropriate, and safe equivalents of those compelling experiences, and complement them with educational presentations and media to connect visitors to wildlife in ways that are positive for both the zoo's animals and its visitors.

Where we differ from our predecessors in zoo and aquarium education is that the severity of threats to wildlife and our resulting focus on our role as conservation centers require that we become extremely explicit about our desired conservation communication outcomes. Current efforts are driven by the recognition that we must measure our success and modify our methods to get the maximum conservation impact from our most important assets—our living collections, our visitors, and our conservation stories. Only through informed, strategically focused efforts that evolve as our knowledge increases can we capitalize on our essential experience, the human-animal connection, and realize our potential as agents of conservation.

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13

Managing Captive Mammals in Mixed-Species Communities

Jake Veasey and Gabriele Hammer

INTRODUCTION

The first step in establishing a mixed-species exhibit is to carry out an objective cost-benefit analysis of the projected exhibit. The analysis should incorporate known or predicted benefits for the animals, keeping staff, and the visitors; these must exceed the potential risks for the animals. A cost-benefit analysis is useful not only in deciding whether or not to proceed, but also in deciding how to minimize, through design, many of the identified risks. A broad range of input should be sought, from keeping staff and veterinarians and also from experienced studbook keepers/species coordinators. In this chapter we hope to outline both the advantages and the disadvantages of mixed-species exhibits to assist in just such an analysis, and combine this with some guidance on the principles of establishing and maintaining successful mixed-species exhibits.

THE BENEFITS OF MIXED-SPECIES EXHIBITS

EFFECTIVE USE OF RESOURCES

Zoos need to ensure that their limited financial resources and space are put to effective conservation use. Space in zoos is becoming more limited by the tendency to increase individual enclosure sizes. By maintaining more than one species within a single enclosure, zoos can significantly increase the conservation return on their space and infrastructure.

BEHAVIORAL ENRICHMENT

Mixed-species exhibits can be developed by the addition of new species to preexisting enclosures and by combining smaller enclosures into larger areas. Increased space can improve animal welfare (Veasey, Waran, and Young 1996) by allowing increased opportunity for environmental complexity and consequently greater behavioral opportunities for the residents. In mixed-species exhibits, scope for social interaction and social complexity can also increase; this is probably one of the most enduring forms of enrichment, as both predictability and the probability of habituation are less likely than with most enrichment devices.

Many animals in zoos do not spend species-typical amounts of times feeding, foraging, and avoiding predators (Veasey, Waran, and Young 1996; Veasey 2006; Seitz 1998); thus, large portions of an animal's daily time budget may be unoccupied, potentially resulting in stereotypic behaviors and other indicators of impoverished welfare. Activity levels are typically higher in mixed-species enclosures, especially with primate species (Baker 1992; Veasey 2005), and so long as such activities are not antagonistic there will typically be a positive effect on both the physical and the mental health of the animals. Having established a mixed-species lemur enclosure at Woburn Safari Park in the United Kingdom, we saw a more diverse ethogram with more play behaviors in the black and white ruffed lemurs, *Varecia variegata variegata*, previously held in a single-species exhibit (Veasey 2005). Though some of the behavioral changes may be attributable to the change of enclosure, the black and white ruffed lemurs did interact regularly with the red-bellied lemurs, *Lemur rubriventer*, and red-fronted lemurs, *Eulemur rufus*.

One of the most common concerns with mixed-species enclosures is the likelihood of negative interactions between species. However, many positive interspecific interactions have been recorded (Hammer 2001). In a community of Barbary sheep, *Ammotragus lervia*, and gelada baboons, *Theropithecus gelada*, at the Zoological Garden of Wilhelma, Stuttgart, the gelada baboons commonly groom the sheep. Similar behaviors have been noted elsewhere, such as Barbary macaques, *Macaca sylvanus*, grooming Grevy's zebra, *Equus grevyi*, at Woburn Safari Park, and Hamadryas baboons, *Papio hamadryas*, interacting with Cape buffalo, *Syncerus caffer caffer*, at Knowsley Safari Park in Prescott, United Kingdom. Such interspecific interactions need not be restricted to mammals. In an exhibit that housed pygmy marmosets, *Callithrix pygmaea*, and green iguanas, *Iguana iguana*, the mar-

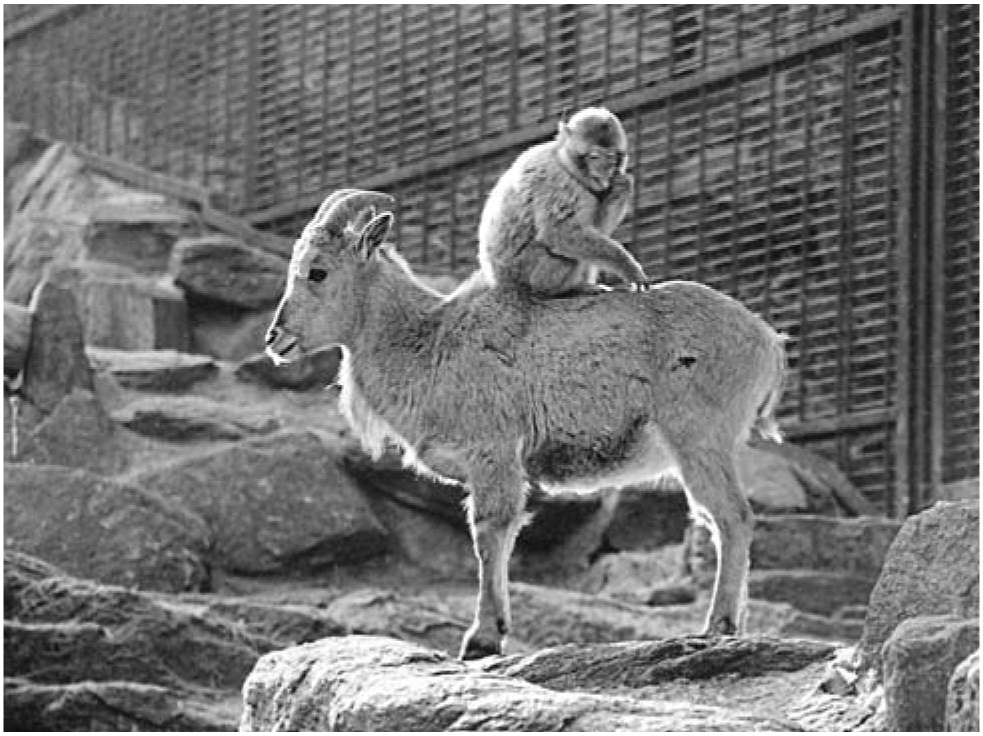

Fig. 13.1. Young Barbary macaque feeding on the back of a young Barbary sheep. (Photography by J. Kircher, Zoo Schönbrunn. Reprinted by permission.)

mosets were regularly seen grooming the iguanas and eating the dead skin from the grooming process.

Zoos currently restrict breeding in order to maintain stable populations. As a result, fewer young are born and juveniles may develop in the absence of a peer group, which reduces the opportunity to play in juveniles and adults alike. However, in a mixed-species environment, juveniles can still benefit from the presence of juveniles of another species during development. Zoo studies have shown considerable interspecific play between juvenile primates (Freeman and Alcock 1973), carnivores (Curry-Lindahl 1958), and ungulates (Zscheile 1980) in mixed-species enclosures.

MANAGEMENT

Mixed-species exhibits can solve management problems existing within single-species exhibits. At Los Angeles Zoo following the death of the dominant male gelada baboon, the baboon group fractured, since the remaining male was not yet old enough to lead the troop. To create a diversion and reduce intraspecific aggression, 2 female chimpanzees, *Pan troglodytes*, were introduced into the group. Aggression immediately ceased among the baboons, who were more preoccupied with the chimps than one another. The situation also appeared to trigger the young male's development of dominance, and order was restored to the troop (Thomas and Maruska 1996).

At Copenhagen Zoo, in a South American exhibit housing guanacos, *Lama glama guanicoe*, capybaras, *Hydrochaeris hydrochaeris*, rhea, *Rhea americana*, and Patagonian mara, *Dolichotis patagonum*, the introduction of anteaters, *Myrmecophaga tridactyla*, resulted in the "demotion" of the guanacos, who previously had aggressively dominated all other species. The guanacos were nervous of the anteater, possibly due to the similarity of the anteater's silhouette and gait to that of a predatory species such as jaguar, *Panthera onca* (Hjordt-Carlson 1997). Long after the introduction, the guanacos remained cautious of the anteaters, and although not always in the enclosure, the anteaters still functioned as a stabilizing element within the community; the introduction of the anteaters was used to control specific incidents by distracting the male guanaco, e.g. when he chased the female guanaco or panicked the other species.

Different species can also function as a shield to vulnerable individuals within social units. At Tiergarten Schönbrunn, Vienna, where Barbary sheep and Barbary macaques are mixed, the young macaques, which were either born in the mixed exhibit or very young during the introduction period, tend to be less fearful of the sheep than macaques introduced to the sheep as adults. The younger macaques exploited this, often hiding from more dominant macaques by climbing under or on top of the sheep (Hammer 2001) (fig. 13.1). Moreover, the younger macaques could forage among the sheep in comparative safety, since the adult macaques maintained a rigid interspecific distance from the sheep.

When chased by older conspecifics, young primates may flee to related animals higher in rank than their pursuer, and often groom their protector enthusiastically. The Schönbrunn Barbary macaques sometimes demonstrated the same behavior toward the sheep, even spontaneously grooming the sheep; sheep also appeared to seek out the younger monkeys to initiate grooming (Hammer 2001). Grevy's zebra likewise solicited grooming from young Barbary macaques at Woburn Safari Park.

At Woburn Safari Park, in a temporary mixed-species exhibit with Bactrian camels, *Camelus bactrianus*, and a bachelor group of scimitar horned oryx, *Oryx dammah*, the camels reduced aggression in this highly aggressive all-male oryx herd. If the camels showed an interest and approached the oryx performing their antagonistic displays, the oryx would then display to the camels and not attack conspecifics. Also, some subordinate oryx would stand close to the camels, thus reducing the likelihood of an aggressive encounter with a more dominant conspecific.

REINTRODUCEABILITY

There are many prerequisites for a successful reintroduction (Kleiman 1996), but one of those must surely be behavioral flexibility and preparedness for a complex environment. Animals exposed to a wide diversity of appropriate external stimuli in captivity, including a complex social and physical environment, are more likely to cope with the complexity of their natural habitat after reintroduction.

Even "negative" interspecific interactions in captivity may be beneficial in survival postrelease. An antelope that has had its calf attacked by a zebra, *Equus* sp., in captivity is likely to avoid zebra if ever released into a habitat with zebra present. Although appropriate legal and ethical considerations must be applied, a degree of "negative" interaction might be considered a requirement for prerelease animals, e.g. controlled nonlethal exposure to predators.

VISITOR BENEFITS: EDUCATION AND ENTERTAINMENT

Mixed-species exhibits also offer educational and entertainment advantages over comparable monospecific mammalian exhibits. Chosen species can exploit different resources within the enclosure; thus, there is the potential to increase the stocking density without compromising animal welfare or resource usage. As a result, visitors are more likely to see animals that are active within the enclosure (Veasey 2005). Visitors not only prefer to see active animals, but also are more likely to learn something about the animals when they are more active (Bitgood, Patterson, and Benefield 1986). Informative displays can then draw attention to diversity and adaptations by highlighting interspecific similarities and differences in behavior, morphology, ecology, natural habitat, and even conservation status (Thomas and Maruska 1996). Combining arboreal and terrestrial species or diurnal and nocturnal species reduces the likelihood of negative interspecific interaction, ensures that visitors can always observe an occupied enclosure, and offers considerable educational/interpretive possibilities.

In mixed-species exhibits with popular species, there are also opportunities to draw visitors' attention to endangered species that are less well known or less "attractive." Likewise, exhibits of species that are naturally solitary, form monogamous pairs, or are being maintained in small single-sex groups for management reasons can be enhanced by adding compatible species that are more conspicuous.

POTENTIAL RISKS AND DISADVANTAGES

UNDESIRABLE BEHAVIORS

Certain undesirable behaviors can occur in mixed-species exhibits that would not have occurred in monospecific enclosures. At Stuttgart, male gelada baboons have been observed attempting to mate with young Barbary sheep, and young lactating Barbary sheep have even been suckled by opportunistic baboons (fig. 13.2). As a result, the zoo now separates the primiparous sheep during rearing.

Other behaviors can occur that may be harmful to the species sharing the enclosure. For example, in one zoo capuchins, *Cebus albifrons*, used red eared sliders, *Trachemys scripta*,

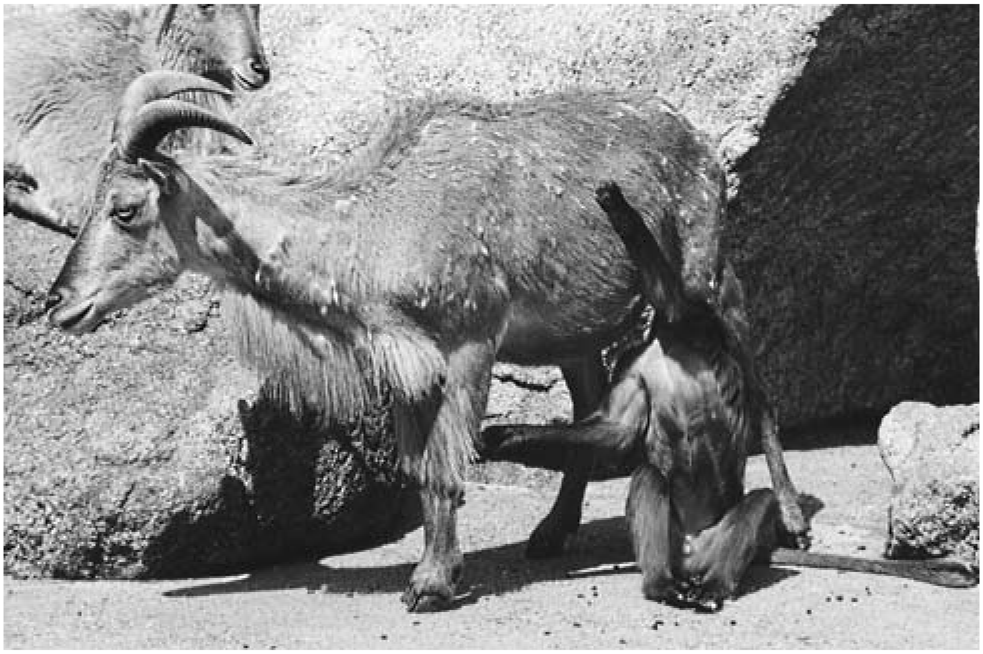

Fig. 13.2. Gelada baboon suckling from a Barbary sheep. (Photography by H. Mägdefrau. Reprinted by permission.)

caught from the moat surrounding their enclosure, in an attempt to break open nuts! This example highlights the need for contingency plans to separate species if there is a clear and insoluble problem in a mixed-species exhibit.

SPECIES IDENTITY CONFUSION AND HYBRIDIZATION

Close interspecific relationships formed in mixed-species exhibits are generally viewed as positive, but not if imprinting or confusion over species identity occurs, since this can reduce breeding success of individual species and may in some circumstances result in hybridization. Mal-imprinting typically occurs when juveniles have limited intraspecific contact or when mothers without young "steal" young from the mothers of other species. This cross-species adoption behavior is not restricted to primates; e.g. Grant's zebra (*Equus burchelli boehmi*) attempted to adopt young from eland, *Taurotragus oryx*, in Hannover Zoo (Dittrich 1968). At the Smithsonian National Zoological Park, in Washington, DC, a mixed exhibit of Geoffroy's marmoset, *Callithrix geoffroyi*, and pygmy marmosets was disbanded when the female Geoffroy's marmoset forcibly adopted a young pygmy marmoset (Xanten 1992).

Mixing different sexes of the same genus or otherwise closely related species should be treated with caution, particularly where intraspecific reproductive opportunities are limited. For example, bongo, *Tragelaphus euryceros*, sitatunga, *Tragelaphus spekii*, and greater kudu, *Tragelaphus strepsiceros*, as well as addax, *Addax nasomaculatus*, and scimitar horned oryx, *Oryx dammah*, have been known to hybridize in captivity, despite some of these species' being sympatric in the wild and in separate genera.

HEALTH RISKS

There are many diseases that have minimal or no apparent impact in the host species, but are lethal when transmitted to other, usually related, species. We advise all zoos to evaluate health risks before proceeding with a new mixed-species exhibit. With a wise selection of species and an effective quarantine and monitoring program, interspecies transmission of disease should be rare and should not be viewed as an impediment to developing carefully selected mixed-species exhibits.

As an example, when housed together, squirrel monkeys, *Saimiri sciureus*, can cause lymphoproliferative disease in black tailed marmosets, *Mico melanurus*, by infecting them with *Herpesvirus saimiri* (McAloose 2004). Salmonella has been transferred between African elephants, *Loxodonta africana*, and hamadryas baboons (Deleu, Veenhuizen, and Nelissen 2003). Parasites are also a major interspecific health consideration, particularly among hoofstock.

STRESS

Stress as a result of interspecific interaction can have a profound effect on the health and welfare of the individuals concerned (see Kagan and Veasey, chap. 2; Hodges, Brown, and Heistermann, chap. 33; and McPhee and Carlstead, chap. 25, this volume). Particular attention should be paid to mixed-species enclosures with primates, as primates are generally more curious and persistent in their attention to other species. For example in the Los Angeles Zoo, silver langurs, *Trachypithecus cristatus*, and Indo-Malayan giant squirrels, *Ratufa bicolor*, had to be separated, because the squirrels began to lose coat condition and became anorexic despite apparently cohabiting without incident. The squirrels were suffering from a low but steady level of chronic stress, despite the fact that the langurs seldom came into contact with them (Thomas and Maruska 1996).

Historically, Woburn Safari Park had housed North American black bears, *Ursus americanus*, with a large colony of rhesus macaques, *Macaca mulatta*. Although the bears were not apparently stressed by the species mix, their behavior did change when they were moved to a new enclosure containing a pack of timber wolves, *Canis lupus*, a far more geographically appropriate species! Female bears that had previously spent considerable time in underground dens now spent more time in trees, where they previously would not have been able to avoid the macaques. The male bears also spent more time in the open, and while the wolves do try and steal bear food, all bears appeared markedly more relaxed at feed times in the presence of the wolves when compared to the presence of large numbers of rhesus macaques. Since all features in the old enclosure were present in the new enclosure, the behavioral changes seen in the bears suggest a response to the absence of the macaques rather than an effect of the enclosure.

AGGRESSION

Aggression is perhaps the most obvious concern when establishing mixed-species exhibits. However, in most instances (notwithstanding predator/prey mixes), intraspecific aggression is more likely than interspecific aggression, because competition for resources will be more intense within a species as individuals compete directly for identical resources, including shelter, food, and mates. In mixed-species exhibits, the likelihood of aggression can be significantly reduced by a careful selection of species and enclosure design. For example, mixing grazers and browsers or arboreal and terrestrial species will reduce the likelihood of certain types of conflict.

Once the species have been selected, an assessment and acclimatization period during which the animals have visual and olfactory contact will allow the individuals to habituate to one another's presence, and zoo staff can evaluate potential problems. However, even if aggression does not occur at first, it can happen in the future. Mothers can become aggressive when rearing young, and some equids and other herbivores may become fatally aggressive in the presence of young of other species. Seasonal or pubertal changes in male reproductive status may also result in aggression. For example, in one paddock, a small bachelor herd of Kafue Flats lechwe, *Kobus leche kafuensis*, had coexisted for a number of years with Southern white rhinoceros, *Ceratotherium simum simum*, common eland, Ankole cattle, *Bos taurus taurus ankole*, sitatunga, and Chapman's zebra, *Equus burchellii antiquorum*. When the lechwe reached the age of 5 years, they turned on one another and all the other bovids, resulting in their removal from the enclosure and separation from one another. Staff thus needs to be vigilant throughout the life of a mixed-species exhibit, and be prepared to respond to outbreaks of aggression.

MANAGEMENT AND DIET

Different species with different dietary requirements and tolerances may need to be fed separately. Ensuring that every individual within complex multispecies exhibits receives the correct amount of appropriate food requires careful observation and mechanisms to feed species or individuals separately. In a 10-ha, mixed-primate exhibit at Woburn Safari Park housing hoofstock with vervet monkeys, *Chlorocebus aethiops*, Barbary macaques, patas monkeys, *Erythrocebus patas*, and colobus monkeys, *Colobus guereza*, staff ensured that citrus fruit fed to the macaques and guenons were not available to the colobus, since the latter are naturally a predominantly folivorous species. They conditioned each primate species to a different auditory signal, and they never scatter-fed citrus fruit.

One of the other complicating factors in mixed-species exhibits is access to housing and especially critical resources such as sleeping sites, heat spots, and refuges. Though species may share an outdoor enclosure without problems, difficulties may arise when individuals are indoors and in closer proximity. Where multiple housing is not an option, houses should be as large, complex, and generously furnished as possible, with multiple entrances and exits to avoid aggressive encounters from which individuals cannot readily escape.

Having adequate housing is most difficult with primates. Woburn Safari Park has 2 mixed-species primate exhibits, one with 4 Cercopithecine species and one with 3 species of lemurs. In both cases primary indoor houses have been supplemented with additional smaller, modular-heated units, so that if individuals are driven out of the main houses, they always have access to shelter. In the Cercopithecine exhibit, each species has its own houses in which it is fed and trained to enter via auditory signals. Staff do not permit nonresident primates to remain in the house of another species.

GUIDANCE ON ESTABLISHING MIXED-SPECIES EXHIBITS

Historically, birds, amphibians, reptiles, and fish have been kept in mixed-species enclosures far more than mammals. Recently, increasingly ambitious mixes exist for mammals. The Miami Seaquarium has mixed bottle-nosed dolphins, *Tursiops truncatus*, with tiger sharks, *Galeocerdo cuvier* (Gray 1962), and the Zoo Schwerin in Germany has mixed slender-tailed meerkats, *Suricata suricatta*, yellow mongoose, *Cynictis penicillata*, and lions, *Panthera leo* (Hammer 2001).

Institutions have different benchmarks for the success of mixed-species exhibits; e.g. a fatality or injury in one mixed-species exhibit might lead to the cessation of the exhibit, while the same incident in another institution might result in altered management or design rather than abandonment. We believe that zoos tend to tolerate fewer negative incidents in mixed-species exhibits than in single-species exhibits; e.g. at Woburn Safari Park, keeping staff seemed willing to accept the sometimes substantial injuries inflicted on conspecifics by both bears and wolves as inevitable, but found less acceptable the idea of lesser injuries inflicted interspecifically, despite clear benefits for relocating and mixing the 2 species. In this instance, effective management combined with considered design has minimized conflict between the species, and as was anticipated, injuries invariably occur within each species rather than interspecifically.

Conflict management between species is essential to the success of a mixed-species exhibit. It is best achieved by first identifying resources that create competition and then either providing an abundance of them or spatially and/or temporally separating these resources.

ENCLOSURE SIZE AND COMPLEXITY

Enclosure size is an important factor in the likelihood of a successful mixed-species exhibit, since space facilitates inter- and intraspecific avoidance (Thomas and Maruska 1996). Including visual barriers such as hills, mounds, partitions, or vegetation facilitates avoidance even further, particularly with primates, for whom visual contact can generate both stress and aggression.

Social spaces between species can be created using carefully constructed barriers. In Woburn Safari Park's bear and wolf enclosure, a core wolf area is maintained to which bears do not have access through narrow wolf-appropriate entranceways of just 20 cm wide. The wolves can thus escape the bears—with the more timid female bears climbing trees if they feel the need to avoid the wolves—and be separately fed if necessary. Such separation zones should be sufficiently large to permit the species to function adequately within them. Such zones can also benefit subordinate individuals within a species; e.g. in Woburn's bear and wolf exhibit, subordinate wolves use the core wolf area to avoid dominant wolves rather than the bears.

Isolation zones can come in many forms; at Safari Beekesbergen in the Netherlands, African elephants and hamadryas baboons are maintained successfully in the same enclosure with a large rocky outcrop at the center of the exhibit which only the primates can access. Likewise, small antelope such as klipspringer, *Oreotragus oreotragus*, can readily avoid larger ungulates by seeking refuge in similar outcrops. In mixed-species primate enclosures, isolation zones can be achieved by exploiting the differences in size, strength, and agility of the species. Refuges for smaller species can be established by the use of branches that would not support bigger species or that are out of reach to larger, nonjumping primates.

Establishing a zone of retreat for the bigger species is far more problematic than creating retreats for smaller species. With ungulates and other terrestrial animals, a low fence that can be traversed only by the bigger species may be possible; doors that only the larger species can open may be another viable solution.

Applying consumer demand theory (where animals have to work or overcome aversive stimuli to receive a reward, e.g. refuge from other animals) may be valuable for refuge design within mixed-species exhibits. For example, an electrified cattle grid has been used to deter bears and wolves from approaching exit gates in Woburn's drive-through exhibit.

Though effective in eliminating approaches by bears and most wolves for the majority of the time, subordinate wolves use the area beyond the grid as a refuge when being chased by dominant members of the pack, since pack members appear not to be motivated sufficiently to pursue the subordinate animal and risk receiving a shock.

Very timid species, such as small antelopes and cervids, have a greater tendency to run into barriers in small areas, since fences generally act as a barrier to flight; whereas in larger enclosures, fences tend to direct the forward movement of the fleeing animals (Backhaus and Frädrich 1965). A number of factors are likely to account for this. First, as enclosure size increases, the ratio between barrier length and area within the enclosure decreases; thus, animals are statistically less likely to run into a fence. Second, when startled within a larger enclosure, an animal is more likely to be further from a fence compared with a smaller enclosure and so can direct its flight. Third, in smaller enclosures, the animal is less likely to have a choice of direction for fleeing, since the stressful stimulus may block part of its path. Thus, exhibits should have corners exceeding 90° where possible so that fleeing animals will not become trapped or reach a dead end when running along a fence line.

Occasionally, larger species are subordinate to smaller species, as has been the case in groups of fallow deer, *Dama dama*, and wild boar, *Sus scrofa*; dik-diks, *Madoqua piacentinii*, and gerenuks, *Litocranius walleri*; lechwe and eland as well as orangutans, *Pongo pygmaeus*, and stump-tailed macaque, *Macaca arctoides*.

If there is interspecific tension, there should be sufficient housing provided so that each species has a retreat, either via separate houses for each species, or at the very least separate stalls or areas within the houses. However, effective separation is possible even within a single house. In Woburn's mixed lemur enclosure, with 3 houses available, the red-fronted lemurs always chose to shelter in the largest house, in which the black and white ruffed lemurs typically resided. The large group of ruffed lemurs is dominant and regularly drove the red-fronted lemurs out of the house. However, placing additional shelving higher up within the house reduced conflict dramatically, since the ruffed lemurs stayed on the lower shelves and the red fronted lemurs resided higher up.

Pens within primate houses should have multiple entrance and exit points at different heights and locations to prevent individuals from being trapped by dominant animals, and to ensure that flight options are always available. Multiple entrances and exits also can prove essential in exhibits where species have been mixed, but do not share the same internal areas. Multiple entrances/exits to the underground burrows of meerkats have proved to be critical to the elimination of predation by lions, who could more readily exploit solitary entry/exit points, with potentially fatal consequences for meerkats.

BEHAVIORAL ECOLOGY

An in-depth understanding of the behavioral ecology of all species concerned is essential when establishing mixed-species exhibits, particularly for species that had not been combined elsewhere.

Feeding behavior and competitive overlap. With the possible exception of conflict relating to reproductive seasonality, conflicts relating to feeding are probably the most common cause of aggression in mixed-species enclosures (Hammer 2001). Thus, reducing competitive overlap during feeding is fundamentally important and is best achieved by combining species which occupy different habitat niches in the wild or can be fed at different times and in different areas.

Where there is overlap, e.g. mixed exhibits of grazing species, differences in size or taxonomy can help to reduce competition; e.g. although both are tragelaphines, sitatunga do not compete with eland within a large safari-type enclosure, because they are significantly different in size and their use of the enclosure habitat is dissimilar. The sitatunga inhabit the swampy edge areas of the reserve, and the eland occupy the central grassland areas. However, when 2 hippotragines (i.e. oryx and addax) were housed together, there was interspecific aggression, although the 2 species are historically sympatric in the wild and are arguably as closely related to each other as eland are to sitatunga.

Feeding animals separately may be the most obvious solution to avoid conflicts, but this is not always possible, effective, or desirable. For example, it is difficult to separate primates from ungulate food, and ungulates often take dropped or discarded food from the primates, a situation regularly observed between Barbary macaques and Barbary sheep at Vienna's Tiergarten Schönbrunn. To avoid the problem, the macaques were fed in the indoor enclosures, but subadults would take as much food as they could carry and flee to the trees, where they would then drop food that was consumed in turn by the sheep. The macaque diet included foods that, in large quantities, could potentially cause problems for ruminants, and so this situation needed careful monitoring and management.

In St. Martin de la Plaine Zoo, France, Tonkean macaques, *Macaca tonkeana*, housed with babirusa, *Babyrousa babyrussa*, competed for food. Despite separating the species at night and when each species was fed, they had to be separated when a babirusa was injured during a fight with a male macaque over discarded food available to both in the exhibit (Hammer 2001).

Social structure. Individuals of social species living naturally in large herds or groups tend to join other species groups when kept as the lone representative of the species. When Suffolk Wildlife Park in the United Kingdom was awaiting the arrival of the remainder of a herd of white rhinoceroses, they gave their temporarily lone bull rhinoceros several African pygmy goats, *Capra hircus hircus*, for company, with whom he associated amicably. The goats, who could readily escape from the rhinoceros between the steelwork, frequently climbed on the rhinoceros, which became considerably calmer in their presence.

Solitary species and species that might typically fight conspecifics if maintained together in close proximity in captivity can also be successfully socialized in mixed-species exhibits. In Smithsonian's National Zoological Park, 3 males of different species of marmoset were maintained together and regularly observed grooming each other, sharing food, and huddling (Xanten 1992).

In Le Parc Zoologique Cerza, Lisieux, France, Indian rhinoceros, *Rhinoceros unicornis*, are maintained in an enclosure to which blackbuck, *Antilope cervicapra*, and spotted deer, *Axis axis*, have access. There is a core rhinoceros area into which the deer and blackbuck can enter and a peripheral area free of rhinoceros, but accessible to blackbuck and spotted deer.

Surplus individuals from typically gregarious species can often be successfully mixed with other species due to their need for social contact. In fact, being able to maintain successfully solitary species with a low tolerance for conspecifics in mixed-species exhibits is highly desirable from a public perception and potentially from an animal welfare perspective.

Antagonistic behavioral ecology. Zoos should avoid mixing species in which interspecific aggression is likely due to similarities in ritualized intraspecific fighting, e.g. many horned and antlered ungulates.

In most zoos, ungulates are maintained in harem groups with only one adult male, or as bachelor herds. Often lone males have no real outlet for their aggressive behavior, despite being provided inanimate branches or posts to attack. If we consider that Walther (1965a) observed as many as 11 fights per day in a wild herd of 15 Grant's gazelle, *Gazella granti*, it is perhaps understandable that inanimate diversions might not eliminate aggression directed to other animals. Some male antelope are so motivated to fight that they have destroyed stables and enclosure fixtures, and even attacked and killed females and juveniles within their harem (Walther 1965b). Likewise, Zscheile (1980) reported that fallow deer stags in rut have gored females. Thus, combining 2 harem species within the same enclosure may result in serious interspecific conflict.

Many artiodactyls have evolved strongly ritualized threat and aggressive behaviors, which result in minimal injuries during intraspecific encounters. However, conflicts between similar species may result in serious injuries or even fatalities due to differences in size and morphology. For example, the ibex, *Capra ibex*, is very vulnerable to fatal injuries from the chamois, *Rupicapra rupicapra*, since, when fighting, chamois keep all 4 feet on the ground and strike upward with their horns, compared with ibex, which rise up on their hind legs and strike downward with their horns. As a result of the ibex's downward force and the chamois's upward attack, the much larger ibex may be seriously injured.

The ordinary behavior of one species may also be misinterpreted as a threat display by another species and subsequently result in interspecific aggression. For example, Hediger (1950) describes how kangaroos raise up on their hind limbs in a posture apparently similar to that of a cervid rearing, and how this can be misinterpreted by stags as an aggressive display, resulting in the stag attacking the marsupial.

Walther (1965a, 1965b) suggested that interspecific aggression is most likely to occur in closely related species that have similar antagonistic behaviors, and that mixed-species antelope exhibits can survive without problems only when the species have different antagonistic behavioral patterns and are more distantly related. Hammer (2001) confirmed this hypothesis; she found more aggression in mixed-species exhibits of closely related horned mammals.

By contrast, Popp (1984) suggested that interspecific aggression is more likely to occur among more distantly related species, specifically because they do not "understand" each other's antagonistic and submissive behaviors. For example, zebra may not perceive an antelope's presentation of horns as a threat display, and likewise an antelope may not understand the zebra's raised hind leg as an intention to kick. However, individuals have shown that they can learn the meaning of interspecific threat behaviors when these are reinforced by a kick or a blow from horn or antlers (Heck 1970).

Dittrich (1968) describes an incident where the failure of a zebra foal to behave "appropriately" to the threat display of an eland bull led to the foal being fatally gored. However, we believe that more distantly related species are less likely to trigger aggressive behaviors in each other, since with large physical differences and little competitive overlap, individuals typically will not perceive members of the other species as a threat.

Zoo staff needs to understand and monitor the species differences and similarities in aggressive and submissive postures when developing and managing mixed-species exhibits. When threat behaviors are similar and submissive behaviors are different, species are more likely to fight, regardless of taxonomic relatedness. Thus, the submissive kneeling behavior of bongo (Estes 1991) may be perceived "incorrectly" by hartebeest, *Alcelaphus buselaphus*, or wildebeest, *Connochaetes* sp., for whom kneeling behavior may be a precursor to aggression.

Morphology and fighting behavior are also critical when mixing horned hoofstock. Wildebeest and oryx have similar antagonistic behaviors, but very different horn morphology. The wildebeest bull is at a considerable disadvantage with his small horns, since he cannot lock with the longer horns of the oryx (Walther 1965b). Eland and lesser kudu, *Tragelaphus imberbis*, lock horns at different heights; eland lock horns just above the ground, but lesser kudu bind higher. If the lesser kudu's head slips between the horns of the eland and the eland exerts an upward pressure while the lesser kudu exerts a downward force, the more slightly built lesser kudu can suffer a broken neck.

Marked differences in conflict behaviors can actually inhibit fights. For example, a bull eland and a wildebeest or hartebeest will use a lateral presentation in their dominance displays (Estes 1991), but thereafter, their aggressive behaviors differ (fig. 13.3). The eland lowers its horns, and the hartebeest raises its horns. The hartebeest will then drop to its knees in order to start species-typical shoulder swiping or soil horning. Meanwhile, the eland, which fights in a standing position, will wait for the hartebeest to stand and fight, while the latter is waiting for the eland to kneel and fight (Dittrich 1971).

One method of avoiding such aggression is to separate bulls selectively during their mating season, but this approach requires detailed observations to ensure that animals are

Fig. 13.3. A wildebeest waits for an eland to accept his challenge. (Photography by G. Hammer, Zoo Münster. Reprinted by permission.)

moved before serious aggressive encounters and, of course, facilities to house the separated animals. However, the removal of a bull may result in females of the species being attacked by bulls of other species in the enclosure. Dittrich (1968) describes just such an event when an impala, *Aepyceros melampus*, bull attacked a female eland with which he had shared the enclosure for some time before the removal of the bull eland.

Estes (1991) and Walther (1965a) provide excellent accounts of antagonistic and dominance behaviors in a wide range of ungulates that are well worth referring to when considering a mixed-species ungulate exhibit.

TAXONOMY

Although the success of a mixed-species exhibit is ultimately dependent on the individual behavior of the occupants, certain tentative generalizations can be made regarding taxonomic differences in behavior. Monotremes, many marsupial orders, Chiroptera, Sirenia, Hyracoidea, Pholidota, and Xenarthra seem to be very tolerant toward most other species, whereas members of the Cetacea are often rough when playing with other species and members of the Scandentia are often very timid. While some carnivores may readily mix with nonprey species as juveniles and then maintain good relationships as adults, rodents generally become very aggressive after reaching sexual maturity. Members of the Equidae often attack the offspring of the other species, and in the Artiodactyla, fighting between males during the mating season is common.

At species levels also, there seem to be differences in individual behavior. Within the Bovidae, Thomson's gazelle, *Endorcas thomsonii*, Rocky Mountain goat, *Oreamnos americanus*, chamois, wapiti, *Cervus elaphus*, spotted deer, fallow deer, cape buffalo and forest buffalo, *Syncerus caffer nanus*, roe deer, *Capreolus capreolus*, and moose, *Alces alces*, are considered very aggressive, whereas bushbuck, *Tragelaphus scriptus*, and eland are generally described as docile. Mountain zebra, *Equus zebra*, appear to be more aggressive than plains zebra, *Equus burchelli*, and white rhinoceros and South American tapirs, *Tapirus terrestris*, seem to be more tolerant than black rhinoceros, *Diceros bicornis*, and Malayan tapirs, *Tapirus indicus* (Bartmann 1980). Pygmy marmosets are described as very shy, whereas emperor tamarins, *Saguinus imperator*, as highly aggressive (Hammer 2001).

GENDER AND AGE

Gender may have a significant impact on the success of a mixed-species exhibit. The males of many mammal species display more aggression than females (Kummer 1971; Bygott 1972; Paul, Miley, and Baenninger 1971, etc.). However, in a mixed lemur enclosure, the females may be most aggressive both within and between the species.

The presence of females from one species may also trigger aggressive behaviors in the males of another species. Also, aggression may vary seasonally and differ across the sexes. Males are typically more aggressive during the mating season, whereas females are typically more protective and hence potentially aggressive when rearing young. Zoo staff therefore need to consider the effect of gender and how to establish appropriate sex ratios within each species due to be mixed.

Generally, younger animals are more adaptable and capable of dealing with change and novelty than adults. As a result, the likelihood of success may well be greater for mixed-species exhibits that start with younger animals.

BODY SIZE

A large size differential is thought to be advantageous in mixed-species exhibits, since this may reduce competitive overlap between species. Furthermore, large herbivores in particular are considered more calm, tolerant, and robust than smaller species. This perception may reflect real differences in species-typical predator risk perception and antipredator behavior, with larger species being less fearful of predation and adopting defensive strategies compared to more fearful smaller species relying on flight and crypsis. However, at this stage there is insufficient evidence to support either of these claims, and exceptions will, of course, always exist. We would encourage an analysis of mixed-species exhibits to see if size differential could be considered a predictor of success in mixed-species assemblages.

INTRODUCTION OF SPECIES

Whether or not animals of different species or of the same species are being introduced, similar principles apply (see Powell, chap. 5, this volume). We will focus mainly on those issues not covered in Powell (ibid.). New exhibits need facilities to allow animals to familiarize themselves with each other without making contact. Such facilities can subsequently be used to separate animals for management reasons, e.g. parturition, and thus are not just useful for the introduction phase.

However, individuals may establish these introduction zones as territories and may defend the space more strenuously than an individual without prior claim to the resource who has invested less in the territory and so has less to lose. This so-called Bourgeois Strategy (Maynard Smith and Parker 1976) increases the likelihood of a resident fighting to defend a territory, whereas a potential invader might just exhibit threat displays.

Mixed-species introductions should attempt to equalize any potential imbalances during the mixing phase. Thus, one might consider allowing members of the "disadvantaged" species more time to establish within the enclosure, or first mix only a few selected lower-ranking individuals of the more dominant species (see Powell, chap. 5, this volume). If species are considered equally dominant within a proposed mix, zoo staff may familiarize the animals with each other and introduce them simultaneously to the exhibit, since the novelty of the new facility will be more significant and distract their attention from each other.

In establishing a mixed lemur enclosure at Woburn Safari Park, we released the black and white ruffed lemurs last, since they were more numerous and considered the dominant species. The nonaggressive red-bellied and red-fronted lemurs with equivalent group sizes were introduced simultaneously into the enclosure after a prerelease familiarization period. Later, the ruffed lemurs were introduced into the enclosure and familiarized with the other 2 species while in an introduction pen adjacent to their house.

Woburn Safari Park staff employed a different strategy for introducing 4 species of Old World primates into a much larger enclosure. All 4 species were confined to their houses and associated introduction pen so that they would establish that area as a territory to the exclusion of other species. Keepers also linked feeding within the house to specific acoustic signals, unique to each species.

Similar principles apply when reintroducing mothers and offspring back into a mixed-species enclosure after separation. Additionally, it may be beneficial to maintain other species, especially equids, on a reduced food ration before reintroduction to ensure that they will be more preoccupied with food and less interested in the newly reintroduced or introduced animals. Introducing the female and infant to a conspecific resident male may protect the female and offspring from aggression by conspecifics and heterospecifics (Dittrich 1968).

POSTMIXING PROBLEMS

There are many examples of mixed-species communities that have worked successfully for many years and then quite suddenly broke down. At Los Angeles Zoo, zebra duikers (*Cephalophus zebra*) and talapoin monkeys (*Miopithecus talapoin*) were separated after several months of peaceful cohabitation because the monkeys started to jump on the duikers and bite at and tear their hair (Crotty 1981). As with single-species exhibits, critical effective monitoring must be in place, combined with contingency plans to remove animals or even whole species from exhibits which "fail," either permanently or temporarily, until appropriate adjustments and reintroductions can be made.

PARTURITION AND REARING THE YOUNG

Postpartum changes in female mammals can be quite dramatic (see Thomas, Asa, and Hutchins, chap. 28, this volume). Some females demonstrate an increased tendency to attack other animals postpartum, and there appears to be a correlation between increased aggression and the length of lactation (Scott 1966; Flandera and Novakova 1971). Often, interspecific interactions previously considered inconceivable are observed postpartum, e.g. cervids attacking and injuring ursids to protect their young (Altmann 1963).

Some species have been reported to predate young of other species with whom they had previously cohabited without incident, including peccaries and anteaters predating young mara (Hammer 2001) and duikers, *Cephalophus* sp., eating young springbok, *Antidorcas marsupialis* (Schanberger 1998).

Facilities to isolate a mother and young from other animals in an exhibit may be critical in most mixed-species enclosures in which breeding occurs. Separation, if required, should ideally occur before parturition so that the dam can acclimate to new surroundings.

There are considerable species differences in the degree to which mothers protect their young. Zebra females are typically quite aggressive in defense of their young, whereas gazelles and hartebeest tend to lead their young away from threats. Cervids use a cryptic approach and hide their young, only returning to suckle. In the latter case, particular care should be taken, since even in large enclosures, young may be found and harmed by cohabiting individuals.

THE FUTURE

Making broad generalizations about mixed-species exhibits is difficult. Although there may be species trends, individuals or circumstances will always provide exceptions to the "rules." Our examples will likely contradict experiences elsewhere. Mixed-species enclosures have risks, but when managed appropriately, and with judicious selection of species, the potential disadvantages are outweighed by the advantages of this approach to captive mammal care (Anderson 1982, Felton 1982, Killmar 1982). A multidisciplinary approach should be taken to assess the risks and benefits for each exhibit and each species combination in advance of establishing a new mixed-species facility. Management strategies need as much consideration as enclosure design in order to ensure success. As zoos quite rightly strive to provide more complex and spacious environments for their animals, and more educational and inspiring exhibits for zoo visitors, the role of mixed-species enclosures will become more important as conservation demands on zoo space increase.

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14

Structural and Keeper Considerations in Exhibit Design

Mark Rosenthal and William A. Xanten

INTRODUCTION

When designing exhibits, there are general issues that zoo planners should address so that exhibits will be safe and easy to maintain (Veasey 2005). Not only should the animal's biological and psychological needs be taken into account (Curtis 1982), but the people who daily manage and maintain the exhibit need to be considered (Simmons 2005). Since animal keepers and maintenance personnel are responsible for the upkeep of the exhibit, the more thought and consideration given to the construction of the area, the easier it will be for them to maintain and to manage responsibly. The need for preplanning cannot be overstated—e.g. once concrete has been poured and set, it is impossible to change the pitch of the floors for better drainage without expensive change orders.

STRUCTURAL CONSIDERATIONS FOR THE VIEWING EXHIBIT

WALLS

Wall composition and form will vary depending on the animal species and how they are to be exhibited. Square territories do not exist in nature, but in most exhibits the walls meet at perpendicular angles—the perfect place to catch dirt and debris. Rounding the corners of walls is an expensive option, but rounded corners accumulate less dirt and are easier to clean. A rounded joint at the junctions of walls and floors can eliminate a crevice where pests can hide or fecal matter can gather.

Walls may be made of precast concrete (Arnott, Embury, and Prendergast 1994), and there are a variety of treatments possible. When applying paint to walls, the preliminary application should be done correctly or peeling may rapidly occur. Nothing detracts more from an exhibit's visual appeal than peeling paint. All paint in animal exhibits should be nontoxic, since many animals bite, lick, or peel off paint and then ingest it. At one zoo, the mandrills, *Mandrillus sphinx*, ate old paint off the bars, resulting in lead poisoning in some troop members. In areas for elephants and rhinoceroses, the walls should be unpainted, because the animals rub against the walls; a concrete stain is preferable.

Tile, available in many colors, can also be used as a wall covering and is easy to clean and maintain (Johann and Salzert 1999). However, the appearance of tile may be too sterile. Brick may be relatively inexpensive as a wall covering, depending on the type chosen, but it often requires filling and finishing joints with cement, mortar, or sealing as the years go by. Brick is also hard to clean and has a rough surface. Fiberglass can be colored and easily cleaned, and it provides little shelter for insect pests, much like tile, brick, and reinforced concrete.

Wood walls offer the advantage of being easily replaced when damaged, and there are a wide variety of woods available. However, wood walls offer abundant shelter for pests. In one giraffe, *Giraffa camelopardalis*, exhibit, wood was used as a façade on top of the concrete walls, and although the giraffes did not damage the wood, mice and cockroaches sheltered in it. Elephants and rhinoceroses damage wood planking by gouging it with their tusks or trying to remove planks using their horns. Wood can be cleaned, but with daily cleaning and spray from animal urine, certain woods absorb liquid and may rot more quickly.

Waterproofing wall surfaces by covering them with sealant makes cleaning much easier. At one zoo, a concrete block wall was not sealed properly, and over the years, the constant use of water on the surface resulted in leaching of the limestone in the mortar joins, leaving a crystallized substance that could not be cleaned.

Murals are often used as a backdrop on walls but can be expensive to replace or touch up when damaged. They need to be sealed for protection against water and animal urine. All murals, regardless of how well they are protected, eventually get damaged and need to be refurbished. Thus, current and future budgets need to be considered before deciding to use murals.

Many species scent mark their living area with urine. The long-term damaging effects of urine on the wall surface include discoloration and staining, especially on wood walls.

Wall coverings of artificial rockwork also must be sealed, and depressions should be created to permit adequate drainage to floor drains when the wall is washed and cleaned. Rockwork should incorporate pathways to allow keepers access to the upper portions of the exhibit for cleaning.

FENCING

In many outdoor mammal exhibits, fencing encloses and thus defines animal territories. A number of fencing types are available, such as chain-link, stock fencing with standard square design (sometimes called hog wire), welded mesh, metal horizontal bars, and wood palisades (Hediger 1969a). Newer types of mesh composed of finely handwoven stainless-steel cable have proved effective for a variety of species (www.pwrconcepts.com). The type of animal to be exhibited and budget considerations typically influence the fencing chosen.

Long-term maintenance is a prime consideration in deciding what type of fencing material to use. Strength and tension are best when the fence runs in a straight line. Wire fencing that is too loose may result in animal injury. In ungulate enclosures, fencing should be attached to the paddock side of the posts to create an unbroken interior surface; this prevents an animal from running along the fence line and injuring itself on protruding posts. The designer needs to consider the animal's strength in the final choice of materials. As Hediger (1964, 53) has stated, "Overexcitement weakens all barriers."

Fencing for ungulates should be 1.8 to 2.4 m high (Manton 1975). Depending on geographic location and the presence of local predators, the designer may need to incorporate barriers to discourage digging and climbing predators. The type and dimensions depend on the species involved and their behavior. Belowground barriers can be of numerous designs. The most effective types are the ones that are installed 15.2 to 45.7 cm belowground and then extend into the enclosure for a distance of 0.6 to 1 m, since most burrowing or digging animals approach a fence and begin digging. Fence overhang topping can consist of outriggers at either 90° or 45° angles (Embury and Arnott 1995). These outriggers can have solid metal or wire or cable strands to prevent escape. Wire or cable can be electrified if needed.

The location and size of transfer gates along a fence perimeter should be designed so that the animal manager can access them safely for opening and closing. A very narrow opening in the transfer gate may result in herd animals bunching up as they attempt to move from one paddock to another (Knowles and Bickley 1992). However, larger gates may be more difficult to operate manually. Gates can be of the swing or slide variety and should be large enough to drive a vehicle through. Sliding gates are more costly, but allow much more flexibility for transferring animals.

FLOORS

One of the most important factors in exhibit design is the slope of the floor and its drainage. During cleaning, excess water should drain rapidly. Poorly drained floors may need to be wiped down to eliminate excess water that has gathered in low spots and to prevent algae buildup, a time-consuming task. To ensure proper drainage, the slope to the drain should not exceed a 5% grade. The slope needs to be predetermined and approved before pouring the floor. Correcting a poorly designed floor is very difficult and expensive. To test whether an exhibit has an adequate slope, a bucket of water should be poured onto the floor from anywhere in the exhibit. If it does not flow easily toward the drain, the slope needs correction.

Floors of most exhibits should have a nonskid texture, to prevent potentially dangerous falls. A broom finish, light or heavily applied to a freshly poured cement floor, provides a degree of firm footing. For painted floors, only specialized paints that can withstand daily wear by animals and animal keepers should be used. Paints with added abrasives can severely wear away the pads/hooves or feet of animals and should be avoided. State-of-the-art cushioned flooring material is now available and can be used successfully for heavy-bodied species such as elephants, hippopotamuses, and rhinoceroses.

PADDOCKS

Drainage is a major consideration in paddock construction. A poorly drained yard results in unsightly pools of standing water, a condition not only detrimental to general animal health, but also requiring more paddock maintenance by animal keepers. Both the top and subsurface substrate materials should promote good drainage. One of the better and inexpensive new products on the market, which works well with ungulates, is blue stone, a dense type of slate. The application of graduated-size stones and a top layer of fine stone creates a very tough and long-lasting paddock surface. If the top substrate does not allow adequate drainage and water starts to erode the soil and form small gullies, the yard should be graded and sloped to facilitate water runoff to a drainage area.

Natural substrates, while aesthetically pleasing and easy on an animal's feet, do present medical issues, e.g. grass. Moreover, parasites may thrive in this environment, although it is less of a problem in temperate climates, as the encysted larvae usually die during the winter. Animals on natural substrates need to be on a scheduled prophylactic parasite program.

CEILINGS

Skylights are excellent for exhibits that have plants or for animals that depend on photoperiods for specific activities (Chew 1990), such as reproduction. Skylights should not block the ultraviolet rays; there are now products that allow approximately 70% UV transmission. Skylights that open to the elements allow the animal manager flexibility in exposing the exhibits to the weather. If they operate via electricity, a manual method of operation needs to be available if the power fails. Exhibits with primates or birds may need a mesh barrier installed at the skylight opening to prevent escapes. Remote operation of skylights is essential, because they are usually installed at high points in the exhibit ceiling.

Wire-mesh or barred ceilings provide good sites from which to hang a variety of ropes, vines, or logs in an exhibit (Dickie 1998). For a solid concrete ceiling, staff needs to preplan the locations for light fixtures and hooks. Suspended ceilings need to be high enough to prevent animals in the exhibit from reaching them; otherwise, zoo staff may be constantly searching for escaped animals above the false ceiling.

KEEPER ACCESS DOORS

Access doors to animal exhibits should be large enough for any keeper to gain entry without having to crawl or stoop, and also allow the entry of exhibit materials, such as soil, rocks, plants, and dead trees, as well as equipment needed for daily maintenance (e.g. high-pressure washers or ladders). All doors need a viewing window to allow keepers visual access before entering, thus preventing animal escapes. Most doors should open inward from a safety standpoint, but there are some exceptions. Small exhibits with decorative materials should open outward to allow more room for the exhibit material and easier access of the material into the exhibit. Dutch doors, where the top half can open separately from the lower half, can provide visual access to prevent escapes.

OFF-EXHIBIT HOLDING AREAS

Holding areas, whether directly connected to or separated from the exhibit area, are essential for proper animal management. Many exhibits lack adequate off-exhibit holding areas. Such areas adjacent to an exhibit permit regular transfer of animals during cleaning. Moreover, the manager can allow the animals to move away from the public, if desirable. In addition, animals can be separated for feeding and for sleeping. When introductions are performed, introduction screens or doors can be placed between the exhibit and holding areas, thus enabling introductions to proceed out of public view. Holding areas are also useful for isolating animals, e.g. to obtain individually identified urine or fecal samples. Urine traps can be incorporated into the drains for ease in collection by keeper staff.

For outdoor exhibits, holding areas in the rear may provide greater security at night. In addition, separate nighttime holding areas for ungulates allow paddocks to recover from the damage caused by grazing, browsing, and trampling of the substrate. Holding facilities separate from the exhibit are indispensable for maintaining surplus animals or for situations that require separation of an animal from the exhibit, e.g. females that are due to give birth, introducing individuals that may initially fight, or animals under medical treatment.

The adage that "nature abhors a vacuum" applies especially to animal holding areas. Certainly, any design for new or remodeled exhibits should include maximum space for holding facilities and, if at all possible, allow room for additional later expansion. Design of a holding facility should follow the basic rules for any animal containment area: the plans should include proper drainage, lighting, water, climate control and/or ventilation (if indoors), shade (if outdoors), and pools (for aquatic animals). In addition, there needs to be sufficient capability for shifting animals within the holding area. Shift areas are perfect sites to install restraint cages that the animals must pass through to go on and off display, and a scale can also be placed either in the restraint cage or as a stand-alone feature. Placement of drains under the restraint cage should be avoided, because access will be extremely limited if not impossible.

Holding areas need to be easily accessible to staff and designed for vehicular entry and the accommodation of equipment for loading and unloading animals and exhibit furnishings. An ideal off-exhibit holding facility should be as flexible as possible. The floors should slope, and the facility should have a pool at one end (front or back). A correctly designed pool, when dry, can be an extension of the main holding area, or can be used as a shallow pool for small aquatic animals. Shelving should be easily removable.

TRANSFER OF ANIMALS FROM EXHIBIT TO HOLDING AREAS

The ability to transfer animals easily and safely from one exhibit to another or between holding areas is of paramount importance and should involve minimal stress to the animals. The proper design of shifting facilities must first take into account the species' natural behavior. Doors should be located at the junctions of walls, since most mammal species run to a corner or can be forced into one; however, door-operating mechanisms should be located at the opposite end of the exhibit, as mammals tend to move away from keepers and not toward them.

Shift doors for arboreal mammals, such as primates, need to be at heights that promote natural behaviors. Elevated shift doors must still be accessible to keepers, and will need a wide shelf just beneath the doorsill to hold crates for catching animals. These shelves also provide a resting site for the animals and a secure anchor for limbs and vines.

Runs should allow keepers access to at least one side, with either sliding or descending (guillotine) doors where the holding or exhibit cage entrances are located. This design allows an animal to be directed from the run into the holding cage and prevents it from doubling back on the keeper. We recommend not shifting animals through cages, since the keeper may lose control over the animal once it is in a larger area. Squeeze cages and scales can be built into runs so that the animals are habituated to them. Squeeze cages can also be built as a connection between 2 rows of holding cages.

Clear identification of shift doors is extremely important. Color coding and numbering of the doors and operating mechanisms make shifting easier and safer for both the animal and the keeper. Door size is also important (Collins 1982). Doors that are too small may cause injuries to the sides and back of an animal moving through them; doors that are too large may not be usable for trapping an animal in a crate, because additional materials will be needed to block the entrance and prevent escapes around the sides and/or top of the crate. Low overhangs above doors can prevent the effective use of crates with guillotine doors.

Either guillotine or sliding doors are best for most carnivores and primates (Blount 1998). Manually operated doors are the least expensive to build and to maintain, but are not recommended for great apes, who can grab the door as it is being closed and throw it back open. However, without strong track stops, a door may be thrown off the track, possibly injuring the keeper. Also, some primates can actually push guillotine doors up unless the doors are extremely heavy and have a slot at the bottom to prevent fingers from slipping under the door. Keepers need to be careful that guillotine doors do not drop on the long tails of some large cats and primates.

While sliding doors eliminate the problem of injury, they are harder to operate. Guide tracks often become clogged, making operation even more difficult. Designers need to consider the amount of horizontal space available for sliding door placement and operation. Sliding door handles can be hinged in the middle in tight areas where a door handle sticking out in the aisle would be problematic.

A cable with a handle that lifts the door when pulled and lowers it when slowly released can operate guillotine doors. Such doors must be light enough for a keeper to operate or have counterbalances provided. Another method uses a cable attached to a ratchet that can be turned with a crank, but this type of door operation can seriously injure animals and keepers if the door is very heavy and drops too fast for the keeper to maintain a hold on the crank handle.

Hydraulic, pneumatic, and electrically operated doors have recently become widely used in great ape and pachyderm facilities. Hydraulic and pneumatic doors are generally of the sliding type and have the advantage of being stoppable at any point during movement by releasing the operating switch. They can also be fitted with automatic pressure stops, which prevent animals from being crushed should they get trapped in the doorway. The speed at which the doors close is important, since some hydraulic doors move so slowly that the animals cannot be closed into or out of their exhibit.

Electrically operated doors are less frequently used because, like manually operated doors, they can be forced open during operation if they have a chain drive. Worm-screw drives can eliminate this problem, but they are very expensive to design and build. In all cases, manual overrides should be provided in case of any type of mechanical failure.

Manually operated sliding doors are preferred for ungulate stalls and for small mammal enclosures. They are easily operated, inexpensive, and offer great flexibility. The size of the door opening can be controlled to facilitate crating and reduce drafts, and the door can be closed quickly if needed. Designers need to remember that keepers vary in height, so placing handles too high will handicap shorter keepers in operating the doors efficiently. Keepers should always have a clear line of sight when shifting animals. If this is not possible, then mirrors can be used to view the transfer doors directly.

Sliding and guillotine doors increase the total usable area of a stall or exhibit. This is particularly important in small mammal exhibits, where space is usually at a premium. A swinging door should not be used to move animals into or out of an exhibit or holding area. However, swinging doors for keeper access should open into the enclosure to create a barrier between the keeper and the animal(s); should an animal hit the door, the door will be forced backward into a closed position. To prevent an escape, swinging doors opening into the enclosure must close automatically and have self-locking latches, in the event they are accidentally left open. If available space prevents positioning a door to open inward, other options (such as a sliding door) may be used.

Dutch doors, swinging doors that are divided in the middle, are common in ungulate barns and small mammal exhibits. They allow the keeper to view the enclosure through the upper half with little risk while preventing terrestrial small mammals from escaping. Again, it is preferable that these doors open inward.

Another door design recently used has been the garage-style door. We do not recommend use of this door type due to its complexity (at least 2 hinged sections) and the possibility of sticking if large mammals hit it. Cats can gain access to the top of an improperly designed door and escape or hide. Also, this type of door moves very slowly when electrically operated and still needs a manual override.

Door thickness and strength depend on the strength and size of the species. Heavy solid-metal or barred doors are generally used for large carnivores, pachyderms, and great apes. For greater security, doors or gates for dangerous animals should have 2 lock hasps, one at the top and the second at the bottom. Lightweight alloys may be used if they meet structural strength requirements. Thick, transparent plastic of high-impact strength which allows the keepers to see what is on the other side of the door has been used successfully with great apes (McDonald 1994) and large carnivores.

Pachyderm facilities have had excellent success using reinforced-concrete doors, while wooden doors are generally adequate for most ungulates. Hollow-core doors offer a lightweight alternative and can be quite strong if properly designed. However, they tend to rust from the inside out unless properly rustproofed; they also harbor rodents and cockroaches unless totally sealed.

KEEPER SERVICES AREAS

Planners often forget the service areas when designing an exhibit, an oversight that can reduce keeper morale and overall operational efficiency. Service areas should be roomy, well lighted, and well ventilated, and have proper drainage. Once these 4 criteria have been met, other needs are much simpler to provide.

Corridors and entry doors must be sufficiently wide for access by crates, food deliveries, and exhibit materials. Service areas should have ramps rather than stairs, again to provide greater ease of access. Floors with the proper pitch will allow good drainage, and nonskid materials or brushed-concrete floors will eliminate slipping. Trench drains are preferable, since they drain quickly and are easy to maintain (fig. 14.1).

Adequate storage areas for food, tools, and exhibit materials are crucial for proper care of the exhibits. Freezer and refrigerator space provides for long-term and short-term bulk storage of foods, which saves time, prevents spoilage, and requires fewer food deliveries.

Racks are necessary for holding a variety of tools in accessible, secure areas. Hose racks should be located conve-

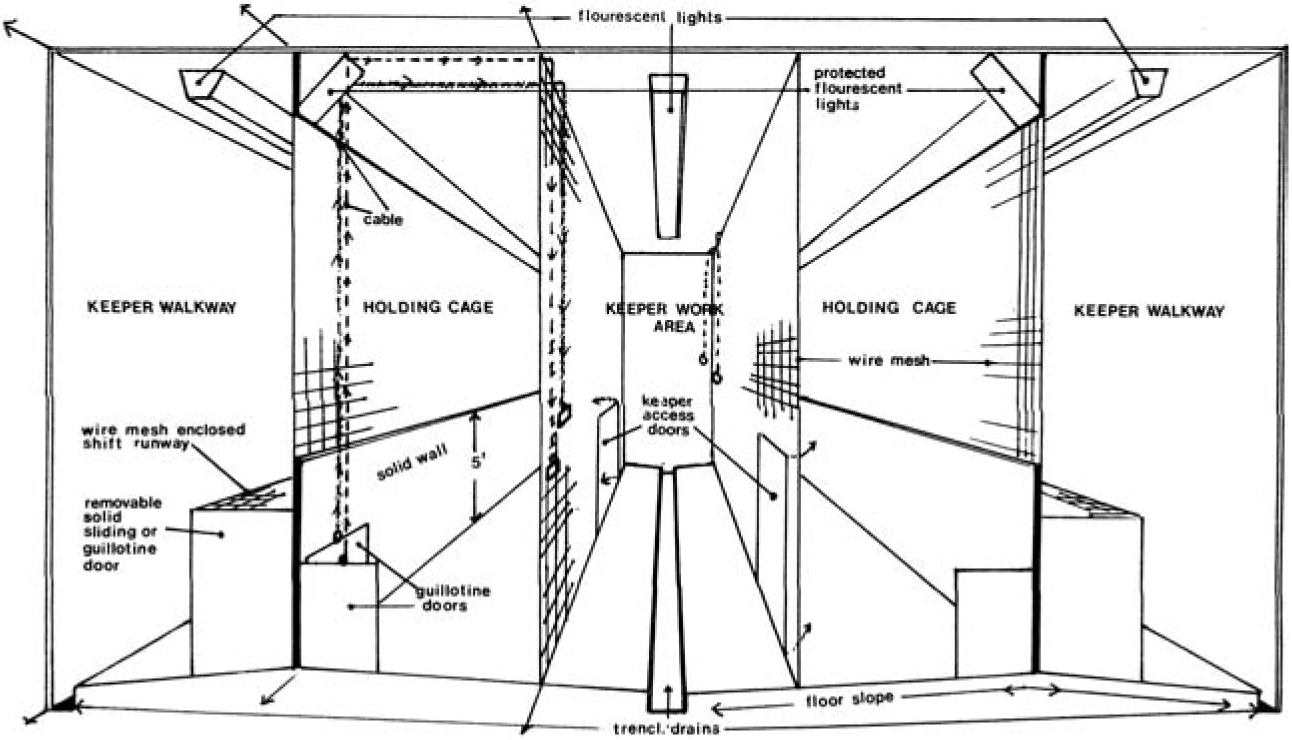

Fig. 14.1. Generalized plan for animal/keeper holding, shift, and work areas (median horizontal section).

niently near the hose connections and in sufficient numbers to allow the use of a short length of hose (less than 7.6 m). Hose racks that are able to recoil hose automatically are a convenience and, if located on the ceiling or high on the walls, save space along corridor walls. These automatic hose racks may break down, however, rendering them useless. Thus, stationary units, which require hand coiling of the hose, may be preferable even though they occupy more space and are more time-consuming to manage.

The space between the rear of the exhibit and the rear wall of the service area should be sufficient for introducing and removing animals and materials from exhibits. Corridors that are too narrow or too low to permit access with exhibit materials or crates can negate the advantages of designing wide and high doors into the exhibits. For example, designers may overlook the need for height to open crates with guillotine doors. Installing rings or hooks for the attachment of chains or ropes to secure crates against a door frame is also useful, especially when transferring large, powerful mammals such as cats, bears, great apes, large ungulates, and pachyderms. Large animals are best moved by crate or chute at ground level; e.g. maneuvering a large, heavy crate holding a rhinoceros off a loading dock is very cumbersome.

Designers also need to consider the possibility of animal escapes. What happens when an animal gets loose? Is there a safety vestibule? Sections for dangerous animals should always have a safety gate before the entrance. A slide bolt in addition to other locking devices can add a secondary measure of safety to the gate.

Ideally, a keeper should have an unobstructed view of the entire service area. An animal keeper was saved in one instance when he noticed bear footprints on the floor just before opening the safety gate leading into the service corridor. He realized that the bears had escaped from their den and was able to summon help. Blind angles should be avoided, but mirrors or closed-circuit television can be used to see around corners. For small mammals, netting or wire mesh should cover any ceilings where there are overhead lights, ducts, or pipes in order to confine the escapees to a height that allows easy recapture. In areas housing large cats, bears, or primates, hiding areas (especially above or beneath cages) should be eliminated. Good lighting is always essential.

Service areas should make a keeper's daily work easier. Discussions with keepers before design and construction usually elicit excellent ideas and lead to less-troublesome facilities.

UTILITIES

PLUMBING

Designing a good drainage system is important at the outset, since future alterations can be costly. Selecting the proper size and number of drains and the location of each requires considerable thought. Drains placed on the outside of the exhibit are accessible to both keepers and maintenance personnel while the animal remains on display. Obviously, the floor must pitch correctly to each drain.

Trench drains must be wide enough to accommodate a shovel or pitchfork in order to clean out accumulated waste. Catch baskets and strainers allow the waste to collect in one location and prevent it from entering and blocking main pipes. One great ape exhibit has an open drain located inside the enclosure which is large enough to accept produce such as apples and oranges. The keeper can thus hose the entire area with the animals still on display and later retrieve the uneaten food and waste from the large, cone-shaped strainer.

If drains are located inside exhibits, the covers must be secured so that the animals cannot remove them. In one case, a polar bear, *Ursus maritimus*, removed a metal drain cover and struck and broke a pane of glass with it in the animal's underwater viewing area. Apes, too, can use their hands to remove covers that are not securely attached.

When constructing pools, it is preferable to place the overflow drain at the end of the pool opposite the fixture for filling the pool. As water fills the pool and is drained by the overflow, it will cause maximum water movement and help skim debris from the water surface.

In any pool, it is a bonus to be able to set the water level to the desired depth. Also, all water elements within the exhibit or holding areas should have outside and conveniently located off/on switches for safe keeper operation.

The location of the hose connections depends on the type of animal exhibited; e.g. outside connections are best for dangerous animals. Usually, if a hose connection is located in a central area, the hose can serve a large number of exhibits. There should be enough hose connections to avoid a keeper's having to manage more than 30 m of hose each day. With nondangerous animals, hose connections can be located within the exhibit.

Hot water is best for cleaning exhibits, but budget may play a role in the size of the water heater installed. Mixing valves are needed when temperate water is used, e.g. for bathing elephants.

Self-filling water bowls are excellent for hoofstock. One type allows the animal to fill the bowl by pressing a lever with its snout. Some antelopes and gazelles have trouble with this type, but another good mechanism is regulated by a float device that automatically fills the bowl when the water level drops. Primates and carnivores are able to destroy self-filling water bowls with their teeth, hands, or paws. For them, "lick-it" watering devices may be more effective: the animal licks the device or presses a small lever that releases water for as long as the lever is depressed. When the action is stopped, the water ceases to flow. Water containers should be above floor level to reduce the possibility of a carnivore's defecating into them. The precise height will depend on the size of the animal.

Adequate water pressure gives keepers the volume of water they need when using hoses or filling pools. Cutoff valves should be easy to reach, and away from direct contact with the animals. The major locations for cleaning out pipes should be located for easy access by maintenance crews. Adequate access to the key plumbing area will permit regular maintenance, including by pest control personnel, who may need to lay traps or spray in plumbing areas.

Pools in naturalistic exhibits need natural-looking handholds for keepers who must enter the water. Since these pools may hold fish, it is not always possible to drain them for routine cleaning. Any drain inside an exhibit or holding area needs to be easily accessed to permit its adequate cleaning and servicing.

ELECTRICAL SYSTEMS

During design of the electrical systems of an exhibit, the future needs of the section must be considered. Adding power for unplanned additional electrical loads can be costly. A sufficient number of electrical receptacles/outlets can accommodate high-pressure water sprayers or medical equipment near where they are needed.

The demand on an electrical system depends on the number of loads of current in operation and the level of energy consumption. Grounding guards against fire and shock help to ensure that a faulty circuit is not dangerous. Outdoor receptacles need waterproofing with a special cover plate and doors that seal the receptacle sections when not in use.

Other special receptacles providing greater safety include one in which a plug can only be inserted by rotating a solid cover that protects the slots, or one in which the cover snaps back into place when the plug is withdrawn. Locking receptacles have a device that grips the prongs of a plug to prevent it from being pulled out accidentally; this is especially useful with equipment moved frequently while in use.

Incandescent bulbs emit light when the fixture is turned on and the filament inside the bulb becomes hot and luminous. Fluorescent lights work on the principle of a flow of electrical current through an ionized gas. While their installation cost may be greater, fluorescent lighting is more uniform and the tubes produce less heat, eliminating heat buildup in smaller exhibits. Fluorescents also use energy more efficiently, thus saving money. Fluorescent tubes designed for special uses, such as growing plants indoors, are available. In certain exhibits, heat lamps or sunlamps will be necessary and may require special fixtures within the exhibit.

Different types of switches are available with variable settings to adjust the lighting level from a faint glow to full brightness. They also save electricity, and when set at lower ranges, the bulbs will last longer. A dimmer switch must be matched to the type of lighting it controls. Incandescent dimmers do not work on fluorescent lights, but special dimmers can be purchased to use with fluorescents. A timer switch, which turns lights on and off at preset times, is controlled by a built-in electric clock and can be operated manually. Timer switches are ideal for controlling photoperiods in nocturnal sections.

An outdoor light switch needs a weatherproof cover that makes it impervious to water and the elements. When access to light switches must be limited for safety or security, locking switches can be used; these are turned on and off by inserting a special key. Light-handle switches, with small bulbs that glow when the handle is turned off, make switches easy to see in darkened areas.

The locations of electrical receptacles, switches, and fixtures should be easy for keepers and maintenance personnel to use and service. In one instance, safety switches were located on the inside of a gate, making it necessary for the keeper to open the safety gate before turning on lights—a potentially dangerous situation. Service panels and electric meters also need to be in locations that do not require an acrobat to reach them. In one zoo, fluorescent lights were placed above a series of small mammal exhibits, but with only one small door in the ceiling to provide access. The electrician had to crawl on his belly to service the lights. Receptacles need to be high enough above the ground so that when floors are washed down, they are not sprayed.

Obviously, fixtures should not be placed where animals can reach them. In one orangutan, *Pongo pygmaeus*, exhibit, wire mesh prevented the adults from reaching the exhibit sunlamps, but the juveniles could easily extend their arms out far enough to damage the fixtures. Luckily, the animals did not injure themselves. Fixtures located within animal enclosures must have a strong-enough protective cover to take all forms of abuse. Certain types of heavy-duty plastic, used in prison construction, function well.

It is critical to have a backup generator to run life support systems in times of power outages. Generators can now run on propane and natural gas, thus eliminating the need to store gasoline or diesel. Backup generators can also power electric and hydraulic door systems during power failures.

VENTILATION

All facilities need adequate ventilation for animals and zoo staff. The size and number of animals in an enclosure will determine the required rate of air exchange. Proper ventilation assures adequate drying of exhibit and work areas, which, along with good drainage, limits the buildup of algae and prevents mildew. If possible, ventilation should be controlled separately for each exhibit and holding area. All controls should be out of the reach of animals but easily accessible to staff and maintenance crews.

WASTE DISPOSAL

Disposing of daily accumulations of waste products from a variety of mammals probably poses one of the most difficult logistical problems faced by the modern zoo. There are basically 2 types of animal waste: soluble materials that can be flushed into the sewer system, and nonsoluble materials that must be disposed of separately. Local or federal laws may dictate the waste disposal method.

Disposal through the sewer system normally involves washing down exhibits, flushing fecal and food materials into a drain. Strainer baskets, placed in the drains to catch large particles that do not break up in the water, prevent sewer blockages. The baskets can then be emptied into garbage containers (fig. 14.2).

There are a number of manual disposal methods for waste, involving carts, wheelbarrows, tubs, buckets, and manure pits. Manual disposal systems are simple and relatively inexpensive; the drawbacks are, of course, that they take time and energy.

Recently, a number of innovative mechanical methods for waste removal have been tried with varying degrees of success, e.g. the use of conveyors to carry waste material (including browse and straw) to an outside pit or dumpster from inside a building. These conveyors can be belts, buckets, or a baffle-type design; all break down periodically and require maintenance for efficient operation. Mechanical assistance, where possible, will help ease any manual operation.

One difficult disposal issue in the United States is the

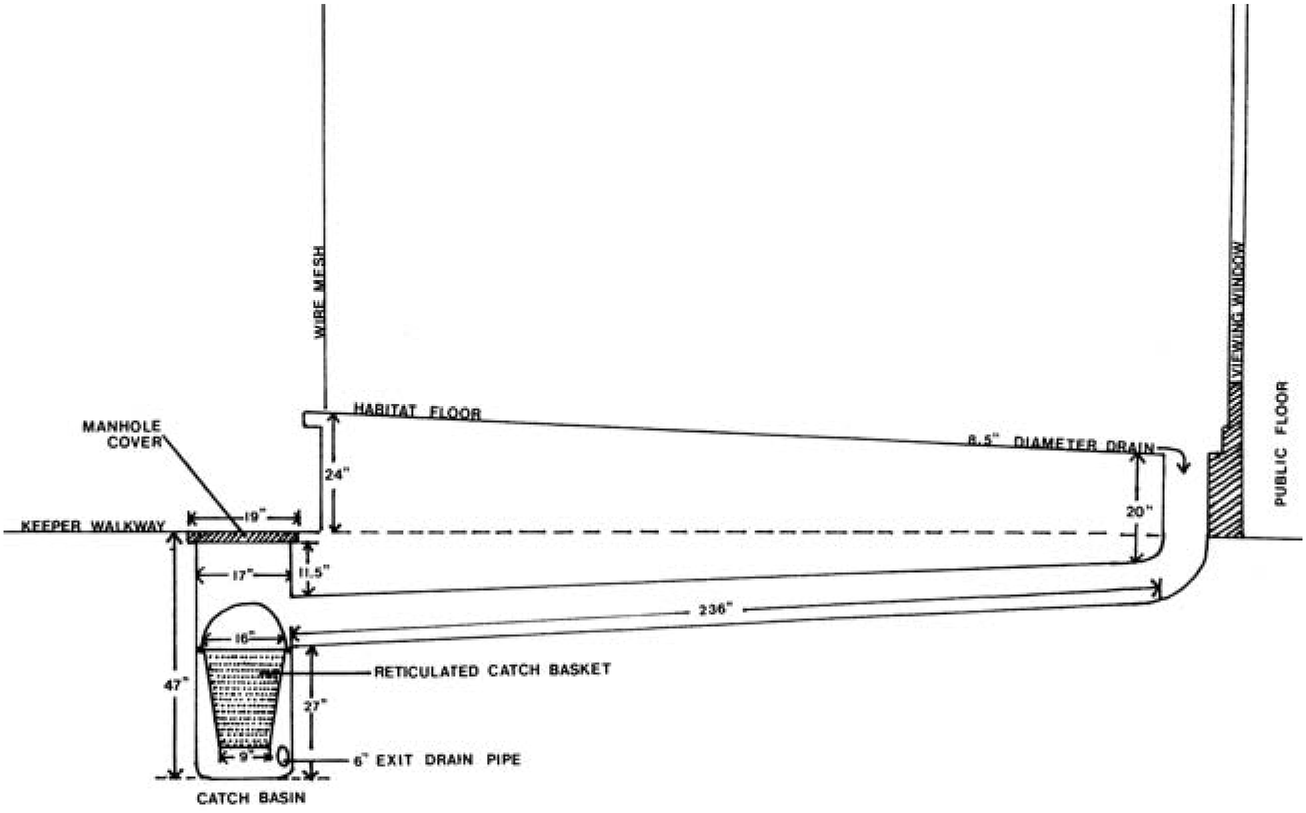

Fig. 14.2. Drainage system, North Side orangutan habitat, Great Ape House, Lincoln Park Zoological Gardens, Chicago.

removal of waste from Permanent Post Entry Quarantine (PPEQ) animals. Manure produced by PPEQ animals must be sterilized before leaving zoo grounds, either by composting or by chemicals. Incinerating the manure is another approach, although many municipalities have limitations on burning. Most zoos have areas on the grounds for composting or have approved sites elsewhere for storing manure. Zoos should consult their local authorities regarding regulations for the disposal of certain types of manure before designing new facilities.

A large, centrally located collection pit can be used to dispose of large amounts of fecal matter from ungulates and pachyderms. Wheelbarrows, dump scooters, or front-end loaders can collect small amounts of waste. Waste can then be removed weekly to a composting site (either on or off zoo grounds) using a vacuum-equipped truck.

Manure can also be placed in a sealed vat, where bacterial action produces methane gas. If large amounts of gas are produced, it can be used to augment other fuels for heating. This technique has not yet met with a strong positive response by zoos, due to the initial costs of equipment and the limited use of methane gas; however, as fuel costs escalate, the use of methane may increase.

Another innovative and successful approach to waste disposal is to sell the composted animal waste to the public for fertilizer. This strategy not only disposes of quantities of manure but also generates revenue from a normally unwanted and expensive disposal item. Obviously, certain manure cannot be sold without being treated first.

Many naturalistic exhibits require that more natural products are used; this requires a system for the efficient removal of the tan bark, sand, straw, leaf litter, or other natural products.

PEST CONTROL

Pest control in animal exhibits is an ongoing problem (Golding 1992; Roberts 2004). Mice, *Mus musculus*, rats, *Rattus norvegicus*, and cockroaches, *Blattella germanica*, need the following conditions to proliferate: (1) shelter, (2) accessible food, and (3) a temperate water source—all easily found in many zoo exhibits and zoo service areas. Controlling pests is possible only if problem areas are known and an integrated pest control program is initiated.

Exterminators usually will not visit and inspect areas that have difficult access. Therefore, all utilities, such as electrical vaults and plumbing mains, must be accessible for treatment (Curtis 1982). Hollow artificial rocks, logs, and trees in exhibits need access ports for spraying insecticide or inserting rodent bait stations.

Small mammal exhibits should be sealed as tightly as possible to prevent rodents from entering. In one small mammal exhibit, a pair of rock elephant shrews, *Elephantulus rupestris*, shared their area with a population of mice. When food was placed in the exhibit, the mice were the first to feed, consuming not only the shrew diet but also the potted plants. After the exhibit was sealed with a finer mesh on the ceiling, the plants thrived and the keepers were able to halve the amount of food provided.

Sealing utility pipes and electrical conduits that open in the floor, walls, or ceiling prevents rodents from using these artificial pathways to travel from section to section (Hediger 1969b). Having entry doors to exhibits and service areas flush to the ground will prevent rodents from entering. A mouse can enter through a mesh size as small as 8 mm. Whenever possible, cracks, crevices, and shelters where roaches can hide should be sealed or eliminated (Doherty 1977–78). Proper design should be coupled with an active management program, in which exhibit and service areas are regularly treated. Pest control is a never-ending battle.

The philosophy of integrated pest management is an important concept for keepers to understand, since they are usually the first line of defense in the fight against pests. Keepers need to understand that pest control is a normal part of their job function, and not an extra chore. If a zoo has a full-time pest manager on staff, the keepers should work together with this person.

TRAINING AND ENRICHMENT

Training collection animals has become an integral part of zoo work. The benefits are many and include easier crating, working with the veterinarians for medical procedures, visitor education, and general animal management (see Mellen and MacPhee, chap. 26, this volume). Zoo management should consider training needs when designing a new exhibit.

Many facilities only allow the option of training in the holding or off-exhibit areas, which means that animals must be taken off public display. However, training sessions in public view can be a powerful educational tool; thus, exhibits should allow for training to be performed both in holding and on exhibit.

The keepers' typical day involves providing enrichment activities for their animals (Bukojemsky and Markowitz 1999; Shepherdson 2003, chap. 6, this volume; Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume). Enrichment opportunities can range from quite simple to very complex (Shepherdson 1992; Gilkison, White, and Taylor 1997; Powell 1997; Wooster 1997). When developing new facilities, designers need to consider the provision of enrichment opportunities for both display and off-exhibit holding areas, e.g. eye bolts in the ceiling to hold ropes or a hanging food puzzle.

Many exhibits have a naturalistic theme, and managers do not want non-naturalistic enrichment devices to be seen by the public. However, such devices can be hidden so that they function but are not seen by visitors, e.g. plastic tubes to hold browse for primates. Painting the plastic tubes will allow them to blend into the exhibit.

SAFETY

Safety is an important part of exhibit design for animal keepers who work with dangerous animals (see Rosenthal and Xanten, chap. 8, this volume). Alarms can be used in areas where keepers work with bears, elephants, large cats, great apes, and large ungulates; the alarm buttons should be of easy access for keepers in an emergency. Alarms should sound not only within the section, but also outside the immediate area and in a central administrative office, since the purpose is to alert as many people as possible that an emergency exists. If more than one area has an alarm, different alarm sounds for different sections will permit the emergency control personnel to pinpoint exactly where the alarm has been activated; e.g. bear exhibits can use a siren, while the elephant house uses a horn. Phones with outside lines are important safety features, to permit calling both within the zoo and to summon fire and police assistance. Emergency procedures and phone numbers should be posted next to the phones in all areas.

With large dangerous animals, predetermined keeper escape routes to exit the exhibit can save human lives. Some zoos have small doors for keepers that larger animals cannot use, thus allowing them an escape route in addition to the entry door of the exhibit. Bars that are spaced properly can contain a rhinoceros but allow room for a keeper to escape.

Blind spots are very dangerous. An animal may be out of the keeper's sight, giving a false impression of safety when entering an area. Some polar bear exhibits have convex mirrors located in the corners of the den that allow keepers to see in the entire area. Properly placed viewing ports also assure optimum viewing.

With dangerous animals, all doors to an exhibit should have double-locking devices. Key-retaining locks ensure that the keeper does not place the lock on a shelf and forget to replace it. When designing new exhibits, a single master key for the section is preferable, so that one master key will allow staff to gain access to all areas in an emergency.

Moving through naturalistic exhibits can be dangerous, especially if adequate natural-looking hand- or footholds are absent. Such areas can be inaccessible, because there is no safe way to access that section of the exhibit. If an animal keeper needs to clean areas that are high off the ground, a safe route to the top should have already been designed in the development of the exhibit.

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15

How to Develop a Zoo-Based Environmental Enrichment Program: Incorporating Environmental Enrichment into Exhibits

Cynthia Fernandes Cipreste, Cristiano Schetini de Azevedo, and Robert John Young

INTRODUCTION

Research, conservation, leisure, and education are the main goals of zoos. To achieve these aims, zoos need to maintain a high level of animal welfare. One action undertaken to improve the psychological aspects of the captive animal's life has been the abandonment of "hard" architecture (enclosures with iron bars and concrete walls and floors) and the adoption of "naturalistic" architecture (exhibits that imitate the appearance of animals' natural environments) (Hagenbeck 1909; see also Hancocks, chap. 11, this volume), but this approach, too, can be criticized, since "green spaces are not always enough" (Coe 2003, 977). Studies have shown that captive animals can be stressed and perform abnormal behaviors in large naturalistic enclosures (Carlstead et al. 1999; Stoinski, Hoff, and Maple 2001; Young 2003).

Environmental enrichment, as stated by Shepherdson, Mellen, and Hutchins in their book *Second Nature* (1998), is a principle of animal husbandry that enhances the quality of captive animals' lives by identifying and providing the environmental stimuli necessary for optimal psychological and physiological well-being. Many studies have confirmed the welfare benefits of environmental enrichment for captive animals (for a review, see Young 2003; see also Shepherdson, chap. 6, this volume).

Environmental enrichment can be built into animal exhibits in the form of structures that the animals can use, such as undulating terrain and elevated resting sites (Tudge 1991; Mallapur 2001), or in the form of enrichment devices, which provoke or allow animals to express species-specific behavior patterns (Chamove and Anderson 1989; Evans 1994; Young 1995; Vick, Anderson, and Young 2000; Grindrod and Cleaver 2001). Environmental enrichment benefits should transcend their costs and be a useful tool in improving animal welfare. However, enrichment needs to be well planned to achieve its goals; otherwise it can be more damaging than beneficial (Baer 1998).

In this chapter, we will outline the necessary steps for the creation and establishment of an environmental enrichment program for zoos and the steps to incorporate environmental enrichment into exhibits; with a few adjustments, laboratories, farms, and other institutions that hold captive animals could also use these guidelines to create their own environmental enrichment programs. An overview of the process necessary to implement a successful enrichment program can be seen in figure 15.1.

GETTING STARTED

PLANNING

The first step in the creation of an environmental enrichment program is to define the person who will be responsible for the planning and implementation. This person obviously should be someone working directly with the animals, but also needs an in-depth knowledge of the institution's activities, and above all must have the interpersonal skills to work with people at all levels within the institution. The most frequent reason for the failure of an environmental enrichment program is not the lack of resources, but the failure of the responsible person to communicate effectively within the institution (Young 2003). The implementation of an environmental enrichment plan needs to be done in a manner that enhances the work of other departments (e.g. Marketing, Education, etc.) and does not nullify their activities.

The activities of an environmental enrichment program appear to be easy to develop; however, much research and therefore time is necessary for a successful program. This research includes collecting information about the individual history of animals within the collection; developing a database of information about the species behavior in the wild and in captivity; and developing an understanding of species-specific (and sometimes individual) safety requirements in relation to the implementation of environmental enrichment. It is important to contact other institutions to share information about the animals' behaviors and enrichment ideas.

One of the most important steps in implementing a suc-

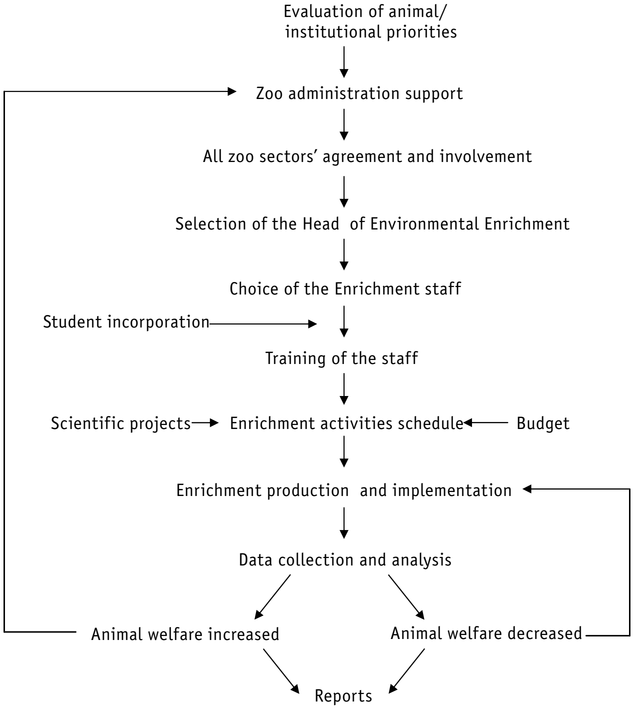

Fig. 15.1. Overview of the process necessary to implement an environmental enrichment program.

cessful enrichment program is to have the zoo administration's support and the whole staff's confidence; otherwise enrichment will fail, because enrichment activities are frequently seen (particularly in zoos in underdeveloped countries) as a "luxury" that the animals can live without. Many zoo staff think that enrichment activities will bring them additional work, others that enrichment may injure the animals, and still others that simply do not believe that enrichment can positively influence animal welfare. With uncooperative staff, the best solution is to educate them about the value of environmental enrichment, which should include information about how enrichment activities will empower them and make their work more interesting (demonstrations of animals interacting with enrichment devices is a great tool for this).

All the zoo's sectors (mammals, birds, reptiles, nutrition, plants, education, etc.) must be involved in enrichment activities, including the animal keepers, who are an excellent resource for enrichment ideas.

With the confidence of zoo staff, enrichment activities will be enhanced, as more ideas will be contributed by a wider variety of people. Typically, enrichment programs start small and get larger because of an empowered zoo staff. Furthermore, visitors generally like to know that the animals are being treated well; enrichment, through its promotion of natural and new behaviors, is a great way of attracting them to the zoo, thereby creating greater educational opportunities for the public (Bitgood, Patterson, and Benefield 1988; Margulis, Hoyos, and Anderson 2003).

HOW MANY ANIMALS AND WHICH SPECIES WILL BE ENRICHED?

To begin enrichment activities, the first step is to create a schedule, which states the animals involved, the date of the activity, the time the activity took place, the enrichment item, and the person responsible for implementing each item (table 15.1). The use of this procedure will organize the enrichment process and minimize mistakes, as the only thing the enrichment staff will have to do is follow the schedule for any particular week. This scheduling creates a routine, thus making the enrichment program easier to control, and it facilitates the writing of a monthly report, which can be sent to the zoo's administration to help demonstrate the program's effectiveness and construct a budget.

When planning an environmental enrichment program, it is important to evaluate initially which species will be enriched and how many animals will be participating in the enrichment activities. Since different species have different needs, each should receive species-specific enrichment. The wrong application of good enrichment can reduce animal welfare and may encourage behavioral habits that are incompatible with conservation and education objectives.

Difficulties may increase with the number of species involved (at least in the beginning of an enrichment program); therefore, it is preferable to initiate enrichment activities with only a few species (4 species per day, in our experience, is a good start number). Behavioral data, such as the percentage of time animals engage in abnormal behavior, can be used to help choose which species should be enriched first (Wallace 1997; Barber 2003; Kiley-Worthington and Randle 2005).

THE ENRICHMENT STAFF

After the zoo chooses a head of Enrichment, keepers need to be chosen to be part of the team. In the selection process, the zoo should consider how many people will be working in the sector; their experience with, knowledge of, motivation concerning, and interest in animals; and whether they would accept working with nonzoo staff, e.g. students. For institutions that cannot dedicate keepers to work solely in the environmental enrichment sector, we suggest creating a committee involving keepers from all sectors (mammals, birds, reptiles, veterinary) to define, implement, and evaluate the enrichment devices. The ideal situation is to have staff that works exclusively with enrichment activities; 2 keepers is enough to attend to 28 species in separate enclosures per week (divided into 4 species per day).

With a dedicated program, the number of animals being enriched should increase rapidly, and in a few months almost every animal should be receiving enrichment at least once a week. Volunteers or university student interns (paid or unpaid) can contribute to the program. The number of staff needs to be limited to that which can be managed effectively by the person responsible for the sector. The selection of student interns and volunteers must consider the same parameters used in selecting keepers. Adult volunteers are also a good source for help in enrichment activities. The enrichment coordinator can have regular volunteer or student in-

TABLE 15.1. Weekly enrichment report for mammals

				Behavioral responses (%)			
Date/period of day	Animal	Exhibit	Enrichment	Baseline	Enrichment	Postenrichment	Comments
12/06 Morning	Grison (*Galictis vittata*)	MPN18	Aniseed (*Pimpinella anisum*) mount and 3 nests with 2 quail eggs each	60%M 30%A 10%NV	70%A 5%IE 5%NV 20%M	22%A 60%M 18%NV	Animals did not interact with the aniseed mount, spending most of their time searching for eggs in the quail nests.
12/06 Afternoon	Coati (*Nasua nasua*)	MPN15	Aniseed (*Pimpinella anisum*) mount and 3 nests with 2 quail eggs each	Male 90%M 10%A Female 80%A 10%SI 10%M	Male 40%IE 20%O 20%SA 20%M Female 60%IE 20%M 20%F	Male 50%M 40%F 10%A Female 70%F 30%A	Male spent most of his time searching for eggs in the quail nests; female, initially interacts with the aniseed mount, sniffing it, but she soon began to search for eggs with the male, ignoring the fennel mount.
13/06 Morning	Raccoon (*Procyon cancrivorus*)	MJ1	one nest with 4 quail eggs	100%NV 10%SA	90%SI 10%A	90%I 10%A	The animal ignored the enrichment and slept or stayed inactive most of the time.
13/06 Afternoon	Capuchin monkey (*Cebus apella*)	EX	6 hanging Flintstones wheels filled with fruit and 5 hanging boxes filled with dried grapes and yellow mealworm beetle larvae	72%O 20%M 4%NV 4%A	55%IE 21%SA 12%M 6%NV 3%F 2%I 1%O	31%A 25%I 17%M 14%O 9%NV 4%F	The animals interact with both items immediately after their arrangement inside the enclosure.

Source: An internship student of the Environmental Enrichment Sector of Belo Horizonte Zoo, Brazil, made this report in June 2005.
Note: See table 15.2 for the abbreviations of the behaviors recorded.

tern meetings to brainstorm enrichment ideas and encourage each person to build, implement, and evaluate an enrichment device for one specific animal.

All the individuals selected to work with environmental enrichment need to receive specific training. Where possible, students and volunteers should be encouraged to participate in relevant conferences, training courses, and scientific meetings. If feasible, prizes, promotions, or financial incentives can be used to motivate keepers and students.

COSTS OF THE ENRICHMENT PROGRAM

With few exceptions, annual zoo budgets are insufficient for all the improvements and actions planned by the administration. Many zoos are maintained by governmental support, and many governments still do not understand the value of having a good zoological park (IUDZG/CBSG [IUCN/SSC] 1993).

The materials used to build the items for the enrichment program can be recyclable (boxes, paper rolls, plastic bottles, etc.). For zoos with natural areas (or wildlife reserves) or with cultivated crops, alternative food items could be collected and offered to the animals. The use of sandboxes (which should be avoided for perissodactyls, since the ingestion of sand causes colic: Rich and Breuer 2002), different mealtimes, hidden food items, rearranged enclosure furniture, toys, or simply the possibility of seeing conspecifics are powerful and cheap enrichment techniques for many species (Young 2003). Manufactured enrichment items can be purchased in pet shops and other specialized stores, but it is preferable to use natural materials where possible (e.g. use bamboo and not plastic tubes). Artificial materials are often more durable, readily cleaned, and disinfected, and easier to modify without compromising the structure of the material (e.g., adding small holes to PVC for a puzzle feeder). Although artificial devices may look unnatural, they can be hidden within a landscape and/or effectively naturalized (Markowitz 1982; Maple and Perkins 1996). Easy decontamination, compliance of use, and durability are also characteristics of some natural enrichment devices. Choosing which device is the best will depend on the objectives of the enrichment, the cosmetic standpoint, and the animals that will receive the device.

By having an annual budget for the buying of enrichment material, staff can vary the items used and find the most appropriate ones. This budget can be developed by counting the enrichment devices used in the first (previous) year and comparing the number with present animal requirements. A budget must consider estimations and simulations of what is really needed to enrich the animals' lives. For example, the list could include plastic (PVC) pipes; aromatic herbs; yogurts; jellies; additional fruits; raisins; nuts; ropes of varied diameters; plastic boxes; plastic barrels; dog bones; and cat and dog food (wet). An enrichment budget needs to include material for the whole year, both permanent and consumable. The first budget and purchase list will likely be the most difficult, as there will be some questioning by the zoo's administration about what items are really necessary. The production of a monthly report is important, since administration can then do a cost-benefit analysis and decide the importance of the enrichment sector and its activities.

Donations from other institutions as well as the zoo's merchandising and research agreements with commercial companies can attract funds for enrichment activities (along with donated items such as plastic bottles, phone books, pumpkins, and ropes). The zoo's marketing and advertising sectors will make the enrichment program better known, thereby helping to bring more money to the program (Mason and Carson 2003).

ENRICHMENT STUDIES

The efficacy of enrichment has been shown scientifically (see Shepherdson, chap. 6, this volume). Ideally, staff should evaluate all enrichment items using a detailed scientific protocol, but sometimes this is impossible due to the state of the animal studied (e.g. animals displaying high rates of stereotypic behavior should be enriched immediately) (Garner 2005). To evaluate an enrichment item, staff can study the behavior of the animals in 3 phases: *before* the introduction of the item into the enclosure, *during* a period with the enrichment item inside the enclosure, and *after* the enrichment item has been removed. If a positive behavioral change occurred when the enrichment item was inside the enclosure, then the enrichment item has most probably improved animal welfare (e.g. reduction in the expression of abnormal behavior). If an item placed in an animal's enclosure does not result in a reduction of abnormal behavior, it probably has not improved animal welfare. Thus, the simple fact that an animal interacted with an enrichment item does not indicate that the item improved its welfare (Ringdahl et al. 1997). Enrichment research projects should follow methodologies and experimental protocols used in behavioral studies; these increase the validity, reliability, and repeatability of the experiments (Altmann 1974; Martin and Bateson 2007; Lehner 1996). Internship students are good candidates for conducting enrichment studies.

Developing an enrichment project approval process will minimize delays and bureaucratic involvement and lead to safe enrichment. Questions to be considered for assessing a possible enrichment research project are as follows:

1. Does the chosen species really need this project?
2. Is it likely that the enrichment project proposed will enhance animal welfare?
3. Are there any safety concerns with the enrichment proposed?
4. How many enrichment items will be necessary to avoid competition for such items in a group?
5. If the enrichment is food based, could it cause nutritional problems?
6. Could the animals use the enrichment to escape their enclosure?
7. Is the enrichment relatively hygienic?
8. How much money will be needed for the development of the project?

These questions will help to evaluate a proposed enrichment study and its methodology. Obviously, an enrichment study should not conflict with ongoing enrichment goals.

Since most zoos have limited financial resources for research projects, the enrichment should be as natural and cheap as possible. Projects using expensive manufactured items or requiring huge alterations of animal enclosures are unlikely to be approved by the zoo staff. This is not, of course, an excuse for not renovating; poor enclosures should be renovated. Animal welfare is probably improved more if a bear or big cat is given a new naturalistic exhibit rather than being given a ball or other toy in a concrete cage (Laidlaw 2000; Pitsko 2003).

The students need to be aware that their projects are important for the zoo, and that they must take responsibility for completing their research. As part of the students' commitment to the zoo, they should be expected to write a report and give a presentation about the project upon its completion. Ph.D. researchers on the enrichment team can assist in coordinating the scientific studies and help in the statistical analyses.

Behavioral data have to be collected with full scientific rigor and follow the methods and schedule in the proposal. Results should be statistically analyzed (sample sizes are often too small for appropriate statistical analysis for these types of projects; graphical analysis, confidence interval analysis, or randomization tests are most appropriate—Festing and Altman 2002; Wehnelt et al. 2003) and the data published, preferably in peer-reviewed journals. Communication of results to as many researchers as possible is important.

Researchers who study animal behavior know that all that is necessary to collect data are an ethogram (inventory of a species' behavior patterns), a check sheet, a pencil, and a stopwatch; more-sophisticated materials, e.g. handheld computers with specific software, telemetry devices, and movement sensors, may be too expensive for many zoos. When a particular species will be studied, staff may need to create an ethogram and a check sheet for recording data (Martin and Bateson 2007; Lehner 1996). Many ethograms have already been published in behavioral journals or on the Internet (see the appendixes to this chapter) and should therefore be used, as this allows comparisons between different studies. To avoid having to create an ethogram for each species a zoo houses, we suggest that a universal ethogram be created, which includes the most common behaviors expressed by animals (see table 15.2). Similarly, one or two universal check sheets can be prepared and used in most enrichment evaluations (e.g. doing focal observations for animals housed singly and scan observations for animals kept in groups). For more detailed studies, a species-specific ethogram and check sheet can be developed. Typically, data collected using a universal ethogram and check sheet are more general, but provide the opportunity to evaluate the duration of certain behaviors, thus indicating the efficiency of the enrichment devices.

ENRICHMENT LIBRARY

Researchers and zoo staff need to keep abreast of scientific findings and methods by reading the literature. There are

TABLE 15.2. Universal check sheet and ethogram used by the Environmental Enrichment Sector of the Belo Horizonte Zoo in the evaluation of enrichment devices given to the animals

Environmental enrichment check sheet										
Date:			Hour:		Climate:					
Responsible:					Enclosure/Species:					
Enrichment device:										
Ethogram: A: Active; I: Inactive; M: Moving; F: Foraging; IE: Interacting with the enrichment device; SI: Social interaction; V: Vocalizing; AB: Abnormal behavior; NV: Not visible; O: Other behaviors.										
Baseline (before the introduction of the enrichment device into the enclosure)										
Time	A	I	M	F	IE	SI	V	AB	NV	O
1										
2										
3										
4										
5										
6										
7										
8										
9										
10										
Notes:										

Note: Enrichment and postenrichment phases use similar check sheets, not shown here

many good books on animal welfare and animal behavior (see also in this volume Kagan and Veasey, chap. 2; Shepherdson, chap. 6; McPhee and Carlstead, chap. 25; Crockett and Ha, chap. 30). Peer-reviewed journals and non–peer reviewed magazines are also available on these subjects. Basic books on ecology and biology of different animal classes are useful as well. We suggest that books listed in appendix 15.1 are essential, and the journals in appendix 15.2 are ideal for any zoo. Appendix 15.3 includes Internet sites that are good sources of information and enrichment ideas.

University libraries may be available for zoo staff, at least on a consultation basis; however, there is no substitute for a good zoo library. Donations can help in the acquisition of the books, but buying or subscribing to magazines and journals is necessary. Funds for such purchases should be included in the annual budget of the enrichment sector.

INCORPORATING ENRICHMENT INTO EXHIBITS

To avoid animal boredom, different stimulation must be offered. Incorporating environmental enrichment devices into exhibits can be done in 2 different ways: (1) items incorporated every day (movable devices) or (2) items incorporated during renovation or construction of exhibits (nonmovable devices, i.e. furniture).

Movable devices may be provided for animals during daily activities. Food, sensory, and cognition items are part of this category. Social stimulation can also be a source of enrichment, thus providing social interactions (interspecific, intraspecific, and human-animal) for captive animals (Crockett 1998; Young 2003) by allowing them to see or touch other animals (when this is not possible, the introduction of mirrors into exhibits can simulate conspecifics) (Heyes 1994; Lutz and Novak 2005). Other changes in the physical and social habitat are in the second type of enrichment: those that cannot be moved from the enclosure easily. Enclosure shape and size, water provisioning, substrate elements, infrastructure for offering enrichment, perches, temperature, humidity, mixed-species exhibits, and conspecifics (for some species) are examples.

Enrichment devices, tools, and options. Many of the enrichment items used in daily scheduled activities are in the movable-items category, e.g. toys, puzzles, hidden food, special food devices like frozen fruit, meatballs covered with fur, different feeders, piles of sticks or stones, and mirrors. The type of movable items depends on the species to be enriched. For example, food items placed in treetops can elicit climbing behaviors in felids (Law 1993; Mallapur 1999).

Novel food items (items not offered in the normal diet) and a change in food presentation (scattered or hidden food, puzzle feeders, and novel presentations) are easy to implement and can simulate the difficulties of acquiring the food in the wild (Porter 1993; LeBlanc 2000), including hunting activities (Williams et al. 1996). While pacing often increases a few minutes before standard food presentation (Hutchins,

Fig. 15.2. Western lowland gorilla's renovated enclosure. Note that the enclosure is landscaped with natural vegetation, artificial rock mountains, waterfall, and cave. (Photograph courtesy of Fundação Zoo-Botânica de Belo Horizonte, Brazil, 2004. Reprinted by permission.)

Hancocks, and Crockett 1984; Mellen, Hayes, and Shepherdson 1998; Sandhaus 2004), providing the opportunity to forage and to hunt for hidden food items diminishes the amount of pacing (Carlstead 1991; Williams et al. 1996; Cipreste 2001).

Sensory enrichment can be tactile (toys and textures: Lutz and Novak 2005), olfactory (scents: Hadley 2000; Schuett and Frase 2001), auditory (playback recordings, music: Wells 2004), visual (view of activities outside the enclosure: Tudge 1991; Mallapur 2001), or taste (foods, scents: Baumans 2005). Puzzle feeders are cognitive devices that provide the animals with an opportunity to learn; they are often given to primates (Lutz and Novak 2005), but they can be used for other mammals (Shepherdson, Brownback, and James 1989).

Enrichment devices may be used for a variety of species or individuals, which can facilitate the transmission of diseases (Novak and Drewsen 1988). Thus, all items should be cleaned and sterilized before being introduced to an animal. Sanitation can be achieved using an autoclave, chloride baths, boiling water baths, freezing, alcohol, radiation, or filtration (for a complete guide to microorganism growth control, see Madigan, Martinko, and Parker 2002). Artificial materials may be easier to clean and sterilize, but natural materials can also be cleaned and sterilized.

During the development of new enrichment devices, the safety of the animals, keepers, and public needs to be carefully evaluated. A list of questions, mentioned earlier in this chapter, should be answered before items are used. A complete list of questions can be found in Young (2003).

Supplying new enrichment items at least twice a week can create an unpredictable environment, and thus stimulate natural behaviors (Shepherdson et al. 1998). Nocturnal animals should be enriched at night (Tardona 2000).

Renovation/construction of exhibits. When renovating old exhibits or constructing new ones, how newly built structures will relate to enrichment activities needs thought. Typically, the architect draws up the new enclosure plan, but a multidisciplinary team is best, and should include zoologists having good knowledge of the animals' needs and botanists who can recommend planting materials to be used both as ornament and as food (Embury 1995). Horticultural staff can also reproduce landscapes by planting associations of species that reproduce the animal's natural habitat. Educators can help in

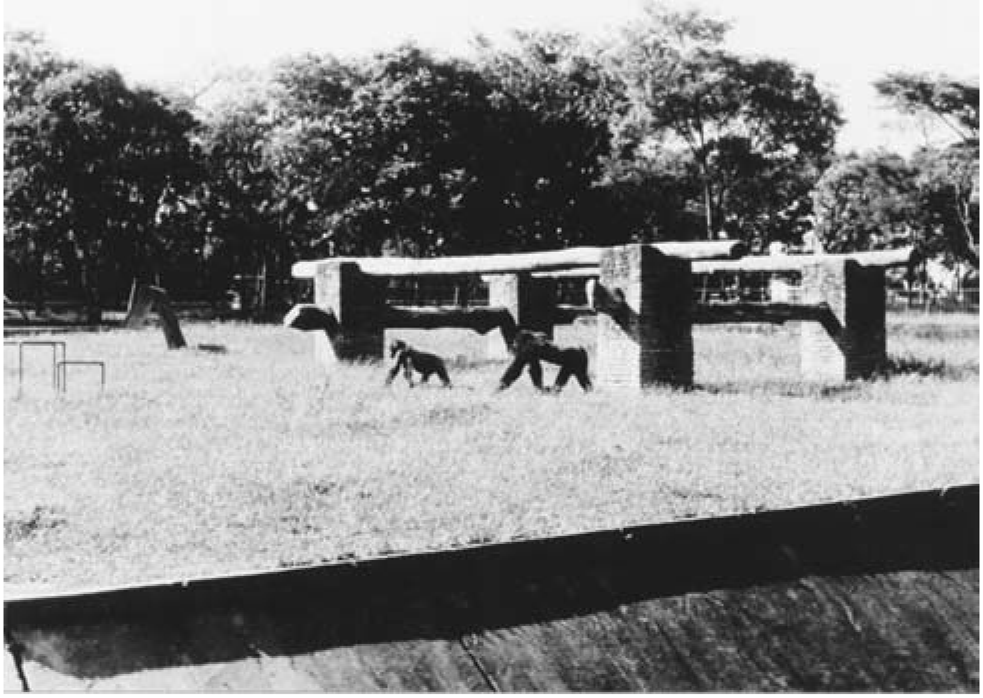

Fig. 15.3. Western lowland gorilla's old enclosure. Note that the exhibit had high concrete walls and only a wood structure for enrichment. In this enclosure, the gorilla male developed many abnormal behaviors, such as regurgitation and reingestion (RR). (Photograph courtesy of Fundação Zoo-Botânica de Belo Horizonte, Brazil, 1982. Reprinted by permission.)

the development of the labels, routes, viewing sites, and all the educational material inserted in the new exhibit; thus, they are important in defining the final enclosure plan (Mitchell, Herring, and Tromborg 1990; Bitgood 2000).

Enrichment features, such as artificial termite mounds, trees and caves, roof feeders, pools, waterfalls, nests, and burrows can be constructed in the renovation of exhibits. All structures linked to enrichment, like those that allow keepers to retrieve and clean the devices, have to be considered during the construction, since it is extremely difficult to change structures after the completion of a renovation. For mixed-species exhibits, there need to be multiple species-specific escape areas, barriers, and more than one feeding area, since each species has its own requirements (see Veasey and Hammer, chap. 13, this volume).

Habituation is the reduction of certain behavioral responses by animals to a neutral stimulus after learning that it has no consequences for them (Young 2003). To avoid habituation to permanent structures, staff can maintain the novelty characteristic of enrichment devices (Kuczaj, Lacinak, and Turner 1998). We recommend periodically moving items, such as ropes, logs, stone piles, and mirrors. Artificial feeders, such as termite mounds and roof feeders, should not be used daily, adding unpredictability to the animals' lives.

Many exhibit renovation plans are available in the specialized literature and we recommend reading them. *International Zoo Yearbook* (www.blackwellpublishing.com/journal.asp?ref=0074-9664) devotes an entire section to renovation and new construction. We also recommend a visit to the Web sites of the architect Jon Coe (www.joncoedesign.com) and the Association of Zoos and Aquariums (www.aza.org), where much information about exhibit planning is available.

An example of a renovation that incorporated enrichment concepts is the redesigned enclosure for a solitary male western lowland gorilla, *Gorilla gorilla gorilla*, at the Belo Horizonte Zoo in Brazil. The new, 2100-m^2 naturalistic enclosure has an irregular topography and is landscaped with grass, live and dead trees, a bamboo grove, different shrubs and herbs, a rockwork hill and cave, and another rockwork that forms a waterfall and pond with a recirculating water system. Some of the trees and plants are protected by "hot wire," while others are unprotected to allow the gorilla to climb on or eat palatable plants and fruits (fig. 15.2; to see more photos of the enclosure, visit the Web page www.pbh.gov.br/zoobotanica/gorillainfo). Since the new gorilla exhibit was opened in December 2000, the solitary male gorilla has shown an increased quality of life. Figure 15.3 shows the pre-renovation exhibit, where the male frequently displayed abnormal behaviors such as RR (food regurgitation and reingestion); in addition, he used to carry an old car tire around and did not have a well-developed stomach or muscles. Since the gorilla moved to the renovated enclosure, RR has not been observed, he no longer carries around his old car tire, and his stomach and other muscles are better developed.

There are many opportunities to get ideas for renovations that include significant enrichment. Each year, zoos renovate and enrich their old enclosures. Many examples have been published in the Exhibits section of the *AZA Communiqué* (now *Connect*), a publication of the Association of Zoos and Aquariums (check Web site www.aza.org/Publications). The ZooLex Zoo Design Organization Web site (www.zoolex.org) also has much information about zoo exhibit renovations from around the world. Unfortunately, almost all examples come from developed countries, showing how the lack of money obstructs exhibit building/renovation in zoos in underdeveloped countries.

All renovations should include plans for behavior studies to evaluate the effectiveness of the new portable and permanent devices in the animals' lives. We recommend making behavioral comparisons of data collected before and after the exhibit renovation. Movable enrichment items should be scheduled for the animals in the new enclosure, taking into account the safety, cosmetic factors, and purposes of the materials and devices.

CONCLUSIONS

The importance of zoos implementing an environmental enrichment sector for their captive animals should now be evident; the benefits of environmental enrichment for the welfare of these animals are unquestionable (Young 2003). We strongly suggest that zoos create an environmental enrichment sector, and we now provide summarized guidelines for its creation:

- The animals' needs and the possibilities of creating an environmental enrichment sector should be analyzed.
- The institution's needs for an enrichment program should be analyzed.
- The enrichment sector head has to be chosen.
- Meetings about the implementation of the enrichment sector should be carried out with the zoo's staff (all sectors must be involved).
- The enrichment staff have to be chosen.
- The annual budget for the sector needs to be calculated.
- Weekly schedules of enrichment need to be implemented;
- A training program for enrichment staff needs to be implemented;
- Enrichment devices should be constructed and used, with data collection and analysis, followed by the publication of results.
- The number of animals enriched should increase until all zoo animals are receiving enrichment.
- Staff must remember that improving animal welfare is not a static process, but one that requires constant attention and updating.
- An enrichment program must contribute to the goals and the mission of the zoo.

ACKNOWLEDGMENTS

We would like to express our sincere thanks to all the staff of the Belo Horizonte Zoo who have endorsed and continue to support its enrichment activities.

APPENDIX 15.1

Books Recommended for an Enrichment Library

Alcock, J. 2005. *Animal behavior: An evolutionary approach*. 8th ed. Sunderland, MA: Sinauer Associates (ISBN: 0878930051).

Appleby, M. C., and Hughes, B. O. 1997. *Animal welfare*. Oxford: CABI Publishing (ISBN: 0851991807).

Begon, M., Harper, J. L., and Townsend, C. R. 1996. *Ecology: Individuals, populations and communities*. 3rd ed. London: Blackwell Science (ISBN: 0632038012).

Broom, D. M., and Johnson, K. G. 1993. *Stress and animal welfare*. London: Kluwer Academic Publishers (ISBN: 0412395800).

Fraser, A. F., and Broom, D. M. 1996. *Farm animal behaviour and welfare*. 3rd ed. Oxford: CABI Publishing (ISBN: 0851991602).

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Lehner, P. 1998. *Handbook of ethological methods*. Cambridge: Cambridge University Press (ISBN: 0521637503).

Manning, A., and Dawkins, M. S. 2002. *An introduction to animal behaviour* 5th ed. Cambridge: Cambridge University Press (ISBN: 0521578914).

Martin, P., and Bateson, P. 2007. *Measuring behaviour*. 3rd ed. Cambridge: Cambridge University Press (ISBN: 0521446147).

Moyle, P. B., and Cech, J. J. 2003. *Fishes: An introduction to ichthyology*. 5th ed. Upper Saddle River, NJ: Prentice Hall (ISBN: 0131008471).

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Young, R. J. 2003. *Environmental enrichment for captive animals*. Oxford: Blackwell Publishing (ISBN: 0632064072).

Zug, G. R., Vitt, L. J., and Caldwell, J. P. 2001. *Herpetology: An introductory biology of amphibians and reptiles*. 2nd ed. San Diego: Academic Press (ISBN: 012782622X).

APPENDIX 15.2

Journals and Magazines Recommended for an Enrichment Library

Animal Behaviour (Academic Press)
Animal Welfare (UFAW)
Applied Animal Behaviour Science (Elsevier Science)
Ethology (Blackwell Wissenschafts-Verlag Gmbh)
International Zoo News
International Zoo Yearbook (Blackwell Publishing)
The Shape of Enrichment
Zoo Biology (Wiley-Liss)

APPENDIX 15.3

Recommended Internet Sites

Animal Diversity Web (information about the biology of almost every living species): www.animaldiversity.ummz.umich.edu
Environmental Enrichment Ideas: www.enrichmentonline.org
Environmental Enrichment for Zoos and Aquarium Animals: www.nal.usda.gov/awic/enrichment/zooandaquariumenrichment.htm
Ethograms (ethograms of many animal species): www.ethograms.org
Jon Coe's Web site (ideas and real projects dealing with exhibit renovations): www.joncoedesign.com
The American Association of Zoo Keepers: www.enrich.org/aazk
The Association of Zoos and Aquariums: www.aza.org
The Shape of Enrichment: www.enrichment.org

Primate Enrichment Database: www.awionline.org/lab_animals/biblio/enrich.htm

Universities Federation for Animal Welfare: www.ufaw.org

ZooLex Zoo Design Organization: www.zoolex.org

Web of Science (search for scientific papers): isiknowledge.com

Many zoo Web pages contain enrichment ideas, such as the Honolulu Zoo (www.honoluluzoo.org) and the Oregon Zoo (www.oregonzoo.org).

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16

Special Considerations for the Maintenance of Marine Mammals in Captivity

Brian Joseph and James Antrim

INTRODUCTION

Marine mammals are a unique group of warm-blooded animals that, with the exception of a few freshwater species, make their living from the sea. However, marine mammals did not evolve in the sea, but rather descended from a number of different taxonomic groups, all of which independently deserted the land less than 60 million years ago (Williams 1999). An excellent and comprehensive review of the history of marine mammals in captivity is presented by Reeves and Mead (1999). The term *marine mammals* as used in this chapter includes all cetaceans (whales, dolphins, and porpoises), all pinnipeds (seals, sea lions, and walrus), all sirenians (manatees and dugong), sea otters, and polar bears (Rice 1998).

Living in a fluid, 3-dimensional, marine environment has resulted in numerous differences between marine mammal and terrestrial mammal physiology, structure, and behavior, many of which are important in the successful maintenance of marine mammals in captive environments. The ocean is cool compared with most terrestrial habitats, and water has a thermal conductivity of more than 25 times that of air (Beckman 1963), rapidly carrying heat away from immersed warm-blooded animals. Marine mammals are characterized by several adaptations to preserve homeothermy within cool aquatic environments. Constantly buoyed by water, larger marine mammals, such as killer whales (*Orcinus orca*) and baleen whales, can afford larger heat-conserving masses than terrestrial mammals. With the exception of sea otters, marine mammals are insulated by layers of blubber, coats of fur, or both. Blood circulation is enhanced by peripheral arteries, which are surrounded by veins capturing arterial warmth as the blood returns to the body core (Scholander and Scheville 1955).

The design and construction of appropriate marine mammal habitats should consider the natural history and behavior of the species to be maintained and should permit the performance of most, if not all, of their natural behaviors (fig. 16.1). Aesthetics must always be weighed against practicality—environments that become too cluttered may be difficult to maintain and/or dangerous to the animals living within them. We cannot reproduce the biocomplexity of a natural environment for any species maintained in a captive environment. Our goal in this chapter, then, is to provide some understanding of key factors facilitating the successful care of marine mammals in zoos and aquariums. While design and construction of the habitat is an essential element, the 3 most important components of husbandry techniques and protocols necessary for the successful maintenance of marine mammals are maintenance of a healthy environment, provision of adequate nutrition, and implementation of a good preventive medicine program.

Some government entities, such as the U.S. Department of Agriculture (USDA 1979), have promulgated laws or regulations regarding the keeping of marine mammals in captivity. Nongovernment organizations such as professional trade associations have also created their own standards or guidelines for the care and maintenance of marine mammals (EAAM 2001; AMMPA 2004). Such regulations or standards always constitute minimum requirements, and in our opinion, facilities built to or operated at minimum standards will not promote the best marine mammal health and welfare and should not be considered acceptable.

FACILITY DESIGN

The design and construction of a facility must meet the physical, psychological, and behavioral needs of the animals as well as the goals and objectives of the host organization (fig. 16.2). There are 2 basic zoological facility types: (1) the public display or exhibit feature and (2) the off-exhibit or restricted entry component. Most marine mammal facilities combine the two, and physically connect these elements to facilitate the movement of the resident animals from one area to the other without the need for transport containers and/or physical

Fig. 16.1. Design and construction of appropriate marine mammal habitats should permit the performance of most, if not all, of their natural behaviors.

Fig. 16.2. Design and construction of a facility must meet the physical, psychological, and behavioral needs of the animals as well as the goals and objectives of the host organization. (Photograph courtesy of UNEXSO: The Dolphin Experience, Freeport, Grand Bahama Island. Reprinted by permission.)

or chemical restraint. All marine mammal facilities should have underwater viewing areas, not only for the public but also for staff observations. Public display can be designed for continuous open, unstructured viewing, structured or programmed viewing, or scheduled educational presentations. The off-exhibit elements may be designed for, but not limited to, functions such as adding or removing animals from the facility, mating and birth, rearing of offspring, medical treatment, medical quarantine, or holding nondisplay animals. An important component of off-exhibit holding of cetaceans is the inclusion of a medical pool featuring a false, lifting bottom. This false bottom allows animal caretakers, handlers, and cetaceans in need of physical restraint to be at a shallow depth for the safe performance of medical and husbandry procedures without having to drain the pool and without endangering personnel through attempting restraint in deep water, where the size, strength, and mobility of the cetacean places them at a profound advantage. False, lifting bottoms are inexpensive, constructed of PVC or fibergrate grating. Lifting apparatuses use city freshwater pressure, hydraulic pressure, or cable lift systems to raise the false bottom.

The design and construction of a facility that promotes good health includes consideration of the size and configuration of the captive environment and maintenance of that area in a clean (not sterile) state. Marine mammals need enough space to allow them to perform natural behaviors with freedom of movement. Surface finishes should be hard, durable, and impervious to water and, to facilitate sanitation, resistant to chemical and mechanical damage. Epoxy coatings work well within marine mammal environments (Watts 1998). Due to the highly corrosive nature of saltwater, the use of corrosion-resistant materials during construction, such as fiberglass reinforced plastic (FRP), polyvinyl chloride (PVC), and type-316 stainless steel, will extend the effective operational life (while reducing the maintenance cost) of any marine mammal facility.

Captive marine mammals have abundant time to investigate, manipulate, damage, or destroy vulnerable elements within their facilities, such as surface coatings, acrylic or glass viewing panels, electrical or plumbing fixtures, exposed hardware or fasteners, gates or doors, and even decorative artificial or natural rockwork. The results of their actions may create significant safety and/or mortality hazards for both the animals and the human caretakers. Toxic plants, shrubs, or trees should not used in landscaping around a facility housing marine mammals, since accidental or deliberate ingestion of such plant items may cause serious health problems or even death. In addition, construction activity adjacent to marine mammal environments can expose the animals to air-, soil-, and waterborne pathogens contained in soil under excavation or used as fill.

ENVIRONMENT AND HEALTH CONCERNS

Constant attention is necessary to prevent littering of poolside areas, to avoid foreign bodies inadvertently falling or being knocked into the marine mammal's environment. Foreign objects entering the environment should be removed immediately. Additional sources of foreign objects that marine mammals can ingest are portions of their environment that they disassemble (Sweeney 1990). Marine mammals frequently pick up foreign bodies in their environment, play with them, and intentionally or unintentionally swallow the objects. Small foreign bodies ingested by cetaceans rarely leave the forestomach, due to the minute opening to the glandular stomach; the presence of foreign bodies may cause mechanical damage to the gastric mucosa and result in ulcers. If coins are digested in the forestomach, copper or zinc intoxication may result. Larger foreign bodies such as air-filled volleyballs and footballs may be lethal to cetaceans. If an animal dives with a ball in its mouth, the ball may be driven back into the throat by buoyancy, where it can lodge in the caudal oropharynx and result in fatal respiratory arrest. Smaller foreign bodies may be vomited and reingested or ingested by other resident animals. Staff should never offer toys that are potentially dangerous to marine mammals, e.g. small balls, sharp objects, and objects that can be dismantled by the animals and then ingested. Ropes dangling in the water and tethered to the pool bottom can result in entanglement followed by drowning.

An ingested foreign body must be manually removed from the animal's forestomach, after identification of its presence and location via gastroscopy. It is unsafe to induce vomiting in cetaceans, as they may expire due to aspiration pneumonia or occlusion of the esophagus and resultant pressure on the heart and trachea.

Pinnipeds are at great risk from foreign body ingestion, since the opening from the simple stomach to the small intestine is large enough to allow some foreign bodies to pass into the intestine, where they may lodge, producing a fatal obstruction if untreated. Pinnipeds are less likely than cetaceans to regurgitate ingested foreign bodies, but can safely be made to vomit by feeding syrup of ipecac in food items. An observer must remain poolside to recover the foreign body when the pinniped vomits.

TERRESTRIAL SPACES

Deck and dry resting areas are most effectively disinfected through the use of dilute sodium hypochlorite solutions (less than 0.5%). Zoo staff should avoid using chlorine within confined spaces, since the resulting chlorine gas can be very irritating to eyes, mucous membranes, and the respiratory epithelium of both marine mammals and caretakers. In addition, workers should always use personal protective equipment when using chlorine and should never apply it in the presence of animals. Residues must be neutralized through the application of a saturated sodium thiosulfite solution and/or thoroughly rinsed from surfaces to prevent harm to the animals.

WATER QUALITY

Staff must attend constantly to the water quality of the marine mammal's environment to ensure and promote the health of the animals. Pathogens are more concentrated within the cleanest zoological environments compared with the oceans, where animal waste products are constantly diluted by large volumes of water and current activity. Good water quality is maintained through the use of adequate mechanical filtration, chemical treatment, continuous surveillance, and proper record monitoring. Boness (1996) and Arkush (2001) review the management of water quality in aquatic exhibits for mammals.

TYPES OF WATER SYSTEMS

Three basic types of water systems are in use today for captive marine mammals (Arkush, 2001; Reidarson 2003; Spotte 1991). The first is an *open system*, generally used when facilities are located adjacent to natural bodies of clean seawater. In open systems a supply of filtered or unfiltered water flows through the animal enclosure and then exits. Such systems, in which water continuously enters the system from a natural source of seawater, are subject to uncontrolled pollution and contamination and are not recommended. Incoming makeup water from a natural source generally should be filtered and chemically treated before use. *Semiclosed* systems use a controlled addition of filtered or unfiltered water, recycling the water through a life support system and discharging a volume equal to that of the influent minus losses to evaporation. *Closed systems* continuously recycle pool water through the life support system. An alternative, used by some coastal facilities, is the netting-off of a portion of a natural bay or inlet. Semiclosed systems and closed systems present difficulties in maintaining salinity, alkalinity, and pH (Reidarson 2003).

Many marine mammal facilities use a closed water system with artificial seawater when access to natural seawater is unavailable. Artificial seawater is made by adding 25 to 35 parts per thousand (ppt) sodium chloride (Geraci 1986a) and, in our experience, important trace minerals to freshwater. In a closed system it is important to add freshwater to offset the effect of evaporation and any other water losses from the system. A closed system requires water recirculation through filters and fractionators as well as chemical treatment before returning water to pools where marine mammals are kept.

WATER TESTING

Regardless of the system used, water should be sampled and tested frequently and regularly for temperature, pH, turbidity, salinity, ammonia content, free and total chlorine, bacterial contamination, residual ozone, and, if necessary, total organic carbon.

WATER TEMPERATURES

Although marine mammals are capable of coping with a wide range of water temperatures, a relatively constant water temperature is important for successful maintenance. Various temperature ranges have been proposed for bottlenose dolphins (*Tursiops truncatus*), but there is general agreement that 20° C is a good average temperature. Other optimal temperature ranges for maintaining marine mammals have been suggested (e.g. AMMPA 2004; Couquiaud 2005). If lower or higher temperatures than ambient are required, water may be passed through a chiller or heat exchanger to provide the desired adjustment. Discussions of ambient water temperature requirements can be found in Geraci (1986a) and Sweeney and Semansky (1995).

Water temperature affects marine mammals both behaviorally and physiologically. Cetaceans and other marine mammals consume proportionally larger quantities of food when maintained at lower water temperatures. Additionally, warm water appears to be a pronounced physiological stressor for many marine mammals. For example, in our experience anemia is more often seen at warmer water temperatures in cetaceans, accompanied by elevations in certain serum enzymes, decreased activity, and decreased appetite (Cornell et al. 1990).

pH LEVELS

A second physical parameter, pH, affects water quality in a variety of ways. The ocean is naturally safeguarded with a carbon dioxide buffering system and pH averages around 8.2 (Toorn 1987). Within a closed system, the accumulation of nitrogenous waste products can raise pH to levels inducing irritation of eyes, airways, and skin. Maintenance of pH is important for animal and handler comfort and affects the bactericidal effectives of free chlorine. An acceptable pH range is 7.5–8.2 (Geraci 1986a). Bactericidal effectiveness of free chlorine is maximal at the lower end of this range (ibid.), but in our experience we have found that handlers frequently complain of eye irritation at pH values of 7.6–7.8. Marine mammal eyes are well protected by mucus and do not seem to be irritated at this lower range (ibid.). Harmful chloramines also form more readily at the lower end of this pH range. Caustic soda, sodium hypochlorite, or sodium bicarbonate can be used to elevate pH into a range more comfortable for animals and the staff (Spotte 1991).

TURBIDITY

Turbidity is a measure of the clarity or optical transmission of the water. Water should appear crystal clear and slightly blue, and measure roughly 0.15 to 0.20 nephelometric turbidly units (NTU). The upper limit of the acceptable range is 0.45 NTU. Turbidity is not entirely dependent on particulate content, but also depends on dissolved oxygen, ozone, entrained gases, and other chemicals contained within the system (Case 1998).

TRACE MINERALS

The chemical composition of water should be similar to natural seawater, which contains many minerals in addition to sodium and chloride. Marine mammals likely make optimum use of their environment, including the extraction of existing trace minerals. Although marine mammals are seen swallowing seawater, trace mineral absorption may be limited to the oral mucosa (Manton 1986).

SALINITY

Salinity in the open ocean averages approximately 3.5%, of which about 2.6% is NaCl and 0.9% is composed of other elements (Turekian 1968). Dolphins must expend more energy to stay afloat at low salinities, which is particularly important in the case of ill, injured, or neonatal marine mammals. Although reversible, a patchy necrosis of the epidermis, accompanied by ulceration, may occur in bottlenose dolphins if salinity drops below 1% and remains there for an extended period. Pinnipeds maintained in freshwater may develop corneal edema (Dunn et al. 1996).

NITROGENOUS WASTE

Successful elimination of nitrogenous waste products is one of the key problems in the proper management of marine mammal water systems. Marine mammals pollute their environment to an amazing degree. A 136-kg dolphin, eating 6.6 kg of food daily, is estimated to pass 4 L of urine and 1.4 kg of feces per day into its pool (Ridgway 1972). Nitrogenous wastes enter the water primarily as urea, which is rapidly converted to ammonia through a process termed mineralization. Ammonia is toxic to most organisms, and high levels of ammonia suggest inadequate chlorination or inadequate removal of organic compounds through protein fractionation. Nitrogenous wastes also provide a good culture medium for bacteria and fungi; thus, their levels must be controlled by flushing waste products back to the natural body of seawater in an open system and by either chemical oxidation (Manton 1986) or removal by protein fractionation in a closed system.

COLIFORM TESTING

Total and fecal coliform testing can be done using a variety of techniques. One of the most common is referred to as the most probable number (MPN) technique and is obtained by the multiple tube fermentation (MTF) method (American Public Health Association 2005). Sometimes membrane filtration or the use of McConkey's agar is substituted for MTF to quantify total or fecal coliforms. The results obtained by these different methods are not directly comparable (Spotte 1991).

TOTAL ORGANIC CARBONS

Total organic carbons, contained in feces, build up within closed systems unless discarded to waste, oxidized with ozone or chlorine, or removed by protein fractionation. In combination with chloramines and other chemicals, organic carbons can produce a green or yellow discoloration of the water.

FILTRATION AND CHEMICAL TREATMENT OF WATER

Filtration and chemical treatment are essential to maintain marine mammal water quality; they serve many purposes, including removal and/or oxidation of organic material, limitation of microbial growth, provision of a relatively toxic-chemical-free environment, and maintenance of water clarity, which facilitates adequate animal observation.

The goal of physical filtration is the removal of particulate material to maintain or restore good water clarity (Manton 1986). Although many types of filtration are available (Boness 1996), the most commonly used filters are high-speed sand and gravel filters. Sand and gravel form a matrix within which particulate matter is trapped. Little biodegradation of organic debris occurs in sand and gravel filters due to the high speed of water flow and loss of sand bacterial populations during backwash procedures (Kinne 1976). Pumps and filters should be appropriately sized to produce a complete water volume turnover rate of between 2 and 3 hours in most marine mammal systems. These filters generally have a filtration rate of 200–500 gals. (760–1900 L)/hour/m^2 of media. Filtration efficiency can be increased through the use of a flocculating agent such as iron-free aluminum sulphate or aluminum hydroxychloride. Filtration efficiency increases as particles are caught in the matrix, but the pressure differential that results as the matrix is plugged with particulate matter results in a pressure differential across the filter bed which can be flow limiting and requires backwash.

Chemical treatment, sometimes referred to as disinfection, involves the oxidation of organic debris, including microbes, with ozone, chlorine, or both. Chemical treatment of marine mammal pools has been traditionally based on human freshwater swimming pool technology (Manton 1986). Problems occur because the necessary chemical reactions cannot go to completion at the usual temperatures at which marine mammals are maintained, and the animals continuously produce waste products that combine with chlorine to form irritating compounds. Constant chlorine exposure for marine mammals and their caretakers can result in health problems for either or both. Although the use of chlorine as an oxidant has been discontinued by many facilities, institutions that still use it generally maintain total chlorine at 1 part per million or below, half of which is free chlorine (Reidarson 2003).

Ozone is potentially toxic and can irritate eyes, skin, and respiratory systems, so extreme care must be taken to avoid exposing personnel and animals. Ozone often is added to a vertical column, called a "contact tower," or as an oxidant in protein fractionators or ozofractionators. For either technique, ozonated water is then passed over a waterfall or through a degassing tower containing plastic or nylon rings, which increase surface area for ozone dissipation before returning the water to the animal facility. An efficient bactericide and powerful oxidizer, ozone is unstable in water. It also acts as a decolorizing agent by attacking carbon double bonds, removing color pigments (Toorn 1987). Ozone is more effective than chlorine against fecal coliforms, such as *Escherichia coli*, plankton, insects, and, possibly, viruses. However, ozone decreases in effectiveness at higher densities of microorganisms and at higher turbidities. Unlike chlorine, ozone does not leave a residual disinfecting agent in the aquatic environment if the oxidation reduction potential at the point of introduction is maintained at below 600 millivolts (Reidarson 2003). At higher levels, ozone is also capable of producing corneal, skin, and respiratory damage (ibid.). It is advantageous to maintain ozone at a level that does not leave a residue in the pool, because preservation of the normal marine mammal's skin microflora is more likely (Ramos and Ring 1980). Arkush (2001) provides an in-depth discussion of the use of ozone in marine mammal systems.

Chlorination is a widely used technique for disinfection of marine mammal pools, but considerable care must be taken in handling chlorine. Chlorine gas at 10 parts per million (ppm) produces marked irritation of the respiratory tract, while 1 ppt is fatal if breathed for 5 minutes (Goodman and Gilman 1954). Chlorination is less effective against fungi than bacteria. Skin infections in marine mammals maintained in chlorinated water may be the result of destruction of normal, beneficial microflora and inactivation of antimicrobial substances secreted by the skin (Geraci, St. Aubin, and Hicks 1986).

Chlorination is accomplished by the addition of either sodium hypochlorite (liquid) or chlorine dioxide (gas), or through electronically facilitated chemical processes that remove naturally occurring chlorine from seawater. Chlorination does not, however, completely remove organic compounds from water systems. Over time, the amount of total organic carbon gradually increases in a semiclosed or closed system, and as much as 7% of the carbon introduced into the system as food remains in this form. Many institutions cope with this carbon buildup by periodic water replacement.

Chloramines, which are nitrogenous wastes combined with free chlorine, can be especially irritating to marine mammals' mucous membranes. High concentrations of chloramines can cause skin sloughing, and in the eyes cause bluish corneas and squinting. Chloramines are more harmful at lower pH values. Free chlorine is effectively bactericidal at concentrations of 0.2 ppm–2.0 ppm. Bactericidal effectiveness decreases with increased temperature, sunlight, pH, and increased organic load.

In the future, biological filtration may replace much of today's mechanical and chemical treatment. Systems will likely include fixed-bed bioreactors or trickling filters, which have been used successfully for aquarium water treatment (Wolff 1981). In a trickling filter, water flows slowly over a filter bed, above and on which microorganisms attack suspended and dissolved organic matter. Trickling filters accomplish 3 things: (1) dissolved organic matter is mineralized; (2) particulate organic matter is either converted to dissolved organic matter and mineralized, or is removed onto the resultant biofilm with flocculants; and (3) inorganic matter can react or be adsorbed onto the biofilm and be removed with the flocculation. From the trickling filters, water flows to settling tanks in which it flows slowly enough to allow flocculants to settle. Sludge can be collected and removed from the bottom of the tank, while clarified water leaves the tank by overflow (Toorn 1987). The addition of new technology, such as movable bed filters, removal of organic materials through biodegradation, and ozofractionation or protein fractionation (Spotte, 1992), has recently led to improvements in the management of nitrogenous compounds in marine mammal systems. Biological filtration occurs slowly, requires a large amount of space, and will be used in conjunction with high-speed and gravel filters and protein fractionation for removal of most particulate matter and soluble nitrogenous compounds. Ozonation will continue in use as a final effective decolorizing and bactericidal agent.

Indoor marine mammal facilities need adequate air filtration and turnover and proper lighting (Geraci 1986a). In nature, marine mammals come into contact with fewer airborne bacteria and fungi-bearing dust particles than in captivity. Fatalities have occurred due to pulmonary mycosis in cetaceans maintained in indoor facilities with suboptimal ventilation (Joseph et al. 1986). Adequate lighting, including proper spectrum and photoperiod, is necessary for vitamin D conversion (Kirby 1990) and may affect reproductive cyclicity (Geraci 1986a).

BEHAVIOR

To maintain a healthful environment for marine mammals within zoological facilities, behavioral stimulation appropriate for the species is necessary, as well as the maintenance of standardized behavioral observations recorded by trained personnel. Behavioral stimulation includes training and behavioral stimulation by caretakers as well as providing social stimulation by other marine mammals that may or may not be conspecifics.

Mellen and Ellis (1996) provide an excellent discussion of training and its importance to the care of marine mammals (fig. 16.3). Training and behavioral stimulation aids in enhanced animal management. Training facilitates the collection of physiological samples such as blood, urine, stomach contents, blowhole cultures, and feces, and the performance of ultrasonographic examinations, thus reducing stress to the animal. In addition, trained behavior can increase the amount of exercise by captive marine mammals, which promotes good health. Zoo staff can train specific behaviors, such as fast swims around the pool periphery and high bows. Training also provides a method for diversifying and changing the environment of the marine mammal. Trainers become, in effect, either members of the marine mammals' social group or elements of change in their environment. By using variable reinforcements, altering the sequencing of trained behaviors, and habituating new behaviors, training makes the environment more diverse and stimulating for the marine mammals.

Fig. 16.3. Training facilitates the collection of physiological samples such as gastric fluid.

Many marine mammals display complex social structures both in the wild and in captive facilities. When forming and maintaining captive groupings, staff needs to consider natural group composition, the behavior of individual animals, and associational preferences (Cornell et al. 1987). In general, cetaceans are social and are more likely to thrive within zoological environments if placed with conspecifics or closely related species. On the other hand, not all individual cetaceans are behaviorally equal. Animals that have demonstrated a previous history of aggression should be placed with conspecifics with great care and continual observation.

Social hierarchy and dominance relationships also have

Fig. 16.4. Behavioral observations provide as much or more information concerning the health of marine mammals than is provided by laboratory analyses. (Photograph courtesy of UNEXSO: The Dolphin Experience, Freeport, Grand Bahama Island. Reprinted by permission.)

an impact and are important for marine mammals' successful maintenance in captive settings. More dominant marine mammals can displace less dominant animals from feeding, steal offspring, and even seriously injure or kill conspecifics. Expressions of dominance can be very subtle, mandating careful observation by skilled personnel.

Behavioral observations and casual subjective observations provide as much or more information concerning the health of marine mammals than is provided by the results of laboratory analyses. Staff should record daily observations into each marine mammal's permanent record for current and retrospective evaluation (fig. 16.4).

Agonistic encounters between marine mammals are noteworthy and can be precursors of sexual behavior, reflect changes in the social order, or be a reaction to changes in the environment, including routine practices. Although aggression is a normal behavior in all social animals, marine mammals whose quality of health is declining may be the target of aggressive behavior by conspecifics. Accurate recorded observations can therefore permit evaluation of changes in behavior and health.

Staff should always record sexual behavior; parturition in a marine mammal should never be a surprise. Although most marine mammals care for their young adequately, first-time mothers may need additional observation and accommodation. Aggressive animals, dominant animals, or males may need to be removed from the mother's environment before parturition in order to facilitate a successful birth and the development of the mother-young bond.

Ill animals frequently tend to isolate themselves from caretakers and conspecifics, as do females close to parturition. Segregation and inattentiveness to caretakers are important behavioral health indicators.

Deviation from normal behavior is cause for concern, e.g. an animal's sudden dramatic decline in performance in a training program. A gradual decline in performance may signal the slow onset of illness or may imply training challenges. Trainers within a given institution should use standardized performance criteria to allow for consistent evaluation of performance. Astute, detailed observations and their documentation are the cornerstones of a good marine mammal management program (fig. 16.5).

NUTRITION

In nature, marine mammals feed on a wide variety of food items which vary seasonally. Marine mammals in captivity are generally given a narrower spectrum of food items, the quality of which is dependent on sources and handling procedures. Staff should provide marine mammals with a variety of food items in case the supply of one or more of the items in their diet becomes unavailable. Proper attention to food quality and preparation and vitamin and mineral supplementation can assist in the prevention of illnesses.

When handling food, keepers and trainers must diligently search for rocks, fish hooks, plastic bags, or other foreign bodies that the animals might ingest. We strongly discourage the use of hook-and-line-caught fish due to the possibility of embedded hooks, but net-caught fish such as mackerel or salmon may also contain fish hooks. Some facilities have exhibits that contain both marine mammals and live fish together or use live fish to feed or enrich the marine mammals. Staff should also check these fish for hooks.

FISH HANDLING AND STORAGE

Staff must give considerable attention to fish handling and storage from the moment of collection to the moment the fish is provided to the marine mammal. Fish freezer shelf life is dependent on 3 things: (1) packaging; (2) storage temperature,

Fig. 16.5. Astute, detailed observations and their documentation are the cornerstones of a good marine mammal management program.

and (3) the type of fish stored. Fatty fish, such as mackerel and herring, tend to deteriorate in quality more rapidly while frozen than do less fatty fish, such as capelin and smelt.

Many species of schooling fish act as intermediate hosts for parasites that can affect marine mammals. Many professionals recommend reducing the present USDA maximum allowable freezer temperature of −18° C to −30° C in order to reduce further the number of viable parasite eggs and cysts with the food items (Gauckler 1982; Geraci 1986b).

Marine mammal food should always be fit for human consumption. Staff should carefully thaw and examine samples from each shipment of fish before purchase or acceptance to make sure it has been properly handled, packaged, and stored since capture. Fish should not have thawed at any time during transport. Boxes that are frozen together imply thawing and refreezing. Food should be discarded if any doubt exists as to quality. Thawing should occur in cool room air or under refrigeration (protected from insects), or rapidly in cool running water (Ridgway 1972). If freshwater is used for thawing, fish should be removed promptly once it has thawed to avoid leaching of sodium. Bacterial growth occurs rapidly, so fish should be covered with a thick layer of ice immediately after thawing if to be used within an hour or two or be immediately refrigerated in closed containers. Thawed food should always be refrigerated or iced until use and must not remain on pool bottoms or be used more than 12 hours after initial thawing.

CRITERIA FOR ASSESSMENT OF FISH QUALITY

We recommend applying the following criteria to all fish received for marine mammal food. A sample should be thawed for examination and evaluation before the entire shipment is accepted. Criteria for examination include smell, color, texture when thawed, and the condition of skin/scales, eye covering, eye lens, gills, and blood. The smell of good quality fish has been variously described as like seaweed, "fresh fish," or "like the sea." Poor quality fish is easier to recognize and smells like decomposing fish that has been left in the sun, ammonia, or rancid food. Good quality fish is typically bright, with distinct margins between colors and with a metallic sheen. Poor quality fish is dull, faded, often appears to have a heavy mucus coating, and may appear slightly granular on the surface from freezer burn. Properly stored and handled fish has a firm, resilient texture, while poor quality fish is mushy. Pressing a finger into poor quality or overthawed fish will often leave an indentation. Very few scales will be shed from good quality fish compared with poor quality fish, and the skin is easily torn in the latter.

The eye covering of the cornea of good quality fish should be translucent to transparent, slightly wrinkled, and convex. Sunken, badly wrinkled, and cloudy corneas are signs of poor quality fish. If there is any doubt concerning quality of the fish, it should not be accepted or used for animal food.

VITAMIN AND MINERAL SUPPLEMENTATION

Vitamin and mineral supplementation is necessary, since there is loss of vitamin content during fish collection, transport, and storage. An enzyme produced by bacteria, thiaminase, breaks down thiamin, especially in poorly preserved fish. Thiamine supplementation at a rate of 200 mg per kilogram of food fed is recommended for marine mammals (Geraci 1986b; Reidarson 2003). Vitamin E breakdown occurs rapidly in fatty fish, especially if it has been handled poorly or improperly stored, but will break down over time in all frozen fish. Cetaceans appear incapable of *in vivo* synthesis of vitamin C, and reports of deficiencies exist for bottlenose and Pacific white sided dolphins, *Lagenorhynchus obliquidens* (Miller and Ridgway 1963; Reidarson 2003). Clinical signs include necrotic stomatitis, anorexia, and weight loss that respond to supplementation (Miller and Ridgway 1963; Reidarson 2003).

HYDRATION

Although there is evidence that dolphins swallow small amounts of saltwater, most of the water that marine mammals use for hydration derives from their diet (Telfer, Cornell, and Prescott 1970; Ridgway 1972; Worthy 2001). Pinnipeds, especially ill animals that are not eating normal quantities of food, should always have freshwater available. Walrus ingest ice in their natural environment and are known to drink freshwater in captivity. An extensive discussion of water balance in marine mammals can be found in Worthy (2001).

FEEDING

Daily feeding and behavior records are useful for keeping track of marine mammal health. Records can include subjective and objective comments of the amount of food given, the vigor with which food is eaten, and the animal's behavior and appearance during the feeding session. Feeding and training sessions foster maximum interaction between caretakers and animals, allowing close observation. Frequent small feedings encourage more dependable food consumption and often result in higher daily food consumption. Marine mammals should receive at least 3 feedings per day.

Food items should be placed near the marine mammal's mouth, or chest in the case of sea otters, and not merely dumped into the pool. Close observations will determine if the marine mammal is ingesting food or merely carrying food items around. If the animal begins to tear or drop food items, the feeding session should be ended. Causes for this behavior may include too high a food base, and supervisory and veterinary personnel should periodically review feeding protocols. Healthy marine mammals, especially cetaceans, rarely miss meals, unless there are changes in their environment or physiology.

The quantity of food needed on a daily basis by marine mammals depends on several variables, including diet composition. Larger amounts of smelt or capelin are generally necessary compared with fatty fish such as herring and mackerel, but fat content varies seasonally in all fish species. Many institutions use a daily caloric analysis of fish to monitor the caloric value of food ingested. Increased activity and cooler water tend to increase food intake, while reproductive activity and warmer water generally decrease intake (Abel 1986). Appetite may or may not increase with pregnancy, but increases significantly during lactation. Geraci (1986b) and Ridgway (1972) present the basic amounts of fish to be fed daily.

Sea otters can consume 25 to 30% of their body weight each day, depending on age, water temperature, and activity (Geraci 1986b; Kenyon 1969). These values vary with the caloric content of food provided, making it necessary to monitor the animal's body condition through regular weight measurements and calculation of caloric values of fish fed daily. A more extensive discussion of marine mammal nutrition and energetics is in Worthy (2001).

FEEDING ABNORMALITIES

Healthy marine mammals, especially cetaceans, do not miss a feeding unless something alters in their environment, social structure, or physiology. A sudden loss of appetite can signify the development of an acute disease, but usually reflects appetite depression due to the gradual progression of an illness. Reproductive activity can result in changed feeding habits, but there should also be other behavioral and physical changes. Most cetaceans stop eating 6 to 8 hours before parturition, but some individuals continue feeding even during labor.

Changes in social structure can depress appetite if larger and more aggressive animals intimidate subordinate individuals. If consecutive feedings are missed, it is cause for staff concern; staff should immediately investigate when a marine mammal does not eat for an entire day.

CLEANING OF FEEDING APPARATUS

As a high priority, staff should clean and disinfect nets, buckets, countertops, and sinks immediately after use. Chlorine-containing cleansers are best for scrubbing, and quaternary ammonia compounds or dilute chlorine are effective disinfectants for environmental surfaces. Freezer and refrigerator door handles, shelves, and floors are locations commonly overlooked when cleaning.

PREVENTIVE MEDICINE

A sound preventive medicine program is the third basic aspect of maintaining captive marine mammals successfully. Program goals include prevention and early detection of disease before such problems become life threatening. Preventive medicine can decrease morbidity, increase life span, and increase the quality of life of captive marine mammals.

QUARANTINE

Strict quarantine of new arrivals is absolutely necessary. New arrivals can be examined, tested, and treated during this period, avoiding the introduction of diseases that might not be present in existing stock. The quarantine protocol should depend on what is known about the health history of the newly acquired animal. If animals from other zoos or aquariums are tested before transport, quarantine may be shorter

Fig. 16.6. Regularly scheduled physical examinations are an important component of keeping marine mammals healthy.

in length. However, animals acquired from the wild, especially stranded marine mammals, require a longer quarantine and more rigorous testing. Quarantine also allows caretakers to begin observing individual variations in the behavior of new animals.

PHYSICAL EXAMINATION

Regularly scheduled physical examinations are an important component of preventive medicine for marine mammals (fig. 16.6). More is learned from examining apparently healthy animals than when they are affected by disease. Routine physical examinations also provide learning opportunities for caretakers in the handling and restraint of their charges. Marine mammals tend to become less excited and more cooperative with increased frequency of handling. Routine examinations permit the collection of samples, measurements, and ultrasonography, which provide baseline information, thus allowing better management of marine mammals. As noted previously, many samples can be collected regularly from well-trained individuals.

MASKING ILLNESS

Marine mammals, like all wild animals, have developed the ability to hide the presence of disease from conspecifics as well as predators. Although cetaceans are often represented as kindly creatures, ill group members are often driven from the pod or killed by conspecifics (Joseph, personal observation). In captive marine mammals, an illness may be well advanced before the demonstration of clinical signs. No laboratory examination can replace the information provided by regular, thorough written observations, both objective and subjective.

CONCLUSIONS

The information in this chapter may serve as a basic template for the successful care of marine mammals and is based on collective knowledge and experience that has developed over the last 40 years. The most important factors for the successful maintenance of marine mammals within controlled environments are a well-designed and properly constructed facility; a healthful environment, including the provision of appropriate and compatible social groupings; adequate nutrition; and a good preventive medicine program.

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17

Zoological Horticulture

Merle M. Moore and Don Peterkin

INTRODUCTION

The practical application of the science and art of horticulture in zoos, aquariums, and wild animal parks defines the profession of zoological horticulture. The Association of Zoological Horticulture (www.azh.org), a nonprofit membership organization dedicated to the advancement of horticulture in zoological parks, gardens, and aquariums, is the primary supporting organization for information exchange between professionals in North American zoos who are responsible for landscape design and maintenance. Elsewhere, a number of regional zoo horticulture groups have formed or are being formed in Germany, the United Kingdom, Ireland, Holland, and Scandinavia. These groups host periodic conferences and provide a network to promote and support the advancement of zoological horticulture in zoos, aquariums, and related institutions.

To appreciate the enormous impact the profession of zoological horticulture is having on animal exhibits and the welfare of captive animal species, one only needs to visit the Web site of the ZooLex Zoo Design Organization (www.zoolex.org). A recent search of the ZooLex Gallery turned up detailed descriptions of recent zoo exhibits in Mexico City, the Czech Republic, Germany, South Africa, England, and 4 North American institutions. The role of professional zoo horticulturists and their staff in designing, installing, and maintaining effectively landscaped exhibits and grounds is the primary focus of this chapter.

As a critical member of a diverse and creative team involved in planning new exhibits or renovating existing ones, the zoo horticulturist contributes to the development of the overall exhibit theme, landscape design, and maintenance protocols by

- recommending plant material and its proper placement to support and enhance an overall exhibit theme while surviving animal and guest impacts
- recommending methods for protecting and using plants preexisting within the construction site, and advising on methods and products to protect plants accessible to animals in exhibits
- recommending plant-growing media suitable for the types and numbers of animals that will reside in the exhibit
- contributing to discussions on planned animal densities and husbandry routines within planned exhibits, to ensure pastures and exhibit landscapes remain viable over the long term
- contributing to the design of irrigation systems where appropriate
- recommending types and placement of plant-related exhibit furniture and other enrichment elements
- contributing to the development of an overall landscape budget for the project

A second and parallel aspect of the zoo horticulturist's role is to develop an ongoing maintenance program to promote the health and sustainability of the plant material in the exhibit and general zoo landscape. Zoos invest substantial financial and human resources to develop comprehensive plans for long-term development of their physical plants. Such plans should include a comprehensive landscape plan that includes the guiding philosophical and aesthetic goals for future plantings, conveyed through a written manual that the zoo horticulturist uses to guide future plant selection and maintenance. The existence of such a plan facilitates a process whereby the zoo horticulturist revisits the zoo landscape periodically to make necessary changes reflecting the original interpretive intent.

The zoo horticulturist may also work with the education department staff in facilitating appropriate uses of exhibit and general landscaping, to impart education and conservation messages through interpretive graphics, youth and adult education programs, and conservation projects or demonstrations.

A successful, well-landscaped zoo exhibit will encour-

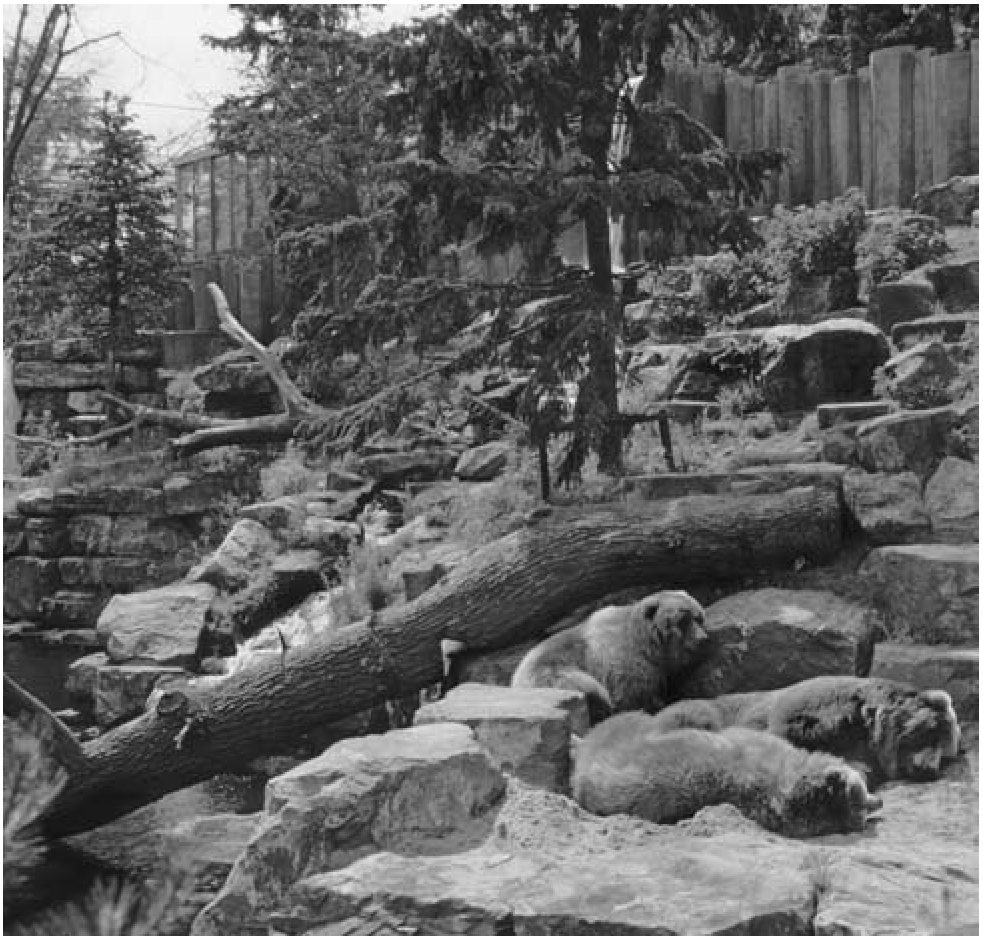

Fig. 17.1. A well-landscaped habitat immersion exhibit for bears, Emmen Zoo, the Netherlands. (Photography by Merle Moore. Reprinted by permission.)

age natural animal behaviors, promote breeding where that is a curatorial objective, and ease transmission of important conservation messages to zoo guests. Today's zoo horticulturists appreciate the importance of habitats and their preservation as paramount to long-term preservation of the earth's wildlife. The zoo horticulturist's challenge is to create, using plant materials appropriate for their specific regional growing conditions, landscape settings that allow animals to be perceived in the context of their natural surroundings (fig. 17.1). Zoo administrators are responsible for ensuring that the horticulturist has the opportunity to influence design decisions for effective, sustainable habitat/visitor immersion exhibits.

The value of a well-designed and well-installed landscape appreciates with the passing of years, unlike the investment in buildings and equipment, which ultimately depreciates over time. The zoo horticulturist can provide the expertise and ongoing management of a zoo's investment in landscape to ensure that this future value is maximized.

While it would be ideal if every zoo had a professional horticulturist to plan, purchase, plant, and maintain the plantings that comprise their zoo landscape, this may not be feasible for smaller zoos. The guidelines and recommendations presented in this chapter should, however, provide a structure for sound zoo horticulture practices whether managed in house or through the use of contracted resources.

PLANNING AND DESIGN: CREATING A "SENSE OF PLACE" FOR THE ZOO GUEST

The geographic location of a particular zoo will have a significant impact on options for creating an effective habitat/visitor immersion exhibit. If the zoo's location is closely similar in climate and other ecological conditions to those of the natural habitat of the animal to be exhibited, then it may be possible to replicate the actual habitat conditions and plants. In such a bioclimatic exhibit, the plants would be identical to those growing in the animal's natural habitat. For a zoo having a strong botanical focus, the plants may actually be collected from the natural habitat or propagated from those plants, with appropriate collection data taken and recorded. An example of such an approach may be found in the Mountain Woodlands exhibit at the Arizona-Sonora Desert Museum in Tucson. Another example, the Canadian Wilds exhibit at the Calgary Zoo in western Canada, combined extensive research and "plant rescue" operations in replicating a series of habitats and plants of the Canadian aspen parkland and Rocky Mountains.

Where the zoo's climate and environmental conditions are radically different from those of the animal, it will be necessary to simulate rather than replicate the habitat through the selection of locally native or adapted plant material similar in appearance and growth characteristics to those growing in the animal's habitat. In the case of the Denver Zoo's 2-ha, outdoor Primate Panorama exhibit, this is accomplished by a dense arrangement of plants able to tolerate high-altitude growing conditions. Hardy, leguminous trees and shrubs with pinnately compound leaves simulate a variety of nonhardy Asian rain forest species. Hardy bamboo, large ornamental grasses, perennials having large, tropical-looking foliage and flowers, and various climbing vines complete the "jungle" ambiance, at least during the spring, summer, and fall. This contrasts starkly with the Denver Zoo's Predator Ridge exhibit, where mixed native and adapted grasses, low, thorny shrubs and trees, and African daisies and ice plants from the high Drackenberg Mountains of South Africa are combined to simulate an African savanna scene for the exhibit of lions, hyenas, and African wild dogs.

The percentage of exhibits that will be primarily outdoor or indoor will be determined by the geographic location of a facility. Immersion techniques may be applied to both kinds of exhibits. However, indoor exhibits pose some major and potentially detrimental challenges that are not as common in outdoor exhibits.

The first challenge is light quantity and quality within the enclosed space. Indoor exhibits with living plants invariably run up against opposing engineering objectives when they are being designed. The mechanical engineers, and the administrators who pay the heating/cooling bills, are looking for energy-conserving designs and materials. The horticulturists, on the other hand, are looking for the maximum intensity of light, penetrating all the way from the tree canopy to the understory plantings. Animal staff may also be looking for critical levels of full-spectrum light penetration to ensure animal health and reproductive success. Suffice it to say, compromise is required if all members of the design team are to be satisfied to the greatest extent possible.

There are modern design techniques and glazing materials for indoor exhibits that will facilitate high light levels while providing significant reductions in heating/cooling costs. The challenge is to select those materials that permit adequate light intensity into the exhibit space to encourage plant growth and flowering. The most likely compromise is one that inevitably will mean not quite as much energy savings as the bill payers would like, and a little less light than the plant growers would consider optimum. The overall result can be an exhibit where plants may be successfully grown, albeit with less variety of plant types than one might otherwise choose. Once light levels decline to 3229 lm/m^2 or less, an exhibit will become nearly devoid of flowering plants unless the horticulture budget permits regular purchasing of "disposable/expendable" plants or a support greenhouse facility is available.

When possible, natural light entering an exhibit space should come from the sides as well as from the top. When light penetration occurs only at the top of the exhibit, plants will stretch for the light and eventually topple over. In small exhibits, special full-spectrum lights that deliver a balanced light spectrum for plant growth may be substituted for natural light, assuming appropriate plants are also used.

The second most challenging condition in indoor exhibits is finding a growing media that will support plant growth while adequately draining away excess water from irrigation, washing animal feces from exhibit surfaces, and hosing walkways to clean them. Exhibits will benefit greatly by having designed into them at the outset a complete drainage system installed under the planting beds and at the edges of paved pathways. Excess water in the plant root zone, especially when combined with low light conditions, will eventually kill even the hardiest of plants. A drainage system that will allow all free water to be directed out of the planting bed is critical to the success of the exhibit plantings.

Using light-textured, often soilless mixes with low percentages of bark in them is recommended over topsoil as an indoor growing media. Adding 10%–15% by volume of pea gravel to the soilless mix may also be advisable to create maximum pore space in the root zone. Whenever a planted area is renovated, new soilless growing media should be brought in and the old removed and discarded. This is especially true in aviaries, where nitrate nitrogen levels quickly elevate in the media due to bird droppings. Planting areas with underdrainage may reduce the frequency of changing growing media by allowing for leaching of nitrates from the media without its becoming waterlogged. In the case of small planters or vertical plant wall structures using live sphagnum moss and no other growing media, fertilizing with frequent but diluted liquid fertilizer formulations may be a preferable growing technique.

For a habitat/visitor immersion exhibit to be effective, the public side of the exhibit must also create a replication/simulation of the animal's natural habitat. The objective is to transport the zoo guests vicariously to the ecosystem being represented, where they may experience the flora and fauna in a simulated wild state, thus counteracting the perception that we are merely bringing exotic plants and animals into our urban environment.

Many of the same plants used within animal enclosures can be duplicated in the visitor area. In addition, there may be a variety of other more interesting plants that would not likely survive in the animal exhibit but which are important in completing the overall theme. For example, plants that are key food species for the animal on display could be planted adjacent to interpretive signage that explains the relationship between the plant in question and the animal within the enclosure. Similarly, plants that have important cultural connections for native peoples as food, shelter, textiles, or medicines may be included to enhance the understanding of how ecosystem health impacts human well-being.

Plantings in public areas of exhibits are also critical to controlling sight lines to enhance exhibit views while screening service areas, holding buildings, and other necessary infrastructure. They can help create a sense of intimacy for the visitor and encourage a sense of discovery, removing the perception of a barrier between guest and animal. When matched appropriately, the blending of animals and plants within a specific ecosystem fosters the greatest potential for meaningful interpretation and education.

CARRYING CAPACITY OF A SUSTAINABLE LANDSCAPED EXHIBIT

The degree to which one can successfully maintain a high-quality immersion exhibit is directly proportional to the size of the exhibit and the type and number of animals in it. In every case, the carrying capacity, or density of animals within zoo exhibits, is many times that of natural ecosystems. Generally, the larger the space and the smaller the number and size of the animals in it, the easier it will be to maintain the original landscape concept. Conversely, exhibits housing too many large, heavy herbivores in minimal area have little chance of success. Where possible, duplication of exhibit spaces to allow the rotation of animals from one space to another will allow for sound pasture management practices and will significantly improve the exhibit experience. While the emphasis is on authenticity and natural appearance, the reality is that satisfactory results depend heavily on intensive management practices to overcome wear and tear generated by animals within any simulated or replicated habitat.

Many other challenges confront the zoo horticulturist in successfully maintaining an immersion exhibit. Appropriate plant species are often not available in the commercial nursery trade, because little is known about how to propagate them. Reliable information about their ability to thrive under cultivation is also often lacking. In the Calgary Zoo's Canadian Wilds exhibit, one of the habitats was designed for woodland caribou, *Rangifer tarandus caribou*, including trees as a major interpretive feature. To the caribou the trees represent an opportunity for antler rubbing, which damages the bark, and browsing, which reduces the amount of foliage. Compaction of the soil around the base of each tree is also problematic. The end result has been a very heavily used habitat. If the habitat is properly interpreted, one may capitalize on the opportunity to explain the carrying capacity of a natural ecosystem where caribou live.

Ultimately, the closer an exhibit habitat parallels the true ecosystem, the greater the opportunity for meaningful interpretation and education. An experienced professional zoo horticulturist is best equipped with the knowledge and skills to design management and maintenance strategies that overcome the inherent challenges of an immersion exhibit. Some considerations for basic plant growth needs are given in a later section of this chapter.

PROTECTING AND/OR RELOCATING EXISTING LANDSCAPE RESOURCES

In designing a new exhibit or renovating an older one, the zoo horticulturist's most valuable resource is vegetation currently existing on the site. Preservation and use of existing trees, shrubs, grass, and other vegetation that may dramatically alter the appearance of the finished exhibit should be a high priority from the earliest conceptual design phase. The architects, general and subcontractors, and zoo horticulturist must work to develop a plan that identifies and protects existing vegetation before the first piece of demolition or construction equipment comes on the site. During the demolition and construction phases of the project, the zoo horticulturist needs the authority to stop a contractor's work if plants designated for preservation are being threatened, so that a resolution of the problem can be achieved. Portions of the site not directly affected by construction activity can be barricaded to avoid their being used as parking areas for equipment and storage areas for construction materials and chemicals, as well as to prevent soil compaction and damage to existing vegetation.

Large trees are a critical asset in any exhibit where a forest or jungle theme is being considered or where shade is an important consideration. According to the National Arbor Day Foundation, damage during construction kills more trees and plants than insect and disease outbreaks combined. Tree roots are most often damaged during construction, since the root zone of a tree extends horizontally from the tree for a distance at least equal to the tree's height. To maintain the health of a tree, an absolute minimum of 50% of the root system must be preserved. If construction damage exceeds this requirement, the resulting decline in tree health and vigor, and the eventual death of the damaged tree, may not become obvious for several growing seasons, long after the contractor has left the site.

Providing this minimum root-damage percentage does not imply that contractors should be free to damage 50% of the roots in existing trees; this would only be acceptable under extraordinary circumstances. Additionally, the level of root damage that trees can tolerate varies widely by species, age, and health of the tree in question. Decisions regarding acceptable levels of root damage should always be made in consultation with a qualified arborist.

As a general rule, trees closer than 1.5 m from a new structure should be removed. If the tree is less than 3 m tall and has a trunk diameter less than 5 cm, it may be possible for the horticulture staff to relocate it. Larger trees will require a tree spade to move them successfully, and this work is best done by a contractor with special equipment.

Protecting the health of trees may involve several or all of the following strategies:

1. In the design development stage of a project, conduct a thorough evaluation, using the services of a certified arborist if necessary, of the health and potential longevity of trees within the project site before determining which trees should be preserved.
2. Set guidelines for tree protection within contracts and impose adequate penalties for noncompliance. Require the contractor to have tree preservation bonds to cover noncompliance fines.
3. Protect trees with chain link fence with steel posts driven into the ground. This may involve individual trees or groupings of trees.
4. Aerate and fertilize those trees that will be preserved and commence root pruning trees that will be moved one full growing season in advance of demolition/construction.
5. Before work begins on the site, have an arborist or staff horticulturist remove low-hanging branches that are likely to be damaged by moving equipment or that may be in the way of improvements. If preserving those branches is important, barriers for tree protection must extend outside the drip line.
6. Install siltation fences to prevent soil in disturbed areas from flowing over tree root zones, burying root systems and cutting off oxygen to the roots.
7. Mulch with wood chips layered 20 cm–25 cm deep,

Fig. 17.2. Tree protection during construction, Denver Zoo. (Photography by Merle Moore. Reprinted by permission.)

beginning 30 cm away from the trunk and extending at least to the drip line (fig. 17.2).

8. Clearly designate on construction drawings where supplies and materials may be placed/stored on the site to ensure these activities do not occur under the tree canopy. Similarly restrict parking of vehicles and equipment in the immediate vicinity of trees being preserved.

When existing trees cannot be successfully moved or used and must be removed from the construction site, the zoo staff should assess their potential use as exhibit furniture (fig. 17.3). Whole trees and portions of trees may have value as props, deadfall, and logs for antler rubbing and scent marking. Removed trees may be placed upright, nearly intact, in concrete culvert sections with large rock and gravel placed around their trunk, providing natural climbing structures in outdoor exhibits for primates. Using rock and gravel to stabilize the tree rather than cementing it in place allows for its replacement once the trunk begins to decay. When trees growing on the site have been identified for such purposes, their removal can be planned and carried out in such a way as to minimize saw-cut limbs and branches, which detract from the desired appearance of a naturally downed tree.

Trees being removed that are too large for deadfall may have individual limbs with contortions and "character" removed, before the tree is cut down and converted to wood chips. Those branches can be used for perches in bird and reptile exhibits. Branches from other large trees, the species of which are suitable for browse, may be taken to the keepers to be fed out to large herbivores. Wood chips generated by tree removal may be used for mulch. Large limbs with hollow cavities in them are also valuable for certain exhibits and animals, and may sometimes be available from local forest or parks districts where hazardous trees are being removed.

PLANT SELECTION AND ACQUISITION

The most critical aspect of plant selection and acquisition is whether the new or renovated exhibit is to be bioclimatic or a simulated version of a habitat. Although it may seem that creating an exhibit like Calgary Zoo's Canadian Wilds is simply a matter of going out to the nearest native plant nursery and buying the necessary plants, that is often not the case. Appropriate plant species common to the animal's habitat may not be commercially grown if they lack ornamental characteristics desired by landscapers and home gardeners. Consequently, those plant species, or propagules from them (e.g. seeds, stem or root cuttings, bulbs or tubers), must be collected from the wild, requiring permission from landowners or appropriate authorities. Then there is the digging and transportation of live plants to the project site, or germinating seed, rooting cuttings, planting bulbs or tubers, and growing them in greenhouses and nurseries until large enough to survive when planted in the exhibit. Depending on construction schedules, collected plants may need to be acquired many months or even years ahead of the landscaping phase of the project. Even then, the species most critical to the habitat re-creation may be poorly suited for cultivation, being slow to recover from transplanting, very difficult to propagate, or poorly adapted to the environment in the desired site.

When selecting plants to simulate rather than replicate a particular habitat type, the options are greater. In that case the focus is on acquiring plants that have an appearance similar to those that would be found in the natural habitat of the exhibited animal(s).

Fig. 17.3. Use of deadfall as climbing structures in a gorilla exhibit, Busch Gardens, Tampa, Florida. (Photography by Merle Moore. Reprinted by permission.)

Plant analogs are often useful within naturalistic exhibits modeled after a particular habitat where native plants of that habitat would not survive. In using plant analogs, the emphasis is on the appearance of reality rather than botanical exactitude (Hohn 1986).

Another tactic is to use plants that are unfamiliar and/or have features perceived as exotic (large foliage, unusual flowering and fruiting), e.g. bigleaf magnolia, *Magnolia macrophylla*, with leaves up to 90 cm long, and Kentucky coffee-tree, *Gymnocladus dioicus*, with very large, bipinnately compound leaves and thick, gnarly twigs. Devil's walking stick, *Aralia spinosa*, also has large, compound leaves and spines covering all plant surfaces. False indigo, *Amorpha fruticosa*, combines tolerance for wet soils with fine-textured, pinnately compound foliage simulating acacia shrubs of the African savanna. Closely related and similar in texture is wild indigo, *Indigofera heterantha*, a simulator for many different plants native to temperate and tropical Africa and Asia, and certain desert shrubs.

Toxicity is another key consideration when selecting plant species for an animal habitat. Given the wide range of animals housed in international zoo collections and the many thousands of plant species available for immersion exhibits, the potential for toxicity is significant and potentially deadly, particularly in exhibits housing grazing or browsing animals. In recognition of this challenge, the Association of Zoological Horticulture has undertaken several extensive studies on toxic plants and their use in zoos and is sharing the information from these cooperative studies, another example of how zoo professionals can work together to their mutual benefit.

In an ideal situation, space would be available within a zoo or nearby for a plant nursery and a greenhouse complex where plants may be custom grown specifically for supporting habitat immersion exhibits. With a properly designed support facility, even zoos in geographic areas with short growing seasons and cold winters may grow and hold exotic plants (e.g. palms, bananas, bamboo) in large containers. Those plants can be moved out into the zoo during the growing season, and then returned to the greenhouse for overwintering. Access to a greenhouse also greatly enhances the horticulturist's ability to support, with live plant material, indoor exhibits, especially of the bird, reptile and amphibian, and aquarium tank varieties. The horticulturist can then purchase small, less expensive plants in quantity and raise them to larger sizes for future exhibit needs.

In many cases plants, particularly trees, that are well suited for zoo exhibits are considered substandard or culls by the nursery industry. For example, in the creation of a northern boreal forest in the Calgary Zoo's Northern Forest exhibit, zoo staff traveled from nursery to nursery, buying up all the "seconds" remaining in the white spruce, *Picea glauca*, field after the commercial-quality stock was removed. These trees had double leaders or were poorly shaped, but otherwise in healthy condition. Not only did the resulting planting look much more realistic than would have been the case with perfectly symmetrical specimens, but they were acquired at a small fraction of the cost of specimen trees. Working with local nurseries in this fashion can have tremendous advantages for the zoo horticulturist.

BASIC PLANT GROWTH

While the conditions for basic plant growth—sufficient light, suitable growing media, nutrients, and water, ability to survive browsing/grazing and other animal impacts—are no different in zoos than in the wild, the new habitat immersion exhibits provide horticulturists and zookeepers with many new challenges and management techniques. Plants are selected and managed today to accentuate their natural appearance; e.g. they are not planted in evenly spaced rows or grids, but are often randomly mixed in communities. Turf-type grasses are replaced with native and exotic grasses that are allowed to mature and set seed. Volunteer suckers and seedlings are not discouraged or removed, but allowed to become a component of the habitat being created. Even dead trees and shrubs, standing or fallen, become part of the exhibit.

Zoo staff needs to employ intensive management practices to overcome the wear and tear generated by animals within a habitat. However, many of the normally accepted horticultural procedures either are not available to zoo horticultur-

Fig. 17.4. Elephants removing bark from an unprotected tree, Toledo Zoo, Ohio. (Photography by Merle Moore. Reprinted by permission.)

ists or are restricted; e.g. chemical pesticides cannot be used, regardless of the seriousness of an insect or disease problem. Irrigation and pruning must be scheduled to avoid the nesting season or planned movements of animals from one pen to another, or the medical concerns of the veterinary staff. In applying fertilizer, staff needs to consider the danger of its ingestion by grazing animals. Even the location and pruning of trees and shrubs must accommodate the animals' territorial nature and/or need for a degree of privacy, and the public's need for an unobstructed view.

The greatest challenge of all is finding a suitable growing media that resists compaction and allows excess water to drain away quickly. Options and techniques suitable for outdoor exhibits include an extensive underground drainage system below all areas to be landscaped to carry away excess water from irrigation and natural sources, especially critical for maintaining landscaping and grass in exhibits with large, heavy animals (e.g. hoofstock and pachyderms). An alternative is grading the exhibit so that it is crowned in the center of all landscaped areas and has a "dry well" around the perimeter to collect and disperse excess water.

The greatest success seems to come from using a growing media similar to that installed under athletic fields, which have high quantities of sand with some organic matter added to retain moisture and nutrients. These types of growing media dry out quickly and allow nutrients to leach away, thus requiring an irrigation system and a frequent fertilization/chemigation program to maintain them properly. The other key to success is an adequate period of establishment time (4–6 months minimum; one full growing season is best) to allow for sufficient root growth. This minimizes movement of the growing media when walked on. Appropriate staff of a local parks department, football stadium, or golf course can suggest the mix of sand and organic matter that works best for them, which can then be modified to meet specific exhibit requirements.

Compacted soils benefit greatly from aeration once or twice during the growing season; a tractor-mounted, commercial-grade aerator that pulls a soil plug out of the ground is better than the smaller machines used for residential turf. The resulting holes may be backfilled with compost, gravel, or a combination of the 2. We also recommend that overseeding the existing grass be done each time the area is aerated, if not more frequently. In small- to medium-size exhibits, overseeding as frequently as every week or two during the growing season might be considered, as grass seed is relatively inexpensive. Other techniques include thoroughly incorporating 2.5- to 5-cm stone into the existing soil and then applying 5 cm of topsoil, or using applications of gypsum to help loosen clay soils.

Sharp, angular, 15- to 20-cm rock may be used as mulch over the root zone of trees, extending to or beyond the drip line. Where compaction of the soil in the root zone is severe, having a contract tree-care company use special equipment to "soil fracture" and inject aerating material into the soil below grade may be beneficial. Zoo staff can use boulders and/or deadfall to prevent animals from walking over the root system of trees and shrubs or even a variety of electrified "hot-grass," "hot-wire," or "hot-vine" applications, alone or in conjunction with the deadfall or large boulders.

Protecting tree trunks from having the bark eaten or rubbed off may be necessary in hoofstock exhibits (figs. 17.4 and 17.5). We wrap around the trunk and secure with wire or plastic clips a barely noticeable, black vinyl-coated fence wire with 2.5-cm squares that are small enough to discourage bark feeding. Other techniques include wrapping the trunk with chain-link fence wire, wooden planks secured with steel banding, or boards specially cut with the bark still intact on one side and wired together. However, zoo staff should check the protective materials annually and loosen them, if necessary, to prevent constriction of the trunk and the cutoff of sap flow. Electrified "hot vines" on the trunk and "hot grass" installed toward the tips of the branches may discourage browsing animals from eating both the bark and the outer branches of trees and large shrubs.

INSTALLING THE HABITAT/VISITOR IMMERSION ZOO LANDSCAPE

WORKING WITH CONTRACTORS AND SUBCONTRACTORS

The installation of the landscape in a larger new or renovated exhibit of 1.2 ha or more frequently involves a very substan-

Fig. 17.5. Protecting tree from elephant browsing using large boulders and hot wire, North Carolina Zoological Park, Asheboro. (Photography by Merle Moore. Reprinted by permission.)

tial amount of nursery stock coming from numerous local and distant suppliers. The zoo may not have adequate space to hold the plants or adequate staff to care for them properly until installation. Contracting with a local wholesale nursery to act as the zoo's "agent" in acquiring, holding, and staging the plants is one approach to ensure that they are being cared for properly, but are readily available to the landscape crew as installation proceeds.

By taking responsibility for acquiring the plant material, project staff can avoid the overhead a contractor will add for this service. Staff can also set up a schedule for delivery of the plants that corresponds to phased completion of various components of the exhibit. While the nursery providing this service may add a modest service charge to the plant order to cover its expenses, it will generally be less than a contractor's overhead and well worth the additional cost.

Before starting large landscape projects, key project staff responsible for the outcome should visit one or two other zoos that have recently completed similar exhibits and meet with their horticulturists. Staff can thus learn firsthand what problems were faced through the landscape installation process and how they were resolved. In addition, such visits lead to the development of ongoing networking relationships that are useful long after the completion of the current project.

Accurate records and drawings are critical to the success of a major landscape installation. Staff should keep a regular log of discussions, decisions, and observations as the project unfolds. These notes will be an invaluable source of information should any disputes with suppliers, subcontractors, or general contractors occur, and will provide background data that can be passed on to maintenance crews once the project is complete. Pay particular attention to gathering information on elements of the finished landscape, such as locations of irrigation lines or subsoil conditions, that will not be obvious in the future. An inexpensive digital camera is ideal for this purpose.

Contractors are often unaware of the impact their actions might have on the health of existing vegetation, particularly trees. For example, while it is considerably cheaper for a contractor to widen a trench rather than making a narrow trench safe with shoring material, the number of tree roots destroyed will increase geometrically with the increasing trench width. Similarly, incorporating herbicides in the road base under new asphalt to retard weed growth, a common practice in some areas, may kill trees if the asphalt crosses over the root systems. In Nilsson (2003), a landscape contractor offers a number of suggestions so that zoo staff and contractors can together accomplish a project goal most effectively.

The professional membership of the Association of Zoological Horticulture (AZH) represents a huge pool of practical experience in all aspects of landscape installation and maintenance in zoological parks, gardens, and aquariums. Comprising horticulturists, arborists, irrigation specialists, and others who work in zoo settings, the AZH brings together hands-on expertise from a wide range of climatic zones and exhibit types. An annual conference brings AZH members together for networking, training, and observation of zoo horticulture in other institutions. Any zoo that is installing or maintaining habitat/visitor immersion exhibits should have a staff member who is also a member of AZH, for access to the many resources the organization and its professional members provide.

ZOO LANDSCAPE SUSTAINABILITY: SUPPORTING A GREEN FUTURE

The modern zoo must play a leadership role in environmental stewardship in its local community if it is to maintain relevance in today's society. This need to demonstrate visibly the organizational commitment to a sustainable world extends to all aspects of the operation of the institution, including the zoo horticulturist. Fortunately, tremendous strides have been made in redefining traditional horticultural practices to be more environmentally responsible.

The use of pesticides in the zoo landscape should be a last resort when all other options have been exhausted. Sound horticultural practices that maintain healthy plant growth are always the first line of defense. In many cases, the use of biological control agents will allow adequate pest control without resorting to chemicals. Appropriate plant selection for a given project should include an assessment of the potential for disease and insect problems, and species known for a high level of susceptibility can be eliminated from the landscape wherever possible. When all else fails, habitat/visitor immersion exhibits are unlikely to be significantly compromised by modest outbreaks of disease or insect infestations; in fact, these natural occurrences may even lead to interesting and innovative interpretive messages.

Zoo staff needs to be mindful about the potential of introducing an invasive plant species inadvertently. If a zoo is considering using an unfamiliar exotic plant species for landscaping, we recommend research, possibly combined with a small trial planting of the plant for several years' duration, to determine its potential for becoming invasive in the region. We do not recommend using a plant species that is already known to be invasive.

The sustainable use of water is a growing issue that zoos need to address. A properly designed zoo landscape can provide a highly public example of how plant selection and appropriate horticultural practices can significantly reduce or even eliminate the need for ongoing irrigation. Zoos should select drought-resistant plant species that are well adapted to the local growing conditions wherever possible. Proper soil preparation and mulching will also reduce the quantity of water required to maintain plant health. Drip irrigation or an automated system that allows irrigation during the coolest part of the day makes a real impact in reducing water consumption.

Composting programs are beginning to reduce the amount of organic waste sent to landfill. A zoo horticulture department can take a leadership role in demonstrating the benefit of composting, from the perspectives of reducing waste to landfill and reusing nutrient-rich compost as a soil amendment and natural fertilizer. The combination of animal manure, animal bedding, and landscape waste provides the ideal raw materials for a highly successful composting program. Zoos should inform the visiting public of the benefits of this natural process in reducing waste. Some zoos even package and sell small bags of zoo compost to visitors, thus creating a revenue source.

Recycling is a core responsibility of the zoo horticulturist. Plant stakes, plastic pots, and bedding plant trays and many other materials used on a daily basis can be recycled and/or reused. Brush and tree limbs can be mulched for use around the zoo. Dead trees can be used as exhibit furniture to support enrichment activities in animal enclosures. Waste reduction is a core responsibility of everyone working in the zoo environment.

THE ROLE OF PLANTS IN COMMUNICATING AND EDUCATING

Pohlkowski (1991) has suggested that the immersion-style zoo exhibit sets the tone for an educational opportunity by advancing the notion that zoo visitors are the "guests" and the animals are the "hosts." This exhibit type can develop a visitor's respect for living creatures and demands participation of the individual observer. Immersion or landscape exhibits make visitors work for the reward of observing natural animal behaviors. The purpose of an immersion exhibit is to attract attention, increase curiosity, and thereby encourage intellectual involvement, eventually creating a memorable image in the mind of the observer. Visitors to the zoo should feel that they have left *their* "habitat," whether it is urban Denver, Colorado, or downtown Calgary, Alberta, and entered the habitat of the animal or group of animals that they are observing. All the elements of the exhibit should contribute to enhancing the "realism" of this experience.

Robert L. Fry, director of the North Carolina Zoological Park, Asheboro, shared the following thoughts at the 1990 AZH Conference:

> There can't be a comprehensive program of species conservation unless plant life is included. There can't be an intelligent presentation of the natural environment unless the vital role of plant life is demonstrated and explained. There can't be strong zoological education programs unless plant life is seen to be of equal importance to animal life. There will never be believable natural habitat exhibits unless horticulturists bring them to life with rich, authentic plant collections representing the environment shared with animal collections. (Fry 1990)

Ertelt (1990) describes the complexity of properly using plants in zoos to achieve maximum educational potential, including the correct placement of epiphytes (e.g. orchids, ferns, bromeliads, certain cacti) in a naturalistic exhibit. The challenge for the zoo horticulturist is to make the correct plant choices, know how to encourage their establishment and growth, and understand their ecology and the various interrelationships they may have with animals in their habitat. By sharing this information as part of the design process, the horticulturist can make a significant contribution to the authenticity of an exhibit while at the same time providing a valuable interpretive feature that may be used to convey important education and conservation messages.

Additionally, to impart a conservation message to a zoo guest, we must first engage their imagination, and the zoo horticulturist has the important responsibility of incorporating as many plants as possible to make critical links between the animals in the exhibit, their natural habitats, and indigenous people who may interact with this biodiversity. In doing so, the zoo horticulturist provides the education department staff with a wealth of opportunities for whole ecosystem interpretation.

"The increasing value of horticulture in zoos has as its basis, four underlying factors: esthetics, a new understanding of ecology, greater insight of animal behavior, and the desire to achieve higher levels of public education" (Hohn 1986). The development of new exhibits displaying and interpreting animals and plants as interdependent life-forms is our means of conveying important principles of an ecological reality. As zoo professionals, we need to ensure that our exhibits encourage a better-informed populace to recognize that they, too, have an important role to play in the preservation of wild animals and wild places. The practice of zoological horticulture is evolving to help zoo visitors understand more fully the critical balance between habitat survival and animal survival, and, ultimately, our own survival.

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18

New and Sustainable Directions in Zoo Exhibit Design

Jon Coe and Greg Dykstra

INTRODUCTION

> Exhibits are a zoo's natural voice, the best means to communicate to the public our message about the animals that are so important to us.
>
> —Jon Coe (1996)

We believe that this observation remains as true today as when it introduced exhibit design in the first edition of this volume. In the ensuing years, design techniques, which give meaning and motivation to zoo exhibits, have improved and taken surprising new directions that add to visitors' awe and enjoyment, such as "rotation exhibits," "night safaris," and the "unzoo alternative." Enriched by collaborations with theme parks, animal trainers, anthropologists, ecologists, educators, horticulturists, and sustainability specialists, zoo designers have advanced both the depth and the breath of their work. At the heart of these advances lies the same enthusiasm for synergy and innovation that resulted in the breakthrough techniques of immersion design introduced in Hancocks (chap. 11, this volume). We continue that discussion, building on innovations presented in earlier chapters. We also introduce the important subject of sustainable, or "green," zoo design and speculate about other future design opportunities.

This chapter is organized according to the interests of the users: husbandry (animal care staff), animal well-being (the animals themselves), education, and entertainment (zoo visitors).

LANDSCAPE IMMERSION UPDATE

Principles of immersion design (Coe 1985; Hancocks 2001, chap. 11, this volume) have changed little since they were introduced nearly 30 years ago (Jones, Coe, and Paulson 1976). Exhibit construction techniques were greatly advanced in the award-winning work done in New York at the Bronx Zoo's Jungle World 20 years ago. Today that zoo's Congo exhibit excels in horticulture, exhibitry, multimedia, and conservation inspiration. Authentic-looking artificial trees not only contain enrichment devices for the apes, they also provide places for physical activity and social interaction. Visitors enjoy nose-to-nose encounters, enhanced by a glass visitor tunnel that gorillas, *Gorilla gorilla gorilla*, cross over, putting zoo guests in the midst of gorilla families. "Congo" demonstrates a high point in immersion design in cold climates.

The scale of projects continues to grow, with indoor immersion exhibit complexes of great size and complexity at Henry Doorly Zoo (United States), the Eden Project (United Kingdom), Zoo Zürich (Switzerland), and Burgers' Zoo (Netherlands), to name significant examples. Sea World, Busch Gardens, and Disney's Animal Kingdom, (all in the United States), Tennouji Zoo (Japan), Singapore Zoo, and many Australian zoos have built extensive, advanced immersion displays. Immersion design has clearly achieved the standard of international best practice, the level to which less-developed zoos worldwide aspire (fig. 18.1). In the last 20 years, 90% of the Association of Zoos and Aquariums' (AZA's) annual awards for zoo exhibits have been won by immersion exhibits, as have the last 3 exhibit awards by the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA).

CULTURAL RESONANCE

Ethnic art, artifacts, architecture, and even villages also can be simulated in zoo exhibits. This adds an interesting cultural dimension to the visitor experience, often telling a story of interactions between people and wildlife. This concept was first popularized by Carl Hagenbeck (1909). When the idea reemerged in U.S. theme parks and zoos, it was seen as an extension of immersion design (Jones 1989) and has been developed to an unprecedented level of thoroughness and integration at Disney's Animal Kingdom in Florida (Malmberg 1998) (fig. 18.2).

Fig. 18.1. The Polar Bear Conservation and Education Habitat (Cochrane, Ontario, Canada) encourages children to swim with polar bears separated by large reinforced-glass windows, taking immersion design to even greater depths. (Photograph © Jean-Pierre Ouellette. Reprinted by permission.)

Cultural resonance reemerged in Europe when the Burgers' Zoo, Arnhem, Netherlands, developed a Southwest Native American pueblo (village) as part of its desert animal display, and is well demonstrated in Zoo Zürich's Masoala Rainforest exhibit with its Madagascar architecture.

Recently, excellent cultural immersion displays have been developed at Melbourne Zoo's Trail of the Elephants (Australia). This 2004 ARAZPA exhibit award winner tells the story of traditional Southeast Asian people's complex relationship with both wild and domesticated elephants. Evaluations show that the design is well received by the public and meets the zoo's learning objectives (Fifield 2004). Cultural presentations are now a common part of immersion exhibits.

MODERNIST UPDATE

Immersion design has joined rather than replaced the earlier modernist style (Coe 1995a). This approach, including the obvious use of modern construction materials and technology, is used in nearly all off-exhibit areas, and also is the style of choice in displays where durability, flexibility, and functionalism are paramount (see fig. 18.3). The primary goal of Philadelphia Zoo's PECO Primate Reserve was to provide large, accessible, and behaviorally enriched year-round indoor space for great apes and other primates (Baker 1999). The project was themed to resemble an abandoned tropical sawmill converted to a primate rescue center. Industrial features such as scaffolds and cranes provide both apes and animal care staff safe access to a vertically oriented and changeable array of behavioral opportunities. Staff reports desirable levels of animal activity and excellent reproductive success (Baker, personal communication).

Fig. 18.2. Disney's Animal Kingdom, Orlando, Florida, uses a simulated ruin under repair as part of its gibbon display, blending natural and cultural elements to evoke a memorable sense of place. (Photograph © J. Coe. Reprinted by permission.)

NEW DIRECTIONS

New design directions have resulted from improvements in related areas such as husbandry, enrichment, education, and entertainment, as well as evolving concerns for animal well-being.

EXHIBIT DESIGN AND ANIMAL HUSBANDRY

Appropriately designed facilities can support animal training, husbandry, and health care, and improve animal welfare as well. In our opinion, the growing use of animal behavioral management, such as training and enrichment, has resulted in the most exciting new directions in exhibit design. It also forms the basis for animal rotation exhibits and demonstrations supporting the zoo's entertainment and education objectives, as will be discussed later in this chapter (fig. 18.4).

Training. Facilities designed for reward-based training (Pryor 1985) and operation should be arranged differently from those using coercive techniques (fig. 18.5). Before positive reinforcement was emphasized, staff often used their dominant status to coerce animals into using transfer gates located at the far side of the exhibit or night room. The opposite situation applies in facilities designed for positive reinforcement training. Here, animal transfer gates are near keeper aisles, giving staff convenient access for training and rewarding desired behaviors. Keeper paths should parallel animal raceways and vertical transfer situations, and provide access to both sides of transfer gates whenever possible.

In "free contact" management of elephants and other species, training is done anywhere in the animal's area. Perimeter access is unnecessary and solid walls are often used. In "protected contact" management (Desmond and Laule 1991), training and interaction usually occur along the perimeter of the enclosure, where keeper access is essential. The ideal design configuration depends on the type of husbandry to be used.

Rotation exhibits. While the concept of rotating or alternating animals between display yards is not new, the ability to transfer animals dependably has made elaborate rotation exhibits practical (Coe 1995b; Steel 2004). For example, orangutans, *Pongo pygmaeus*, siamang, *Symphalangus syndactylus*, tapir, *Tapirus indicus*, babirusa, *Babyrousa babyrussa*, and tiger, *Panthera tigris*, species rotate through 4 display areas at the Louisville Zoo, Kentucky (figs. 18.6 and 18.7). The rotation sequence, direction, and duration is randomized daily by keeper staff to maximize novelty (Herndon 1998). Animals rotating through a variety of interconnected enclosures have access to additional space and more varied environments, including traces of animals previously occupying the space, compared to animals occupying single yards. Extended behavioral analysis found that the animals responded well to this time-share situation, and that rotation was enriching for animals (White et al. 2003).

Fig. 18.3. Modernist design principles are widely used where functionalism is paramount, exemplified in zoo animal holding areas and facilities such as the Primate Research Institute, University of Kyoto, Japan. (Photograph © J. Coe. Reprinted by permission.)

Fig. 18.4. Designers need a good understanding of husbandry methods such as operant conditioning and behavioural enrichment to design facilities that function well for both keepers and animals. This facility is at Louisville Zoo, Kentucky. (Photograph © Louisville Zoo. Reprinted by permission.)

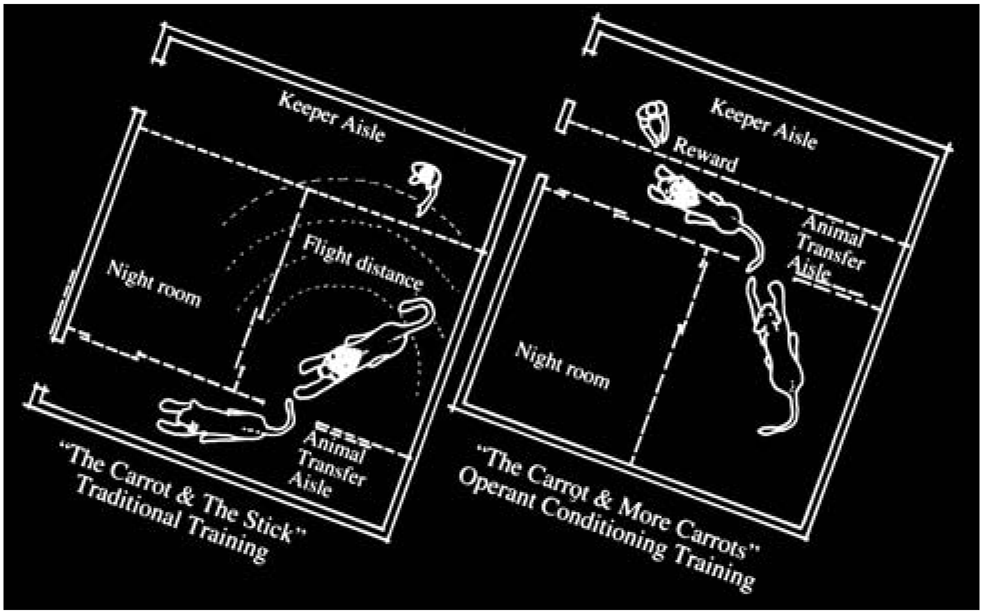

Fig. 18.5. In this traditional arrangement (*left*), caregivers drive animals through gates located on the opposite wall. In reward-based training (*right*), gates should be near the staff to facilitate training and giving rewards. (Diagram © J. Coe. Reprinted by permission.)

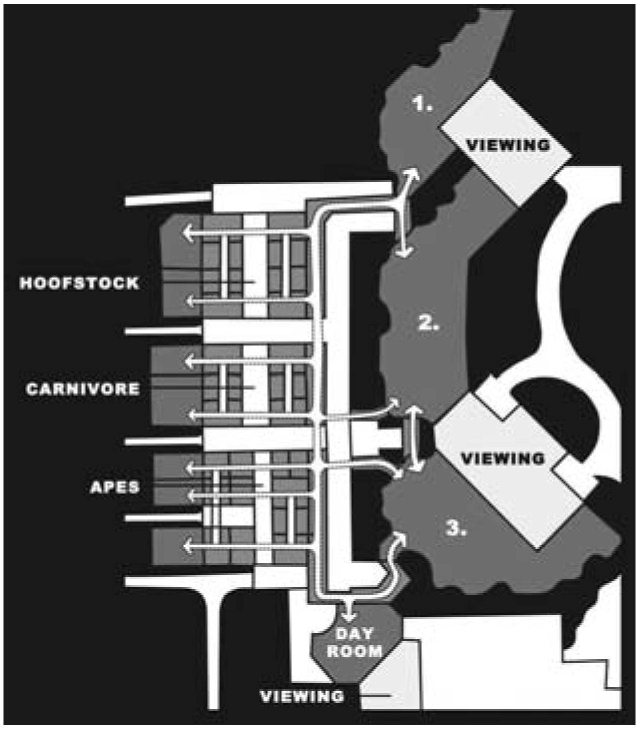

Fig. 18.6. This plan of the Islands exhibit at Louisville Zoo, Kentucky, shows the complex system of raceways designed to rotate multiple species through 4 display areas. (Drawing © J. Coe. Reprinted by permission.)

Point Defiance Park Zoo and Aquarium, Tacoma, Washington, displays animal species similar to those in the Louisville Zoo exhibit, but it has added small-clawed otters, *Aonyx cinerea*, and langurs, *Semnopithecus* spp., in an even more extensive rotation exhibit complex. Both zoos are also mixing some species, such as siamang and tapir, and plan to combine other species in groupings that will vary throughout the day.

From a disease control perspective, rotation displays are like any other mixed-species exhibit: good quarantine, health checkups, and cleanup procedures are essential for success.

From a design and operational perspective, rotation displays are complex and relatively expensive to build and operate. Barriers must be appropriate for the most robust and demanding species to be rotated. However, staff using such exhibits strongly endorse the approach based on their observance of increased animal activity levels and public appeal (Walczak 1995).

EXHIBIT DESIGN AND ANIMAL WELL-BEING

While the previous section described training, enrichment, and rotation exhibits from a husbandry perspective, they are also important advances for improving the overall well-being of zoo animals. Good design benefits animals by facilitating environmental enrichment and physical exercise.

Environmental enrichment. There is occasionally unproductive disagreement between immersion advocates ("keep it natural") and enrichment advocates ("keep it changeable and easily available"). Forthman-Quick (1984) concluded that immersion exhibits are inherently enriching, but that such exhibits still need additional enrichment. Coe (2003) has pointed out that many enriching features gradually lose their attraction because of habituation. Thus, we must constantly seek additional strategies to maintain reasonable levels of animal well-being. We suggest considering the following when designing enrichment features (see also Coe 2006):

1. Keep the enrichment features natural or within the theme whenever possible, especially in immersion exhibits. As Hancocks points out (chap. 11, this volume), why spend large sums of money on finely tuned im-

Fig. 18.7. Keepers transfer a tiger at Louisville Zoo's Islands exhibit facility by operant conditioning. Note that the keepers have excellent visibility and access to animals at multiple levels. (Photograph: © Louisville Zoo. Reprinted by permission.)

mersion displays and then dilute their message to the public by inserting commercial toys?

2. Build in permanent features of enduring interest to animals, including sun-heated and shade-cooled overlooks, visible basking and rest areas, water features, and some climbing features.
3. Provide novelty by using changeable naturalistic features, including vines, scratching posts, balancing logs, browse, real or artificial fruit, and simple treat-delivery systems.
4. Use hidden enrichment systems so appearance is not an issue, including artificial heating and cooling systems, treat delivery systems, and animal-controlled water jets or air bubbles in pools and streams. Tether artificial toys so that the animals' play behavior, but not the toys, is visible to viewers.
5. When all else fails, especially in artificial-looking exhibits, use commercial products and adapt the overall educational message to fit the exhibit.
6. Use any and all enrichment features imaginable in off-display areas, where many zoo animals spend the majority of their time. Designers should work with zoo staff to provide abundant attachment points and adequate storage and access for enrichment programs.
7. Budget for evaluation and replacement. Wild animals live in self-renewing landscapes. Zoo animals require us to provide this service.

Physical fitness. Most zoo animals have very limited opportunity for strenuous physical activity compared to their wild counterparts. Taronga Zoo, Sydney, Australia, will allow elephants, *Elephas maximus*, to plunge through a 60-m-long "river meander" of 3-m-deep water, following trainers moving along the adjacent shore (fig. 18.8). This intensive, low-impact aquatic aerobic exercise should increase physical fitness of the elephants and is likely to be an impressive display for the public as well. Similar opportunities are planned for greater one-horned rhinoceros, *Rhinoceros unicornis*, at Woodland Park Zoo, Seattle, Washington.

The Smithsonian National Zoological Park, Washington, DC, uses moving lures to encourage pursuit by cheetah, *Acinonyx jubatus*. Designers should develop features to encourage exercise in all animal facilities.

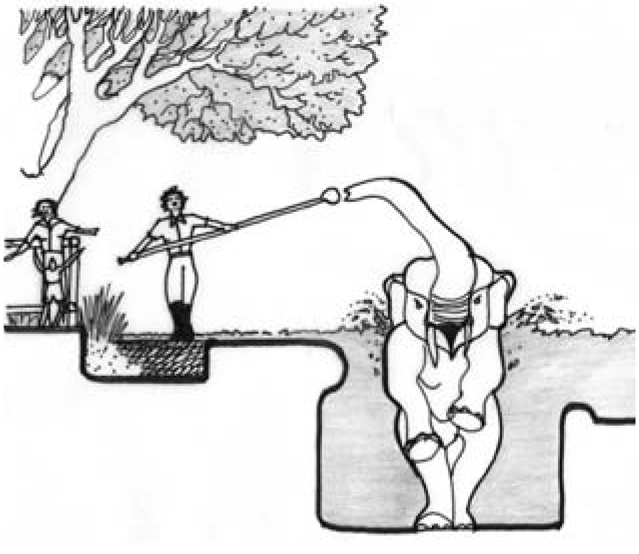

Fig. 18.8. All zoo animals need opportunities to maintain high levels of physical fitness. This example of aquatic aerobic exercise for elephants was designed for Taronga Zoo, Sydney, New South Wales, Australia. (Drawing: © J. Coe. Reprinted by permission.)

Choice and self-determination. Perhaps the next frontier in improving animal well-being through design is to devise means for zoo animals to have more behavioral choices and also greater participation in their own care (fig. 18.9), resulting, eventually, in greater self-determination. Coe (1995c) suggested that the organism with the greatest number of choices has the greatest freedom; therefore, we should provide the greatest reasonable number of choices to zoo animals. Coe also argued that animals competent to survive and evolve through millions of years without human assistance may be competent, with adequate training, to provide many services for themselves which today are provided by keepers. For example, common remote sensing devices such as infrared motion detectors and microchip implants could allow animals to activate showers (fig. 18.10), heaters, fans, food dispensers, and sound, light, and aroma systems, and open or close keeper-approved doors (Coe 1995c).

Integrated planning. In our experience, exhibit design and construction often precede design of husbandry procedures, including behavioral training and enrichment. Activity-based design and management (Coe 1997) is an integrated approach to coordinating training, enrichment, general husbandry, and design from planning through operation of new facilities, with the goal of improving animal well-being. The design of facilities at the Louisville and Point Defiance zoos described above responded to the husbandry plan and not vice versa.

Fig. 18.9. Bears at Northern Trail, Woodland Park Zoo, Seattle, Washington, have been given back their occupation—catching fish for themselves. (Photography by L. K. Sammons. Reprinted by permission.)

EXHIBIT DESIGN AND EDUCATION

Hancocks (chap. 11, this volume) points out the inherent educational value of immersion design, which is based on the premise that perceiving an animal within a multisensory context that convincingly presents the habitat in which the species evolved contributes to a greater public appreciation of the animal's significance as an ecological being, not merely an object of curiosity. Evaluation work by Bronwyn and Ford (1992) supports this approach.

Presentation, perception, and embedded meaning. While education and interpretation are addressed by Routman, Ogden, and Winsten (chap. 12, this volume), we will focus on design of the overall environmental context within which the educational strategies are carried out and interpretive features are placed.

To the trained observer, a natural or cultural landscape is filled with meaning and significance. An ecologist, for example, could identify the plant and animal species and the stage of natural succession, make an informed guess as to soil type and underlying geology, and know the biome and perhaps even the approximate global position of the site. An anthropologist could identify the ethnicity of local people, as well as their status, economy, and, perhaps, religious beliefs. Both experts could discuss the relationship between local people and the surrounding landscape.

Good zoo exhibits, too, are filled with embedded meaning. It is the exhibit designer's responsibility, working with educators, ecologists, behaviorists, and others, to give appropriate form, filled with appropriate meaning, to the total exhibit environment.

Environments for active learning. Exhibits today encourage active participation in free-choice learning environments. Werribee Open Range Zoo, Australia, designed its Lions on the Edge exhibits to activate Howard Gardner's (1983) concept of multiple intelligences by designing landscape and indoor environments "that deliberately arouse and use a range of intelligences in a provocative mix" (Landells 2004) (fig. 18.11).

EXHIBIT DESIGN AND ENTERTAINMENT

While education is often given as the main reason for a zoo visit, we believe entertainment is the engine that powers attendance, especially when paired with education. Theme parks, beginning with Hagenbeck's combined zoo, circus, and park in Germany a century ago through today's leaders such as Sea World, Busch Gardens, and Disney's Animal Kingdom (all in Florida) as well as Ocean Park (Hong Kong), Taman Safari Indonesia, and Sea World (Australia), blend education and entertainment. Like zoos, their presentations are evolving to present nature and wildlife more respectfully.

Fig. 18.10. Animals should have the opportunity to do things for themselves. This elephant operates a shower at Columbus Zoo, Ohio, by activating a simple motion-activated device. (Photography by Grahm Jones, courtesy of the Columbus Zoo and Aquarium. Reprinted by permission.)

Amphitheaters and animal demonstrations. Theme parks and some highly visited zoos like Singapore Zoo have designed facilities ranging from vast amphitheaters to small, terraced seating or standing areas outside popular displays. Show venues give visitors a much-appreciated chance to rest and provide the institution with a captive audience able to focus on its message. Amphitheaters at the Desert Wildlife Park (Australia) and Sea Life Park (United States) feature dramatic natural backdrops.

Positive reinforcement training was largely developed in oceanarium and zoo animal demonstrations, and animal rotation exhibits evolved from this technology. Building on this new direction, San Francisco Zoo, California, once considered a plan where animals could be transferred from their exhibits along publicly viewed raceways to a central demonstration amphitheater. Animals could arrive by flying, brachiating, walking, or swimming, depending on their preferred mode of locomotion (G. H. Lee, personal communication).

The Smithsonian National Zoological Park's modernist-style O-line allows orangutans to move along 10.6-m-high cables over the public walkways for 150 m, from their display area to the "Think Tank" demonstration and interpretive complex (Gilbert 1996) (fig. 18.12). A similar system recently opened at Tama Zoological Park in Japan (Wako, personal communication). In Australia, Adelaide Zoo is building overhead lines and towers to allow orangutans and siamang to pass over and rest above the adjacent tiger display.

Habitat theater. Midsize and smaller show venues are also being developed in zoos. Using a concept called habitat theatre, Zoo Atlanta (USA) developed a themed character, "Mr. Zuma," to play the role of a game warden in an African safari park. Mr. Zuma confronts a "poacher" (another actor) outside the black rhinoceros display, and after a heated exchange, Mr. Zuma escorts the poacher to the Elders' Tree (minitheater), where Mr. Zuma and the poacher each present their case and the audience votes to convict or release the poacher. These themed venues allow complex social and conservation questions to be presented to the pubic in insightful and provocative demonstrations within the immersive display area.

Ray Mendez has said, "Make the landscape your theatre and the animals and staff your actors" (Coe and Mendez 2005). Habitat theater may also be staged in dispersed, trailside demonstrations. Visitors to San Diego Wild Animal Park, California, may see a large python moving across a clearing in a simulated safari camp while the keeper, appearing to be inattentive, sits quietly some distance away. The sight of this active, unconfined snake was electrifying, to judge from the reaction of visitors Coe observed. This example shows just how simple, inexpensive, and immersive habitat theater can be.

Continual renewal. Novelty seems to have a strong influence on attendance, and zoos are learning that continual renewal with new and varied exhibits, shows, and other features usually results in increased attendance and revenue to support education and conservation goals. This factor has led us to question the desired life expectancy of exhibits and other facilities. When we observe the rate of change in exhibit philosophy and technology over the last 25 years, we suggest that future projects be planned for a life no longer than 20 years.

Story-based displays may have an especially short relevant life. Woodland Park Zoo's elephant display told the story of traditional elephant logging programs when it opened in 1989. Such logging is now all but obsolete, and today's story concerns the conservation of both domesticated and wild elephants in a rapidly industrializing world. This has led to discussions of changing the display theme from a logging camp to an elephant sanctuary and breeding center.

Another way to renew exhibits is by adding or updating operating programs. Using computer terminology as a metaphor, the physical infrastructure of the exhibit can be considered "hardware." With frequent "software upgrades," such as staff training, keeper demonstrations, behavioral enrichment, and interactive features, old exhibits can take on a new life and address contemporary issues.

Behind-the-scenes tours. Behind-the-scenes tours build on the entertainment value of close-up animal encounters as well as the visitors' desire for special treatment. Sea World designed a behind-the-scenes polar bear display pool. On a smaller scale, Adelaide Zoo is building behind-the-scenes visitor facilities in its new South East Asian Rainforest Stage 2 display. Visitors, including school groups, will be able to watch orangutan and tiger training sessions and learn about the care that goes into maintaining animals in modern zoos.

Louisville Zoo and Philadelphia Zoo both provide on-exhibit public viewing of animal training, making the fascinating interchange between trainers and trainees an important attraction. As an alternative to staged shows, the extensive dolphin facility at Mirage Hotel and Casino, Las Vegas, Nevada, provides public viewing of its nearly continuous dolphin, *Tursiops truncatus*, training and behavioral enrichment activities.

Night zoos. Night zoos are an exciting design direction that combines aspects of entertainment and immersion exhibits. The best-known example is the Singapore Night Safari. The obvious difference between a night zoo and a traditional zoo

Fig. 18.11. The Lions on the Edge display at Werribee Open Range Zoo, Victoria, Australia, provides an excellent environment for active learning while exercising multiple intelligences. (Photograph: © Werribee Open Range Zoo. Reprinted by permission.)

Fig. 18.12. The O-line at the Smithsonian National Zoological Park, Washington, DC, is entertaining for guests and gives orangutans both behavioral choice and physical exercise. (Photograph © Jessie Cohen, Smithsonian Institution. Reprinted by permission.)

is that "in a night-time facility everything the visitor sees will be determined by lighting" (Graetz and Coder 1999, 31). This affects not only what is seen and what is hidden (not lit), but also the overall quality of the viewing experience. Lighting design is a form of naturalistic stage lighting. Cost savings occur when service buildings and some barriers can be hidden in darkness, but the development and operation of massive lighting systems add costs.

Night safaris are most suitable in lower latitude regions, where the hour of sunset varies little and evening temperatures often are more pleasant than daytime temperatures. Cultures in these climates often have an active evening social life, enabling night zoos to attract a more affluent audience and to provide profitable dinner venues and even overnight accommodations.

New night zoos and safaris are being considered in India and the United Arab Emirates, and one recently opened in Chaing Mai, Thailand. Some established zoos are adding lighting and evening event areas to increase visitation and extend use of their existing facilities. Of course, animal species suitability, increased staff and operation costs, and variable admission fees must be considered in planning evening extensions of day zoos.

Fig. 18.13. Some zoos are re-creating the overnight experiences of wildlife safaris, as demonstrated here by Werribee Open Range Zoo, Victoria, Australia. (Photograph: © Werribee Open Range Zoo. Reprinted by permission.)

Safari parks. Wildlife safaris form the inspiration for a growing number of entertaining venues. Drive-through displays are especially common in Asia and Australia. More of these facilities are adding safari-like tented camps, campfire experiences, torchlight walks, and early morning bird viewing. The Werribee Open Range Zoo and Earth Sanctuaries (both in Australia) and Fossil Rim Wildlife Center (United States) are good examples of this trend (fig. 18.13). Al Maha (United Arab Emirates) provides luxurious accommodations in the midst of a restored 225-km^2 desert reserve (G. Simkus, personal communication).

GREEN DESIGN

There are 4 ways to protect and conserve wildlife and the wild lands that sustain them: (1) protect and preserve remaining intact ecosystems, (2) restore and repopulate damaged ecosystems, (3) sustain viable relic wildlife populations in zoos and sanctuaries, and (4) reduce human demand for resources that threaten wildlife habitat if removed. But sustainable design intends more than simple reduction of resource consumption.

> Ultimately, the goal of sustainable landscapes is the transformation of culture—the taming of technology, the emergence of a new environmental ethic, a new measure of life quality, and a substantially broadened sense of community including not only humans, but all of life. (Thayer [1994], 317)

With hundreds of millions of people worldwide visiting zoological institutions, zoos can influence the world by example. Sustainability aligns perfectly with zoos' missions of conservation and education.

HOW GREEN?

The U.S. Green Building Council's Leadership in Energy and Environmental Design (LEED) program (USGBC 2000) is a point-based rating system for certification of high-performance green buildings, focusing on 6 key categories: energy, water, materials, site, indoor environmental quality, and "green" innovations. Buildings can be awarded one of 4 certification levels: certified, silver, gold, and platinum. Other related initiatives include the World Green Building Council and green building councils in Australia, India, Spain, Canada, and Japan, to name a few. They are at the forefront of transforming building and design industries. The International Organization for Standardization (ISO) 14001 environmental management system standards (ISO 1995) assist organizations in meeting environmental policies and goals, and the ISO works globally to that end.

A few zoos have established environmental management systems (EMS) accredited under IS014001, such as Aalborg Zoo (Denmark) and North Carolina Zoo (United States). Some U.S. zoos also have projects registered with LEED, though we know of no certified zoo projects at this time.

GREEN HEART

> Yet I believe much of this progress has unduly relied on a largely negative emphasis on avoiding environmental harm and injury, a stress on physical and material benefits, and changes more at the level of building systems than at the experience of individuals and groups. By contrast, I believe sustainable design has insufficiently considered how people derive a host of intellectual and emotional, as well as physical and material, benefits from connections with natural process and diversity. I conclude by suggesting green development will not achieve its full promise and potential until it more positively motivates individuals, developers, and planners by capturing in the built environment the widest range of physical, emotional, and intellectual values of nature.
> —Stephen Kellert (1999)

Architecturally, the present sustainability movement overemphasizes engineering and materials technology. Where is the "green heart" of green design? What if we designed buildings and landscapes to encourage natural plant succession? What if we preplanted walls and roofs as living habitats and biofilters? What if present timid steps for growing "green roofs" of succulents, moss, and herbs were extended to create buildings supporting and supported by forest communities (fig. 18.14)? Why can't wild owls, bats, and squirrels have nest boxes in our attics?

Zoos have been quiet leaders in developing some of these ideas. Buildings with living landscapes on their roofs were developed nearly 100 years ago (Hagenbeck 1909). More recent examples include the small cat grottoes at the Arizona Sonora Desert Museum (mid-1970s, United States) and the administration/education facilities and big cat exhibits at the Smithsonian National Zoological Park (mid-1980s). Extensive indoor "living walls" have been developed at Central Park Zoo (United States), Smithsonian National Zoological Park's Amazonian exhibit, and Denver Zoo. Outdoor living walls were developed at the New York Aquarium, Woodland Park Zoo's Northern Trail, Brookfield Zoo's Wolf Woods (United States), and the Bristol Zoo (United Kingdom). Zoos and aquariums are now poised to lead development of a new sustainable architecture based on humane and ecological principles.

Fig. 18.14. Zoos have a unique opportunity and responsibility to demonstrate sustainable designs. Could zoos design buildings that also provide habitats for wildlife, fix atmospheric carbon levels, produce oxygen and energy, and treat effluent as a tree does? (Drawing © J. Coe. Reprinted by permission.)

THE GREEN INSTITUTION

Campus ecology is a 20-year or even longer plan for sustainably rebuilding and operating zoological institutions that was embraced by the Denver Zoo. The U.S.-based Wildlife Conservation Society (WCS) also developed a green master plan to guide its future growth. Perth Zoo (Australia) established a Sustainability Management Policy (Perth Zoo 2005) to integrate green initiatives at all levels of operation and management.

Other zoos have begun to look at energy use on a campuswide basis. New York Aquarium (United States) utilizes hydrogen-fuel cell technology to supply up to one-fifth of its electricity load. Tama Zoological Park, Rosamond Gifford Zoo (Syracuse, New York), Denver Zoo, and the WCS are studying the feasibility of renewable energy sources, including the use of manure and other wastes from animal and food services, to generate energy. Zoo Heidelberg (Germany) and the City of Heidelberg are building and operating a biogas combined heat and power plant that also uses zoo animal and other organic waste (Energie-Cités 2005). Los Angeles Zoo (United States) benefits from a districtwide reclaimed water system.

The World Association of Zoos and Aquariums views sustainability as a core component of its world conservation mission (WAZA 2005).

GREEN FUTURE

Zoos and aquariums practicing and advocating sustainable environmental design provide positive demonstrations of wilderness preservation, regional resource collaboration, and urban reforestation for their millions of visitors. Green roofs and living walls can produce oxygen, collect rainwater, fix atmospheric carbon levels, and recycle wastes while creating habitats for humans and other animals. Zoos can realize Thayer's (1994, 317) vision of a "broadened sense of community including not only humans, but all life." Zoos can also advance global green design practice by following Kellert's (1999, 39) advice to elucidate "how, by adequately relating to natural processes and diversity in the built environment, we may achieve lives of meaning and satisfaction."

Zoos and aquariums worldwide must interpret green design in terms of their unique climates, cultures, plants, and animals, which will result in a rich diversity of new design directions.

EVALUATION

How well do zoo and aquarium exhibits serve their animals, visitors, and employees? And how well integrated are their multiple functions? In our experience, exhibit designers generally rely on their own inspiration, intuition, and unsophisticated evaluations to learn from their work and that of their colleagues. Reliable, valid, and integrated evaluations simply have not been available. Designers can access unrelated studies on subsets of design such as environmental enrichment, behavioral management, and exhibit interpretation. Yet despite the very substantial expenditures on immersion exhibits, to our knowledge there remains not a single integrated evaluation of immersion theory itself. Early evaluations attempted to reduce carefully choreographed, multidimensional immersion exhibit experiences to simple, preselected, 2-dimensional photographs or used what we consider substandard immersion exhibits for testing. We know of no studies that cross-reference benefits to viewers, animals, staff, and conservation action. Woodland Park Zoo (L. Sullivan, personal communication) is developing a Fully Integrated Program to integrate these primary exhibit functions in new projects, but as yet it has not evaluated its award-winning exhibits using these terms of reference.

We understand that a multi-institutional research project is now under way to explore the fundamental motivation of conservation actions by zoo visitors (J. Gwynne, personal communication). As designers, we enthusiastically await the results. But as of this date, we believe the lack of relevant, integrated evaluation is the single largest constraint to knowledgeable exhibit design.

BACK TO BASICS, BACK TO NATURE

Innovations may come from introspective analysis of the basic assumptions on which present zoos are based. Coe and Mendez (2005) point out that all zoos have evolved using a policy of animal containment and coercion. But what if a new zoo model emerged—they call it the "unzoo"—based on principles of animal attraction and reward? Other chapters of this volume demonstrate how behavioral conditioning, enrichment, and reward can be used not only to improve animal husbandry and well-being, but also to improve visitor encounters with animals. Could attraction and reward replace caging and fencing? Disney's Animal Kingdom used many of these techniques to manage an impressive variety of African hoofstock in its Kilimanjaro Safari, using few internal barriers. Use of the walk-through or drive-through model of confining visitors on trails, boardwalks, or canopy walkways or in vehicles within extensive multispecies enclosures can be easily expanded. This is especially true when displaying free-ranging, smaller native species (fig. 18.15). For example, the 3 Earth Sanctuary facilities (Victoria, Australia) have only a perimeter predator fence, and the Asa Wright Wildlife Sanctuary (Trinidad) has no fencing at all, yet visitors see abundant wildlife close at hand. New wildlife research tools like telemetry, night-vision goggles, "bat finders," and surveillance cameras can help enhance visitors' senses in sanctuaries and zoos.

The unzoo model is most applicable for animal species well adapted to local climate, but free-access shelters could extend the possibility of displaying a wide range of animals with minimum containment, maximum choice, and self-determination without coercion. This greatly reduces the need for traditional buildings and infrastructure, reducing the impact of human structures on visitor perception of nature and the environmental impact of zoo construction and operation. A major result of this approach would be a shift from capital-intensive facilities such as exhibit and holding buildings to labor-intensive programs, such as training and demonstrations, with a corresponding shift in business strategy.

Evolution toward the unzoo model, pressured by increasing difficulty in importing animals and increased zoo spe-

Fig. 18.15. Could zoos evolve into "unzoos," where animals are attracted and rewarded rather than constrained and coerced? (Photo simulation © Jon Coe Design, P/L. Reprinted by permission.)

cialization, could result in a regionalization of zoos. Tropical and subtropical zoos could specialize in the display and conservation of animals from similar biomes, while zoos in temperate climates could specialize in animals from these zones. All zoos should place greater emphasis on providing memorable encounters with native species, making them as entertaining as many better-known exotic animals. Expanding regional and global ecotourism would make *in situ* sanctuaries more available to animal lovers.

CONSERVATION INSPIRATION

If exhibits are a zoo's or aquarium's natural voice, what should that voice say to our millions of guests?

> The most important function of the 21st century zoo will be to inspire conservation action. Few other communication tools are as effective as well-done exhibits of living animals for creating powerful bonds between human and animal. The best exhibits will be those where the close-up potency of living animals connects visitors directly to field conservation action via inspiration messages. These must combine affective and cognitive elements based not just on designer's whim, but upon that which is proven to be relevant to the visitor. (J. Gwynne, personal communication)

CONSERVATION CONNECTIONS

The most effective projects are those that have a field component,
an exhibit component and an education component.
—D. Jensen (2003)

Exhibits at Woodland Park, Atlanta, Los Angeles, Louisville, and Philadelphia zoos and others have built exhibits mimicking imaginary *in situ* research and conservation projects; Bronx, Denver, Louisville, and Point Defiance zoos have raised considerable funds for conservation projects with donation machines in exhibits. Now there is a movement to dramatize connections to actual, specific *in situ* projects. Bronx Zoo's Congo exhibit raises over $1 million annually for WCS projects in the Congo region. (J. Gwynne, personal communication). Zoo Zürich's Masoala Rainforest exhibit helps fund Masoala National Park in Madagascar. Adelaide Zoo, Taman Safari Indonesia, and Ocean Park Zoo are presently arranging *in situ* conservation connections.

CONCLUSION

For zoo staffers dreaming of exhibit improvements and for professionally trained zoo design specialists, this is a great time to be active. As the range of information in this single volume alone shows, never before have so many advances occurred in so many related fields, offering unprecedented opportunities for synergy and innovation. Never before has there been greater opportunity and need for good design to integrate diverse opportunities and objectives.

The epicenter of zoo design is also shifting as information and expertise become globalized. Zoos in Europe, Australia, and New Zealand are now producing excellent exhibits supporting their long-standing conservation programs. Japan, long limited by tradition (Wako 1993), is producing world-class exhibits at Osaka Zoo. Asia and especially India and China are creating what may become the world's greatest market for zoos as well as a proportional need for conservation literacy and supportive action.

Zoo exhibits, in partnership with other programs, continue to evolve in new and existing directions. The question for the next worldwide generation of visionaries and designers will be how to respond to a culturally diverse global market while still advancing the well-being of wildlife *in situ* and *ex situ*.

APPENDIX 18.1

Glossary

A specialized exhibit vocabulary is emerging from the interaction of zoos, museums, and theme parks, and the entertainment and construction industries. This glossary is offered to help regularize meaning and improve the integration of ideas from these valuable traditions.

Content. Intended communication. Basically, this is what interpretive signs say. It is the cognitive information that the zoo or aquarium wants people to perceive, understand, and remember (Coe 1982).

Context. The exhibit viewers' perceptual surroundings. This is everything that exhibit viewers perceive consciously or unconsciously while experiencing an exhibit (Coe 1982).

Contextual exhibits. A museum term similar in meaning to *immersion exhibits*.

Exhibit. In educational discussion, the term often derives its meaning from its historic connection to museum exhibit design. Thus, it is used to describe a well-defined object, display, or group of displays.

Exhibit. In the context of immersion design, the term has a broader meaning, including the entire environmental surround. This could include everything from the surfacing underfoot, to the themed character interacting with guests, to vistas of distant landscape, and, of course, the animals being displayed.

Immersion exhibit. A shortened form of landscape immersion. This term could also apply to exhibits in cultural, agricultural, or other settings as well as natural landscapes.

Landscape immersion. Exhibit or experience: "Ideally the viewer should move through the characteristic landscape of the natural habitat zone seeing its sights and savoring its moods. Only then can we become aware that the landscape is also inhabited by animals separated by unseen barriers. The success of this landscape immersion depends entirely upon 2 factors: (1) the completeness and correctness with which the characteristic landscape is projected, and (2) the care and accuracy with which the viewpoints and views are located and composed, concealing barriers, enhancing perspectives, composing light and shadow and, most importantly, visually unifying animal space and visitor space" (Jones, Coe, and Paulson 1976, 44).

The term is developed from 2 definitions: *landscape*, an expanse of natural scenery; and *immersion*, to involve or engage deeply (*Webster's New Universal Unabridged Dictionary*, 2nd ed.).

Message. The actual communication received and remembered by zoo visitors. This may include the (cognitive) information, concepts, or ideas that the visitors glean from the actual interpretive information, filtered through the (affective) context of the setting and the distractions, prejudices, or attitudes of visitors themselves (Coe 1982). The message that counts most is the one the visitor remembers. Serrell (1996) emphasizes the importance of clearly and finitely defining the message as the first step in the exhibit design process. Since the message is communicated through the entire immersive environment, the entire team of designers, educators, and other stakeholders should participate in framing the intended message.

Naturalistic: "In accordance with or in imitation of nature" (*Webster's New Universal Unabridged Dictionary*, 2nd ed.).

The terms *naturalistic* and *immersion* are used interchangeably in general conversation about zoo exhibits. However, as designers we apply these terms differently, and find that confusion over specific means can lead to misunderstanding.

Immersion design theory emphasises the "in imitation of nature" part of the definition and calls for highly realistic simulations of nature. An example would be an artificial tree cast from a real tree.

Naturalistic design has come to signify design "in accordance with" or functioning like nature. An example would be a treelike structure built using manufactured logs and timbers.

Scenario. The outline for a proposed natural or cultural setting which carries out the intended theme; setting the scene. Examples include providing charred logs, exposed permafrost, and fast-moving braided streams, all to suggest the effects of fire, frost, and flood in shaping the boreal landscape and to provide the setting for encountering indigenous wildlife (as in the Northern Trail exhibit, Woodland Park Zoo).

Storyline. The narrative or pictorial sequence of active events or experiences envisioned in a themed setting. Storylines and storyboards, annotated sequential illustrations or computer-generated simulated walk-throughs, were long used in the motion picture industry and are now used in zoo design to visualize the intended visitor experience in detail.

Sustainable. The United Nations' World Commission on Environment and Development's definition in 1987 suggests that development is sustainable when it "meets the needs of the present without compromising the ability of future generations to meet their own needs" (quoted in Bruntland 1987).

Theme. The subject of the overall presentation or experience; the overall character-giving concept. Examples could include life with elephants in an Asian village (Melbourne Zoo); visit to a remote greater one-horned rhinoceros rescue center (proposed for Woodland Park Zoo); or visit to a gorilla research camp in West Africa (Zoo Atlanta).

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Part Five

Conservation and Research

Introduction

Devra G. Kleiman

This section focuses on conservation and research within the zoo community and the greater expansion and integration by zoos of their *in situ* and *ex situ* activities, starting with a useful and detailed analysis of the techniques currently being used by zoos to manage captive mammals demographically and genetically for the long term. Over the past decade, there has been an incredible increase in the sophistication with which professionals manage zoo populations, and in the degree of national, regional, and international cooperation. The zoo mission also is coming closer to being a real conservation mission, with zoos becoming ever more involved in reintroduction programs for captive-bred animals and even supporting considerable conservation research and field activities. Many institutions now partner with and provide support to protected areas (reserves and parks) within "Hotspots" (Conservation International) or "Ecoregions" (World Wildlife Fund) in habitats that are disappearing with human development and environmental degradation. Certainly, the essential role of research in the development of zoo *in situ* and *ex situ* programs continues.

The section starts with the longest chapter of the book, the detailed analysis of current approaches to genetic and demographic population management by Ballou et al. The length of this chapter is a testament to the advances in population management strategies. The authors first ask why we need and want to manage populations, and then provide the theoretical and practical basis for demographic and genetic management of zoo populations. Ballou et al. examine how we develop the goals and objectives for different species we wish to maintain, how we

Cheetah cubs at the Smithsonian's National Zoological Park, Washington, DC. Photography by Jessie Cohen, Smithsonian's National Zoological Park. Reprinted by permission.

evaluate status at any given time, and then how we go about constructing the animal-by-animal recommendations needed for species Masterplans.

Allard et al. look at how population management techniques have been applied to regional collection planning, an area of cooperative zoo activity that has expanded greatly since the first edition of this book. They examine the potential tension and conflict between regional collection planning and a single institution's needs. For both institutions and regions, each species' role must be defined—whether for exhibit, research, education, or conservation.

Carter and Kagan examine the perennial problem of dealing with individuals which are surplus to institutional needs or to the more broadly managed population. They summarize the traditional methods of managing surplus, e.g. selling animals to dealers. They suggest a paradigm shift, i.e. that zoos accept birth-to-death responsibility for all animals that they produce. To reduce the surplus problem, the authors recommend greater research into contraception and control of reproduction. They also plea for more high-quality off-exhibit space for surplus animals and the development of multizoo managed "retirement" facilities.

Earnhardt's chapter on reintroduction summarizes the costs and benefits of using captive-bred animals in reintroduction programs and how zoos have contributed to such programs. She discusses the genetic and demographic considerations in managing population growth when the animals being produced are targeted for reintroduction, and the use of computer models for planning. As with population management, strategies for harvesting animals from a captive population have become ever more sophisticated. Earnhardt ends with a discussion of the methods for, and benefits of, monitoring after release.

Zimmermann's chapter on zoo involvement in *in situ* conservation provides a summary of the change in the zoo community's attitude and behavior concerning the support of research and conservation in the field. Many zoo scientists and zoos now consider a portfolio of *in situ* activities as a prerequisite for a zoo to call itself a conservation organization. The limitations of *ex situ* conservation are obvious: zoos simply do not have the facilities and infrastructure to "save" many species in their institutions, especially large mammals. Captive breeding space is just too limited, and the costs of that space are very high. While many zoo professionals have believed that maintaining large mammals like elephants as "ambassadors" will change the attitudes and behavior of their visitors, there is little evidence that zoo visitors actually contribute to conservation or live more sustainably after seeing large, expensive installations with large, charismatic mammals. Zimmermann recommends that zoos contribute directly to *in situ* conservation, and summarizes the recent increases in just those types of contributions; she does, however, suggest that the percentage of most zoos' budgets that is spent on *in situ* research and conservation is extremely low, a comment also made by Maple and Bashaw in their research chapter and originally made by Kurt Benirschke in the first edition of this book.

Zimmermann sees an evolving path for zoo *in situ* conservation contributions: from starting out as a zoo that gives funds directly to a program in the field, to being a zoo that manages *in situ* conservation programs, to being a conservation organization that just happens to run a zoo, e.g. the Wildlife Conservation Society.

Maple and Bashaw analyze publications from zoo-based scientists in journals such as *Zoo Biology* and also look at zoo-based publications in the *Basic Biosis* database to chart the trends in zoo-based research since publication of the first edition of *Wild Mammals in Captivity.* As before, behavior is most strongly represented, and reproductive biology, genetics, and veterinary medicine are also prominent topics. New areas of research over the last decade include behavioral management and enrichment as well as conservation psychology. As previously, there is a strong bias toward the study of mammals. Maple and Bashaw argue that all zoos need to support research, either through hiring scientists and building dedicated facilities/departments or through collaborations with other zoos or universities. They also argue that zoo researchers need to publish more in the peer-reviewed literature, and that zoo research needs greater visibility, e.g. through the presentation of more awards to zoo-based scientists.

19

Demographic and Genetic Management of Captive Populations

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Laurie Bingaman Lackey, and Thomas J. Foose (deceased)

INTRODUCTION

The purpose of population management is to ensure that populations of species of our choosing are available, healthy, and viable for the foreseeable future. Thus, the contribution of zoos to *ex situ* conservation via captive breeding programs requires prudent population management planning. Population management does result in successful conservation. The rescue from extinction of species like the black-footed ferret, *Mustela nigripes*, California condor, *Gymnogyps californianus*, Guam rail, *Rallus owstoni*, Lord Howe Island woodhen, *Gallirallus sylvestris*, greater stick-nest rat, *Leporillus conditor*, and mala, *Lagorchestes hirsutus*, testifies to the potential of the international zoo community's response to the needs of species under the imminent threat of extinction. Successful reintroduction of captive-born individuals into the wild to reestablish natural free-ranging populations of golden lion tamarins, *Leontopithecus rosalia*, black-footed ferrets, Przewalski's horses, *Equus caballus przewalskii*, chuditchs, *Dasyurus geoffroyii*, and greater bilbies, *Macrotis lagotis*, is also a testament to the direct role of zoos in conservation. All these programs and more reflect the implementation of successful population management programs.

The World Zoo and Aquarium Conservation Strategy developed by the World Association of Zoos and Aquariums (WAZA 2005) recognizes this need and calls for increased attention to and implementation of animal management at the population level, and the establishment of truly viable populations. This is both a biological and an organizational challenge.

Some of the biological challenges are illustrated in figure 19.1, which shows a hypothetical, but not atypical, history of a population rescued by captive breeding. The original wild population may have declined for any number of reasons—habitat loss, competition with invasive species, or disease. Some or all of the few remaining wild-born individuals may be captured to establish the captive breeding program in the founding phase. If these founders are the last remaining individuals of the species, they represent the total genetic future of their species (e.g. black-footed ferrets). Unfortunately, captive breeding programs are often initiated with few founders, compromising the genetic health of the program from the start. Basic husbandry knowledge may also be lacking, so the population initially remains small, further compromising the genetic health of the population. Lack of reproduction may even cause the population to go extinct (e.g. several species of Hawaiian birds). As knowledge is gained, reproduction becomes more reliable, generating the population's growth phase. Population managers will set a target size for the population based on resources available, the genetic and demographic status of the population, and the captive breeding needs of similar species competing for limited captive resources. The population will be maintained during the management phase at zero population growth to establish a stable population. And for certain populations, reintroduction of individuals into the wild may be an option (see Earnhardt, chap. 22, this volume).

The overall demographic goal for captive populations is to increase the population, as rapidly as possible, to a sufficient size to avoid extinction due to accidental or chance events, and then to maintain that population with an age and sex structure that promotes reliable reproduction when needed (and possible surplus reproduction for a reintroduction program). The demographic challenges here are to maintain stable populations that neither overshoot the capacity available, nor leave zoos with empty exhibits.

The genetic goal for these populations is to retain the founders' genetic diversity, as unchanged as possible over time, so that the population can serve as a genetic reservoir for the species (from which genetic diversity may be reintroduced into the wild). Achieving this goal means confronting the challenges of loss of genetic diversity, inbreeding and inbreeding depression, and adaptation to captivity (Bryant and Reed 1999; Frankham, Ballou, and Briscoe 2002). Management strategies attempt, as much as possible, to retain every aspect of the genetic diversity of the founders over time: essentially stopping evolution in the captive population.

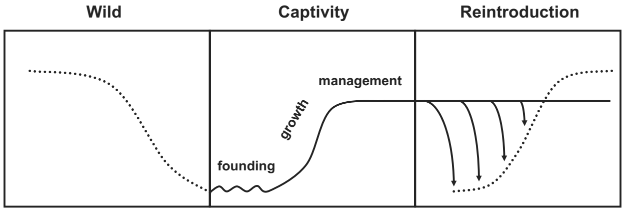


Fig. 19.1. A hypothetical history of the events in a captive population.

There are organizational challenges involved in managing groups of individual zoo collections as cross-institutional biological populations. The international zoo community has responded to this additional responsibility by forming regional zoo associations and programs to organize and coordinate cooperative population management efforts, e.g. Species Survival Plan (SSP) of the Association of Zoos and Aquariums (AZA, based in the United States and Canada); European Endangered species Programme (EEP) of the European Association of Zoos and Aquaria (EAZA); and the Australasian Species Management Program (ASMP) of the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA) (Shoemaker and Flesness 1991; see Allard et al., chap. 20, this volume; Bingaman Lackey, appendix 3, this volume). However, plans based on the science of population management do not always coincide with desires of individual institutions. More zoos may want to breed than is needed for zero population growth during the management phase. Ideal genetic management recommendations to transfer a particular animal to another zoo may conflict with the holding zoo's desire to keep that individual. Managers of captive breeding populations are continually struggling to balance the science with institutional wishes.

This chapter does not address the sometimes competing needs of population management versus institutional wishes. Rather, it presents and outlines the basic principles, concepts, and techniques that are involved in managing captive populations, concentrating on those aspects critical to the long-term maintenance of genetic diversity and demographic security (Ballou and Foose 1994). The chapter begins with the basic data needed for a management plan, followed by a description of the overall purpose and goals of the captive population. We present the demographic and genetic characteristics that are used to define the current status of a population, followed by a description of the basic management strategies that are applied to population management and a description of the more detailed analyses that form the basis of the individual-by-individual animal recommendations—the heart of any population management plan. We end by addressing particularly difficult issues (how to proceed when data are poor and how to manage groups of individuals where individual identity is not known).

THE VALUE OF POPULATION MANAGEMENT

Managing captive populations is time consuming (maintaining the data, making recommendations), costly (shipping animals), and sometimes risky (disease transfer between institutions, stress on animals). However, its benefits are clear, and are delineated in the rest of this section.

INCREASING VALUE TO CONSERVATION

Intensive management can help populations to retain the genetic characteristics of wild counterparts. This increases their value as genetic reservoirs for use in reintroduction, should this be needed.

ENSURING THE AVAILABILITY OF CAPTIVE ANIMALS

Many captive populations that were once large and well distributed have subsequently crashed, particularly populations of small mammals and birds (Amori and Gippoliti 2003; fig. 19.2). Although there are many reasons why populations crash, many do so because individual collections are not managed as an integrated population. The result is not having specimens available when desired. For example, when the giraffe, *Giraffa camelopardalis*, SSP was changed to a Population Management Plan (PMP) in 2004, recommendations became voluntary rather than mandatory (PMP recommendations are voluntary, as opposed to recommendations made in a SSP). Over the next 2 years, 35 giraffes, representing over half the giraffes shipped in North America, were transferred out of the AZA population. This resulted in a waiting list of 17 institutions wanting roughly 50 giraffes; an additional 6 institutions wishing to build and stock new giraffe exhibits found few available.

IMPROVING ANIMAL WELFARE

Population management attempts to avoid inbreeding, as inbred animals often suffer from a vast assortment of ailments. These include reduced longevity, inanition (failure to thrive), metabolic diseases, morphological deformities, abnormal birth weights and growth, organ (eye, brain, spleen, adrenal gland, thyroid) malformations, impaired reproductive traits,

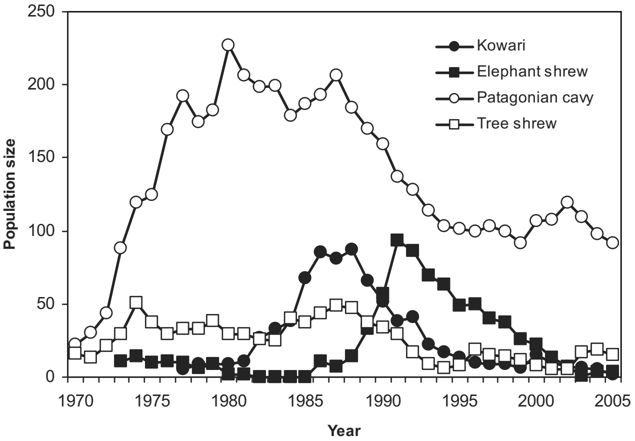


Fig. 19.2. Captive population crashes and declines in 4 small mammal species: kowari, *Dasyuroides byrnei*, elephant shrew, *Macroscelides proboscideus*, Patagonian cavy, *Dolichotis patagonum*, and tree shrew, *Tupaia glis*.

modified temperament, immune diseases, reduced temperature tolerances, and increased susceptibility to stress (Wright 1977; Frankham, Ballou, and Briscoe 2002). In theory, any trait partially or wholly determined by genetics is a candidate for being degraded by inbreeding (see below). Though considerations of animal welfare alone should be enough to encourage inbreeding avoidance, there is also the increased cost of treating such a variety of ailments. For example, Willis (personal communication) found that inbred prairie chickens, *Tympanuchus cupido attwateri*, at the Minnesota Zoo received veterinary attention significantly more often than non-inbred chickens.

VERIFYING TAXONOMIC ORIGIN

Because captive breeding plans require effort in ensuring accurate studbook data, working within a population management plan increases the chances that zoos actually receive what they ask for. When the giraffe SSP program was initiated in the early 1990s, a studbook was compiled and for the first time a complete pedigree was available. Many curators were unpleasantly surprised to discover that about 30% of living giraffes were subspecific hybrids or had minimally traceable pedigrees. Furthermore, between 1979 and 2000, 27 giraffes were purchased by Japanese zoos from U.S. zoos. Having assumed these were reticulated giraffe, *G. c. reticulata*, they were surprised to discover, on consulting the studbook after the animals had already been shipped, that 13 of them were subspecific hybrids and therefore useless to their breeding programs. Failure to examine the studbook cost these zoos up to $50,000 for each giraffe.

MANAGING ZOO SPACE EFFICIENTLY

Population management is not only for species that we want to maintain over the long term, but also for controlling populations of common species that compete for space with more endangered species. Examples among AZA populations include limiting population growth in plains zebra, *Equus burchellii quagga*, and warthog, *Phacochoerus africanus*, to increase available space for Grevy's zebra, *E. grevyi*, and Red River hog, *Potamochoerus porcus*, respectively.

BUFFERING AGAINST UNEXPECTED CHANGES IN REGULATIONS

Unexpected and unplanned-for regulations that limit imports can result in populations becoming closed, and, unless managed, vulnerable to extinction. For example, Australia suspended all artiodactyl imports in 2001 due to disease concerns, which so far has resulted in demographic extinction of the Australian populations of greater kudu, *Tragelaphus strepsiceros*, sable antelope, *Hippotragus niger*, and collared peccaries, *Pecari tajacu*, with other species in decline. Only demographically robust, cooperatively managed populations are likely to survive these restrictions. Similar effects on native taxa can result from changes in policy/attitude toward wild collection or retention in captivity of injured wildlife. Zoos need to be able to weather these shifts in policies and regulations.

REDUCING COLLECTION FROM THE WILD AND SHIPPING COSTS

Programs are designed to reduce the frequency and distance of shipping and/or to reduce the rate of wild collection, thus saving time and costs of collecting trips, permit applications, and international transaction arrangements.

DATA FOR POPULATION MANAGEMENT

The most important task in the development of a captive breeding plan is compiling the basic data required for population analysis and management. Data may already have been compiled in a variety of different forms if a captive population exists or has existed in the past. The best source of compiled data is a studbook, which is a chronology of a captive population listing vital information on animal identities, sex, parentage, and birth and death dates, as well as information on animal movements between institutions (Glatston 1986; Shoemaker and Flesness 1996; see also Bingaman Lackey, appendix 3, this volume). Studbooks serve as excellent data sources because studbook keepers validate and edit data to enhance quality. Currently there are over 1150 regional and 145 international studbooks (ISIS 2007), most of which are available as computerized databases on the ISIS/WAZA Studbook Library CD-ROM distributed annually (ISIS/WAZA 2004).

If a studbook does not exist or is out of date, one must be compiled from original sources. Historical and current data should be collected from all institutions that have had or currently have individuals of interest. Historical data are critical for determining the relationships between living animals and estimating important population parameters.

Potential sources of data are as follows.

INTERNATIONAL SPECIES INFORMATION SYSTEM (ISIS)

ISIS is a computerized database containing information on animal identities, birth and death dates, genealogies, and movements (Flesness 2003; ISIS 2007; Bingaman Lackey, appendix 3, this volume). ISIS collects data from over 700 institutions from 70-plus countries worldwide and is the best starting point for compiling population data if no studbook is available. ISIS is currently developing a single, Web-based global Zoological Information Management System (Cohn 2006; ZIMS 2007; ISIS 2007). This will provide, for the first time, a single unbroken record of an animal's significant events throughout its life. ZIMS will be replacing the current ISIS animal record-keeping software currently being used by most zoos worldwide (ARKS, SPARKS, MedARKS).

INTERNATIONAL ZOO YEARBOOK (*IZY*)

Published yearly by the Zoological Society of London, *IZY* provides an annual list of birds, mammals, reptiles, amphibians, and fishes bred in captivity from 1961 until 1998. Although only numbers and locations are presented, these annual listings are useful for identifying institutions that once held specimens of a particular taxon.

IN-HOUSE INSTITUTIONAL RECORDS

In-house inventory records are the primary source of data. Once institutions that have had or currently have specimens of interest are identified, they can be contacted for information on the history, status, and details of their collection.

The basic data required for each animal for population analysis and management are as follows:

- individual identification: a simple numeric lifetime identity (e.g. studbook number): to achieve this identification, it may be necessary to link a series of different local institutional ID numbers assigned to an animal as it has moved among institutions
- sex
- birth date and location
- death date and location (it is vital to record stillbirths and aborted fetuses)
- parentage
- rearing type

If an individual is wild-caught:

- date and site of capture
- estimated age at time of capture
- possible relationship to other wild-caught animals (e.g. several animals captured from a nest or herd)
- date and institution when animal entered captivity
- date animal left captivity or was lost to follow-up (e.g. reintroduced into the wild, escaped, sent to an animal dealer and no longer tracked)
- institutions where it has been, with dates of transfers and the local ID at each institution
- information on circumstances and cause of death
- reproductive condition (e.g. castrated male, postreproductive female, with relevant dates)
- group compositions (which animals are housed together and during what time period)
- reproductive opportunities (whether animal was given opportunities to breed, and when)
- information on past breeding experience (e.g. proven breeder)
- tattoo or other permanent identification marks (e.g. transponder number)
- carcass disposition and tracer (e.g. "Sent to University of Kansas Museum. #12345")
- miscellaneous comments (e.g. unusual behavior or phenotype) that might affect its reproduction, social behavior, and husbandry

Missing and incomplete information is a characteristic of any kind of data, and animal records data are no different:

1. When dealing with unknown or missing data, as much information should be recorded as possible. However, data should never be invented to fill in missing or incomplete information.

2. Uncertain parentage is a common problem, particularly in herd situations. All potential parents should be recorded with, if possible, their likelihood of being the parent (e.g. based on behavioral data).

3. Records must correctly reflect the extent of uncertainty in an animal's history. While assumptions often need to be made when analyzing a population in preparation for making management recommendations, the practice is to create an "analytical" version of the studbook, where documented assumptions replace missing or unknown data. These assumptions, however, should never be transferred to the official "true" studbook.

4. The fundamental data needed for demographic analysis are birth dates, death dates, and dates of reproduction. Uncertainty of any of these events, especially birth dates and death dates, can have significant effects on the demographic analyses. Any individuals with unknown dates (especially unknown birth dates) are generally excluded from analyses (while some software allows them to be included, but in proportion to rates from known-aged animals). Informed estimates should be recorded wherever possible.

5. The fundamental information needed for genetic analyses is parentage. The complete set of parentage information for a population constitutes the population's pedigree. Captive pedigrees are plagued with unknown or missing parentage. Pedigrees with many unknowns (more than 15% is a rough threshold) can make pedigree analyses useless. Significant efforts go into trying to resolve unknown parentages or making assumptions so that genetic analyses can be completed; these strategies are discussed in their own section below.

Most analyses require that the data be computerized for easy access and manipulation. Standard formats for pedigree data have been developed (Shoemaker and Flesness 1996), and a number of computerized studbook management and analysis software packages are currently available, or soon will be, including the Single Population Analysis and Record Keeping System (SPARKS: ISIS 2004a), PopLink (Faust, Bergstrom, and Thompson 2006), and ZIMS (ZIMS 2007) (see appendix 19.1 for more details).

MAINTAINING VIABLE POPULATIONS: DEMOGRAPHY

The purpose of demographic management depends on the goals of the population. While for most populations of conservation concern, the goal is to establish a stable population of sufficient size to mitigate risks of extinction, for other populations the goal might be to reduce the population to extinction at a managed and predictable rate. The major demographic risks that populations face are small population dynamics, unstable age structures, and unreliable reproduction.

SMALL POPULATION DYNAMICS

Small populations are more vulnerable to extinction than large populations, not just because they are smaller, but because synergistic interactions in their dynamics can lead to an "extinction vortex" (Gilpin and Soulé 1986; Shaffer 1987; Lande 1988; Vucetich et al. 2000; Lande, Engen, and Saether 2003; Drake and Lodge 2004; Fagan and Holmes 2006). One of the main sources of demographic vulnerability for small populations is demographic stochasticity—the random variation in reproduction, mortality, and offspring sex ratio at the individual level. This variability is magnified when population size is small, resulting in fluctuations in a population's vital rates (mortality and fecundity) and sex ratios (Lande 1988; Lacy 2000a; Lande, Engen, and Saether 2003).

In addition to the effects of demographic stochasticity, small captive populations may become demographically vulnerable because of inbreeding depression, which can decrease survival and reproduction (see below). Although there is no rigid cutoff for when a population becomes susceptible to these types of dynamics, general estimates range from 20 to 100 individuals in the population or in a particular life stage (Goodman 1987; Lande 1988; Lacy 2000a; Morris and Doak 2002; Lande, Engen, and Saether 2003) or an effective population size (see below) of fewer than 100 (Keller and Waller, 2002).

UNSTABLE AGE/SEX STRUCTURES

Although there is no strict definition for what makes a population's age structure unstable, there are some situations that can be harbingers of demographic problems, including the following:

- Large discrepancies in sex ratio of age classes or life history stages (e.g. pairing all reproductive-aged females and males) for monogamous species: these uneven sex ratios may result in difficulty in forming monogamous pairs for breeding or social housing.
- Inappropriate sex ratio for polygynous or group-housed species: if sex ratio at birth is equal but management is in polygynous social groups, the excess individuals of one sex must be managed as single-sex groups or solitary individuals (e.g. gorillas [*Gorilla gorilla*], African and Asian elephants [*Loxodonta africana* and *Elephas maximus*], and hoofstock species such as wildebeest [*Connochaetes*], waterbucks [*Kobus*], and gazelles [*Gazella*]) and planned for in long-term space requirements. It is often important, however, to manage these excess individuals as potential future breeders in the population rather than export, neuter, or otherwise remove them from the breeding pool; in the future, they may become important genetically or demographically and be essential to maintaining population stability.
- Few individuals in the youngest age classes: as those individuals become reproductively mature, there may not be enough individuals to form breeding pairs to sustain the population.
- Too few individuals in the reproductive age classes: this leads to relatively few births, which decreases population size; this factor should be taken into consideration in harvesting animals from captive populations for release.
- Large numbers of individuals in the oldest age classes: if these individuals are close to the maximum longevity of the species, managers may want to anticipate their death in the near future and the resulting need to fill empty exhibit spaces.

Managers can detect many of these problems using demographic models that project future population growth (see below).

UNRELIABLE REPRODUCTION

Understanding the reproductive biology of captive species and the husbandry necessary to produce offspring when desired is essential to good population management. When populations are in their initial growth phase, reproduction should be spread across participating institutions rather than focused at a few institutions, to mitigate the risk of wiping out a population's breeding potential if an essential institution experiences a random catastrophe (e.g. disease, natural disaster). When a population reaches the phase when it needs to be maintained at a certain size, the number of allowable breedings will be severely limited. For example, in a tiger, *Panthera tigris*, population at capacity, a zoo might get only one breeding recommendation in 12–15 years; this interval may mean that staff at that zoo does not have relevant breeding management experience. Managers need to think creatively about sharing the collective experiences of those working in the wider managed program to ensure dissemination of valuable husbandry information. Many captive breeding programs have husbandry manuals (and/or other management protocols). For example, the Tiger SSP published a husbandry manual in 1994, which includes not only information about husbandry and veterinary care, but also details on how to introduce (breed) and raise tigers. This manual has been translated into 5 languages (Russian, Chinese, Thai, Vietnamese, and Indonesian) and distributed among zoos in all tiger-range countries.

In addition, managers may need to be careful about ensuring that individual females remain viable, especially if breeding is being delayed because the population is being maintained at zero population growth. There are suggestions that in several species females may need to breed early in their reproductive life span to remain viable breeders in the future (e.g. elephants and rhinoceroses [*Rhinoceros*, *Ceratotherium*, *Dicerorhinus*, *Diceros*], Hermes, Hildebrandt, and Göritz 2004; Hildebrandt et al. 2006; Australian dasyurids such as Tasmanian devils [*Sarcophilus harrisii*], C. Lees, personal communication; lions [*Panthera leo*] [B. Wiese, personal communication]). Although it is not clear whether such examples are exceptions or the rule, individual program managers and scientific advisors should carefully consider whether species may be susceptible to such an effect. Managers should also be careful that if contraceptives are used to limit reproduction, females can be reliably returned to reproduction once contraceptives are removed; the North American population of Goeldi's monkey, *Callimico goeldii*, experienced a serious demographic crash that threatened long-term viability when contraception, believed to be reversible, permanently sterilized females.

MAINTAINING VIABLE POPULATIONS: GENETICS

Maintaining genetic diversity and preserving demographic security are the primary population management goals for long-term conservation. Management for genetic diversity minimizes change in the genetic constitution of the population while in captivity (fig. 19.1) so that if and when the opportunity arises for animals to be reintroduced into the wild, they will represent, as closely as possible, the genetic characteristics of the original founders used to establish the captive population (Lacy et al. 1995). Genetic variation is also the basis for adaptive evolution and must be retained to maintain the population's potential to adapt to environmental change. Furthermore, a large number of studies indicate a general, although not universal, positive relationship between genetic variation and both individual and population fitness (Hedrick et al. 1986; Allendorf and Leary 1986; Vrijenhoek 1994; Frankham 1995b; Saccheri et al. 1998). In addition, most studies on the effects of inbreeding, in both captive and wild populations, have documented deleterious effects (Ralls, Brugger, and Ballou 1979; Ralls, Ballou, and Templeton 1988; Lacy 1997; Crnokrak and Roff 1999; Keller and Waller 2002). Finally, maintaining genetic diversity preserves future management options, a strategy that will become increasingly important as knowledge of the genetic and demographic requirements of wild and captive populations expands.

WHAT IS GENETIC DIVERSITY?

Genetic diversity comes in many forms. It can be haploid (DNA of the mitochondria), diploid, or even polyploid. Genetic traits can be based on the alleles at a single locus or many dozens of loci. Not surprisingly, then, there are several different terms and different types of genetic variation (refer to Frankham, Ballou, and Briscoe 2002 for more details). Two common terms are allelic diversity and heterozygosity. Allelic diversity refers to the number of different alleles at any given locus in the population. Heterozygosity is the percentage of loci that is heterozygous in a population or individual (ibid.). A heterozygous locus is one in which the 2 alleles (one inherited from the dam, the other from the sire) are different (e.g. *Aa* as opposed to *AA* or *aa*). When the alleles are the same, the locus is said to be homozygous. Genetic diversity can be measured in both individuals and populations. Both allelic diversity and heterozygosity are desirable. Allelic diversity is important for a population's long-term ability to adapt, while heterozygosity is important for more immediate individual health (Allendorf 1986).

Both allelic diversity and heterozygosity are lost in small populations (populations with individuals numbering fewer than several hundred) through the process of genetic drift. Alleles are passed randomly from parents to offspring (each parent has a 50% chance of contributing either of its alleles at each locus to an offspring), and thus the alleles the offspring receive across all loci represent only a sample of the allelic variation of the parental generation. When only a few offspring are produced, the genetic diversity of the offspring may be unrepresentative of the genetic diversity present in the parents. By chance alone, some alleles may not be passed to the offspring; others may increase or decrease in frequency. These changes in the number and frequency of alleles, as well as changes in heterozygosity due to this sampling process, are termed genetic drift.

Another term, *quantitative variation*, refers to those traits of high concern that are related to the overall fitness of individuals (e.g. reproductive success and survival rates, litter size). Rather than being determined by a single locus, these traits involve many loci. Quantitative traits vary among individuals due to genetic differences and environmental differences. The most important genetic component of the variation in quantitative traits is called additive genetic variation (Frankham, Ballou, and Briscoe 2002). However, it is difficult to determine how much of the differences observed in a quantitative trait are due to additive genetic variation versus environmental effects without extensive research and experimentation (ibid., 2002). Conveniently, overall heterozygosity and additive quantitative variation are lost at approximately the same rate. Consequently, management strategies based on maintenance of heterozygosity will generally promote the maintenance of additive genetic diversity as well (Lande and Barrowclough 1987).

Genetic traits can also be selectively beneficial, deleterious, or neutral. Thus, selection can potentially retard or accelerate loss of genetic diversity. Little is known about the role selection plays in captive populations, although it is undoubtedly important and has been shown to be a significant factor (Frankham and Loebel 1992). Variation can be selective (influenced by selection pressures) or selectively neutral (influenced not by selection pressures but by the random process of genetic drift) (see Lande and Barrowclough 1987; Lacy et al. 1995 for further discussions of this issue).

Genetic management needs to focus on maintaining all these levels of genetic variation—diversity at the single locus as well as diversity for quantitative traits, loci that are under selection and those that are not (but may be in the future). Average heterozygosity appears to be the best single measure of diversity that encompasses most of this variation. It is often used as an overall indicator of genetic diversity, since it lends itself well to theoretical considerations and usually provides a simple, accurate indicator of the loss of allelic diversity (Allendorf 1986). The genetic goals of most captive breeding programs are currently based on maintaining overall levels of average heterozygosity.

The primary threat to the genetic health of a population is the loss of genetic diversity. This is a function of population size (actually, effective population size; see below) and time. In general, the smaller the population, the faster the loss; and the longer the period of time, the greater the total loss (fig. 19.3). Therefore, those developing breeding programs to conserve genetic diversity must consider the questions, how much genetic diversity is required? and how long should it be maintained? (see Demographic Goal section below).

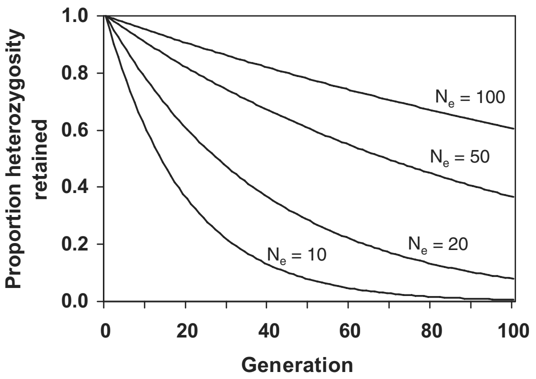


Fig. 19.3. Proportion of original heterozygosity from the source population retained over 100 generations for effective population sizes (N_e) ranging from 10 to 100.

MEASURING GENETIC DIVERSITY

Genetic variation is typically measured by collecting a sample of DNA from an organism (from blood, tissues, hair, feathers, bones, feces, etc.) and, using one of a variety of molecular techniques that are available, measuring the frequency of alleles or the frequency of heterozygotes for a set of loci (see Schlötterer 2004 for a comprehensive review of techniques). Common techniques used at the time of publishing include analyzing microsatellites, mitochondrial DNA haplotypes, and even exact sequences of genes.

Most of these techniques have in common the ability to identify genetic differences among individuals and provide information about allele diversity and heterozygosity. Changes in diversity over time can be measured. In an ideal world, molecular techniques could be used to identify the genetic diversity of the founders and, through continued monitoring of individuals over generations, guide a management program that maximizes retention of all the founders' genetic diversity.

Unfortunately, molecular analyses that measure diversity at the individual level across the entire genome do not (yet) exist. Even the most extensive studies are able to sample only several score of loci among the many tens of thousands of genes that make up an animal's genome. Managing based on the diversity of only a few loci will not achieve the goal of genomewide diversity, as it will tend to result in populations with high diversity at the monitored loci, but loss of diversity at all others (Slate et al. 2004; Fernandez et al. 2005).

However, managing genetic diversity at the whole-genome level can be achieved using pedigrees. When pedigrees are known, calculating kinships among individuals and inbreeding coefficients gives us genomewide estimated or average levels of diversity in individuals relative to the source population. Studies show that genetic management based on pedigree estimates of genetic diversity performs better at maintaining genetic diversity than molecular-based methods (e.g. Fernandez et al. 2005). The primary difference between molecular- and pedigree-based methods is that molecular methods provide empirical estimates of absolute or real levels of diversity of only a few loci, while pedigree-based methods provide a statistical measure of average genomewide diversity, but relative to the source population as opposed to absolute levels of diversity. Since an overall goal of management programs is to preserve the genetic diversity of the source population, the pedigree-based method works very well.

DEFINING A PURPOSE, GOALS, AND TARGETS FOR POPULATION MANAGEMENT

One of the most important steps in population management is to define the reasons why a particular species needs a captive breeding program. The goals of captive programs can be described at 3 levels. At the highest level, the program will have broad, qualitative goals that define the purpose of applying management, such as sustaining a population to meet zoo exhibition needs or generating a sufficient number of animals for release into the wild. These are referred to here as the program's *purpose*. At the second level are the population *goals*, which translate program purpose into quantifiable genetic and demographic measures that answer the questions *how much* (genetic diversity), *how many* (animals), and *for how long*. These are the characteristics of the population that will determine whether the program achieves its purpose. At the third level are a series of targets for those program parameters directly influenced by day-to-day or year-by-year program management of individual animals and which, over time, will determine whether population goals are met. These might include targets for maximum level of inbreeding, annual birth rate, effective population size, rate of input of new founders, and generation length (all are described in detail elsewhere in this chapter). These targets interact closely with each other such that changes in performance of one can often be compensated for by careful management of another. As a result, they are the most dynamic of the 3 levels.

DETERMINING A POPULATION'S PURPOSE

Populations in captivity can serve a number of purposes. Different purposes lead to different management needs, different levels of management intensity, and different goals and targets. Populations that are to be reintroduced soon after a captive colony is established will require less concern about long-term maintenance of genetic diversity than populations destined to remain in captivity for many generations. Similarly, populations primarily managed for zoo display will need less ambitious genetic management, possibly reflecting a need to manage average inbreeding levels only rather than maintain evolutionary potential. On the other hand, a species that is extinct in the wild and exists only in captivity will require long-term intensive genetic and demographic management.

Before a program's purpose can be determined, analyses must be conducted to examine the potential of the population to serve that purpose, e.g. a detailed analysis of the population's current demographic and genetic status. The status will determine whether the population in its current state can meet the proposed purpose and if not, what potential there is for bringing it closer to what is required. For example, a population that currently retains very little gene diversity may not be a useful starting point for a long-term conservation insurance program unless additional founders can be acquired. Similarly, a highly inbred population founded on only 4 individuals may not be a suitable source of animals for restocking a wild area.

ZooRisk (Earnhardt et al. 2005) is a software program that uses the current demographic and genetic structure of a population along with historic fecundity and mortality rates to model and categorize a population's viability in captivity stochastically. This categorization is based on (1) the population's probability of extinction; (2) the distribution of breeding-age groups (e.g. determining whether the population's reproductive stock is limited to only a few institutions); (3) current number of breeding-aged animals (ensuring that there are enough potential pairs); (4) reproduction in the last generation (determining whether there is historic breeding success); and (5) the starting and/or projected level of gene diversity. This multifaceted approach to evaluating viability helps identify the genetic, demographic, and management factors that may be increasing the risk to the population, and is very useful in helping managers evaluate whether a population can meet its intended purpose.

In addition to population characteristics, there are some practical constraints that have an impact on a population's potential to meet its goals. For example, is there sufficient husbandry expertise and adequate cooperation from studbook keepers, program coordinators, and holding institutions to meet a program's proposed purpose? Is there sufficient zoo space available? Consideration must be given to the needs of other taxa competing for similar zoo resources. Frameworks for prioritizing the allocation of zoo space at regional and sometimes global levels have been developed around the world as regional collection plans (see Allard et al., chap. 20, this volume).

Based on an analysis of the current status, practical considerations, and availability of resources, it may be necessary to modify a program's purpose. Determining a population's purpose may be an iterative process. For example, there simply may not be enough space or husbandry expertise to develop a reintroduction program, and the purpose might change to holding the population in zoos for a longer time period with the hope of acquiring additional founders and gaining husbandry experience.

SETTING GENETIC GOALS

Setting genetic goals essentially asks *how much*, *for how long*, and *how many*. The time scale for management programs will vary. Some species may need only the temporary short-term support of a captive population before they can be returned to the wild. However, for many if not most species, captive populations will have to be maintained for the long term, often over hundreds of years.

For these populations, a crude but general strategy is to preserve 90% of the source population's heterozygosity over a period of 200 years (Soulé et al. 1986). This 90%/200-year rule originated from considerations of how long human population growth and development will continue to reduce wildlife habitat, estimated at between 500 and 1000 years. However, Soulé et al. (ibid.) observed that some stabilization of human population growth is expected in the next 150 to 200 years, and concluded that 200 years would be a reasonable time frame for management of captive populations. The recommendation to retain 90% of the original heterozygosity was based on the authors' consensus that the 10% loss "represents, intuitively, the zone between a potentially damaging and a tolerable loss of heterozygosity" (ibid., p. 107). More recently, targets for population size have been formulated in terms of 100 rather than 200 years, since this results in smaller, more realistic population sizes (Foose et al. 1995). Maintaining 90% of the original heterozygosity for 100 years is the starting point advocated here for populations that are without more specific guiding influences.

Once a genetic goal has been selected, then the number of animals needed to achieve that goal can be calculated (Soulé et al. 1986) using PM2000 (Pollak, Lacy, and Ballou 2007), given the population's potential growth rate, effective size, current level of gene diversity, and generation time. Thus, a genetic goal can be directly translated into a demographic goal to answer the demographic question of *how many*.

SETTING DEMOGRAPHIC GOALS

Small populations are subject to demographic as well as genetic problems, and similar questions about demographic security should be considered in establishing goals for captive populations, i.e. *how many* and *for how long*. Risks of demographic problems, like genetic risks, are functions of population size and time; the smaller the population and the longer the time period of management, the greater the risks. The relevant question then is, what is the probability of a population surviving (i.e. not going extinct) for a specified period of time? Or, in other words, what population size is necessary to achieve a high probability (e.g. 95%) of survival over a long time period (e.g. 100 years) (Shaffer 1987)? Or, alternatively, for common display species, what rates of supplementation will confer a 95% probability of persistence for a population at or above the size needed to meet regional exhibit needs? In most cases, captive populations large enough to achieve standard genetic goals will also be large enough to ensure high survival probability over the time period of concern. ZooRisk can help evaluate if this is true.

SETTING TARGETS

Analysis programs such as PM2000 (Pollak, Lacy, and Ballou 2007) and ZooRisk (Earnhardt et al. 2005) convert the genetic and demographic goals to specific targets. They are also often used to explore what combination of management actions and targets would be needed to ensure that the population meets its goals or, conversely, what goals could be met using the population under consideration, within the range of possible management actions. Typically, the first target set is the target for population size. The Goals module in PM2000 allows managers to determine what population size is needed to reach the genetic goals set earlier, which will depend on the population's generation length, effective population size, current population size, population growth rate, founder supplementation rate, and captive carrying capacity—all of which can be influenced directly through management.

Once a specific target population size is set, then a decision can be made about whether the population needs to grow, shrink (and how fast), or remain the same size in order to meet that target. This decision will determine the number of births needed (or the number of animals that need to be removed from the population) to meet the desired growth rate (or to meet zero population growth).

With a realistic set of initial targets for key program parameters established, and population goals and program purpose refined as appropriate, a more detailed management strategy can be drawn up. Program performance should be evaluated regularly against both population goals and parameter targets, and adjustments made as necessary. Through these iterative steps, program management can continue to adapt to population and program needs.

Listed below are a number of scenarios describing programs with different purposes, with examples of the kinds of goals and targets that might be established for each (Lees and Wilcken 2002; AZA 2007). Goals and targets need to reflect realistic benchmarks for the specific populations being managed and hence will vary between different programs and regions.

1. Common display species, species for education and research

   Characteristics: Species is not threatened in the wild and is periodically available to zoos through importation, wild collection, or rehabilitation centers. Breeding is reliable and consistent. Populations that exist in zoos for research or education purposes would also fit into this program category, many having relatively short-term goals with little or no need for genetic and demographic management.

   Program purpose: To sustain a healthy population able to meet zoo display needs.

   Management strategy: Maintain a demographically stable population at the size required without generating unwanted surplus. Minimize inbreeding where possible. Monitor status of supply and intensify management as needed.

   Example population goals: Maintain population size at 50 for 25 years.

   Example targets: Maintain inbreeding below $f = 0.25$; maintain breeding rate at approximately 8 births per year for the next 5 years.

2. Endangered species in captivity for long-term conservation

   Characteristics: Captive population that is closed or has few new founders available. Breeding is reliable and consistent.

   Program purpose: To maintain a long-term viable population and preserve genetic diversity.

   Management strategy: Maximize retention of genetic diversity (using mean kinship values to select optimal pairings) and maintain a demographically stable population compatible with the limits of the captive environment's carrying capacity.

   Example of population goals: Focus on maintaining genetic diversity and program duration. Usual goals would be to maintain 90% of wild-source heterozygosity for 100 years.

   Example targets: Maintain population at 250; produce 30 births next year; raise first age of breeding to 7 years in females to extend generation length; raise N_e/N ratio to 0.4 by increasing ratio of males to females.

3. Rare species being propagated for immediate release into natural habitats

   Characteristics: Management applied from the founder phase. Wild recruitment, if possible, is likely to be limited. Breeding is reliable and consistent.

   Program purpose: To sustain a genetically diverse, demographically robust population able to sustain a harvest of animals for release.

   Management strategy: Manage reproduction to maximize initial growth and retain founder genetic diversity. At captive capacity, manage reproduction to generate required harvest for release. Retain genetic diversity in both captive and release populations until reintroduction is complete. Minimize inbreeding in release animals. Manage appropriate age structures in both captive and wild populations. Ideally, manage population in a captive environment as similar as possible to the natural environment.

   Example population goals: Maintain 95% of wild-source heterozygosity for 25 years. Maintain population size at 100 (to allow a harvest of 20 animals per year for release).

   Example targets: Maintain breeding rate at 40 births per year; maintain inbreeding at or below $f = 0.125$.

4. Species not yet capable of self-sustaining reproduction in captivity

   Characteristics: Breeding is not reliable and consistent. Species may be new to captivity or one for which husbandry remains poorly known. Further recruitment may or may not be possible.

   Program purpose: To establish the conditions required to manage a demographically viable and genetically healthy captive population.

   Management strategy: Encourage proliferation of individuals breeding well in captivity in order to sustain demographic stability. Focus husbandry research and resources on specimens not breeding well. Once techniques are firmly established, document and wind down program or manage as one of the other categories.

   Example population goals: Focus on sustaining the population at a particular size for a specified period (e.g. sustain population size at 50 animals for 5 years; retain at least 85% genetic diversity).

   Example targets: Reduce juvenile mortality to below 20%; maintain breeding rate at approximately 20 births per year; maintain inbreeding at or below 0.125; breed every available female.

Some programs will not fit neatly into any of these categories. Some will span several of the purposes described, and for any program, both the purpose and the supporting goals may change over time with shifting circumstance. Despite this, clearly identifying a program's purpose and setting goals and targets to underpin that purpose remain the key to successful management.

EVALUATING A POPULATION'S DEMOGRAPHIC STATUS

Although zoo and aquarium populations are typically dispersed across institutions, they meet the basic definition of biological populations, since animals are transferred between these institutions. The first step in evaluating a population's status is to assess its current size, structure, and distribution, as well as to determine any historical demographic patterns that may be relevant to future population management; all these analyses are dependent on the data collected in a studbook.

POPULATION SIZE AND DISTRIBUTION

The size of the current population, while seemingly easy to determine using studbook data, is dependent on how the managed population is defined. A captive population may include (1) all individuals of that species (and/or subspecies) held globally; (2) all individuals held in a region; (3) all individuals at a subset of institutions participating in a regional management program (such as an SSP or EEP);

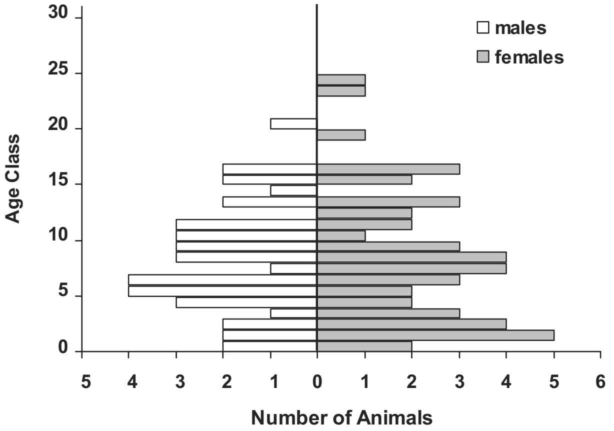


Fig. 19.4. Age pyramid of the Okapi SSP population as of March 2006 (*Okapia johnstoni*).

and/or (4) specific specimens from the set of institutions participating in a regional management program (e.g. an individual institution may have some individuals that are excluded or surplus to the managed population). Also note that in subsequent analyses (see below), specimens are often excluded from the genetically managed population for various reasons; but that these genetically excluded individuals are still regarded as part of the overall population. Thus, they will still be included in the final recommendations, since they occupy exhibit space.

When analyzed, the total population size is also often considered in the context of the amount of space available to the population (the carrying capacity) and/or the target population size set by the management program. For example: “The Okapi SSP population size at the time of analyses was 80 individuals (37.43.0; or 37 males, 43 females, and 0 unknown sex) distributed among 24 institutions. The SSP Management Group has set the target population size at 200” (Petric and Long 2006).

AGE AND SEX STRUCTURE

Populations are composed of individuals that differ in sex, age, birth origin, medical status, and/or other assorted phenotypic or genotypic traits. This underlying structure is important, because these traits influence an individual’s chance of reproducing or dying in a given year, and therefore the population’s overall potential for growth. The most conventional visual representation of a population is an age pyramid, which delineates the number of individuals in each age and sex class (fig. 19.4). Specific regions of interest in an age pyramid are

- the base of the pyramid, or the number of individuals in the youngest age classes: these are the surviving offspring from the most recent years of breeding;
- the individuals in the reproductive age classes (e.g. the middle of the pyramid—bounded by the ages at first and last reproduction): these are the individuals being paired for reproduction, and the sex ratio of these individuals (e.g. relative number of males and females) can influence management and the ability to form pairs or breeding groups; and
- the individuals at the top of the pyramid: these are the oldest living individuals in the population (but note that they may be younger than the species’ maximum longevity); often they are nonbreeding individuals that occupy available zoo space until death.

Understanding the structure of age pyramids can reveal a good deal about a population’s past growth pattern and potential for future growth. Populations that have a strong base of young individuals are usually growing populations (e.g. fig. 19.5a); these populations will have a strong potential for future reproduction as the youngest individuals advance to the reproductive age classes. Populations that have few individuals in the youngest age classes (e.g. they are top heavy:

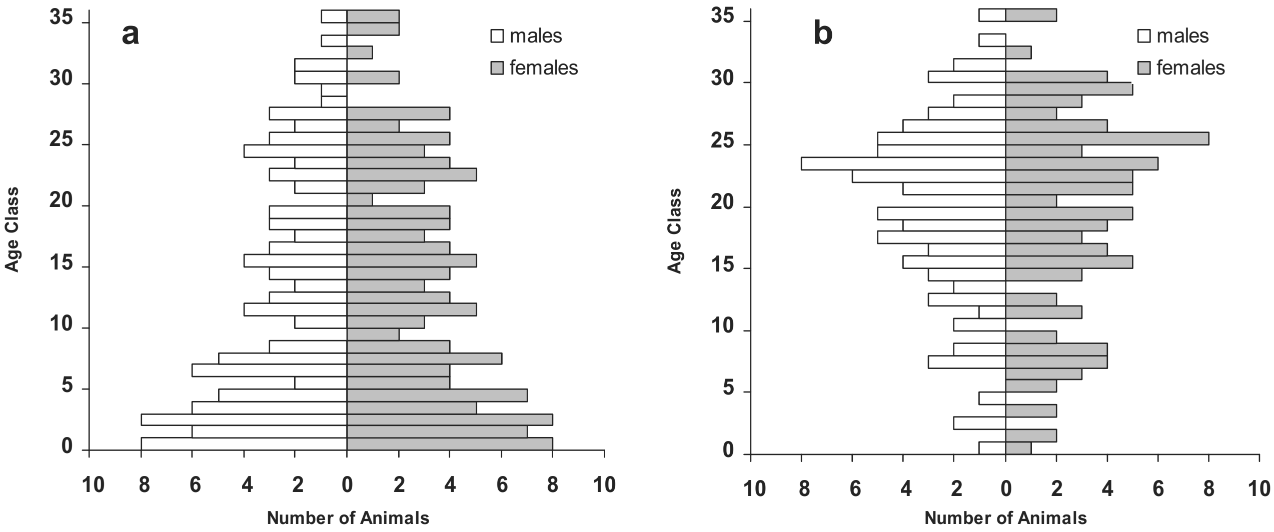


Fig. 19.5. Comparisons of age structures in a growing (*a*) or declining (*b*) population.

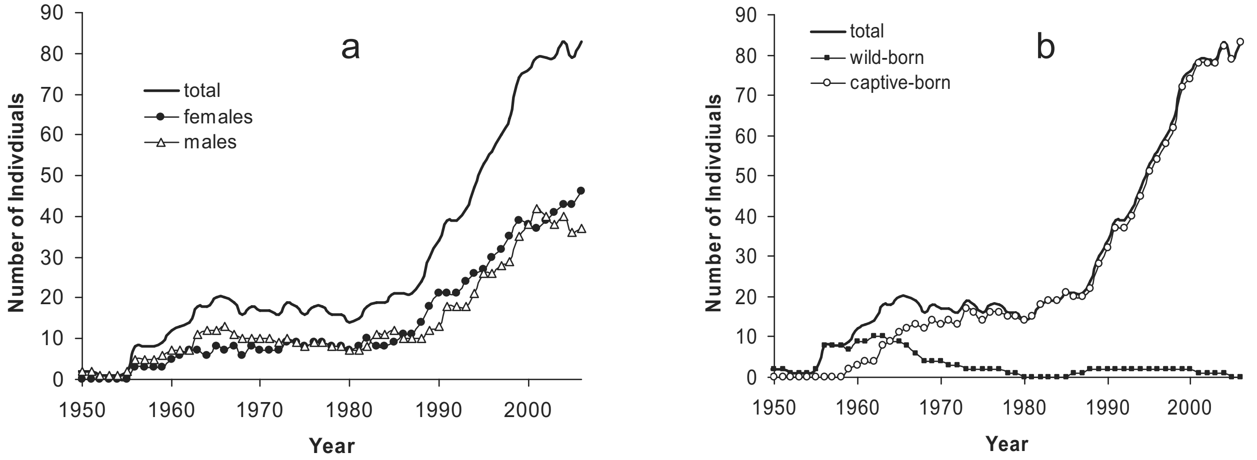


Fig. 19.6. Census of okapi in the SSP by sex (*a*) and origin (*b*).

fig. 19.5b) are usually declining populations; these populations may experience further difficulty as current breeders age and are replaced by a smaller number of breeders, as there may not be enough individuals to form breeding pairs or sustain the population.

HISTORICAL DEMOGRAPHIC PATTERNS

Population size. Assessment of a population's historical pattern of growth is important in determining its potential for future growth. Most commonly, this is done using census graphs of population size over time, often divided by sex (fig. 19.6a) or origin (fig. 19.6b).

These graphs can show important trends, such as the different phases in a population's growth (fig. 19.1), the point when captive births began overtaking importation of wild-caught individuals as a consistent source of population growth (in the mid-1960s for okapis, *Okapia johnstonii*; fig. 19.6b), or patterns of rapid growth or decline. Explanations should be sought for periods of rapid decline, especially if they took place during a period of population management, as they can pose serious threats to population viability. The demographic data that exist in the studbook can provide some indication of reasons for such declines (see life table section below), but ultimately population managers will have to indicate whether the changes were planned or unplanned. If the change was not planned, then managers should attempt to determine whether the changes had a biological cause (limitations in breeding biology or population structure, issues related to health, veterinary care, behavior, husbandry) or resulted from a lack or failure of management (lack of cooperation, failure to monitor births/deaths/aging structure).

Population growth rate. Rates of change in population size, which are called growth rates regardless of whether the population is increasing or decreasing, are typically expressed as a function of time (e.g. percent per year). There are 2 avenues of change in population size: intrinsic, which arise from births and deaths, and extrinsic, which arise from immigration (or importation) and emigration (or exportation). From one year to the next, change in population size is determined by the formula

$$N_{t+1} = N_t + (B - D) + (I - E), \tag{19.1}$$

where N = population size at time t or $t + 1$, B = births, D = deaths, I = immigration, and E = emigration. For most captive populations, immigration and emigration are typically low because of the logistical, financial, and ethical considerations of bringing wild individuals into captivity and/or transporting exotic species across international borders. However, importations are important when a captive population is started, and after a population is established they can still be an important strategy for improving genetic health (by bringing new founders into a population) or demographic stability (e.g. by adjusting sex ratios or bringing in individuals of breeding age). Even so, for the most part managers of captive populations primarily focus on the intrinsic properties of population growth.

Using a population's size over time, managers can calculate a historic average growth rate, or rate of change, symbolized by λ (lambda). When $\lambda > 1.00$, the population is increasing; when $\lambda < 1.00$, population is decreasing; and when $\lambda = 1.00$, the population is stationary. The difference between the value of lambda and 1.00 indicates the magnitude or annual rate of change: $\lambda = 1.04$ denotes a population increasing at 4% annually, while $\lambda = .94$ indicates an annual decline of 6%. λ for an individual year is calculated as

$$\lambda_t = \frac{N_t}{N_{t-1}}. \tag{19.2}$$

An average λ for a series of years is calculated as the geometric mean of each year's λ (Case 2000). Annual and average λs can be found in the census reports of SPARKS (ISIS 2004) and PopLink (Faust, Bergstrom, and Thompson 2006). For example, the Okapi SSP female population experienced an observed average growth rate of 1.072 (7.2% increase) over the period 1981–2006 (fig. 19.6a).

Life tables. Although the most general way to categorize a population's demography is to look at population-level rates of birth and death, in reality population growth is determined by how age-specific patterns in those rates interact with the population's structure. For many species, males and females have different age-related patterns of reproduction and mortality. These differences are conveniently summarized in a life table (Caughley 1977; Ebert 1999). Table 19.1 is a life table for the AZA SSP population of female okapi (Petric and Long 2006).

A life table displays the vital rates (mortality, Q_x; fecundity, M_x; and related rates) for each age class; male and female rates are usually tabulated separately. Vital rates are calculated based on age-specific tallies of birth and death events and the number of individuals at risk for those events using data from a studbook. Studbook data are generally limited to a defined subset of data using a date span and a geographic/institutional filter. Although the specific parameters and calculations used to create life tables for captive populations vary somewhat between software programs (SPARKS, PM2000, ZooRisk, PopLink), the basic concepts are applicable across all software.

Although life tables may display a sometimes overwhelming amount of data, population managers can focus on specific characteristics for key information about their population's demography (table 19.1):

- Age-specific patterns of fecundity (M_x) can indicate the reproductive life span (e.g. those years with non-zero M_x rates, or ages 2–21 for okapi).
- Patterns in M_x can also indicate the period of peak reproduction (those years with the highest fecundity rates, e.g. ages 8–19 for okapi).
- Age-specific patterns of mortality (Q_x) should be ex-

TABLE 19.1. Life table for female okapi, *Okapia johnstoni*, in the AZA SSP

Age (x)	Q_x	P_x	l_x	M_x	V_x	E_x	Risk (Q_x)	Risk (M_x)
0	0.110	0.890	1.000	0.000	1.058	16.336	66.2	59.3
1	0.020	0.980	0.890	0.000	1.200	16.448	55.6	55.6
2	0.020	0.980	0.872	0.035	1.295	15.763	50.4	49.5
3	0.020	0.980	0.855	0.093	1.360	15.065	45.7	45.7
4	0.020	0.980	0.838	0.128	1.367	14.352	44.3	43.7
5	0.020	0.980	0.821	0.143	1.338	13.624	41.7	41.7
6	0.020	0.980	0.804	0.150	1.290	12.882	41.6	41.3
7	0.022	0.978	0.788	0.150	1.231	12.140	38.3	37.3
8	0.027	0.973	0.771	0.153	1.173	11.425	34.6	34.6
9	0.032	0.968	0.749	0.158	1.112	10.747	29.9	29.4
10	0.038	0.963	0.725	0.160	1.046	10.100	27.3	26.3
11	0.040	0.960	0.698	0.160	0.975	9.467	25.4	24.5
12	0.040	0.960	0.670	0.160	0.898	8.819	23.4	22.9
13	0.058	0.943	0.643	0.165	0.820	8.219	18.6	18.6
14	0.093	0.908	0.606	0.175	0.748	7.800	18.0	17.9
15	0.110	0.890	0.550	0.180	0.674	7.562	14.9	14.0
16	0.110	0.890	0.490	0.180	0.587	7.373	10.1	10.1
17	0.110	0.890	0.436	0.180	0.484	7.161	9.0	8.5
18	0.113	0.888	0.388	0.180	0.362	6.931	8.0	8.0
19	0.138	0.863	0.344	0.150	0.219	6.773	8.2	8.2
20	0.180	0.820	0.297	0.075	0.087	6.849	7.0	6.0
21	0.150	0.850	0.243	0.015	0.015	7.018	5.0	4.4
22	0.050	0.950	0.207	0.000	0.000	6.717	4.6	4.6
23	0.000	1.000	0.197	0.000	0.000	5.867	4.5	4.5
24	0.000	1.000	0.197	0.000	0.000	4.867	3.4	2.9
25	0.000	1.000	0.197	0.000	0.000	3.867	2.0	2.0
26	0.000	1.000	0.197	0.000	0.000	2.867	2.0	2.0
27	0.125	0.875	0.197	0.000	0.000	1.992	2.0	1.4
28	0.500	0.500	0.172	0.000	0.000	1.417	1.0	1.0
29	0.875	0.125	0.086	0.000	0.000	1.111	1.0	0.6
30	1.000	0.000	0.011	0.000	0.000	1.000	0.0	0.0
31	1.000	0.000	0.000	0.000	0.000	0.000	0.0	0.0

Source: Based on a demographic filter of data between 1/1/1981–29/2/2006 and restricted to individuals at institutions in the SSP.

Note: See appendix 19.2 for definitions of life table parameters.

$r = 0.0559$; $\lambda = 1.0575$; $T = 9.34$; $N = 43.50$; N (at 20 yrs) $= 132.99$

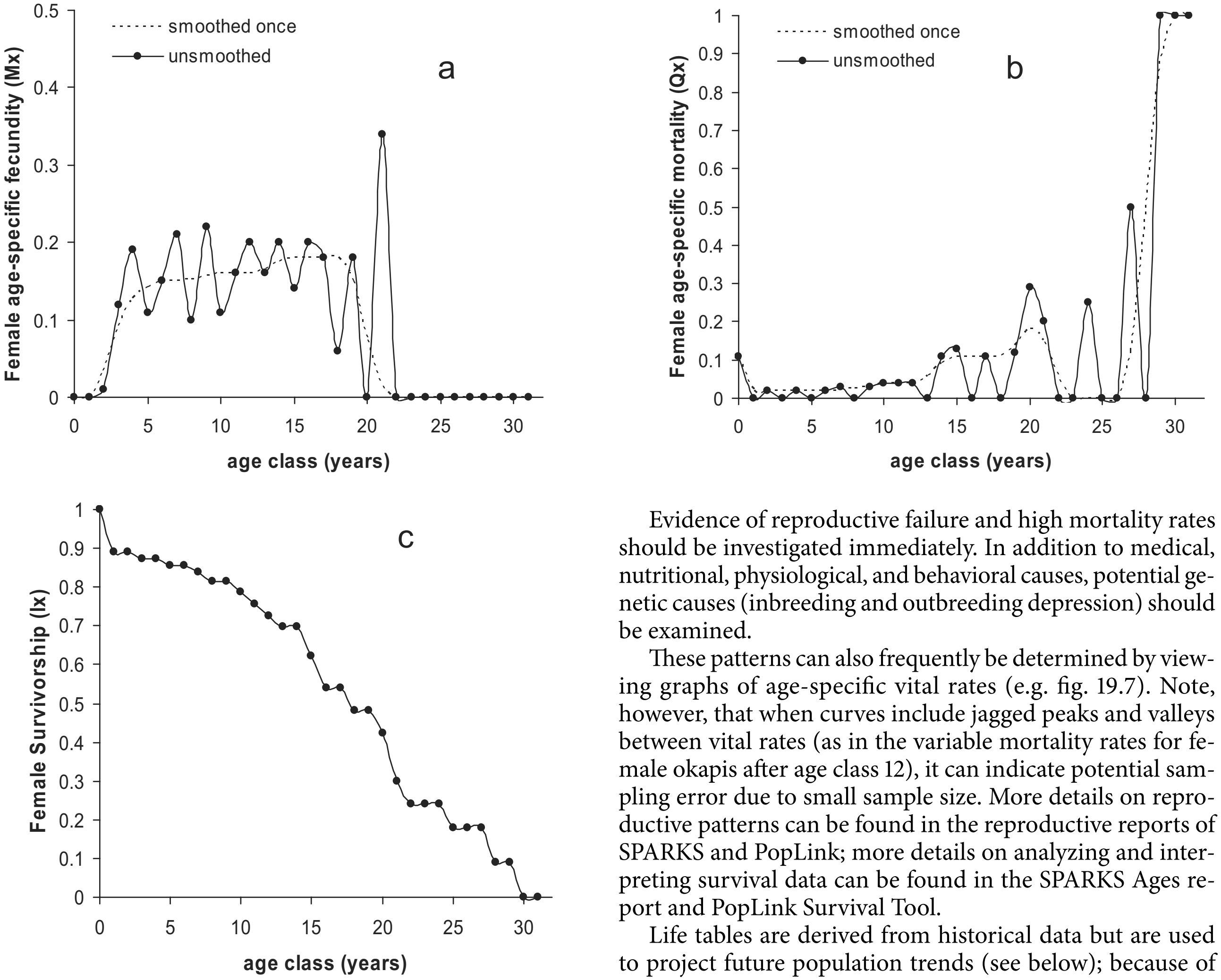


Fig. 19.7. Age-specific fecundity (*a*), mortality (*b*), and survivorship (*c*) rates for female okapis in the AZA SSP population based on a demographic filter of data between 1/1/1981 and 29/2/2006 and restricted to individuals at institutions in the SSP. Note the different scale on (*a*) and (*b*).

amined for the rate of infant (first-year) mortality (0.11, or 11%, for okapi females) and any other unusual age-specific spikes in mortality.

- When the age-specific mortality rates reach 1.0 or l_x = 0, that is generally the maximum observed longevity for the population (30 for female okapis).
- Age-specific patterns of survivorship (l_x) can indicate the median survivorship (the age where l_x = 0.5), also called the median life expectancy; half the individuals in the dataset died before this age and half the individuals survived longer (between 15 and 16 for okapi females).
- The Risk columns indicate the sample size on which the vital rate calculations are based. In general, if a particular age class has fewer than 30 individuals at risk of events (death or reproduction), the vital rates calculated for that age class should be viewed with caution. This occurs after age class 9 for okapi female vital rates.

Evidence of reproductive failure and high mortality rates should be investigated immediately. In addition to medical, nutritional, physiological, and behavioral causes, potential genetic causes (inbreeding and outbreeding depression) should be examined.

These patterns can also frequently be determined by viewing graphs of age-specific vital rates (e.g. fig. 19.7). Note, however, that when curves include jagged peaks and valleys between vital rates (as in the variable mortality rates for female okapis after age class 12), it can indicate potential sampling error due to small sample size. More details on reproductive patterns can be found in the reproductive reports of SPARKS and PopLink; more details on analyzing and interpreting survival data can be found in the SPARKS Ages report and PopLink Survival Tool.

Life tables are derived from historical data but are used to project future population trends (see below); because of this, it is important that the life table is representative of the population's true capacity for reproduction and mortality. The general strategy for defining the filter used to extract these data is to limit the life table to the period of modern management—those years in which a managed program has been in place (e.g. for many AZA populations, from the 1980s to the present) or when modern husbandry was established for the species. A common starting point is when intrinsic growth of the historic population (e.g. growth fueled by births rather than importations) becomes strong. However, several additional items that influence life table vital rates should be considered when setting a filter:

1. The amount of studbook data used to create the life table: In some populations there may not be enough recent data to construct a reliable life table, or there may be specific age classes in which sample sizes are not sufficient to calculate reliable vital rates. The cutoff of 30 individuals in a given age class is a somewhat arbitrary definition but is based partially on statistical conventions of small sample sizes (Lee 1980). More recently, attempts have been made to quantify data quality for data used in mortality analyses; these data quality routines can be found in the Survival Analysis Tool in PopLink.

2. The husbandry practices within the demographic filter: As captive managers' understanding of each species' nutritional, behavioral, reproductive, and medical needs evolves, the species' vital rates are likely to change. For example, when a population is being established in captivity and breeding is sporadic, fecundity rates will be very low; if nutrition and husbandry have not been fully perfected, mortality rates may be higher. Certain aspects of the life table are likely to be more susceptible to these changes, including infant survival (e.g. for species with changing philosophies on hand rearing), maximum longevity (as veterinary knowledge and nutrition practices improve), and fecundity rates (as husbandry knowledge of breeding biology increases). Also, if sample sizes are already small, care should be taken that husbandry practices at an individual institution do not overly affect life table values (e.g. only a single institution has successfully bred the species, but fecundity rates look high because of small sample sizes, or a catastrophe at a single institution inflates mortality rates).
3. Which individuals are considered at risk for events: Life table fecundity calculations in current software consider all females "at risk" for reproduction, regardless of whether they are physically separated from males or contracepted to prevent breeding. Fecundity data are therefore highly affected by whether the demographic filter reflects a time frame where breeding was actively pursued versus being limited to a few individuals or institutions. Because of this, fecundity data are generally underestimates of a population's true reproductive potential (e.g. what reproductive rates could be if all individuals were in breeding situations). When fecundity rates are low or 0, especially for the oldest age classes (for example, 22–30 years in female okapis), one cannot determine from the life table whether these rates are due to reproductive senescence (e.g. they are biologically unable to breed) or lack of access to mates. In the future, better recording of reproductive data (e.g. tracking an individual's opportunities to breed) should enable calculation of more accurate at-risk values and more appropriate fecundity rates.
4. The particular life history of the species: In general, it is more difficult to create accurate life tables for long-lived species, because data accrue more slowly in such populations. Long-lived species will often have small sample sizes, especially in the oldest age classes, which can make it challenging to accurately assess maximum longevity and other parameters of the survival curve.

In situations where data quality is very poor or the life table is not considered representative of the species' life history, population biologists may simply use the data as is or may (1) expand the demographic and/or geographic filter (include additional years or additional institutions/regions), or use another region's studbook to include more data in the analyses; (2) use different filters for mortality calculations and fecundity calculations (this may be appropriate if reproduction in a population is concentrated in a short window but mortality-related management practices have been stable for a wider time frame); (3) smooth mortality and fecundity data to remove some of the variability; (4) adjust data based on basic life history data on the species (e.g. ages of first and last reproduction, litter size, maximum longevity); and/or (5) use data from a closely related species or taxon (and/or a species that may be distantly related but might be expected to have similar demographic rates), which may be accessed on the WAZA/ISIS Studbook Library (ISIS/WAZA 2004).

SUMMARY PARAMETERS CALCULATED FROM THE LIFE TABLE

The age-specific vital rates in a life table can also be summarized into parameters that can be used to describe the population's demographic characteristics over the historic period covered in the life table:

Population growth rate (λ, r). Earlier we described λ as a parameter calculated from observed population sizes; life tables can also provide estimates of the expected growth rate of the population. The λ calculated from life table vital rates is the value of λ that solves the Euler equation:

$$1 = \Sigma\, \lambda^{-x}\, l_x M_x, \tag{19.3}$$

where the summation is over all age classes in the life table (Caughley 1977; Ebert 1999). λ is calculated separately for each sex; if a population level λ is reported, it is generally the average of the male and female rates.

The intrinsic rate of natural increase (r) is an analogous growth rate calculated from the life table, except that r is centered around 0.00 rather than 1.00 (e.g. $r < 0.0$ describes a declining population, $r > 0.0$ describes an increasing one). λ and r can be derived from each other as

$$\lambda = e^r \text{ or } r = ln(\lambda). \tag{19.4}$$

Growth rates calculated from the life table are based on the assumption that estimated survival and fecundity rates remain stable over time and that the population is at stable age distribution (Caughley 1977).

Since λ can be calculated in 2 different ways (from observed changes in N and from the life table), a population may therefore have 2 values of λ for the same time period. For example, the observed historic λ for okapi females from 1981 to 2006 was 1.072, while the calculated λ from the life table for the same period was 1.0575 (table 19.1). Differences between the 2 rates can arise if demographic characteristics of the population have been changing, if imports and exports have contributed to changes in population size, or if the population structure is very different from stable age distribution.

Generation length (T). Generation length is the average age at which all parents produce young. Generation length is *not* the age at which animals begin to reproduce. It can be calculated directly from estimates of survival and fecundity rates in the life table (Caughley 1977; Ebert 1999; Case 2000). T is calculated for each sex separately; if T is reported for an entire population, it is generally the average of the male and female generation lengths. Generation length is important in captive management because it determines the rate at which genetic diversity is lost; a longer T results in a slower loss over time.

Stable age distribution (SAD). The stable age distribution is the eventual sex and age structure the population would reach if the survival and fecundity rates in the life table remained constant over time (Caughley 1977). If a population were at its SAD, the population and each age class within the population would grow at the same rate each year. Although the SAD is a useful theoretical concept, in reality most captive (and likely many wild) populations are not necessarily at or near their SAD. A population's deviation from SAD can arise by stochastic fluctuations in the number of offspring produced from year to year, in survival rates, or in importation and exportation events where groups of individuals are brought in or transferred out, or by other chance events. If a population is not near its SAD, its growth may deviate greatly from the λ calculated from the life table.

Definitions for demographic terms are provided in appendix 19.2.

EVALUATING A POPULATION'S GENETIC STATUS

The genetic history of a population can be represented as diagrammed in figure 19.8. Any population can be traced back to some number of founding individuals. These may be wild-caught individuals derived from a specific wild population or several different wild populations. Some of them may be individuals whose parentage cannot be traced back any further, but that are very likely to be unrelated to one another.

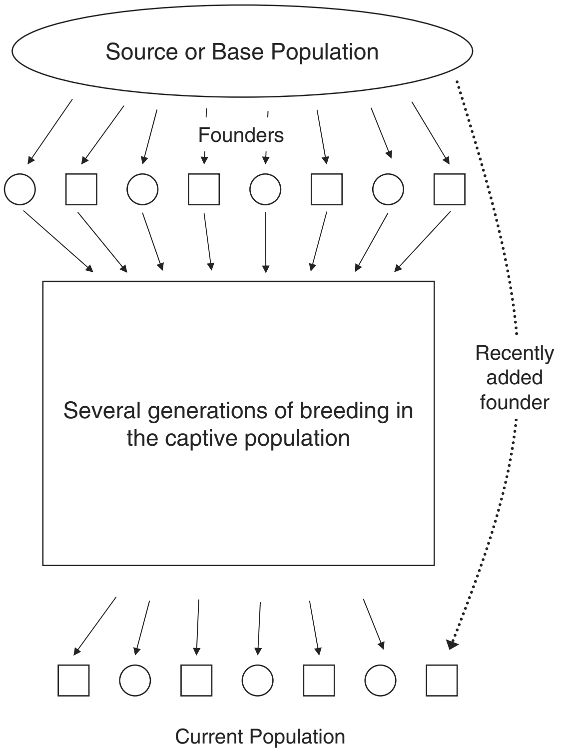


Fig. 19.8. Diagram of the genetic events over time in a hypothetical captive population.

Either way, these original founding individuals are assumed to be a sample of a Source or Base population, and the goal is to preserve, to the best extent possible, the genetic composition of the Source population over time by preserving the genetic diversity of the founders.

There may be several generations of breeding between the founding event and the current living population. The genetic characteristics of the current population can then be described in terms of the following:

- How many founding individuals have contributed genes to the current population (some lineages may have died out)?
- How much of each founder's genome has survived to the current population?
- What proportion of the gene pool of the Source or Base population has been retained in the current population?

The following sections present the concepts needed to answer these questions.

FOUNDERS

A founder is an animal who has no known ancestors either in the wild or in captivity at the time it entered the population and who has descendants in the living population. As such, wild-caught animals are usually founders if they reproduce (and their parents are unknown wild individuals). Wild-caught animals that have not reproduced are not (yet) founders, since they have not contributed genetically to the captive population (fig. 19.9). When the relationships of wild-caught animals are known or suspected (e.g. several cubs captured in the same den), it is necessary to create hypothetical parents (or other ancestors) to define those relationships. These hypothetical ancestors are then defined as founders.

Molecular genetic analyses can be useful in examining relationships of wild-caught animals or even captive-born animals without pedigrees (Haig 1995, Haig, Ballou, and Derrickson 1990, Haig, Ballou, and Casna 1994; Ashworth and Parkin 1992; Geyer et al. 1993; Jones et al. 2002; Russello and Amato 2004). However, these techniques typically have the resolution for determining only first-order relatedness (e.g. full sibling or parent-offspring relationships) and must be based on extensive molecular data to be useful. When information about founder relatedness is available, the PM2000 software does allow use of those data as a matrix of kinships or relatedness to apply to the founding generation.

The number of founders is a rough indication of how well the source population has been sampled to provide genetic diversity to the captive population. A large number of founders is indicative that the source population was well sampled and probably could be managed to retain much of its genetic diversity.

FOUNDER CONTRIBUTION

Founders will typically have unequal genetic contributions to the current population. Founder contribution is the percentage of an individual's or a population's genes that have descended from each founder. Calculations are based on the

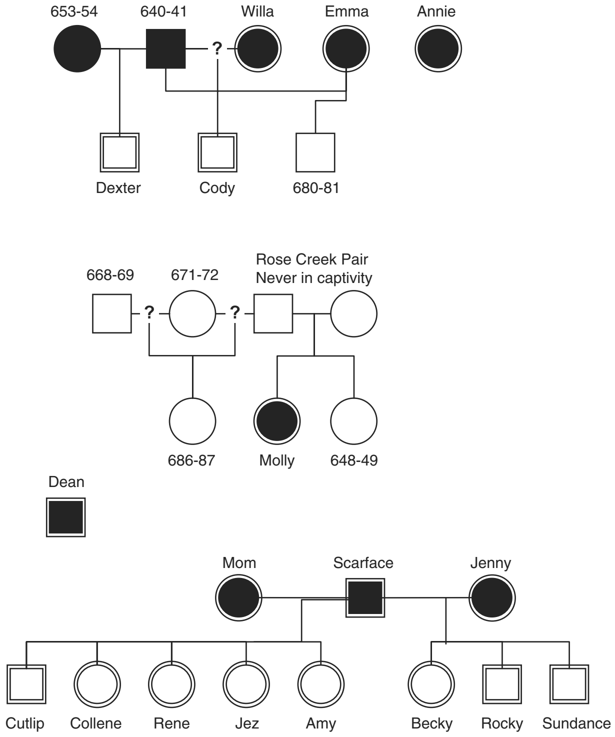
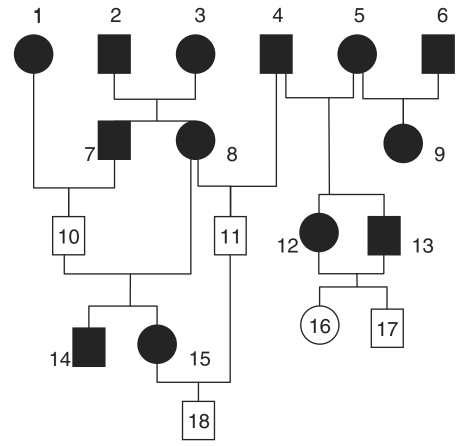


Fig. 19.9. The identification of founders in the last remaining 18 black-footed ferrets brought into captivity (Ballou and Oakleaf 1989). Squares are males, circles females. Solid objects are founders. Question mark indicates uncertain parentage. Double-outlined objects indicate living individuals at that time. Willa, Emma, Annie, Mom, Jenny, Dean, and Scarface are shown as founders, since they are wild caught, have no known ancestors in the group, and are thought not to be closely related to one another. Although Molly has known relatives, they were either never in captivity or died without producing offspring; she is therefore considered a founder. Even though they were never brought into captivity, female 653-54 and male 640-41 are also founders because Dexter, who is living, is an offspring of both and Cody is an offspring of male 640-41.



ID	Sex	Dam	Sire	Status
1	F	Wild	Wild	Dead Founder
2	M	Wild	Wild	Dead Founder
3	F	Wild	Wild	Dead Founder
4	M	Wild	Wild	Dead Founder
5	F	Wild	Wild	Dead Founder
6	M	Wild	Wild	Dead Founder
7	M	3	2	Dead
8	F	3	2	Dead
9	F	5	6	Dead
10	M	1	7	Living
11	M	8	4	Living
12	F	5	4	Dead
13	M	5	4	Dead
14	M	8	10	Dead
15	F	8	10	Dead
16	F	12	13	Living
17	M	12	13	Living
18	M	15	11	Living

Fig. 19.10. Pedigree of a population founded with 3.3 individuals. Squares = males; circles = females; open squares and circles = living animals. Numbers are unique identifiers for each individual. The pedigree listing is presented below.

Mendelian premise that each parent passes (on average) 50% of its genes to its offspring. Each founder's genetic contribution to living individuals can be calculated by constructing each individual's pedigree back to the founders and applying these Mendelian rules of segregation. A pedigree is presented in figure 19.10.

A founder's genetic contribution to the current population's gene pool (p_i) is its contribution averaged across all living individuals (table 19.2). Algorithms and computer programs are available for calculating founder contributions from pedigree data (Ballou 1983). Founder contributions in most captive populations are highly skewed, usually due to disproportionate breeding of a small proportion of the founders early in the population's history (fig. 19.11). Genetic diversity potentially contributed by the underrepresented founders is at high risk of being lost due to genetic drift.

ALLELE RETENTION

Further loss of genetic diversity occurs when genetic drift causes founder alleles to be lost from the population. Extreme cases of genetic drift are often referred to as pedigree bottlenecks, occurring when the genetic contribution of a founder passes through only one or a few individuals. For example, only 50% of a founder's genes survive to the next generation if it produces only one offspring, 75% if it produces 2 offspring, and so forth. Bottlenecks may occur during the first generation of captive breeding if only one or two offspring of a founder live to reproduce. However, the genetic drift caused by such bottlenecks can occur at any point in the pedigree, resulting in gradual erosion of the founder alleles. The more pathways a founder's genes have to the living population, the less likely will be the loss of its alleles. Therefore, even though a large proportion of a population's gene pool may have descended from a particular founder (i.e. its founder contribution is high), those genes may represent only a fraction of that founder's genetic diversity.

The proportion of a founder's genes surviving to the current population is referred to as gene retention (r_i) or gene

TABLE 19.2. Founder contributions for each living individual and allele retention for each founder from the pedigree in figure 19.10

	Living individuals					Average contribution	Retention
Founder	10	11	16	17	18	p_i	r_i
1	.50	0	0	0	.13	.126	.500
2	.25	.25	0	0	.31	.162	.484
3	.25	.25	0	0	.31	.162	.487
4	0	.50	.50	.50	.25	.350	.803
5	0	0	.50	.50	0	.200	.612
6	0	0	0	0	0	0	0

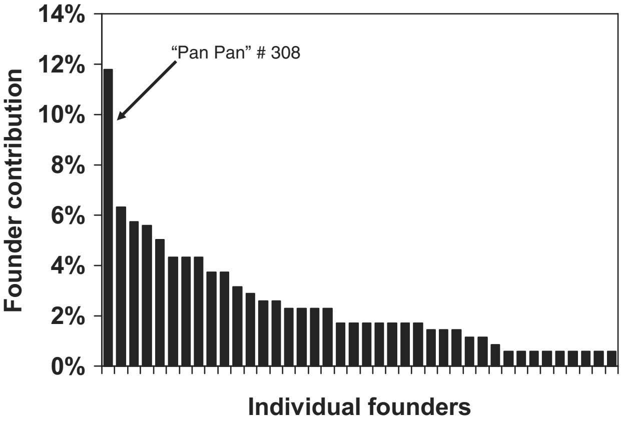


Fig. 19.11. Founder contributions in the 2006 captive population of giant pandas, *Ailuropoda melanoleuca*. The distribution is heavily skewed due to disproportionate breeding among the founders. About 12% of the gene pool has come from one prolific male, panda #308 (Pan Pan), far left.

survival. Although exact methods for calculating retention have been developed (Cannings, Thompson, and Skolnick 1978), it is often estimated using Monte Carlo simulation procedures (gene dropping: MacCluer et al. 1986). Gene drop procedures assign 2 uniquely identifiable alleles to each founder. Alleles are passed, randomly, from parents to offspring according to the rules of Mendelian segregation, and the distribution and pattern of alleles among living animals are examined after each simulation (fig. 19.12). The simulations are repeated several thousand times, and the retention for each founder is calculated as the average percentage, across all simulations, of the founder's alleles that have survived to the living population. The retention estimates for the sample pedigree shown in figure 19.10 are listed in table 19.2. The retention for founder 1 is only 50%, because she produced only one offspring, while the retention for founder 4 is higher because his genes have multiple pathways to the living population. Founder genome survival is the sum of the founder retention across all founders.

Gene drop analyses provide information about the distribution of founder alleles in the living population not available from data on founder contributions. This is particularly true for deep, complex pedigrees, in which using founder contribution alone can be very misleading.

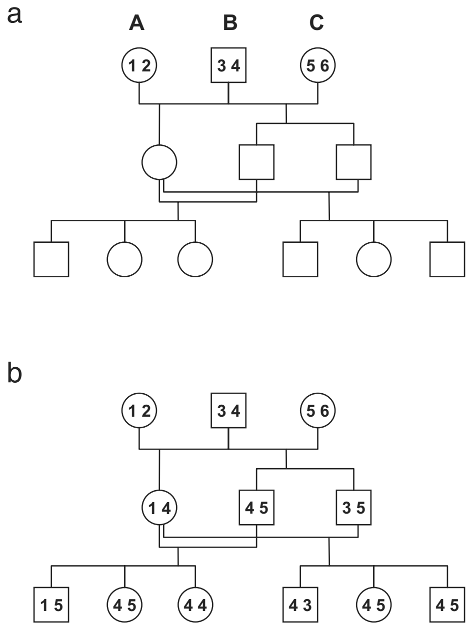


Fig. 19.12. Gene drop analysis. (*a*) Each founder is assigned two unique alleles. (*b*) The alleles are then "dropped" through the pedigree according to the rules of Mendelian segregation; each allele has a 50% chance of being passed on to an offspring. At the end of the simulation, the pattern and distribution of alleles in the living population (bottom row) are examined. The simulation is repeated several thousand times, and results are averaged across simulations to give allele retention. Note that allele 2 from founder A and allele 6 from founder C have been lost in the simulation shown.

FOUNDER GENOME EQUIVALENTS

Since both skewed founder contributions and loss of alleles due to genetic drift result in the loss of founder genetic diversity, the genetic contribution of the founders to the gene pool may be less than expected. Lacy (1989, 1995) introduced the concept of founder genome equivalent (f_g) to illustrate the combined effect that skewed founder contribution and genetic drift have on the genetic diversity of a population. f_g is the number of founders required to obtain the levels of genetic diversity that are observed in the current population if the founders were all equally represented and had retained all their alleles in the living population. It is calculated as

$$f_g = \frac{1}{\sum_{i=1}^{N_f} (p_i / r_i)}, \tag{19.5}$$

where N_f is the number of founders, p_i is the contribution of founder i to the population, and r_i is founder i's retention. Our sample population in figure 19.10 has 6 founders, but because of retention problems and skewed founder contribution, they have an f_g of only 2.8. In essence, they behave genetically like 2.8 idealized founders. The f_g values are often calculated with living founders excluded from the analysis. Living founders have 100% retention, and including them assumes that their alleles have been captured in the population, even though they may not have successfully reproduced or have any living descendants. Excluding living founders provides a more realistic summary of the genetic status of the population, particularly if there are many founders who are not likely to contribute offspring to the gene pool. Comparing the f_gs calculated with living founders excluded versus included shows the contribution that genetic management can make if 100% of the living founder genes can be retained in the population.

GENE DIVERSITY RETAINED

Gene diversity (*GD*) is the level of expected heterozygosity in a population. *GD* ranges from 0 to 1 and is the principal measure of genetic diversity in populations. In genetics of captive breeding, the gene diversity of interest is the proportion of heterozygosity of the Source population that currently survives in the living population:

$$GD_t = \frac{H_t}{H_0}, \tag{19.6}$$

where H_t is the expected heterozygosity in the current population (at time *t*) and H_0 is the expected heterozygosity in the Source population (i.e. time 0). Since there is no estimate of H_0, GD_t can be calculated from the allele frequencies generated by the gene drop simulation as follows:

$$GD_t = 1 - \sum_{i=1}^{2N_f} q_i^2, \tag{19.7}$$

where N_f is the number of founders and q_i is the frequency of allele *i* in the current population (Lacy 1989). Gene diversity can also be calculated directly from f_g:

$$GD_t = 1 - \frac{1}{2f_g}. \tag{19.8}$$

AVERAGE INBREEDING

Inbreeding is the mating of related individuals. If 2 parents are related, their offspring will be inbred; the more closely related the parents are, the more inbred will be their offspring. The degree to which an individual is inbred is measured by its inbreeding coefficient (f), which is the probability of receiving the same allele from each parent (i.e. the alleles are identical by descent). Figure 19.13 shows a father-daughter mating. The allele "A" has a 50% chance of being passed from the father to his daughter. When he breeds with his daughter, this male again has a 50% chance of passing "A" on to his offspring. Likewise, the daughter also has a 50% chance of passing on "A" if she carries this allele. The inbred offspring then have the potential to inherit allele "A" (with 12.5% probability) from both the father and mother. Allele "a" has the same chance. Therefore, the inbred offspring has a 25% chance of receiving 2 duplicate alleles in the form of "AA" or "aa." Inbreeding coefficients range from 0 (parents are unrelated) to 1.0. Offspring of father-daughter, mother-son, or full-sib matings are 25% inbred; offspring of first-cousin matings are 6.25% inbred. Many generations of full-sib matings result in offspring with inbreeding coefficients of 1.0. Inbreeding coefficients are used to examine the effects of inbreeding in the population and to determine the degree of relatedness between individuals. Methods for calculating inbreeding coefficients are available from Ballou (1983), Boyce (1983), and Frankham, Ballou, and Briscoe (2002).

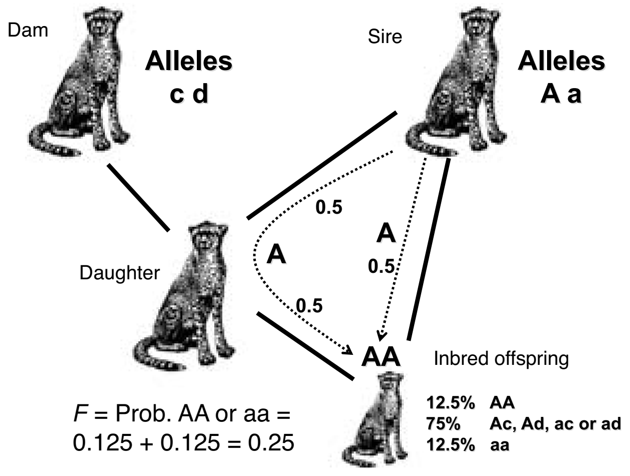


Fig. 19.13. An example of inbreeding: a father-daughter breeding produces an offspring with an inbreeding coefficient of $f = 0.25$.

All naturally outbreeding plants and animals (including humans) have deleterious recessive alleles resulting from mutations. In figure 19.13, if "a" is such an allele, it would not cause deleterious problems in the sire, because it is masked by the dominant "A" allele. However, in the inbred offspring, there is a 12.5% chance of the locus being homozygous (aa) and therefore the alleles being expressed. Inbreeding depression results primarily when inbreeding unmasks these deleterious recessive mutations that reside in animals' genes and is the reason that deleterious consequences are expected and commonly observed in most species when inbred (Lacy 1997).

Average inbreeding is the average of the inbreeding coefficient of all animals in the current population and is a good indicator of the overall level of inbreeding in the population.

POTENTIAL GENETIC DIVERSITY

Living founders that have produced only a few offspring, or living animals that have no descendants in the population but are still capable of reproducing, represent individuals that can potentially still contribute genetic diversity to the population. Living founders who have only produced a few offspring have a chance, by producing additional offspring, to increase their allele retention (r_i) so that more of their genome is captured in the population. Equations (19.5) and (19.8) show that if r_i is increased for any founder, f_g and GD increase as well. Living animals that have no relatives in the population but can still breed are potential founders (e.g. recently acquired wild-caught animals).

A genetic summary of the population should indicate how many potential founders exist, and the values of GD and f_g, if potential and living founders were ideally managed and bred.

EFFECTIVE POPULATION SIZE

The extent and rate of loss of gene diversity depend on the size of the population (fig. 19.2). However, the size of relevance is not simply the number of individuals. Rather, it is the genetically effective population size (N_e), a measure of how well the population maintains gene diversity from one generation to the next. Gene diversity is lost at the rate of $1/(2N_e)$ per generation. Populations with small effective population sizes lose gene diversity at a faster rate than those with large effective population sizes (fig. 19.2).

The concept of N_e is based on the genetic characteristics of a theoretical or ideal population that experiences no selection, mutations, or migration and in which all individuals are asexual and have an equal probability of contributing offspring to the next generation. This "ideal" population is well understood, and loss of genetic diversity over time in an ideal population can be easily calculated (Kimura and Crow 1963). A real population differs greatly from the ideal, but is compared with an ideal population to determine its effective size. If a real population of, say, 100 tigers loses genetic diversity at the same rate as an ideal population of 15, then that tiger population has an effective population size of 15. Strictly defined, the effective size of a population is the size of a theoretically ideal population that loses genetic diversity at the same rate as the population of interest (Wright 1931). Once an effective population size is calculated, the rate at which the population loses genetic diversity can be estimated.

In general, the effective size of a population is based primarily on 3 characteristics: the number of breeders, their sex ratio, and the relative numbers of offspring they produce during their lifetime (their lifetime family size). In general, a large number of breeders will pass on a larger proportion of the parental generation's genetic diversity than only a few breeders. A heavily biased sex ratio in the breeders will result in greater loss of genetic diversity, since the underrepresented sex will contribute an unequally large proportion of the offspring's genetic diversity. An equal sex ratio is preferable, since it assures that the gene pool will receive genes from a larger number of breeders than when the sex ratio is highly skewed. Differences in family size also result in loss of genetic diversity, since some individuals contribute few or no offspring to the gene pool while others, producing large numbers of offspring, contribute more to the gene pool. The amount of genetic diversity passed from one generation to another is generally maximized when all breeders produce the same number of young (i.e. family sizes are equal and the variance in family size is zero).

Management procedures to maximize a population's effective size focus on maximizing the number of different breeding individuals, equalizing the sex ratio of breeders, and rotating breeding among many animals so that each breeding group or pair produces similar numbers of offspring. Managing a population using mean kinships (described below) also is an effective way to maximize a population's effective size.

By knowing the effective size of a population, it is possible to predict how rapidly heterozygosity will be lost in the future. Therefore, N_e is a useful indicator of the population's future genetic status. There are many methods for estimating a population's effective size. Some are based on demographic parameters that can be estimated from studbooks (sex ratios, variance in family size, changes in population size, etc; Nunney and Elam 1994; Lande and Barrowclough 1987; Frankham, Ballou, and Briscoe 2002). Others use changes in genetic diversity over time (Waples 1989). However, all these methods require the assumption that trends in the past represent future trends. Nevertheless, understanding this caveat, N_e is useful as a general measure of how well the population has been managed. It is also needed to predict how well the population will retain future diversity—a measure needed to develop population-level goals. Software (e.g. PM2000) is typically used to estimate N_e for captive populations based on the pedigree and life history (studbook) data as well as changes in genetic diversity over time.

Effective population sizes are also normally presented as the ratio of the effective size to the census size (N_e/N). The value of N_e can theoretically range from 0 to about twice the population's census size. However, rarely is it above N. The N_e/N ratios for most species in captivity typically range from 0.15 to 0.40 (average about 0.3), the low end being species managed as groups with unequal sex ratios (e.g. hoofstock herds) and the high end being long-lived and monogamously paired species (e.g. okapi). In the wild, N_e/N ratios are closer to 0.11 (Frankham 1995b).

USE OF MOLECULAR GENETIC ANALYSES

Estimates of genetic variation are helpful primarily for identifying the extent of genetic differences between populations or taxa. Large genetic differences may be evidence that there is more than one taxon or evolutionarily significant unit (ESU) within a species. If large differences (e.g. chromosomal differences) are found within a managed population, it may be necessary to reevaluate the goal of the program and possibly manage the population as 2 separate units (Deinard and Kidd 2000). Interbreeding individuals from different ESUs may result in reduced survival and reproduction (outbreeding depression). Where managers suspect that there are different ESUs, they should conduct additional morphological, behavioral, and biogeographical analyses and reexamine the purpose and goals of the population.

Levels of genetic variation may also provide information on the demographic and genetic history of the population. However, the goal of maintaining genetic diversity should not be abandoned if little or no variation is measured. Molecular analyses only sample a very small proportion of the genome, and there may be important diversity at unscreened but highly functional genes. Management should strive to maintain what little genetic variation is present for the long-term fitness of the population.

GENETIC SUMMARY TABLE

Table 19.3 shows the summary of the genetic status of the global golden lion tamarin (GLT) captive breeding program. Based on 40 founders, much of the Source population gene diversity (96%) has been retained. If the GD_t was lower than 90% (the typical goal for many captive populations), this should raise some concern. GD_t lower than 80% indicates that a population has lost much of its evolutionary potential

TABLE 19.3. Summary of the genetic status of the international golden lion tamarin (*Leontopithecus rosalia*) population as of January 1, 2007

Founders	40
Potential founders	8 additional
Living descendants	448
GD_t retained	0.9624
Potential GD_t retained	0.9842
Founder genome equivalents (f_g)	13.31
Potential f_g	31.59
Average inbreeding (f)	0.0257

and its conservation value is questionable. In the GLT population, the GD_t represents the level of gene diversity retained if a new population were established by 13 unrelated founders (i.e. $f_g = 13$). There are a few additional potential founders (illegally wild-caught tamarins recently confiscated by Brazilian authorities that have not yet bred). Including them in the program and breeding them to the fullest extent possible as well as successfully breeding the underrepresented founders would bring the gene diversity retained up to 98% and the founder genome equivalents up to 32. A large number of potential founders indicates that there may be opportunities to increase genetic diversity significantly by successfully reproducing them. In the GLT population, the average inbreeding is low at 3%. Population managers' tolerance for the level of inbreeding in a population vary. There is no level of inbreeding that indicates a threshold for inbreeding depression; inbreeding depression is expected to be a linear function of the amount of inbreeding (Frankham, Ballou, and Briscoe 2002). However, many geneticists and population managers would probably feel uncomfortable with levels of inbreeding above 0.125.

Definitions for genetic terms are provided in appendix 19.3.

GENERAL MANAGEMENT STRATEGIES

OBTAIN A SUFFICIENT NUMBER OF FOUNDERS: THE FOUNDING PHASE

How many founders are needed to start a captive population? Allelic diversity is lost much more rapidly than heterozygosity during founding events (Allendorf 1986; Fuerst and Maruyama 1986). Therefore, the primary concern is capturing allelic diversity, since this may require more founders than sampling for heterozygosity alone. Sampling for heterozygosity does, however, establish a lower limit for the effective founder size required. N effective founders retains on average $100 - [1/(2N)] \times 100\%$ of the Source population's heterozygosity. A general rule of thumb is to try to sample at least 95% of the source population's heterozygosity; this requires an effective founder size of at least 10 (Denniston 1978).

The number of founders required to capture allelic diversity adequately depends on the allele frequencies in the source population. Marshall and Brown (1975), Denniston (1978), and Gregorius (1980) discuss the effective founder sizes required given various allele frequency distributions. Unfortunately, information on the distribution of allele frequencies in the source population is often not available. Marshall and Brown (1975) suggest that founder numbers adequate for effectively sampling allelic diversity be based on the most likely allele distributions, and conclude that effective founder sizes between 25 and 50 are sufficient in most cases. They emphasize the need to consider potential differences in genetic variation over the range of a population. Sampling strategies should attempt to compensate for and/or exploit known geographic patterns of genetic variation to optimize the levels of genetic diversity sampled, while at the same time striving to remain within the geographic boundary of the ESU.

Founders will not necessarily or optimally enter the population only at the inception of a captive propagation project. Immigrants from the wild should periodically be incorporated into the captive population if possible. Failure to obtain an optimal genetic number of founders is not justification for canceling plans to establish a captive propagation program. However, before the removal of wild-caught specimens, managers should carefully consider the potential effects of such removals on the wild population.

EXPAND THE POPULATION SIZE AS RAPIDLY AS POSSIBLE: THE GROWTH PHASE

Genetic diversity is lost when growth rates are slow, because small populations lose genetic diversity at a faster rate than large populations; therefore, until the population reaches its target size, managers should increase it as rapidly as possible. This sometimes means compromising genetic management. The 2 primary objectives (population growth and genetic management) are not always complementary. Extreme focus on population growth (ignoring genetic management) might entail using only one or a very few highly successful males to accomplish all the breedings during a given year. This might result in the production of more offspring, and hence a larger population size, but would also result in all or most of the offspring being related. As a consequence, future inbreeding might result in a large, genetically unhealthy population with high mortality and low reproductive rates.

On the other hand, an extreme focus on genetic management (ignoring demographics) might entail trying to breed only the most underrepresented males and females, who may be underrepresented due to advanced age or reproductive or behavioral problems and have little true reproductive potential. The number of animals reproducing and number of offspring produced would thus decline, and reproductive rates might be too low to sustain the population. This strategy would result in a genetically healthy but small or declining population.

Population management then becomes a balance between demographic and genetic management: achieving sufficient (but not maximum) reproduction among a genetically good (but maybe not ideal) set of individuals, which may compromise both population growth and genetic management. There will be some loss of reproduction when inexperienced males and female are paired and some genetic compromises when breedings are set up among some genetically overrepresented pairs to ensure the production of a sufficient number of offspring. This is a challenge that all managed populations face.

The early history of a population is often where many genetic problems originate. For example, institutions that experience successful breeding right away tend to start dispersing offspring to those that are less successful. Underperforming founder males are paired with extremely successful females to kick-start breeding and vice versa, resulting in one of the most difficult genetic challenges to correct: the linking of rare and common genetic lines. These problems will persist through the rest of the population's history and should be avoided if possible. Nevertheless, if populations are extremely small or declining, it is always appropriate to focus more on growth than genetic management.

STABILIZE THE POPULATION AT CARRYING CAPACITY: THE MANAGEMENT PHASE

The current population size and growth rate determine whether the population is at, or when it will reach, carrying capacity. If the population is at or approaching carrying capacity, managers can use demographic analyses to determine how fertility and survivorship rates can be managed by removals of animals (harvests, culls) and/or regulation of reproduction (contraception) to stabilize the population at the desired carrying capacity (Beddington and Taylor 1973). This process may entail substantial "what if" analysis to determine how such managerial modifications of survivorship and fertility patterns will affect population size, growth rate, age distribution, and other population characteristics.

CONSIDER SUBDIVIDING THE POPULATION

Subdivision of a population into several subpopulations or demes among which gene flow (usually exchange of animals but also potential exchange of gametes or embryos) is regulated is advantageous for protection against diseases, catastrophes, and political changes (Dobson and May 1986) as well as for other practical reasons, such as reduction of shipping costs and hazards and simplification of management logistics. In addition, genetic advantages may accrue based on the theoretical argument that, without selection, random genetic drift will drive different alleles to fixation in different demes, and therefore, subdivision will maintain a higher overall level of allelic diversity; however, the theoretical conditions that support this argument do not always exist in real populations. Furthermore, while the smaller subdivided populations lose genetic diversity more rapidly than one single population because they are small and genetic drift dominates the evolutionary process, they experience fewer undesirable adaptations to captivity (i.e. adaptation is less effective in small than in large populations; Margan et al. 1998). Margan et al. (ibid.) proposed that regional populations remain isolated until moderate levels of inbreeding accumulate, then exchange animals among regions to reduce inbreeding. This has the advantage of reducing adaptation to captivity as well as maintaining genetic diversity. However, the role of selection in captive populations is uncertain, and similar types of selection, conscious or unconscious, may actually fix similar alleles in each deme, thereby decreasing the overall levels of genetic diversity. Furthermore, the smaller size of semi-isolated subdivisions may render them more vulnerable to inbreeding depression and demographic stochasticity (Drake and Lodge 2004).

USE AVAILABLE REPRODUCTIVE TECHNOLOGY

Reproductive technology (e.g. semen/ovum collection and storage, embryo transfer and freezing) may be a useful tool for assisting captive breeding programs in the long-term maintenance of genetic diversity. Such technology can facilitate exchange of germ plasm between wild and captive populations as well as effectively increasing the reproductive lifetime of founders and their immediate descendants. By increasing generation length, adequate levels of genetic diversity can be maintained in smaller populations, leaving more resources for populations of other species in need (Ballou and Cooper 1992). Living founders who have not yet contributed to the population should be considered immediate candidates for germ plasm storage. Artificial insemination can also help problem breeders contribute to the gene pool (black-footed ferrets; Wolf et al. 2000). Although reproductive technology is not yet available for most exotic species, it is a major focus of research by reproductive biologists (Spindler and Wildt, chap. 32, this volume).

DEVELOPING POPULATION MANAGEMENT RECOMMENDATIONS

In most captive breeding programs, the status of the population is reviewed periodically, and managers generate or update recommendations for every individual in the population to produce an annual or biannual Masterplan. The steps involved are fairly standard across species.

STEP 1: CALCULATE THE TARGET POPULATION SIZE

This step has been described earlier when setting the goals and purposes for the population, but the target size needed to achieve a goal will vary over time as levels of gene diversity and population characteristics change.

STEP 2: CALCULATE DESIRED GROWTH RATE

The difference between the target population size and the current population size helps to determine the desired growth rate for the population. Population managers will need to decide how rapidly they wish to grow (or decline) to the target size, which may be dependent on genetic considerations, biological constraints, space availability, and other factors. They can then calculate the average growth rate needed over the defined period to reach their goals.

If the desired growth rate is negative (e.g. a population's target size is smaller than its current size), zoo professionals need to consider carefully how to manage the decline. If the final goal is to phase out the captive population, reproduction can be stopped and decline will come from attrition as animals gradually reach the end of their life span. Conversely, if the final goal is to decrease the population size but still maintain a stable population, population managers need to be careful not to affect the age structure of the population negatively. A complete breeding moratorium may jeopardize future viability, since no young individuals will be available to fill the reproductive age classes. As a result, managers often aim for a gradual decline, in which a few births occur each year to ensure future reproduction but not to maintain the current size.

If the desired growth rate is positive, the population will need more births and/or imports than deaths and/or exports. If the population has grown strongly in the past (at the desired rate or higher), it will likely be able to meet the demographic goals. However, the desired growth rate may be much higher than the growth rate observed historically or calculated from the life table as described earlier, which can be potentially confusing. In such cases, it becomes difficult to determine whether the population actually has the biological potential to reach the desired growth rate, recalling that the historically observed rates reflect the management practices of a given time period, and are often affected by small sample sizes. If so, how can we use demographic data to determine what the biological potential of the population might be?

One frequently used method is to look at annual growth rates of the captive-born segment of the population; these annual rates can help managers determine whether the population has ever reached the desired growth rate in the past, and/or how long higher growth rates were sustained. Another important strategy is to evaluate vital rates in the life table and use simple "what if" modeling to assess the impact of potential management changes. If fecundity rates in the life table are low (because they reflect a period in which a large portion of breeding-aged animals were not in reproductive situations), managers can adjust fecundity rates in the reproduction age classes to reasonable levels and determine how much impact those changes have on the projected growth rate. Setting these levels is often challenging, but simple scenarios of likely management actions, such as "what if each female bred once every 5 years" or "what if all females were in a breeding situation, but only half the females bred successfully," would help assess the efficacy of such management actions. Similarly, if mortality rates in the life table are high and specific management practices can be identified that might lower them, population managers can test their impact on the growth rate. Such analyses can help determine if a desired growth rate is achievable, given the population's current structure and potential management actions, and also help managers decide where to invest research and management effort. For an example of the application of these types of analyses to the management of the AZA Asian elephant SSP, see Faust, Earnhardt, and Thompson (2006) and figure 19.14.

If the growth rate is inadequate for the population to be self-sustaining, the focus of the management program should shift to research on reproductive, behavioral, and other biological and husbandry aspects of management to resolve the problems.

STEP 3: CALCULATE NUMBER OF BIRTHS AND BREEDING PAIRS NEEDED

Determining the number of births needed for a given time period involves weighing multiple demographic, genetic, and management factors. The analysis combines the desired target size and time frame for growth to that size with the expected number of deaths in the upcoming year(s), based on the population's age structure and the mortality rates categorized in the life table (this includes infant mortality for the births needed). This produces a deterministic estimate of how many births will be needed to meet the population size goals. Such projections are likely most accurate for the short term (0–10 years); longer-term projections may be very different depending on how the population changes.

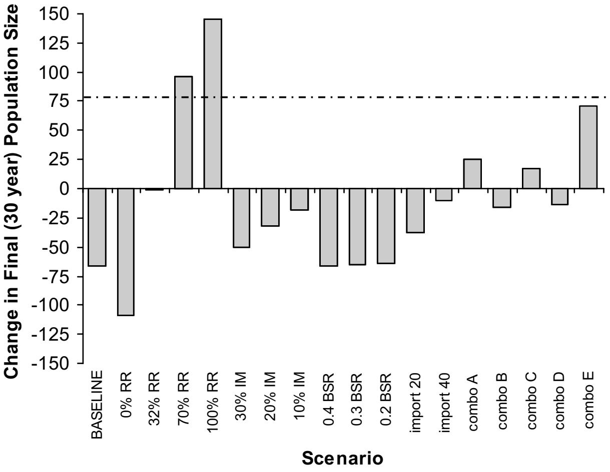


Fig. 19.14. Change in final total size of the Asian elephant SSP population after 30 years under different model scenarios.

The number of breeding pairs needed to produce the desired number of offspring will then be determined by factors such as litter size, the proportion of pairs that successfully reproduce, and the likelihood that some breeding recommendations simply will not be implemented successfully. For example, 25% of the recommended breeding pairs of golden lion tamarins fail to breed each year. Of those that do reproduce, 65% produce one litter and 35% produce 2 litters per year, with an average litter size of 1.9. Therefore, the production of 80 offspring requires 40 breeding pairs.

An alternative strategy is to assign a probability of success to each breeding pair as they are selected and to select enough breeding pairs so that the sum of the success probabilities sums to the number of desired litters. For example, a pair that had been successfully producing young over several years might receive a success probability of 0.9, while a newly established young pair that involved an animal transfer might receive a probability of 0.2. These probabilities can be based on analyses of past successes and failures to breed. For example, an analysis of 101 breeding recommendations from 1992 to 2001 by the Amur Tiger SSP found the greatest predictors of breeding success within one year to be the current location of the recommended breeders (same or different institutions) and previous reproductive success (Traylor-Holzer 2003). Recommended pairs located at the same institution and with both animals having previously produced offspring (not necessarily with each other) had an 87% probability of success; pairs at the same institution but involving at least one unproven animal had a 50% probability of success; and pairs located at different institutions at the time of recommended breeding had a 14% success rate within one year. The Tiger SSP takes these probabilities into account when making annual breeding recommendations (Traylor-Holzer, personal communication).

The ideal goal is to produce the desired number of offspring from the best possible genetic matches. Since pairings among the genetically best choices may not be sufficient to produce enough offspring, genetically less desirable pairings may be needed simply for demographic reasons. Therefore, breeding pairs are selected on the basis of a number of factors, including genetics, age, past breeding experience, and location.

TABLE 19.4. Kinship coefficients between all living animals from the pedigree in figure 19.10

ID	10	11	16	17	18
10	0.500	0.063	0.000	0.000	0.188
11	0.063	0.500	0.125	0.125	0.328
16	0.000	0.125	0.625	0.375	0.063
17	0.000	0.125	0.375	0.625	0.063
18	0.188	0.328	0.063	0.063	0.578
***mk* =**	**0.150**	**0.228**	**0.238**	**0.238**	**0.244**

Note: Mean kinship values are the average of the kinships for each individual and are shown on the bottom row. The genetically most valuable individual is number 10, with the lowest mean kinship.

STEP 4: CALCULATE MEAN KINSHIP VALUES

When selecting animals for breeding, it is useful to rank individuals according to their genetic importance in preserving gene diversity in the population. Individuals carrying alleles from overrepresented founders are not as genetically valuable as those carrying alleles from underrepresented founders. Two measures of genetic value need to be calculated for each individual: mean kinship and genome uniqueness.

Before these calculations are made, animals that are no longer likely to breed should be removed from the data set, as they are genetically senescent and no longer relevant to the genetics of the population. This includes individuals that are sterilized, have debilitating medical problems, whose behavior will not allow breeding, or who are postreproductive.

The mean kinship of an individual (mk_i) is the average of the kinship coefficients between an individual and all living individuals (including itself) in the population (Ballou and Lacy 1995):

$$mk_i = \frac{\sum_{j=1}^{N} k_{ij}}{N}, \tag{19.9}$$

where k_{ij} is the coefficient of kinship between individuals i and j, and N is the number of living animals in the population (ibid. 1995; Toro 2000). The kinship coefficient is the probability that 2 alleles, taken at random from 2 individuals, are identical by descent (Crow and Kimura 1970). It is a measure of the genetic similarity of the individuals and is the same as the inbreeding coefficient of any offspring they would produce. Individuals who are carriers of rare alleles will have low values of *mk* because they have few relatives in the population, whereas individuals who carry alleles shared with many individuals will have a high *mk*. Ranking individuals according to their *mk* values provides a quick method for identifying genetically important animals.

Minimizing mean kinship is directly related to maximizing gene diversity retained:

$$GD_t = 1 - \overline{mk.}, \tag{19.10}$$

where $\overline{mk.}$ is the average of the mk_i in the population. Thus, minimizing $\overline{mk.}$ maximizes gene diversity retained.

Management programs designed to minimize kinship using the mean kinship strategy have been demonstrated to work through computer simulations (Ballou and Lacy 1995) and experimental breeding (Montgomery et al. 1997; Toro 2000). Values of *mk* for the sample pedigree in figure 19.10 are shown in table 19.4.

STEP 5: CALCULATE GENOME UNIQUENESS VALUES

Another measure of genetic importance is genetic uniqueness (gu_i), which is the probability that a gene carried by an individual is unique (i.e. not carried by any other living animal). Genetic uniqueness is calculated using the gene drop analysis described above and can also be used to rank individuals by genetic importance (Ballou and Lacy 1995; Ebenhard 1995; Thompson 1995).

Genome uniqueness and mean kinship are often correlated, but there are certain pedigree configurations where mean kinship does not clearly identify valuable individuals, whereas genome uniqueness does (offspring for which one parent is descended from overrepresented founders and the other is from underrepresented founders; Ballou and Lacy 1995). Typically, when screening individuals for genetic importance, mean kinships are considered first, and genome uniqueness is then checked to ensure that carriers of vulnerable alleles are also included in the breeding recommendations.

STEP 6: CALCULATE KINSHIP COEFFICIENTS OF ALL POSSIBLE PAIRINGS

The kinship coefficient between 2 individuals is the same as the inbreeding coefficient of any offspring they produce. Since kinships are used to calculate mean kinship values, they can also serve to indicate potential offspring's inbreeding levels.

STEP 7: USE THE MEAN KINSHIP TABLE TO IDENTIFY PAIRINGS

A mean kinship table (table 19.5) is often used in conjunction with the kinship table (table 19.4) when making pairings. Selecting breeding pairs involves 3 genetic considerations: the mean kinships of the individuals involved; the difference in their mean kinships; and their kinship to each other. Ideally, the lower the average mean kinship of the pair, the better, since minimizing mean kinship equates to maximizing genetic diversity. The *mk* of the male and female should also be similar. When the *mk* values are different, offspring produced have both rare and common alleles. If this occurs often, it is

TABLE 19.5. Mean kinships from a subset of the European populations of sun bear, *Helarctos malayanus*

	Males					Females				
Rank	Stbk#	MK	Known	Age	Location	Stbk#	MK	Known	Age	Location
1	136	0.0000	100.0	25	ROSTOV	125	0.0000	100.0	27	ROSTOV
2	175	0.0000	100.0	20	JIHLAVA	167	0.0000	100.0	20	FRANKFURT
3	182	0.0000	100.0	18	USTI	173	0.0000	100.0	21	HILVARENB
4	207	0.0000	100.0	13	BELFAST	176	0.0000	100.0	20	JIHLAVA
5	210	0.0000	100.0	16	TOUROPARC	179	0.0000	100.0	18	USTI
6	122	0.0245	100.0	27	BASEL	180	0.0000	100.0	18	USTI
7	206	0.0245	100.0	18	KOLN	181	0.0000	100.0	18	USTI
8	169	0.0368	100.0	20	OLOMOUC	134	0.0245	100.0	25	BASEL
9	204	0.0368	100.0	12	FRANKFURT	172	0.0368	100.0	20	OLOMOUC
10	145	0.0951	100.0	23	LODZ	191	0.0368	100.0	14	BELFAST
11	203	0.1311	50.0	12	MADRID Z	197	0.0397	87.5	13	LA PLAINE
12	205	0.1392	100.0	11	BERLIN TP	159	0.0429	100.0	21	ZAGREB
13	218	0.1444	100.0	3	HILVARENB	201	0.0491	100.0	12	MADRID Z
14	124	—	—	27	KYIV ZOO	214	0.0491	100.0	7	USTI
15	149	—	—	23	BERLINZOO	217	0.0491	100.0	3	OLOMOUC
16	164	—	—	21	MUNSTER	211	0.0511	75.0	7	KOLN
17						213	0.0511	75.0	7	KOLN
18						165	0.0736	50.0	20	HILVARENB
19						185	0.0736	50.0	17	PARIS ZOO
20						192	0.0798	50.0	14	KOLN
21						193	0.0798	50.0	14	KOLN
22						139	0.0951	100.0	24	LODZ
23						142	0.1189	100.0	24	BERLINZOO
24						174	0.1281	100.0	18	BERLIN TP
25						212	0.1311	50.0	7	MUNSTER
26						198	0.1331	100.0	13	BERLIN TP
27						160	—	—	21	TOUROPARC
28						178	—	—	25	SOFIAZOO
29						195	—	—	14	TOUROPARC

Note: Males and females sorted by ascending mean kinship values (courtesy of Dr. Lydia Kolter, Zoologischer Garten Köln). "Known" is the percentage of an animal's pedigree that is known. Mean kinship values cannot be calculated for individuals with 0% known. Animals with mean kinship values of 0.0 are founders that have not yet produced offspring (i.e. potential founders).

difficult to increase the frequency of the rare alleles independently of the common ones. Finally, the kinship of the pair should be evaluated to keep inbreeding low. In some highly inbred populations (e.g. Przewalski's horse, where the average inbreeding coefficient in the population is above 0.30), it is impossible to avoid inbreeding. A common rule is to keep the inbreeding of offspring less than the average mean kinship of the population (some managers use less than one-half the average mean kinship)—this provides a sliding scale that increases as closed populations become unavoidably more inbred. Taking these factors into consideration, the mean kinship table is used until the desired number of pairings has been made.

An alternative to using the detailed mean kinship tables and PM2000 is to use the software MateRx. MateRx (Ballou 1999) calculates a single numeric index indicating the relative genetic benefit or detriment to the population of breeding for all possible male/female pairs in the population. This index, the mate suitability index (MSI), is calculated for each pair by considering the mean kinship values of both animals, the difference in the male's and female's mean kinships, the kinship of the male and female, and the amount of unknown ancestry in the pair. MSI ratings range from 1 (very beneficial) through 6 (very detrimental—pairing should only be used if demographic considerations override preservation of genetic diversity). MateRx is designed to simplify pairing decisions by condensing all that is known about the genetics of a pair into a single number. MateRx is useful for species such as colonial penguins in which managers cannot easily establish good breeding pairs but can discourage detrimental breeding pairs (by removing eggs). It is also useful for finding alternative pairings in species that require mate choice and for facilitating good genetic management in less intensively managed or less cooperative programs.

STEP 8: MAKE RECOMMENDATIONS FOR EVERY ANIMAL IN THE POPULATION

A captive breeding plan usually provides recommendations for every animal in the population. In addition to breeding recommendations, other recommendations are often made:

- separating/contracepting individuals to prevent breeding
- importing individuals to increase population size or improve population structure (age and/or sex)
- exporting individuals to decrease population size or improve population structure
- removing individuals from a captive population for release into the wild (reintroduction)
- maintaining individuals to breed at another time
- designating an individual as surplus to the program (no longer needed in the population)
- conducting a reproductive evaluation (e.g. determine whether females are cycling, examine sperm quality)
- collecting and banking gametes for future use
- culling a specimen to make space available (note that this management option is somewhat controversial and is rarely used in some regions while well accepted in others)

These management actions can be used to manage a population's size and structure, and ultimately to ensure reaching the long-term demographic and genetic goals of population management.

PARTICULAR CHALLENGES

MANAGING NEW FOUNDERS

For species with short generation times, regular importation of founders, when possible, may be an alternative strategy for maintaining high gene diversity when population sizes and growth rates in zoos cannot be high enough to compensate for the rapid loss of *GD* due to drift. For some species, particularly those regularly available through rehabilitation efforts, there may be regular opportunities to incorporate new founders into the population which could completely counteract the loss of genetic diversity due to drift and inbreeding.

The genetic contribution of adding new founders can be measured as the change (increase) of genetic diversity in the population if that founder were to successfully breed. This is done by calculating the current f_g, adding to it 1 or some fraction of an f_g for each founder added, and converting it back to *GD* using the formulas presented above. It is probably unrealistic to assume that each founder will produce enough offspring to contribute a full f_g to the population. Mansour and Ballou (1994) found that over time, the average f_g contributed by a set of new founders of golden-headed lion tamarins, *Leontopithecus chrysomelas*, was $0.4f_g$ per founder. For example, if 4 new founders were added to a population that had retained 92.0% of its gene diversity, how much might they boost gene diversity? 92% gene diversity equates to $6.25f_g$. Assuming each founder contributed $0.4f_g$, then the total f_g would be $6.25f_g + (0.4f_g \times 4) = 7.85f_g$. This equates to 93.6% gene diversity retained; adding 4 founders increased gene diversity by 1.6%. The lower the gene diversity, the more it will be boosted by adding new founders. Odum (1994) provides a method for calculating the number of offspring each new founder should produce to ensure optimal representation of each founder in the population.

Importation of new founders may take 2 forms: one large, one-time importation versus a series of imports of fewer animals over a longer time period. Factors include limitations on quarantine space, the ability to absorb new animals, and founder availability now and in the future. PM2000 allows modeling of these various scenarios to determine optimum strategies for importing new founders into a particular population.

When founders are added, their lineages will be rare and their mean kinships will be 0.0 until they produce offspring. If possible, managers should avoid pairing new founders with overrepresented lineages (high mean kinship animals), as this will link rare and common alleles in the offspring, which is difficult to correct later. However, pairing with a known successful breeder might be necessary to ensure capturing the new founder genetic diversity. If several new founders are available, consideration should be given to pairing them with each other. If several pairs of new founders exist, pairing them in several permutations may be possible. Further pairing of offspring from these founders may allow the *mk* values for the imports to begin to approach that of the rest of the population. Only after several generations would this new lineage be folded into the main population.

IMMIGRATION AND EMIGRATION

Transfers between regions or with dealers can result in situations that compromise good population management. Often animals transferred from one region to another are individuals from the bottom of the mean kinship list in the shipping region. In the receiving region, these may be appropriately treated as founders and their genes incorporated into the population as such. However, if the source region later is interested in importing animals from the receiving region, a global population analysis should be done to determine the relationships of potential imports to the current source population. This also applies to animals sent to dealers.

Sending animals to dealers who do not keep adequate records can result in animals going to another zoo and then reappearing in the managed population with the knowledge that they are related to that population, but without knowing the specific nature of the relationships (pedigree). This is not uncommon in hoofstock; thus, all animals leaving the managed population should be marked with a transponder, brand, or tattoo for permanent identification.

Zoos planning to receive animals from different regions should always check available studbooks (both regional and international) and the ISIS database. In the near future, ZIMS will also be available to provide one lifetime record for each specimen in ISIS zoos and studbook.

UNKNOWN ANCESTRY

Lack of individual identification and uncertain parentage complicate both demographic and genetic analyses, a problem common in species managed as herds (individual dams are often not identified) and in species in which more than one breeding male has access to females, resulting in uncertain paternity. Population managers may develop assumptions for demographic data in order to calculate fecundity or mortality rates for animals whose birth dates are not known. For example, the median age for first reproduction in the population could be used to determine a female's birth date when she gives birth for the first (known) time.

While molecular genetic analyses may be used to resolve pedigree unknowns, this is often too expensive or impossible if the unknown ancestors are no longer available for sampling. For animals with unknown ancestry, the options are to exclude them from the population; to use only the known portion of the pedigree in the calculations; or to make various pedigree assumptions and compare the differences. In any case, replacing unknown parents with assumed parents should only be done in the analytical studbook, not the official studbook.

Exclude individuals with unknown parentage or ancestors from the managed population. This approach is practical only if few individuals are involved and they are not otherwise important to the population. In such cases, a determining factor in the decision will be the percentage of an individual's alleles that have descended from unknown ancestors. Small percentages of unknown ancestry may be acceptable. Animals that have some degree of unknown ancestry but also have ancestors whose alleles are relatively rare could be kept in the population to perpetuate the contribution of underrepresented founders. Deciding what to do typically involves weighing the risks of losing genetic diversity against the risk of inbreeding: removing animals will remove their genetic diversity as well, but keeping them in and assuming they are unrelated may result in unwanted inbreeding. However, the genetic costs of excluding animals with unknown ancestry generally are greater than the costs of including them and making incorrect assumptions about their paternity (Willis 1993).

Leave unknown individuals in the population. PM2000 software will calculate mean kinship values on only that proportion of the pedigree or genome that is known (Ballou and Lacy 1995). Again, this is suitable if only a small proportion of the pedigree is unknown (e.g. less than 20%). As the proportion of the pedigree that is unknown increases, estimates of relationships among animals become unreliable since the genetic calculations are based on a smaller and smaller proportion of the pedigree.

If questionable parentage is limited to only a few individuals, run the genetic and demographic analyses under all possible combinations to give the complete range of outcomes. If the results are insensitive to parentage possibilities, the questionable parentage should have little effect on management decisions. If the results are sensitive, the pedigree should be explored. An alternative strategy is to select the worst-case scenario in terms of gene diversity or inbreeding as the basis for management decisions.

Use the potential parent most likely to be the true parent for the pedigree analysis. When using this strategy, be aware that parental assumptions based on behavior or dominance can be prone to error.

Create hypothetical parents that represent an agglomeration of all potential parents. If the potential parents are all equally likely to be the true parent, then a new average hypothetical parent can be created by giving it a "dummy" ID number for the genetic analysis and considering it the sire (or dam) of the offspring in question. The founder contribution of the hypothetical parent is then calculated as the average of the founder contributions of the possible parents, weighing the average by the probability associated with the likelihood of different parents being the true parent. Creating an "average" parent is most appropriate if the founder contributions of the potential parents are not too different. If the differences between potential parents are very large (especially if the potential parents are founders), other options should be considered. Inbreeding coefficients are calculated by assuming that the hypothetical parent is unrelated to its mate and the rest of the population. In most cases, this will underestimate inbreeding coefficients for the descendants of the unknown parent(s). To avoid inbreeding, one could assume worst-case scenarios: i.e. the closest relationships among putative parents. However, the worst-case scenario for inbreeding is usually not a good strategy for maintaining gene diversity (Willis 1993). Instead, a second set of assumptions and hypothetical pedigree could be constructed to represent the best-case scenario for retaining gene diversity by assuming no relationships among putative parents (Willis 1993).

When groups have been managed for several generations without individual animal identification, create hypothetical pedigrees. "Black box" populations are common for species kept in large groups. The AZA Species Survival Plan for Grevy's zebra is an example of using a worst-case strategy to incorporate at least some of the founder potential. With this species, there were several very large herds without individual parentage being recorded. However, there was considerable useful information: each herd had been established by a number of founder animals (usually one stallion and several mares); there had been limited further immigrants of known origin introduced to the herds; only one stallion was in each herd in any breeding season; and the birth dates of all individual foals born into the herds were documented.

It was first assumed that a single founder female established the herd; that is, all actual founder females were amalgamated into a hypothetical founder female that was assigned a dummy ID number. All offspring born during the first few years (or a period of time equal to the age of sexual maturity for the species) were then considered offspring of the herd stallion at the time of conception and this hypothetical dam. After this first cohort, it was assumed that daughters of this pair would have matured and bred with their father. Therefore, an F_1 hypothetical female was created. The parents of this female were the herd stallion and the hypothetical founder female. Thereafter, all offspring born in the herd traced 75% of their genes to the founder stallion and only 25% to the hypothetical founder female.

Such a strategy is most useful if the herd was established by known founders. Obviously, this strategy will underestimate the actual number of founders for the herd as well as the genetic diversity involved. Inbreeding coefficients will be overestimated when a number of different breeding animals are combined under one hypothetical parent. However, within the herd, inbreeding coefficients will be relative, and closely related individuals will have higher coefficients than less closely related individuals. When hypothetical parents or founders are created to satisfy genetic analysis requirements, individuals with unknown ancestors in their pedigree should be clearly labeled to indicate that both their founder contributions and inbreeding coefficients are based on hypothetical data in the analytical studbook.

Estimate average kinship and create a hypothetical pedigree for a group of individuals with unknown pedigrees. A more quantitative approach to constructing pedigrees in black-box populations is to estimate the average kinship of individuals coming out of the black box. First, estimate the number of individuals that likely founded or provided genetic input into the black box and convert this to the number of unique founder alleles (Willis 2001). For example, if there were known to be one male and 2 female founders, then 3 founders were involved, contributing a total of 6 alleles. If there were 2 males and 2 females, but they were known to be related (brothers and sisters), then only 4 alleles contributed. From the number of founder alleles (A), the average kinship ($\bar{k}$) among the group of animals emerging from the black box (N) can be calculated from

$$\bar{k} = \frac{2N - A}{2A(N-1)} \tag{19.11}$$

(corrected from equation 10 in Willis 2001).

A hypothetical pedigree for the ancestors of the emerging animals can then be created so that the emerging animals have a level of kinship that best approaches $\bar{k}$ (often it is not possible to create a pedigree that exactly produces the desired $\bar{k}$). Table 19.6 shows several common pedigree structures that can be used to create animals with specific levels of kinship (Willis 2001).

For example, if a black box were founded by 3 individuals (so $A = 6$) and there were 10 animals emerging from the black box ($N = 10$), then their average kinship from the above equation would be 0.129. This level of kinship among the 10 is most closely re-created by making them all half-sibs (table 19.6). More details on using the approach are available in Willis (2001).

Other methods for dealing with incomplete pedigrees can be found in Lutaaya et al. (1999), Marshall et al. (2002), and Cassell, Ademec, and Pearson (2003).

MANAGEMENT OF DELETERIOUS AND ADAPTIVE TRAITS

Relatively high frequencies of deleterious recessives have been described in a number of captive animal populations that were founded by a small number of individuals (Laikre 1999). Examples include blindness in wolves, *Canis lupus* (see Laikre, Ryman, and Thompson 1993), albinism in bears, *Ursus* sp. (Laikre et al. 1996), gingival hyperplasia in silver foxes, *Vulpes vulpes* (see Dyrendahl and Henricson 1959), and hairlessness in red ruffed lemurs, *Varecia rubra* (see Ryder 1988; Nobel, Chesser, and Ryder 1989).

TABLE 19.6. Pedigree structures that create specific average levels of kinship among a set of relatives

Average kinship ($\bar{k}$)	Pedigree structure that creates that average kinship
0.375	Full siblings of full siblings
0.25	Full sibs (share 2 parents)
0.1875	Share one parent and one grandparent
0.125	Half-sibs (share one parent)
0.0625	First cousins (share 2 grandparents)
0.03125	Share one grandparent
0	None

Typically, most deleterious alleles will be rare in a large, normally outbreeding population (Frankham, Ballou, and Briscoe 2002). However, when populations pass through a bottleneck, such as founding a captive population, previously rare alleles that survive the bottleneck may increase significantly in frequency. If an allele with a low prebottleneck frequency survives the bottleneck, its frequency will increase to at least $1/(2N)$ after the bottleneck, where N is the number of animals in the bottleneck. After the bottleneck, additional inbreeding will increase the likelihood of expression of deleterious recessive alleles that do persist in the population.

As species in many captive breeding programs become more inbred, we can predict that deleterious alleles will be detected with increasing frequency. Deleterious alleles are a natural component of the genetic diversity of all species, and the temptation will be to exclude from reproduction those animals exhibiting the trait (i.e. select against it). Population managers need to first ascertain, through pedigree analysis, veterinary examination, and other kinds of research, that the traits observed are truly genetically determined. This will be difficult in some cases, since sample sizes may be small and genetic mode of inheritance complicated. Second, it is important to understand the ramifications of strategies to select against the trait. Ralls et al. (2000) and Laikre, Ryman, and Thompson (1993) carefully evaluated the effects of selecting against traits on the overall genetic diversity of the population. Until the genetic basis is determined and the implications of selection are evaluated, captive breeding programs should be very hesitant to automatically impose selection strategies.

Some biologists suggest that population managers select for specific or adaptive traits or allow natural mate choice in captive breeding programs to enhance reproduction (e.g. variation at the major histocompatibility complex (MHC) loci: Hughes 1991; Wedekind 2002). Others have recommended that selection of breeding individuals be based on individual levels of heterozygosity estimated from biochemical methods. As mentioned earlier, heterozygosity at a few loci is often a poor indicator of overall individual heterozygosity. In addition, specific selection for known heterozygous loci (e.g. MHC loci: Hughes 1991) may select against heterozygous loci not sampled and decrease the overall level of genetic diversity in the population (Haig, Ballou, and Derrickson 1990; Miller and Hedrick 1991; Gilpin and Wills 1991; Vrijenhoek and Leberg 1991). Any selection, be it for specific genetic markers or phenotypic traits, will further reduce genetic diversity and increase inbreeding, since selection will reduce the number of animals breeding and hence the effective population size (Lacy 2000b). Additionally, such selective measures will enhance the adaptation to the captive environment and reduced fitness in the wild (Margan et al. 1998; Ford 2002; Kraaijeveld Smit et al. 2006).

GROUP MANAGEMENT

The strategy of minimizing mean kinship may not be practical for populations in which animals are not individually identified (e.g. herd species, tanks of fish, colonies of birds). Such populations, for which detailed pedigree information is unknown and/or specific breeding pairs cannot be reliably controlled, are generally referred to as groups. Groups can range from species in which individuals are identifiable, but pairings cannot be controlled (e.g. some penguins) to species in which individuals cannot be distinguished or counted at any life stage (corals, eusocial insects).

Genetic management of groups is a developing science and not frequently done (except for *Partula* snails; Pearce-Kelly and Clarke 1995). Proposed methods for group management include the following.

Maximizing effective population size. The factors that contribute to increases in effective population size can be manipulated through the introduction and/or removal of individuals. Such management actions include managing for equal sex ratio among breeders, producing an equal number of offspring per female, frequently rotating males in and out of breeding situations, maintaining a constant population size, and regularly moving animals (4–5 effective migrants per generation) among groups. For example, Princeé (1995) proposed a scheme that minimizes inbreeding and maximizes N_e by a regular, systematic procedure of rotating males among groups. How much can be accomplished will depend on the social and husbandry requirements of specific species.

Group mean kinship. In a metapopulation of groups, average inbreeding and mean kinship values of groups (average relatedness of one group to all groups in the metapopulation) can be calculated using information on changes in group sizes (number of individuals), migration among groups, and sexual mode of reproduction (e.g. selfing versus cloning; Wang 2004). Much like mean kinship of individuals, these calculations allow managers to identify which groups should send or receive migrants with other groups. Research in this area is continuing.

Molecular analysis of population structure. Molecular genetic analyses of samples from groups can be used to calculate measures of genetic divergence between groups (F_{st}, genetic distance; Frankham, Ballou, and Briscoe 2002). Animals can then be moved to reduce genetic differences. This strategy is controversial because, as mentioned above, it bases genetic management on maintaining diversity in a small set of loci, but likely reducing diversity over the remainder of the genome.

GENETICS OF REINTRODUCTIONS

The selection of individuals for reintroduction should consider genetics (Ralls and Ballou 1992; Ballou 1992, 1997). A common genetic goal of reintroduction programs is the eventual release into the wild of all the potential genetic diversity contained in the captive population (Earnhardt 1999). Reintroduced animals should not be inbred, as they may be less able to cope with the wild environment than non-inbred individuals (Jiménez et al. 1994). During experimental reintroductions, when risks to animals may be high, managers should choose animals for reintroduction with care so as not to release those whose removal from the captive population will reduce its genetic diversity (e.g. underrepresented animals or founders should not be released; Russell et al. 1994). However, as reintroductions become more successful, release of animals of higher genetic value is acceptable in order to transfer the full component of genetic diversity from the captive population to the wild (Ballou 1992). The software MetaMK (Ballou 1999) and PM2000 (Pollak, Lacy, and Ballou 2007) both assist with choosing individuals to move between populations and have been used in selecting animals for reintroduction (Ralls and Ballou 1992).

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APPENDIX 19.1

Software Programs for Managing and Analyzing Data for Population Management

Software	Developer	Primary purpose	Features	Source
ARKS	ISIS	Animal records management for individual zoos	Animal records management with some analyses; multiple species	Available to staff of ISIS member zoos. (ISIS 2004b)
SPARKS	ISIS	Studbook records management	Manages studbook data with some basic analyses of demography, genetics, census, and reproduction	Available to staff of ISIS member zoos. (ISIS 2004)
GENES	R. C. Lacy	Genetic management	Using a pedigree exported from SPARKS, calculates inbreeding coefficient, mean kinships, founder statistics. Evaluates effect of making pairings on genetics of population. OUTDATED	Free. Distributed with SPARKS software. (Lacy 1993)
Demog	J. D. Ballou and L. Bingaman Lackey	Demographic analyses	A spreadsheet that calculates a life table from data exported from SPARKS. Limited demographic modeling. OUTDATED	Free. (Ballou and Bingaman 1992)
PM2000	J. P. Pollak, R. C. Lacy, and J. D. Ballou	Population management	Pedigree and demographic analyses, population goal setting, genetic management recommendations. Uses data exported from SPARKS and PopLink.	Free. Available from Web site of R. C. Lacy. (Pollak et al. 2007) www.vortex9.0rg/home.html
PMx	J. P. Pollak, R. C. Lacy, and J. D. Ballou	Population management	Update of PM2000 currently under development. Includes genetic management of groups, multiple parents. Bootstrap demographic analyses.	Free. Will be available from Web site of R. C. Lacy.
MateRx	J. D. Ballou, J. Earnhardt, and S. Thompson	Genetic management	Assigns a rating from 1 to 6 for all possible breeding pairs in the population to simplify genetic management. Uses a data file produced by PM2000 and will be a module of PMx.	Free. Distributed with PM2000. (Ballou et al. 2001)
Meta MK	J. D. Ballou	Genetic management	Evaluates effects on genetic diversity of moving animals between 2 populations.	Available from J. D. Ballou Web site at National Zoo. (Ballou 1999)
ZooRisk	J. M. Earnhardt, A. Lin, L. J. Faust, and S. D. Thompson	Population viability analysis	Uses simulations to evaluate the degree of risk for a captive population. Uses data from a SPARKS or PopLink data set.	Available at www.lpzoo.org/zoorisk (Earnhardt et al. 2005)
PopLink	L. J. Faust, Y. M. Bergstrom, and S. D. Thompson	Studbook records management and analysis	Helps maintain, analyze, and export population data for demographic and genetic management. Uses SPARKS data set, user-entered data, or (in the future) ZIMS data.	Available at www.lpzoo.org/poplink (Faust, Bergstrom, and Thompson 2006)
Vortex	R. C. Lacy	Population viability analysis	PVA modeling with options to import studbook information from SPARKS and determine pairings based on genetic criteria.	Free. Available from Web site of R. C. Lacy. (Lacy, Borbat, and Pollak 2007)
ZIMS	ISIS	Global animal records information system	Animal husbandry, health, studbook, pathology, etc., global Web-based information system currently under development. Being built by ISIS to replace ARKS, SPARKS, and MedARKs.	Will be available to staff of ISIS member zoos. (ZIMS 2007)

APPENDIX 19.2

Demographic Definitions

Symbol	Term	Definition
x	Age class	The time interval that includes an individual's age. Age class 0 includes all animals between 0 and 0.999 year of age, age class 1 includes those between 1 and 1.999, etc. Age is denoted by an x in other terms.
	Age pyramid (or distribution)	A histogram showing the structure of the population, in the form of the numbers or percentages of individuals in various age and sex classes.
SAD	Stable age distribution	The age distribution at which the relative proportions of each age class remain stable (change at the same rate) and the population growth rate remains constant.
M_x	Age- and sex-specific fecundity	The average number of same-sexed young born to animals in an age class. Fecundity rates provide information on the age of first, last, and maximum reproduction.
Q_x	Age- and sex-specific mortality rate	The probability that an individual of age x will die during that age class. $Q_x = 1 - P_x$.
P_x	Age- and sex-specific survival rate	The probability that an individual of age x will survive to the beginning of the next age class (age $x + 1$). $P_x = 1 - Q_x$.
l_x	Age- and sex-specific survivorship	The probability that a newborn individual (e.g. age 0) will be alive at the beginning of age x. Survivorship is a cumulative measure—e.g. the survivorship of age class 10 is influenced by all the survival rates in all age classes from birth until 10. $l_x = \prod_{i=0}^{x-1} p_i$.
r	Instantaneous rate of change	The rate of change in population size at any instant in time. If $r > 0$, the population is increasing; if $r = 0$, the population is stable; if $r < 0$, the population is declining.
λ	Lambda or population growth rate	The proportional change in population size from one year to the next. λ can be based on life table calculations (expected λ) or from observed changes in population size from year to year. If $\lambda > 1.0$, the population is increasing; if $\lambda = 1.0$, the population is stable or sustaining; if $\lambda < 1.0$, the population is declining. A λ of 1.11 means an 11% per year increase; lambda of .97 means a 3% decline in size per year.
E_x	Sex-specific life expectancy	Average years of further life for an animal in age class x.
	Median life expectancy/ median survivorship	The age where $l_x = 0.5$; half the individuals in the data set died before this age and half the individuals survived. This is commonly used to describe a population's survival pattern.
	Maximum longevity	The age of the oldest known individual in an analysis; the individual can be living or dead. Note that this value may change frequently, and that it is inaccurate to assume that the majority of specimens will survive to this age (e.g. it should not be used as the sole summary parameter for survival patterns).
T	Mean generation time	The average time elapsing from reproduction in one generation to the time the next generation reproduces. Also, the average age at which a female (or male) produces offspring. It is not the age of first reproduction. Males and females often have different generation times.
V_x	Sex-specific reproductive value	The expected number of same-sex offspring produced this year and in future years by an animal of age x.
	Risk (for Q_x, M_x, or any age- or sex-specific rate)	The number of individuals that have lived during an age class. The number at risk is used to calculate M_x and Q_x by dividing the number of births to and deaths of individuals in age class x by the number of animals at risk of dying and reproducing during that age class.

APPENDIX 19.3

Genetic Definitions

Term	Symbol	Definition
Heterozygosity	H_o, H_e	Observed heterozygosity (H_o): The proportion of individuals in a population that are heterozygous (have 2 different alleles) for a particular trait or genetic marker. Expected heterozygosity (H_e): The proportion of individuals in a population that would be expected to be heterozygous if the population were bred at random.
Allele diversity	A	The average number of alleles existing in a population for a set of traits or markers.
Gene diversity	GD or H_t	Another term for H_e. In genetic management, often refers to the proportion of the wild or source population heterozygosity that is retained in the analyzed population.
Founder genome equivalent	f_g or FGE	The number of equally represented founders with no loss of alleles (retention = 1) that would produce the same gene diversity as that observed in the living, descendant population. Equivalently, the number of animals from the source population that contain the same gene diversity as does the descendant population. The gene diversity of a population is $1 - [1/(2 \times f_g)]$.
Founder retention	r_i	Proportion of a founder's genome surviving in the analyzed population.
Mean kinship	mk_i	The mean kinship coefficient between an animal and all animals (including itself) in the living, captive-born population.
Average mean kinship	$\overline{mk}$	Average of mean kinships of individuals in the population. The average mean kinship of a population is equal to the proportional loss of gene diversity of the descendant (captive-born) population relative to the founders and is also the mean inbreeding coefficient of progeny produced by random mating. Average mean kinship is $1/(2 \times f_g)$. Proportion GD retained = $1 - \overline{mk}$.
Inbreeding coefficient	f	Probability that the 2 alleles at a genetic locus are identical by descent from a common ancestor to both parents.
Average inbreeding		Average of the inbreeding coefficients of all individuals in a population. The average inbreeding coefficient of a population will be the proportional decrease in observed heterozygosity relative to the expected heterozygosity of the founder population.

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20

Regional Collection Planning for Mammals

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COLLECTION PLANNING PRINCIPLES: WHY PLAN?

Cooperative collection planning is essential to the long-term viability of animal populations held in zoos and aquariums (Hutchins, Willis, and Wiese 1995). The primary goal of collection planning is to increase the sustainability of living collections and their relevance to conservation, through the strategic allocation of available zoo holding space. Taxa selected for this space are carefully targeted for their ability to support broad-based conservation goals at institutional, regional, and global levels (Foose and Hutchins 1991). The World Association of Zoos and Aquariums (WAZA) recognizes 22 administrative regions among the current organization of zoos and aquariums (see also Bingaman Lackey, appendix 3, this volume). Zoos within a number of these regions collaborate closely on decisions about which species will receive priority, how many individuals should be held, and how they will be managed. A detailed discussion of population management goals and techniques is provided in Ballou et al. (chap. 19, this volume), but the basic management programs referred to in this chapter are described in box 20.1, using the categories of the Association of Zoos and Aquariums (AZA) as an example. While this chapter focuses on regional-level planning, the 3 levels interact closely; regional planning recommendations must be informed by institutional objectives and limitations, and, similarly, institutional planning decisions need to consider the priorities of regional and global planning processes.

Historically, zoos and aquariums maintained and displayed species that reflected the personal interests and preferences of directors, curators, and zoo benefactors as well as species availability (Thomas 1987; Diebold and Hutchins 1991). The movements of animals to and from the collection did not typically follow any long-term objectives, nor were they evaluated over time to assess their relevance to regional or international conservation and management. With the accelerated decline of species in their habitats, changing attitudes regarding collecting animals from the wild, and the increased regulation of international animal transfers, planning and cooperation have become important components of zoo management. Further, the developing discipline of small population biology underlined the vulnerability of zoo collections operating in isolation (e.g. Wiese, Willis, and Hutchins 1994). Over time the institution-centric approach has shifted. Many zoos have begun planning their collections strategically, working with regional zoo associations to coordinate their planning decisions with other institutions and, in some cases, other regions (Hutchins, Willis, and Wiese 1995; Hutchins et al. 1998).

Regional collection planning has been part of mainstream zoo activities for well over a decade. Though planning activities began before this (e.g. Phipps and Hopkins 1990; Foose and Hutchins 1991; Hutchins and Wiese 1991), the call for zoos worldwide to engage in cooperative planning came in the 1993 World Zoo Conservation Strategy (IUDZG and IUCN/SSC CBSG 1993), which appealed to regional zoo associations to intensify coordination of the composition of animal collections, and to individual zoos to shift their use of space toward threatened taxa with a well-defined, conservation-directed role in their mission (Bruning 1990; Hutchins and Wiese 1991; Foose, Ellis-Joseph, and Seal 1992; Hutchins and Conway 1995). There followed considerable discussion within and between regions about how this should be achieved (e.g. de Boer 1995; Hopkins and Stroud 1995; Hutchins, Willis, and Wiese 1995; Mallinson 1995; Robinson and Conway 1995), and though that discussion continues, the following pages indicate considerable convergence on ideas and approach. Table 20.1 provides an example of the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA) regional collection plan data for felids, which is similar to the basic structure of collection plan data for the European Association of Zoos and Aquaria (EAZA) and AZA Taxon Advisory Groups.

Regional collection planning for mammals, and for larger mammals in particular, can be a slow and difficult process. Populations of long-lived taxa show considerable inertia, are

Box 20.1 Species Management Categories

EAZA, ARAZPA, and AZA have each developed cooperative species management programs; although each region's programs operate under different names, the basic program definitions and goals are quite similar. AZA's programs are described here as a representative example of the types of regional programs in use today.

***Species Survival Plan* (*SSP*)** programs provide intensive genetic and demographic management, including the maintenance of studbooks. SSP programs are led by a species coordinator, who works with institutional representatives and a population management advisor to develop breeding recommendations and a Masterplan for the species. All AZA member facilities holding SSP species are required to fully participate in the SSP partnership and process.

***Population Management Plan* (*PMP*)** programs provide breeding and transfer recommendations for populations in need of more moderate management. The goal is to enhance population sustainability, but, unlike SSPs, compliance is not mandatory. PMP programs require studbooks and a population management advisor.

difficult and expensive to move around, and, as they can be the jewel in the crown of many zoo collections, can require the application of considerable political skill to effect necessary change (Graham 1996). Despite these difficulties, it is now widely accepted that effective strategic, cooperative planning must be in place if zoos are to secure a diverse array of genetically and demographically healthy populations of key species for the future (Hutchins, Willis, and Wiese 1995; Allard and Hutchins 2001; Lees and Wilcken 2002; Smith et al. 2002). Further, cooperative collection planning can reduce the need for importation of animals from the wild, reduce the production of surplus animals and associated ethical concerns (Koontz 1995; Graham 1996; Carter and Kagan, chap. 21, this volume), facilitate permitting processes, make the most efficient use of available resources, and maximize the conservation impact of regional zoo associations and their members.

INTERNATIONAL APPROACHES: DIFFERENT REGIONS, SIMILAR GOALS

Although regional collection planning is by no means a new concept, widespread implementation of strategic, cooperative planning is still gaining traction in the international zoological community. It is a testament to the changing approaches to zoo and aquarium collection management that, in the first edition of this volume, collection planning was not mentioned at all (Kleiman et al. 1996), and it now is the subject of an entire chapter.

Of the 3 zoo regions currently actively engaged in regional collection planning (North America, Europe, and Australasia), all use Taxon Advisory Groups (TAGs) as the primary vehicle for development and implementation. TAGs are specialist groups focusing on higher-order taxa (e.g. felids, antelopes, prosimians) and generally comprise zoo curators, directors, keepers, and other zoo staff committed to the management and conservation of taxa falling under the TAG umbrella (Hutchins and Wiese 1991). External specialists from conservation organizations such as the International Union for Conservation of Nature's Species Survival Commission (IUCN-SSC) Specialist Groups and university researchers frequently act as advisors to the TAGs. Further, all have worked to define priority taxa and to assess how much exhibition, breeding, and holding space should be allocated to each. Although the regional TAGs operate independently, they often share information and, when appropriate, work together toward common goals.

As zoos have begun implementing cooperative, strategic planning, it has become apparent that although the underlying goals are similar, different regions face different challenges, requiring different solutions and approaches.

In North America, the strategic collection planning process was first described in detail in 1995, by Michael Hutchins, Kevin Willis, and Robert Wiese of the AZA (Hutchins, Willis, and Wiese 1995). Under this system, collection planners develop and apply well-defined selection criteria (see table 20.2) to rank taxa according to their potential ability to contribute to conservation action, display needs, education and outreach objectives, research priorities, and more. Each recommended species has a stated role, and all new acquisitions must be justified using the agreed-on selection process. There must always be a degree of flexibility in collection management, but this approach to planning is designed to ensure that exhibit and holding space is optimized for the benefit of captive populations as a whole.

AZA TAGs develop regional collection plans (RCPs) that recommend taxa for cooperative management. Although some TAGs had been developing plans independently for nearly a decade, specific standards for RCP structure and process were first defined by AZA's Wildlife Conservation and Management Committee (WCMC) in 1998 and published in the *AZA Conservation Programs Resource Guide* in 2000 (AZA WCMC 2000). Under these guidelines, RCPs are submitted to the AZA WCMC, which evaluates plan structure, process, and recommendations. Once WCMC approves an RCP, it is published and distributed to AZA members via the AZA Web site. TAGs are required to update and resubmit their RCPs for review every 3 years.

EAZA TAGs follow a similar, though less formal process. EAZA membership encompasses over 250 institutions in more than 30 countries speaking multiple languages and representing a wide range of cultural and economical backgrounds. This raises an assortment of logistical issues that have an impact on planning, ranging from different permitting requirements, husbandry standards, transportation and trade restrictions, and more. Over the years, the vast majority of the 40 EAZA TAGs have produced Regional Collection Plans. At this time, EAZA RCPs do not have to be formally endorsed by the European Endangered Species Programme (EEP) Committee, the EAZA body that oversees all animal collection management issues within EAZA. Draft and final plans are published on the EAZA Web site and updated as needed.

With relatively few zoos, considerable geographic isolation, and complex governmental restrictions, the imperative to plan

TABLE 20.1. Summary of the Australasian regional collection planning process for Asian Felidae

Taxon	Space allocation (01/01/2000)		Recommended for regional collection	Target pop. size	Management category*	Rationale (extracts only)
	Current	Planned				
Lion (subspecies hybrid) *Panthera leo persica x Panthera leo* spp.	3	5	No	0	Phaseout	Region can sustain only one large Southeast Asian felid. Replace with priority large Asian felid (*P. tigris sumatrae*).
Asiatic golden cat *Catopuma temminckii*	6	10	Yes	20+	Population Management Program	Small felid for Southeast Asian geographically themed exhibits. Southeast Asia is the priority region for outreach activities. Opportunities to generate support for and illustrate *in situ* work in Southeast Asia.
Fishing cat *Prionailurus viverrinus*	10	17	Yes	20+	Population Management Program	Small felid for Southeast Asian geographically themed exhibits. Southeast Asia is the priority region for outreach activities. Opportunities to generate support for and illustrate *in situ* work in Southeast Asia.
Clouded leopard *Neofelis nebulosa*	2	8	Yes	20+	Population Management Program	Medium-size felid of conservation significance for Southeast Asian geographically themed exhibits. Southeast Asia is the priority region for outreach activities. Opportunities to generate support for and illustrate *in situ* work in Southeast Asia. *Note: This taxon was later removed from the plan due to lack of availability of good founder stock. The situation will be reviewed annually.*
Persian leopard *Panthera pardus saxicolor*	8	9	No	0	Phaseout	Regional population not viable. No good founder stock available. Replace with priority taxon.
Tiger (subspecies hybrid) *Panthera tigris*	15	20	No	0	Phaseout	Region can sustain only one large Southeast Asian felid. All tiger spaces to be allocated to *Panthera tigris sumatrae.*
Sumatran tiger *Panthera tigris sumatrae*	15	35	Yes	40+	Population Management Program	Large felid for Southeast Asian geographically themed exhibits. Southeast Asia is the priority region for outreach activities. Opportunities to generate support for and illustrate *in situ* work in Southeast Asia.
Snow leopard *Uncia uncia*	8	10	Yes	20+	Population Management Program	Medium-size Asian felid of conservation significance. Requires greater space commitment to be viable.

Source: Data taken from the 2000 ASMP Regional Census and Plan (Wilcken et al. 2000), the 2000 Carnivore TAG Action Plan (Walraven 2000), and from ASMP program outlines for the taxa listed (unpublished).

**Note:* In Australasia, Population Management Programs (PMPs) are similar to AZA PMPs in being primarily aimed at sustaining zoo populations. However, in Australasia, strategic plans are required for all PMPs, and compliance with all recommendations is mandatory and a requirement of ARAZPA membership. Also, within PMPs there are different levels of management intensity—high and low specimen-level management, and group management. All felid taxa are managed at specimen level and at the highest intensity.

cooperatively has been especially strong in Australasia. Zoo populations there are relatively small and require regular supplementation from the wild (for native species) or from captive populations overseas (for exotic species). This can make them expensive to maintain and highly vulnerable to changes in government policy or quarantine restrictions. Planning cooperatively to achieve larger, better-managed populations is essential to maintaining stability and diversity in the region's animal collections and to releasing zoos from prohibitively costly supplementation rates (Lees 2001). Australasian TAGs periodically produce Action Plans. Similar to North American and European RCPs, these plans list priority taxa and target numbers, explain the principles and criteria behind the selections made, and detail the actions required to advance regional collection planning goals. Current Action Plans are published on the ARAZPA Web site as an aid to institutional collec-

TABLE 20.2. AZA species selection criteria

1. Conservation status of the species
2. Existence and viability of captive populations
3. Number of other regional captive programs
4. Husbandry expertise
5. Availability of potential founders
6. Potential to affect *in situ* conservation of species or ecosystem
7. Reintroduction potential
8. Scientific/Research potential
9. Exhibit value
10. Educational value
11. Taxonomic uniqueness

Note: AZA selection criteria are similar to those used in other regions for regional collection plan decision making.

tion planning. The primary collection planning instrument in Australasia, though, is REGASP (REGional Animal Species Collection Plan) (Johnson 2003), a computerized system for collection planning that interacts with in-house animal record-keeping systems. Institutions record their current and planned species holdings in REGASP, submitting these data annually for central compilation and review by the relevant TAGs. First, TAGs use the REGASP system to comment on zoo plans, recommending changes in line with agreed regional principles and priorities, which zoos can use in subsequent planning sessions. Second, TAGs use REGASP to identify new trends in institutional exhibitry and species preferences so that, where possible, these can be accommodated in regional plan updates. In this way, institutional and regional plans progress iteratively and adaptively, with annual snapshots taken and published as the *ASMP Regional Census and Plan*, the first of which was published in 1990 (Phipps 1990). As illustrated in table 20.1 for felids, these documents include all taxa held in zoos, their current and planned numbers, and species-specific regional planning recommendations.

In all regions, a failure to plan zoo and aquarium collections may result in the loss of captive populations, inefficient use of limited resources, and an accompanying loss of credibility (Hutchins, Willis, and Wiese 1995). Many professionally managed zoos and aquariums present themselves as net producers or conservers of wildlife, not consumers (Smith et al. 2002). If animal collections are not managed carefully, many captive populations may not persist (Conway 1987; Quinn and Quinn 1993; Sheppard 1995). The conservation ethic prevalent in today's premier zoos and aquariums throughout the world calls for the careful management of wildlife in their care, and collection planning is the primary way to ensure the future of managed populations.

HOW ARE REGIONAL COLLECTION PLANS DEVELOPED?

Before TAGs make management recommendations, they first assess space availability. ARAZPA TAGs use the current *ASMP Regional Census and Plan* (Johnson, Ford, and Lees 2005) to evaluate current and future holding space. Many AZA TAGs develop and distribute space surveys, through which member institutions report current and planned holdings for TAG taxa. EAZA regularly conducts surveys of animals held and bred by its members, and the results are published in the EAZA TAG Surveys. In addition, TAGs make use of the data available from the International Species Inventory System (ISIS) (www.isis.org). Each of these approaches provides TAGs with a sense of how much space is available for the taxa under their purview, and surveys and/or REGASP data are used to evaluate how institutions would like to allocate that space. This allows TAGs to base their collection planning recommendations on current and future institutional priorities, thereby improving the likelihood of implementation.

In order to determine which species should be managed cooperatively, TAGs develop selection criteria, which they use to evaluate all relevant taxa. Following the first *World Zoo Conservation Strategy* (IUDZG and IUCN/SSC CBSG 1993), conservation needs, combined with zoo capabilities, species availability, and potential conservation impact, are generally used as criteria in determining which species zoos should hold (see table 20.2). There are some regional variations to this approach. For example, a geographic focus is applied in Australasia, reflecting ARAZPA's primary commitment to fauna endemic to Australasia and indigenous to Southeast Asia.

The guidelines outlined in table 20.2 are currently being refined to provide consistent direction regarding the level of management necessary to maintain recommended species. AZA TAGs are not required to incorporate each criterion. However, planners must address why or how the TAG's goals are best met by utilizing their specific approach. For example, due to import restrictions, Australian native mammals raised in North America are not likely to be allowed into Australia (Allard 2000, 2004). Accordingly, the AZA Marsupial and Monotreme TAG does not include reintroduction potential in its selection criteria. AZA TAGs also are given leeway to weigh specific criteria if they believe they deserve special consideration.

In Europe, the situation is fairly similar to that used in the other 2 regions. In the mid-1990s, the EEP Committee decided to let each TAG approach the regional collection planning process in the way the TAG felt was best suited for its specific situation. After all, the decision-making process is very likely to be different for a TAG that has to deal with only a handful of species (e.g. the EAZA Rhinoceros TAG) than for a TAG that is responsible for multiple thousands of taxa, such as the EAZA Fish and Aquatic Invertebrate TAG. After roughly a decade of regional collection planning, in 2005 EAZA established a Standard Regional Collection Plan Format, which outlines the contents and process that needs to be adhered to by each EAZA TAG in producing its RCP. This standard is basically an accumulation of the approaches that were developed by various EAZA TAGs over the years. Although developed separately, the EAZA and AZA formats are remarkably similar.

Species selection criteria can be used in conjunction with a ranking system or decision tree analysis to provide a list of priority taxa recommended for cooperative breeding/conservation programs (Hutchins et al. 1998; Smith et al. 2002; Shoemaker, Smith, and Allard 2004). Tools such as a decision tree analysis allow RCP users to see clearly how planners arrived at the recommendations outlined in the plan, and make the TAG's priorities transparent. For all regions, collection plan recommendations generally focus on the species that will best serve the overall display and conservation goals of their member zoos and aquariums, and reflect the regions' expertise, interest, and resource availability (Hutchins, Willis, and Wiese 1995; Lees and Wilcken 2002; Shoemaker, Smith, and Allard 2004).

Once TAGs have made an assessment of which species are highest priority for the regional collection based on agreed criteria, some assessment needs to be made of how many of the taxa identified as suitable could or should be sustained within the available space. This in turn requires some decisions about what is considered a minimum sustainable population size. In Australasia, due to small size, this hinges on acceptable rates of supplementation, and a minimum threshold is set at 20 specimens. So, e.g., if the region's zoos are planning to create 100 spaces for small felids, a maximum of 5 taxa could be nominated for the regional collection plan. This figure might be revised up or down depending on the feasibility of estimated supplementation rates required to sustain stocks. For AZA TAGs, a similar process is followed, although no minimum threshold has been established.

Once taxa have been identified for the regional plan, the next step is to determine at what level they will be managed and which existing taxa they will replace. The language used to describe species management categories varies among the regional zoological associations, but the basic categories are consistent (see box 20.1). Species may be recommended for population management at greater or lesser intensity or for introduction to or removal from the regional collection, or identified as a species not to be acquired due to its potential to compete with existing programs. These management recommendations communicate the level of investment the regional association feels is appropriate for taxa held in their collections, and for those proposed for future acquisition. We assume that managed species are more likely to be available into the future than unmanaged species, because more institutions are investing resources and energy in maintaining those priority taxa (Smith and Allard 1999; Willis 1999). Some taxa are not given a management recommendation and their numbers are left to institutional discretion, while others are designated specifically for phaseout or as not recommended for acquisition. Taxa in the latter 2 categories would not serve an important role in current captive collections, and could actually impair managed programs by taking up valuable space (Shoemaker 1997).

While planning priorities and TAG recommendations may vary, the importance of stakeholder participation in decision making is standard across regions. TAGs include representatives of participating zoos, who communicate regularly through meetings and electronic discussion lists. In Australasia, proposed amendments to existing regional plans are framed in formal issue papers that are circulated before and decided on at TAG meetings. In North America, TAGs typically work through collection plan development at meetings, and must post final-draft RCPs on TAG e-mail discussion lists or the AZA Members Only Web site for a 30-day comment period before submitting their plans to WCMC for approval. In Europe, the development of Regional Collection Plans is similar to the process used by AZA TAGs, although there is no formal period for members to comment, and no formal approval by the EEP Committee. Table 20.3 illustrates the col-

TABLE 20.3. 2005 REGASP entry for Sumatran tigers, *Panthera tigris sumatrae*

Zoo	Current inventory M	Current inventory F	Current inventory U	Planned inventory M	Planned inventory F	Planned inventory Flexible	Implementation plan
Adelaide	1	1	0	2	2	0	Follow CMP recommendations
Auckland	0	1	1	1	1	0	Acquire male
Beerwah	2	1	0	1	2	7	Acquire
Coomera	0	1	0	1	1	0	Acquire; follow CMP
Crocodylus	0	0	0	1	1	0	Acquire long term >2007
Dubbo	1	1	0	1	1	0	Follow regional recommendations
Hamilton	1	2	0	1	2	0	Maintain >2005
Melbourne	1	1	0	1	1	2	Follow regional recommendations
Mogo	1	1	0	2	2	2	Maintain; spaces available to Sumatran program
Orana	0	0	0	2	0	0	Acquire in 2005
Palmgrove	0	0	0	1	1	0	Acquire long term according to CMP
Perth	2	1	0	1	1	2	Breed; follow CMP in 2005
Sydney	2	2	0	0	2	0	Follow CMP
Wellington	1	1	0	1	1	0	Acquire new genetic stock according to CMP >2005
Yarralumla	1	0	0	1	1	0	Acquire according to program recommendations
Totals	13	13	0	17	19	13	

Draft target population: 40+

IUCN: Critically Endangered; CITES I; VPC 3a

ASMP Carnivore TAG: Population Management Program; Management Level 1a

TAG notes: All tiger spaces are recommended to be allocated to *Panthera tigris sumatrae*.

Source: Johnson, Ford, and Lees 2005.

Note: M denotes male; F, female; U, unknown.

lection planning process, using Australasia's Sumatran tigers, *Panthera tigris sumatrae*, as an example.

Several resources are essential for developing an RCP. To assess available and future holding space, planners use institution space surveys, which assess both current and projected distributions of species in participating institutions. Regional and international studbook data and International Species Inventory System (ISIS) census data can also be used to estimate the current numbers of each species in captivity. To assess species' status in the wild and conservation relevance, planners consult IUCN Specialist Groups, the IUCN Red Lists, Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) data, and regional designations (e.g. Australian Department of Environment and Heritage's Environment Protection and Biodiversity Conservation Act list of threatened species, U.S. Fish and Wildlife Service's endangered species list). RCP authors also review the International Union for Conservation of Nature's (IUCN's) Species Survival Commission's (SSC) taxonomic specialist group action plans, government wildlife agencies' recovery plans, reports from field biologists, and other relevant publications to assess conservation needs of species under review. For captive management and husbandry information, RCP developers rely on the expertise of TAG members and relevant publications, including husbandry manuals.

REGIONAL COLLECTION PLAN IMPLEMENTATION AND REVIEW

As mentioned previously, it is in RCP implementation that the different regional associations' approaches vary most. EAZA and AZA TAGs communicate their plans to members via Web sites and other venues, and institutions are asked to consult RCPs when developing their Institutional Collection Plans (ICPs). Institutional collection plans lay out priorities for current and future use of institutional space, and may detail plans for existing and planned enclosures. EAZA and AZA TAGs present their RCP recommendations in a primarily passive approach, via information transfer. There is an understanding that institutions should use RCPs when planning collections, but no enforcement or regulation currently requires adherence to RCP recommendations.

Limited space in the Australasian region (55 members, compared to more than 200 in AZA and nearly 300 in EAZA) increases the challenge of providing for the diverse exhibitry needs of members while at the same time maintaining sustainable populations. These competing needs are in constant tension, so fundamental to the implementation of plans in Australasia is a commitment by TAGs to balance sustainability with diversity in regional planning decisions, and a reciprocal commitment by zoos to place sustainability above novelty in institutional planning (Lees and Wilcken 2002). These commitments are tested and sustained through the iterative planning process described earlier, through which TAGs identify zoos operating outside regional plans and work with them directly to reach a solution.

AZA TAGs are called on to produce updated collection plans at least every 3 years. In EAZA, reviews and updates are required at least once every 5 years, although most TAGs update their RCP more frequently. Since their populations are relatively small and their status can change quickly, ARAZPA TAGs review and refine regional plans annually.

Regional collection plans are living documents. TAGs make recommendations based on the best information available to them at the time of plan development, but circumstances change and unforeseen opportunities arise. For example, a species may be designated to be phased out if numbers are dropping and no founders are known to be available. However, an unexpected government confiscation of a significant number of individuals may make a managed program possible overnight. The reverse may also occur: a TAG may determine that there are sufficient numbers of a given species to warrant management, but if the animals do not reproduce, the population may collapse despite the management recommendation. Accordingly, RCPs must be flexible if they are to be effective.

DOES REGIONAL COLLECTION PLANNING WORK?

TAGs in EAZA began developing RCPs in the early 1990s, and continue to refine their planning processes. ARAZPA and AZA TAGs have been developing and implementing regional collection plan recommendations since the 1990s, and their RCPs provide an interesting opportunity to see how collection planning at the regional level has an impact on institutional decisions.

Standardized regional collection planning processes are still too new to allow for a robust evaluation. However, there are enough data available to conduct some analyses to assess whether institutions are following TAG recommendations. We looked at the 8 AZA TAGs that have completed first- and second-edition RCPs using the same AZA WCMC–approved processes and guidelines (Antelopes: Shurter 1999, Fisher 2005; Bears: Moore 2000, Carter 2007; Columbiformes: Roberts and Wetzel 2000, Roberts 2005; Coraciiformes: Sheppard 1999, 2004; Marsupials and Monotremes: Allard 2000, 2004; New World Primates: Baker 2000, 2005; Penguins: AZA Penguin TAG 1999, AZA Penguin TAG 2002; Small Carnivores: Lombardi 2001, 2005). Five of these plans were for mammal TAGs and 3 were for birds; the analysis covered programs for 110 species and subspecies in total.

We compared "current population numbers" for species recommended for management from the first edition RCP with "current population numbers" from the second edition to determine whether the populations increased or decreased in size. All species evaluated were recommended for Population Management Plan (PMP)- or Species Survival Plan (SSP) level management in both editions. We then looked at the target population sizes set in the first-edition RCP, and recorded whether the current population reported in the second-edition RCP reflected movement in the direction of the stated target. Populations whose second-edition numbers remained within 10% of the target or went in the direction of the target were considered to have followed the TAG recommendations. For example, if a population numbered 50 animals in the first edition and 75 animals in the second edition, and the first-edition RCP called for a 3-year target of 100 animals, we would count this as following the TAG recommendation.

Sixty percent of the species analyzed moved in the direction of the TAG recommendations. TAGs ranged from 44 to 100% "success," meaning that on the low end, fewer than half the TAG's species recommendations were followed, and on the high end, all species numbers moved in the direction targeted by the TAG.

There are myriad reasons why recommendations may not be followed. For example, planned imports may be delayed, managed populations may go extinct due to stochastic processes, changing institutional priorities may result in significant impacts on population numbers and management decisions, animals in breeding situations may not breed, and contraception failures may result in unrecommended offspring. In addition, space survey data may be incomplete (many TAGs do not reach a 100% response rate on their surveys), meaning that if a significant holding institution does not return the survey for one of the editions of the RCP, the data will not include the full number of specimens. Institutional planners may also willfully ignore recommendations in some instances, or regional planners may not be communicating the urgency of their recommendations clearly enough. By the same token, a TAG's recommendations might be unrealistic or difficult to implement.

The analysis shows that populations move in the direction of AZA TAG targets more than 50% of the time, indicating that regional collection planning may indeed work. Because not all recommendations are followed, the data should also serve to advise TAGs that they may need to be more compelling when making recommendations for those species whose sustainability in captivity is dependent on cooperative planning. Because TAGs cannot simply publish RCPs and hope that institutions will help them meet their collective goals, they need to work with institutions to ensure a future for priority populations. Some TAGs have begun including a "replacement table" in their RCPs (Lombardi 2005; Fisher 2005). By highlighting recommended species that would serve as good alternatives, these tables direct institutional planners away from species recommended for phaseout or not recommended for collections. For example, the AZA Cervid RCP (Fisher 2005) recommends institutions looking for a small cervid for an Asian exhibit should consider replacing Reeve's muntjac, *Muntiacus reevesi*, with western tufted deer, *Elaphodus cephalophus cephalophus*, which are recommended as a PMP.

A similar analysis carried out for a number of Australasian TAGs also showed an overall trend in the direction of regional plan implementation. Through REGASP data, it was possible to assess not only movement of the actual collection toward cooperatively agreed-on targets, but also any directional changes in what zoos are planning to hold. For the same taxa, institutional plans moved much more convincingly toward regional priorities than did the living collections (61% of taxa in the living collection moved toward regional priorities versus 77% of taxa in institutional plans; both managed and unmanaged populations were included in the analysis). This suggests that zoos are committing to regional collection plans, but their progress in implementing those plans is being slowed, possibly by practical issues. For exotic mammals in Australasia (the focus of the study) these issues include long life span—making replacement of one taxon with another a slow process; the difficulty of acquiring good genetic stock from captive populations overseas (often only already overrepresented lines are available); and delays in funding for planned exhibit alterations or expansions.

The analyses described here are not the first attempts to evaluate the extent to which RCP recommendations are followed (Smith and Allard 1999; Searles 2004). In 1999, shortly after the AZA WCMC issued new regional collection planning guidelines, Smith and Allard (1999) looked at 2 TAGs that had each completed first- and second-edition RCPs. They evaluated whether institutions followed recommendations from one RCP to the next and determined that 60% of the recommendations were followed, using methods similar to those described previously in this chapter. As they noted in their conclusions, TAGs need to take past performance and space survey trends into account when making species recommendations in their RCPs. Searles (2004) compared targets set in first-edition RCPs to a snapshot of current population data for January 2004, and determined that 54% of the populations assessed were "in compliance." This analysis included unmanaged populations as well as SSPs and PMPs, so Searles's results cannot be directly compared with the other AZA analyses described here.

A formal analysis on the implementation of RCPs is yet to be conducted for the EAZA region, although a number of TAGs have looked at this for their own species. For example, in the case of the EAZA Prosimian TAG, the analysis revealed a major increase in the numbers of recommended species, whereas the nonrecommended species had by and large declined, thus indicating a positive implementation of the RCP. On the other hand, an analysis by the EAZA Parrot TAG indicated that institutions were not implementing the recommendations in the RCP. The underlying causes for this are not fully clear, but language barriers are certainly a major factor hindering implementation in large parts of the EAZA region.

While these analyses indicate that collection planning recommendations are being followed at least in part, they also show that TAGs continually need to assess the direction their programs are taking, and to communicate directly and frequently with institutions to ensure that they are aware of their role in helping the TAG meet priority objectives. Most important, each population needs to be evaluated to determine the reason or reasons RCP recommendations are not being implemented.

FUTURE CHALLENGES

Regional zoo associations should continue to expand support and commitment to regional programs, as outlined in regional collection plans. Very few managed populations show potential for long-term sustainability (Conway 1987; Quinn and Quinn 1993; Sheppard 1995), and even globally, as many as 50% of taxa show little potential of reaching this goal (Magin et al. 1994). Cooperative planning on a global scale may help solve the issue of limited captive space for managed taxa and the increasing difficulties of collecting animals from the wild (Maguire and Lacy 1990; Hutchins, Willis, and Wiese 1995; Sheppard 1995; Hutchins et al. 1998; Allard 2000; Smith et al. 2002).

Global cooperative planning was introduced in the 1990s, with specific processes designed by the IUCN-SSC Captive Breeding Specialist Group (CBSG, now Conservation Breeding Specialist Group) (Foose, Ellis-Joseph, and Seal 1992; IUDZG and IUCN/SSC CBSG 1993; Hutchins, Willis, and Wiese 1995; Allard and Hutchins 2001). Stakeholder support for these processes could not be sustained, because neither regional nor institutional planning mechanisms were sufficiently embedded in zoo culture at that time. It was therefore not possible for regional or even institutional planning participants to represent their constituency adequately. Without firm stakeholder support, implementation could progress for only a small number of high-priority taxa, such as tigers and rhinoceroses.

Regional plans are now well developed in a number of regions and, for taxonomic groups that find it useful, could provide a platform for renewed attempts at global coordination. Effective global planning requires all the support mechanisms on which regional planning currently relies—in particular, a body providing oversight, policy, monitoring, and regular evaluation—i.e. a body equivalent to the AZA WCMC in North America, the ASMP Committee in Australasia, or the EEP Committee in Europe. Such a body currently exists under the WAZA umbrella, in the form of the Committee on Inter-Regional Conservation Cooperation (CIRCC). CIRCC is responsible for monitoring and evaluating international studbooks and has developed protocols for the effective interregional and global management of captive populations. Both global and interregional planning and management along these lines are already a reality (e.g. golden lion tamarin, *Leontopithecus rosalia*, Partula snails, red panda, *Ailurus fulgens*; and joint ASMP/EEP management of Sumatran tigers whereby a jointly appointed coordinator completes analyses and makes recommendations for the combined population). And more important, global planning could be used to reduce the redundancy of each region trying independently to maintain sustainable populations of all recommended species. Global strategic planning can serve to partition managed space around the world.

As more of these programs develop, global planning will become essential to ensure effective partitioning of global space and to increase population viability as appropriate. Global planning is not necessary or even advisable for all managed species, but for certain taxa it may be the most effective way to maintain sustainable populations and maximize the use of captive space.

Regional differences and distance make it a complex endeavor, but working together may allow us to maintain some self-sustaining captive populations and maximize our conservation impact by increasing the number of species we are able to hold. For example, there may be several species of rodents than would benefit from captive propagation, but not enough space for each region to maintain all species (Riger 2004). A global planning effort could determine which region could best manage each priority species or subspecies, with surplus from one region potentially going to meet the display needs of another. This approach ensures that no single region has to try to build up self-sustaining populations of all priority rodent species, but also demonstrates the international zoo community's commitment to rodent conservation worldwide.

No matter how much effort we put into cooperative planning, there is simply not enough room in the world's zoos and aquariums to maintain sustainable populations of every species of interest (Foose 1983; Soulé et al. 1986; Conway 1986, 1987; Diebold and Hutchins 1991; Hutchins and Wiese 1991; Quinn and Quinn 1993; Willis and Wiese 1993; Sheppard 1995; Smith et al. 2002). In fact, Conway estimated that in 1987 there was only enough space to maintain 230 species for the long term (Conway 1987). One way to meet future challenges for zoo and aquarium collection management would be to revisit Conway's study to determine whether that figure still holds true, and then to work together with the CIRCC and regional zoological associations to develop a list of priority species for which global planning is essential. Each association would have to make a firm commitment, perhaps through a memorandum of participation, in order to formalize its involvement in the program. This approach would be a departure from the current approach to collection planning, but may be what is needed to secure the future of the rarest and most sought-after species in zoological collections. With this in mind, the international zoo community needs to develop assessment tools to evaluate the costs and benefits of global planning. For example, Margan et al. (1998) demonstrated with fruit flies that population subdivision with occasional translocations can, under some circumstances, better preserve genetic variation than does combining all individuals into a single large population. Kevin Willis (personal communication) has begun work to define "cooperation coefficients" for managed populations, which would describe the impact of collaboration on genetic and demographic parameters of managed populations. Ultimately, we cannot assume that a single model of population management or collection planning will be appropriate for all taxa, but we must continue to develop innovative approaches to help us meet our long-term collection and conservation objectives.

CONCLUSION

Historically, some zoological professionals have worried that widespread cooperative collection planning would result in a loss of diversity in zoo and aquarium collections, and that "each zoo will be a clone of another" (Jones 1998, 260). However, an analysis conducted by Willis (1999) suggests that these worries are overstated. Willis compared current and/or past taxonomic diversity in AZA collections to the diversity that would be retained if institutions followed the recommendations outlined in the RCPs available at that time. His analysis showed that following TAG recommendations would not negatively impact taxonomic diversity.

This study shows that working cooperatively does not require sacrificing autonomy. Increasingly, zoo professionals agree that collection planning is essential if we are to have sustainable populations of key species into the future. In addition, both TAGs and institutional planners recognize that institutions' decisions are driven by a number of motivating forces. For example, an institution may maintain a species that is not recommended by the TAG, if it is iconic to that facility or region (e.g. Eurasian otter in Europe). Overall, there is enough space in zoo collections to allow for some flexibility in terms of taxa displayed, which in turn ensures that each zoo or aquarium has an opportunity to develop a distinct collection that meets its individual needs. That said, if institutions do not plan strategically and cooperatively in the long term, they may move from having "a little of everything" to having very little as captive populations dwindle (Hutchins, Willis, and Wiese 1995; Sheppard 1995; Ballou and Foose 1996; Hutchins et al. 1998; Smith and Allard 1999). RCPs should serve to help institutions maintain viable populations of recommended species while reducing the number of surplus animals produced (Hutchins, Willis, and Wiese 1995; Sheppard 1995; Smith and Allard 1999; Allard 2000; Allard and Hutchins 2001; Carter and Kagan, chap. 21, this volume).

Whether at an institutional, regional, or global level, zoos and aquariums cannot maintain viable and diverse collections (for discussion, see Hutchins, Willis, and Wiese 1995, and others from the same volume) without coordinated, cooperative management programs. Careful planning by TAGs can help zoos and aquariums select those species that will benefit most from captive programs (Soulé et al. 1986; Hutchins, Willis, and Wiese 1995; Sheppard 1995; Shoemaker 1997; Smith and Allard 1999; Willis 1999; Allard 2000; Smith et al. 2002; Shoemaker, Smith, and Allard 2004). We are still climbing the steep slope of the learning curve when it comes to collection plan development and implementation. However, it is evident that when fully implemented, cooperative, strategic planning helps ensure the stability of the species managed in captivity and promotes diverse and interesting collections for zoos and aquariums into the future.

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21

Management of “Surplus” Animals

Scott Carter and Ron Kagan

INTRODUCTION

With many habitats and species in decline, the problem of surplus zoo animals seems incongruous to those outside the zoo profession. Nonetheless, the result of successful captive breeding is populations of animals that exceed the collective carrying capacity of zoos. When there are more animals than there is space (or resources) to provide for their care, some individual animals (and sometimes entire species) are designated surplus. The “surplus animal problem” has long been a significant issue for zoos (Conway 1976; Lindburg 1991; Fiebrandt 2004; and others), and it remains challenging on many levels.

This chapter will not simply review the management considerations and public relations issues of surplus animals. We suggest that zoos develop a fundamental change in the prevailing paradigm, i.e. accept birth-to-death responsibility for all animals that they produce. The limited space and resources of zoos are clear. We advocate (1) greater commitment of resources to research in contraception and population management that will reduce the number of unneeded animals produced in captive management programs (see Asa and Porton, chap. 34, this volume); (2) greater commitment to allocating quality off-exhibit space for animals not immediately needed for breeding or display; and (3) development and support of regional retirement facilities for animals not needed for breeding or display. We believe that our commitment to captive animals should be equal to that of animal conservation (see Kagan and Veasey, chap. 2, this volume).

Authors from within the zoo community (e.g. Conway 1976; Lindburg and Lindburg 1995; Lewandowski 2003) and even some from outside the zoo community (e.g. Pressman 1983) have considered surplus animals the “cost of success” of zoo breeding programs. However, disposition of surplus animals is one of the most sensitive public relations issues zoos face (Lindburg 1991; Graham 1996). Media coverage of zoo dispositions has brought negative attention to zoo practices such as culling (Zimmerman 2004) and has also revealed that some surplus zoo animals have ended up in questionable conditions, including roadside zoos, pseudosanctuaries, circuses, research facilities, private ownership, and hunting facilities (e.g. Goldston 1999; Green 1999; Satchell 2001). These reports have led to concern among zoo visitors and the general public and certainly carry the potential to damage the professional image of all zoos.

WHAT IS A “SURPLUS” ANIMAL?

While earlier treatments of the subject of surplus animals in zoos (e.g. Conway 1976; Lindburg 1991) dealt primarily with the “genetic surplus” from cooperative management programs, the issue for zoos is far broader. Regardless of their conservation status or level of captive management, animals become surplus as a result of space limitations in zoos. Lacy (1995, 188) defines *surplus animals* as “those that are not needed for the goals of a program.”

Zoos have 2 different designations or uses of the word *surplus*. One is a designation by population managers for individuals not necessary for the long-term genetic and demographic management of a captive population of a species, and the second is a designation by a holding institution for individuals held, but no longer desired, for display or breeding. The criteria used for each designation differ. Population managers are concerned primarily with the potential genetic contribution of an individual to the population’s viability, whereas institutions are primarily concerned with the display and care (including cost of care) of individuals in a specific physical setting.

Significantly, institutions, and not population managers, are ultimately responsible for the disposition of animals. Thus, institutions can and do designate animals surplus, independently of the designations of population managers and for reasons other than their potential genetic value to the population or program.

The reasons that individual animals are designated surplus by holding institutions include an animal’s age, sex, and physical, behavioral, or social condition (all of which can also be factors in a designation of genetic surplus). Additionally, a lack of space, whether as a result of breeding or changes in regional or institutional collection plans, may result in a surplus designation.

In North America, the lion-tailed macaque, *Macaca silenus*, is a good example of a species in which individuals were designated surplus because of changes in institutional collection plans. The Macaque Species Survival Plan (SSP) currently manages 120 lion-tailed macaques in 22 institutions. Nine institutions no longer wish to house macaques because their collection plans have changed, and they now consider their macaques surplus (Carter 2004). However, some of the macaques designated surplus are in fact genetically valuable to the population. Thus, institutional priorities are here in conflict with the recommendations of cooperative management programs.

THE ORIGINS OF SURPLUS ANIMALS

Conway (1976) and Lindburg and Lindburg (1995) have noted that captive animals do not have pressures like predation that control wild population sizes. Zoo animals are mostly protected from natural causes of death, such as predation and disease, and thus zoos that breed species successfully may have more animals than space and resources with which to provide care.

POPULATION MANAGEMENT

Masterplans for cooperative management programs identify those individuals considered genetically important for breeding and those that are not needed to contribute to the population (see Allard et al., chap. 20, this volume). Individuals with the most genetic representation are usually considered surplus to the population's needs (depending on population size and the criteria used in decision making by the population manager[s]). Production of males, especially for captive mammal species that are polygynous, usually exceeds that required for the populations' long-term maintenance.

Changes in the decision-making criteria used by management groups and population managers during master planning can change the designation of individual animals as surplus to a population's needs. For example, in its 2000–2001 Masterplan, the Association of Zoos and Aquariums' Chimpanzee, *Pan troglodytes*, Species Survival Plan (AZA SSP) included in genetic analyses and breeding recommendations all individuals for whom at least 75% of the pedigree was known (Fulk 2000). Births resulted from these recommendations. Subsequent Masterplans by a different coordinator and management group used different criteria, requiring that 100% of the pedigree be known in order for the individual to be included in genetic analyses. Thus, some individuals born as a result of the 2000–2001 Masterplan are now excluded from analyses and are not recommended for breeding. Similarly, events such as new imports may lower the genetic value of once important individuals and the offspring they produced, thereby increasing the likelihood that they will be considered surplus to the population. Changes in the administration of populations, especially as a result of importation and other events, are normal expected elements of population management.

THE APPEAL OF BABY ANIMALS

As zoos have evolved into conservation organizations and actively marketed the role captive breeding plays in conservation, the public appeal of cute baby animals has been enhanced by equating infants with conservation successes. The joint marketing of conservation and infant mammals provides a strong motivation for zoos to breed animals. While there is evidence that new exhibits at zoos may be more compelling to the public than young animals (Kasbauer 2004), zoos use the appearance of new infants to drive attendance.

STRATEGIC PLANNING

Hutchins, Willis, and Wiese (1995) recommend strategic planning for captive animal populations at global, regional, and institutional levels. While still relatively new in animal management, there has been significant progress in the development and adoption of strategic plans at both regional and institutional levels (see also Allard et al., chap. 20, this volume).

The regional collection planning (RCP) process focuses on maintaining fewer species so that population sizes sufficient to sustain long-term management are possible (e.g. Conway 1976; Hutchins, Willis, and Wiese 1995). Thus, the use of captive space is coordinated to benefit those species in greatest need of a long-term program. The RCP process, especially at its earliest stages, creates surplus animals as institutions attempt to "phase out" species and replace them with recommended species. However, regional priorities may change, and RCPs may later recommend the elimination of a species that was initially desired.

The success of the RCP process depends on institutions following recommendations in the development of their individual collection plans. Thus, an inherent weakness in the RCP process is the expectation that the institutional collection plans on which the population recommendations are based will not change.

CHANGING INSTITUTIONAL COLLECTION PLANS

Zoos evolve over time, both physically and philosophically, as organization leadership changes and new strategic plans and physical Masterplans are developed and implemented. Species (and individuals) suitable in one physical setting or important to one administration often change. These changes in institutional priorities have an impact on the projected carrying capacities for individuals of certain species.

Recognizing that strategic planning, especially at its earlier stages, will result in the designation of animals as surplus is in no way a criticism of institutional and regional collection planning. Both are crucial to the long-term success of population management and the viability of zoos. Integration of institutional and regional collection plans will improve the effectiveness of cooperative management programs, including ultimately reducing the numbers of animals produced that are surplus to the needs of the population.

TRADITIONAL SOLUTIONS TO DEAL WITH SURPLUS ANIMALS

Expenditure of resources to provide long-term housing and care for individuals that cannot be included in breeding programs or cannot be exhibited has been viewed as wasteful of limited resources and even harmful to conservation (Lacy 1995). Removal of animals designated surplus has historically been the action taken by institutions, and zoos have employed a number of means to do so.

REDUCTION OF SURPLUS

The development of reversible contraceptives is one very important solution aimed at reducing the number of animals designated surplus (Porton, Asa, and Baker 1990; Asa, Porton, and Plotka 1996; Kirkpatrick 1996; Asa and Porton, chap. 34, this volume). The need to advance these techniques has catalyzed some research (e.g. Porton, Asa, and Baker 1990; Raphael et al. 2003).

To remove existing surplus, zoos traditionally place individuals in other zoos, sell them to dealers, practice "managerial euthanasia" (more accurately called culling), transfer animals to nonzoo holders, and, in a few cases, release them into the wild.

Placement in other zoos. Placement of unwanted animals in other accredited zoos is usually the desired disposition outcome. Appropriate care and management are normally assured, and the transfer is generally beneficial to both institutions as well as to the species and the individual animals involved. Certainly, transfer recommendations made by population managers in cooperative management programs focus primarily on the transfer of animals among accredited zoos or zoo association members within a region. For some animals, however, transfer to another zoo may not be possible.

Transfer to dealers. Transfer of animals to animal dealers was once commonplace when removing surplus animals from zoos; the practice has been declining significantly in recent decades. Graham (1987) reported a declining number of animal "suppliers" that were members of the American Association of Zoological Parks and Aquariums (AAZPA) (from 30 in 1978 to 11 in 1987). A recent AZA membership directory lists only 4 entities under the category of Animal Transaction (Ballantine 2005). While there are many animal dealers that are likely not members of a zoo association, the decline in AZA member animal dealers may suggest a general decline in the practice of selling animals to animal dealers. Media attention on the transfer of zoo animals into facilities and conditions that compromise their welfare has often focused on the practice of selling animals to dealers (e.g. Goldston 1999; Green 1999; Satchell 2002). Publicized cases of zoo animals ending up at animal auctions, roadside zoos, and other substandard facilities have no doubt been a significant factor in the decline of this type of disposition.

Off-exhibit holding. "Warehousing" of surplus animals in behind-the-scenes areas is described by Lindburg (1991) as perhaps the most common practice zoos employ to deal with surplus animals. *Warehousing* implies that the areas in which animals are maintained are less than optimal, which is probably accurate. Lindburg (ibid.) and Maple (2003) both consider this practice insufficient and inappropriate. Development of high-quality off-exhibit housing, on the other hand, could be considered an important part of the responsible management of nonreproductive surplus animals.

Culling. Though proponents of culling have argued for its greater acceptance and more widespread use (e.g. Graham 1987, 1996; Lacy 1995; Schürer 2004), culling mammals, especially large mammals, is considered one of the most controversial means of dealing with surplus animals (Graham 1996; Zimmerman 2004) and is even prohibited as a systematic means of population management in Germany (Vogel 2004). Killing healthy animals because they are not needed for breeding or exhibition is argued by some as logical and responsible management to conserve resources for other animals (Lacy, 1995), and/or to prevent animals from being transferred into situations that may compromise their welfare (Graham 1987, 1996). While Lacy (1995) argues that culling is avoided to minimize human discomfort (e.g. discomfort of the animals' caretakers and others who have formed a bond with a particular animal), pressure from the general public, the media, employees, and governing bodies is also a significant factor in zoos seeking means of disposition other than culling (Blakely 1983). Lacy (1991, 1995) also points out the inconsistency of many institutions in applying culling decisions, e.g. hoofstock are culled more often than primates, and rats and bats more often than cats.

Public discussion of culling healthy animals requires that the conservation and animal welfare messages of zoos are both consistent and consistently reinforced. As Graham (1996) points out, zoos are often seen as sanctuaries for animals. Zoos market and promote the births of animals, but educational messages of "survival of the fittest," predation, and mortality are normally not included in the press release that announces a new birth. Zoos also generally do not tell their visitors that some young may be killed. Conway (1976) and Lewandowski (2003), among others, have advocated greater public education on this issue as a means of gaining greater support for disposition methods, including culling. However, Lindburg and Lindburg (1995, 203) are likely correct when they state, "A message emanating from zoos that advocates both the saving and the taking of animals' lives is likely to be, at best, a confused one."

Sanctuary placement. Placement of zoo animals in accredited animal sanctuaries has occasionally been done but is generally not considered a viable disposition option. Like zoos, sanctuaries have limited space and resources (sometimes fewer resources than zoos), and surplus zoo animals occupy space needed for privately owned and other animals often found in dire situations. Maple (2003) asserts that assurance of animal care standards consistent with that of zoos is not always possible in sanctuaries; some unaccredited "pseudosanctuaries" have not demonstrated that they provide appropriate care or that they refrain from breeding and selling animals.

Other means of disposition. Transfer to cooperative management programs in other countries, transfer to nonzoo facilities (e.g. private breeders and research), and release into the wild are options, especially for hoofstock and primates, respectively, that are listed in discussions of the surplus issue (e.g. Conway 1976). But, as most authors point out, these options have extremely limited potential to provide appropriate disposition, and some come with significant welfare concerns.

CHANGING THE PARADIGM

Changing the current paradigm of surplus animals is fundamental to solving the "surplus animal problem." Committing to the long-term care of animals that zoos produce helps resolve the public relations issues surrounding the disposition of animals. Public criticism of animal welfare issues in zoos, including disposition of surplus animals, undermines zoos' important conservation initiatives and accomplishments.

Other steps consistent with this shift in paradigm include further implementation of strategic planning, prevention of surplus through more careful management of all mammal species in zoos, greater commitment to quality on site but off exhibit, holding and management, and the establishment of regional retirement centers.

IMPLEMENTATION OF STRATEGIC PLANNING

Cooperative management, especially the integration of institutional and regional collection plans, can and should contribute to a reduction of individuals produced to sustain populations. Integration of regional and institutional collection plans to align the species living in zoos with those recommended in regional collection plans will eventually phase out those species not recommended for management and thereby help to reduce the number of surplus animals.

PREVENTION OF SURPLUS

Contraception is an important component of responsible population management, and can substantially reduce the number of animals designated surplus. Contraception alone will not eliminate surplus animals in captive breeding programs, and it is important to consider the welfare effects of delayed (or permanently denied) reproduction on female mammals as described by Hildebrandt (2004) (see also Asa and Porton, chap. 34, this volume). However, the zoo community needs greater commitment to research on contraception and manipulation of reproduction in order to balance the needs of the individual female mammal, the offspring produced, and the population.

COMMITMENT TO QUALITY, ON-SITE FACILITIES AND MANAGEMENT

Commitment to quality, on-site management of animals that are not exhibited or bred will move the zoo community toward birth-to-death care for the animals zoos produce. Adopting a business model that accepts that the cost of successful conservation and welfare will include more off-exhibit room for old, genetically insignificant, or otherwise unneeded animals is an important first step in changing the current paradigm.

COOPERATIVE RETIREMENT CENTERS

Lindburg (1991) and Lindburg and Lindburg (1995) suggested that it is possible to provide animals with quality living spaces that are more cost effective than the expensive, aesthetically pleasing exhibits typical of modern zoos. Similarly, Maple (2003) emphasized the need for zoos to move toward "life span planning," which includes providing for the retirement of animals that can no longer be exhibited. Development of regional "retirement centers" has been suggested by several authors (Lindburg 1991; Kagan 2001; Maple 2003) to ensure the long-term care of animals that zoos produce.

CONCLUSION

Strategies for dealing with the "surplus animal problem," including the ones suggested here, have been debated for years, but it is clear that the problem of surplus animals remains. Committing to solutions that ensure the responsible management of zoos' populations, from careful planning of their births to responsible care during their "retirement," offers resolution to the welfare and related public relations issues that surround the disposition of zoo animals. Maintaining responsibility for animals throughout their lives exemplifies both ethical appreciation for and professional treatment of animals, both individuals and species.

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22

The Role of Captive Populations in Reintroduction Programs

Joanne M. Earnhardt

INTRODUCTION

Many mammal populations throughout the world are suffering dramatic declines in size or are already extirpated. To avert the extinction of species, conservation biologists initiate wide-ranging actions designed to mitigate the threats leading to population decline, and attempt to restore locally extinct populations through reintroduction programs. Reintroduction is the release of captive or wild-caught animals to a suitable site within their natural range, specifically to reestablish a viable population in an area from which the species has been extirpated (IUCN/SSC RSG 1998). This chapter explores the use of captive mammal populations as a source for a reintroduction program intended to reduce the risk of extinction for a species.

MAMMALS IN REINTRODUCTION PROGRAMS

Among potential candidates, mammals appear to be a taxonomic preference for reintroductions, as studies have found that a large proportion of reintroduced species has been mammals. Even though mammal species are not more prevalent in the wild, Seddon, Soorae, and Launay (2005) found that mammal reintroduction projects accounted for 41% of vertebrate reintroduction publications; the largest shares involve artiodactyls (29%), carnivores (24%), and primates (15%). In a survey of published case studies on translocations (defined by 1998 IUCN guidelines as movement of wild individuals from one part of their range to another for conservation purposes), Fischer and Lindenmayer (2000) found over 50% involved mammals. In an earlier survey analyzing only releases of captive-bred animals, Beck et al. (1994) found that 32% of past reintroduction projects were mammals and 45% were birds; but in programs currently managed by the Association of Zoos and Aquariums (AZA), mammal reintroductions account for 38% of projects in comparison to 31% for birds and 23% for reptiles (AZA ReintroSAG 2005). While this predominance of mammal reintroductions may indicate that mammals are good candidates for reintroduction or have more need of conservation, the higher proportion of mammal projects is more likely due to political issues or taxonomic preferences (Fischer and Lindenmayer 2000; Seddon, Soorae, and Launay 2005).

BACKGROUND ON REINTRODUCTIONS

Reintroductions, regardless of the species, can be complex, extensive, and costly, and success of a program is not assured (Kleiman 1996). Meta-analyses investigating success across programs established that most programs could not be classified as a success: Griffith et al. (1989) found that 44% of programs with bird and mammal translocations were successful, and Beck et al. (1994) found that 11% of programs using captive populations as a source were successful. In a survey of published literature, Fischer and Lindenmayer (2000) classified 26% of translocations as successful, with 27% as failures and 47% as unknown (or uncertain as of analysis date). However, evaluating the success of a reintroduction is difficult; goals vary from program to program, evaluation depends on methodology, and objectives are time-dependent (Sarrazin and Barbault 1996; Seddon 1999).

To enhance the probability of success and encourage the use of scientific methods in the management of reintroduction programs, the IUCN (International Union for Conservation of Nature) in 1988 formed a Reintroduction Specialist Group (RSG). The RSG has a Web site (www.iucnsscrsg.org) and produces a semiannual reintroduction newsletter with reports from projects on a wide range of taxa. In 1998, it published its first set of guidelines as a resource for reintroduction practitioners. The RSG general guidelines have been succeeded by production of taxon-specific guidelines for mammals such as primates, great apes, and elephants (IUCN/SSC RSG 2006). In a similar effort, the AZA Reintroduction Scientific Advisory Group (ReintroSAG) published guidelines in 1992, and these guidelines state that "reintroduction should be regarded as science, with surveys of the pertinent literature, interdisciplinary participation, formulation of testable hypotheses and goals, thorough documentation, rapid publication of results, and review of the program by independent referees"(AZA ReintroSAG 1992, 1). In addition, these 2 guideline documents describe potential program objectives, conditions necessary for reintroductions, considerations for choice of release site, taxonomic issues, characteristics of suitable release stock, socioeconomic and legal requirements, release design, health protocols, and monitoring activities.

While the above guidelines serve as the principal foundations for planning reintroductions, guidelines have also been published by individual authors experienced with reintroductions. Kleiman (1989) published one of the first sets of guidelines and followed it with a relevant chapter in the original volume of *Wild Mammals in Captivity* (1996); in these publications she addressed biological, logistical, and management factors in reintroduction programs, emphasizing the importance of planning and evaluating to improve program success. In addition, she pointed out that reintroductions are not feasible or appropriate for every species or population. Miller et al. (1999) focused on specific biological considerations for reintroductions of carnivore species, but in another paper, Reading and Miller (2001) also called attention to the value of the nonbiological aspects—e.g. values and attitudes of the stakeholders and the public—in reintroduction success. In proceedings from a symposium on reintroductions, Stanley Price (1991) reviewed mammal reintroductions and emphasized the need for adaptive management based on postrelease monitoring; other additional chapters in this volume address policy, politics, logistics, ecology, and genetics and provided species-specific examples.

A "science of reintroduction biology" is clearly developing. Authors advocate the use of meta-analyses to derive general principles; they propose the use of experimental approaches that have hypotheses, controls, and replicated trials; and they promote the use of simulation models to assess factors affecting population dynamics of source and released populations (Sarrazin and Barbault 1996; Armstrong and Davidson 2006; Seddon, Armstrong, and Maloney 2007).

Comparisons of reintroduction programs have identified biological (e.g. demography, genetics, behavior, mitigation of threats, and quality of the habitat) and nonbiological (e.g. politics, society, logistics, regulations, and funding) factors associated with success, with the assumption that managers could use this information to improve their programs (Griffith et al. 1989; Stanley Price 1989a; Beck et al. 1994; Wolf et al. 1996; Miller et al. 1999; Fischer and Lindenmayer 2000). Planning for a reintroduction program should include a literature review, because a survey of the extensive literature can yield important and relevant information on general and specific topics, strategies that were successful, and lessons that were learned from comparable programs.

While analyses of the factors influencing success of a reintroduction have been conducted, the factors associated directly with captive populations have received less attention. In this chapter I examine

- advantages and disadvantages of releasing animals reared in captivity (e.g. disease risk and behavioral and genetic changes);
- the manner in which zoos have contributed to reintroductions;
- the development of captive breeding programs intended to produce animals for reintroduction (e.g. genetic and demographic considerations for management of population growth);
- the use of computer models for research and planning;
- strategies to harvest and release specific animals from a captive population (e.g. when to initiate harvest, how many and which animals to harvest); and
- approaches to and benefits of postrelease monitoring of captive animals.

Because mammals are the focus of this volume, the majority of examples will consider mammal reintroductions, but many of the topics are relevant to reintroductions regardless of taxonomy.

CAPTIVE POPULATIONS AS THE SOURCE

While there is general concern for the effectiveness of reintroduction as a conservation strategy (Griffith et al. 1989; Beck et al. 1994; Kleiman 1996; Fischer and Lindenmayer 2000), specific concerns (e.g. funding, speed and probability of population recovery, disease, and undesirable behavioral and genetic changes) center on the use of captive populations as the source of animals in future reintroductions (Snyder et al. 1996; Miller et al. 1999). For example, Snyder et al. (1996) suggested that money and resources will be directed to captive breeding programs at the expense of other conservation strategies (see also Zimmermann, chap. 23, this volume). By contrast, Conway (1995) contended that such breeding programs do not compete for funds with other conservation actions, as some funding may be targeted only to captive programs.

Regardless of these issues, a captive breeding program is likely to be expensive and complex: funding is necessary to build exhibits and off-exhibit breeding facilities, and to provide food, veterinary care, and support for other collection operations. In addition, a captive breeding program requires longer prerelease time. A translocation in which animals are captured in the wild and released into another location can initiate the recovery process faster than a captive breeding program where animals must be captured and bred before a release can occur. The IUCN/SSC RSG guidelines (1998, 8) state strongly that reintroductions "should not be carried out merely because captive stock exists or solely as a means of disposing of surplus stock." Thus, the decision to use captive animals as the source population requires an evaluation of the advantages and disadvantages for each species program.

DISEASE RISK

Disease infects individuals as a normal feature in any environment, but the risk of transmitting infectious disease appears to be a concern with reintroductions that use captive-bred animals (Ballou 1993; Woodford 1993; Cunningham 1996; Griffith et al. 1993; Snyder et al. 1996; Lafferty and Gerber 2002). Pathogens can be transmitted between animals of the same species or between species, including to and from humans (see Travis and Barbiers, chap. 7, this volume), and the direction of disease transmission can be from captive to wild individuals or the reverse (i.e. newly released animals can acquire a resident disease).

Transmission of disease can increase the risk of decline or extinction of a population by increasing mortality rates. The risk to small populations, typical for reintroduction programs, may depend on the interaction between the infectious agent and population density. For example, small, dense populations may be at greater risk of adverse effects from an epidemic than similar-sized populations with lower densities, because transmission rates will be greater in the former (May 1988; Lafferty and Gerber 2002). Woodford (1993) provides actual examples of disease transmission in different situations, including transmission as a result of animal translocations from one wild site to another.

Concern about accidental disease transmission seems greater when released animals are from a captive rather than a wild source (Snyder et al. 1996). Specific threats in relation to captivity include high densities and exposure to other species with novel diseases (Cunningham 1996; Snyder et al. 1996). On the other hand, animals in well-managed captive facilities benefit from veterinary care, because health can be monitored, diseases may be diagnosed, and suitable actions can be taken to improve an animal's health and to avoid disease transmission, including not releasing individuals with known problems.

There are many suggested actions to minimize transmission of disease (Woodford and Kock 1991; Beck, Cooper, and Griffith 1993; Cunningham 1996; Miller, Reading, and Forrest 1996; Snyder et al. 1996; Mathews et al. 2006), and the IUCN/SSC RSG guidelines (1998) include many veterinary measures, including a prerelease exam with disease screening and preventive actions and/or quarantine before release. In addition, the IUCN guidelines recommend minimizing the risk of infection during shipment by avoiding exposure to animals of the same or other species with poor or unknown health. Of particular importance are postrelease monitoring and necropsies of dead animals (as recommended by IUCN/SSC RSG 1998) to identify disease risks as the reintroduced population matures. While the exams, screenings, quarantines, monitoring, and necropsies increase the cost and logistical challenges for a reintroduction program, these programs do conduct some or all of these measures. For example, the golden lion tamarin, *Leontopithecus rosalia*, conservation program has intensive quarantine protocols that include standard blood screening and screening for callitrichid hepatatis virus before releasing captive-born individuals (Ballou 1993). However, regardless of population size, source of animals, or efficacy of veterinary measures, disease risk always exists. All reintroduction programs should explicitly consider and minimize this risk.

BEHAVIORAL COMPETENCE OF CAPTIVE-REARED INDIVIDUALS

Captive-reared individuals may be less able to survive and reproduce after release than wild-born conspecifics. Indeed, reintroductions using wild populations as the source are approximately twice as successful as those using captive populations (29 versus 15%, respectively—Griffith et al., 1989; 31 versus 13%—Fischer and Lindenmayer 2000). While there may be other factors associated with programs that release captive-reared individuals (e.g. release of limited numbers), captivity does influence the behavior of mammals (Carlstead 1996; McPhee and Carlstead, chap. 25, this volume). Many of the skills needed for survival in the wild, e.g. orientation and navigation, foraging behaviors, finding suitable nest sites, and predator avoidance (Box 1991), are not essential for survival in captive breeding facilities. For some but not all species, such skills may be more readily acquired after release into the wild. May (1991) suggested that species displaying innate or hard-wired behaviors may be more successful candidates than species displaying more flexible behaviors when captive-reared animals are the source for reintroduction.

If captive individuals lack behavioral competencies to survive in wild habitats, using captive populations as a source will reduce the probability of success of a reintroduction program. Behavioral incompetence may occur either through missed developmental opportunities (Stoinski and Beck 2004) or genetic changes resulting from adaptation to captivity (McPhee 2004; McPhee and Carlstead, chap. 25, this volume).

There are different methods available to address the problems of behavioral competence. Mathews et al. (2005) described prerelease screening protocols in which behaviors of wild conspecifics provide the baseline and controlled behavioral experiments assess the suitability for release of specific captive-bred individuals. Beck (1995) suggested that captive breeding facilities prepare animals to cope with challenges in the wild by exposing them to opportunities and impediments while still in captivity. Griffin, Blumstein, and Evans (2000) proposed that captive-bred animals routinely experience antipredator training, because a substantial number of postrelease deaths are due to predators.

Managers believe that some species are more flexible, and individuals can acquire appropriate behaviors; in these cases, the development of specific prerelease training programs may increase postrelease survival (Beck et al. 1988; Biggins et al. 1999). However, Stoinski and Beck (2004) found that prerelease experience (e.g. opportunity to locomote and forage in natural-type conditions) for golden lion tamarins provided few improvements in behavior and no survival benefits, possibly because the prerelease experience was provided to mature individuals and did not occur during the important early developmental stages. Managers should use experiments to identify the most suitable protocols for release, and may need to adapt management to address behavioral concerns (Miller, Reading, and Forrest 1996; Seddon, Armstrong, and Maloney 2007).

CHANGES IN GENETIC COMPOSITION OF CAPTIVE POPULATIONS

Behavioral incompetence as a result of a genetic adaptation to captivity may present a more serious threat than a missed developmental opportunity. Behavioral traits can be heritable, linked to fitness, and vulnerable to selection (McDougall et al. 2006). Natural selection occurs in captivity; behaviors persist that enhance survival and reproduction in captive conditions (Frankham and Loebel 1992; Arnold 1995; Carlstead 1996; Woodworth et al. 2002; Gilligan and Frankham

2003; McPhee 2004). While this selection may be unintentional, it occurs in all species (Frankham, Ballou, and Briscoe 2002; McDougall et al. 2006); individuals that survive and reproduce in captivity leave more descendants than those individuals that cannot adjust. Selection is detectable after only 3–4 captive generations and may result in even more rapid evolution than expected (Lacy 1994; Arnold 1995; Woodworth et al. 2002; Gilligan and Frankham 2003; Stockwell, Hendry, and Kinnison 2003; McDougall et al. 2006). While adaptation appears to be most rapid in earlier generations in captivity, it likely continues although at a slower pace throughout the generations a species is maintained in captivity. Behaviors that are favored in the wild may persist in the population, but the frequency of these behaviors declines. Those individuals that are successful in captivity, but have traits that would have been selected against in the wild, will be less likely to survive or reproduce when released into a wild environment (Frankham et al. 1986; Lynch and O'Hely 2001; McPhee 2004; Mathews et al. 2005).

Genetic drift causes change in a captive population's gene frequencies through the random sampling process, because each generation is only a genetic sample of the previous one. Genetic drift results in a loss of genetic diversity and has a greater impact on small than on large populations (Lacy 1994; Ballou and Foose 1996; Frankham, Ballou, and Briscoe 2002; Ballou et al., chap. 19, this volume). Although some genetic change in captivity is unavoidable, managers of captive populations do and should use strategies that attempt to retain initial genetic variation and minimize evolutionary change (Foose 1991; Arnold 1995; Frankham, Ballou, and Briscoe 2002). Genetic management, which prioritizes individuals for breeding based on a measure of genetic diversity, will retain gene frequencies most similar to the wild founders of the captive population (Ballou and Foose 1996; Frankham, Ballou, and Briscoe 2002; Ballou et al., chap. 19, this volume). This genetic strategy should not only preserve the potential for individuals to adapt when released into the wild, but also minimize the production of individuals whose behaviors are strongly adapted to captivity. Of course, managers may not be able to control fully which individuals leave offspring, because not all individuals thrive in captivity. The optimal genetic management may not be feasible, but application of genetic management practices still retains more genetic diversity than random breeding (Earnhardt, Thompson, and Schad 2004). Thus, if a captive breeding program has reintroduction as a goal, genetic management should be a priority from its initiation.

Other strategies can minimize genetic change while animals are in captivity and should be considered when planning a reintroduction using a captive population. First, increasing the length of generation time results in fewer generations in a specified time; thus, the population's gene frequencies would be less likely to change through selection and genetic drift (Gilligan and Frankham 2003). The common practice of breeding founders before their offspring and breeding the offspring before the grand-offspring extends generation time. Second, regular importation and breeding of animals from the wild can inject new genetic material into the captive population, again reducing the rate of genetic change (Lynch and O'Hely 2001; Woodworth et al. 2002; Gilligan and Frankham 2003). Third, creating captive conditions similar to those in the wild might weaken directional selection for captivity and minimize genetic change (Woodworth et al. 2002; Gilligan and Frankham 2003). Some reintroduction programs construct facilities near (or as ecologically similar as possible) to the planned release site; these facilities house a core group of animals that breed and whose offspring acclimate to local conditions and are then released. For example, black-footed ferrets, *Mustela nigripes*, reared in an environment as close to natural as possible survived better after release than those reared in a traditional captive facility (Miller, Reading, and Forrest 1996). The Mexican wolf, *Canis lupus baileyi*, bongo, *Tragelaphus eurycerus isacci*, and Arabian oryx, *Oryx leucoryx*, reintroduction programs have also used an on-site breeding facility approach (FWS 2006; Fort Worth Zoo 2006; Stanley Price 1989b). An undesirable consequence may be the additional delay before first release while animals transfer to the on-site facility, acclimate, and breed, and the offspring mature (Stanley Price 1989b).

Reintroduction programs using captive-bred animals may be complex and require more detailed planning than those involving wild-to-wild translocations, but programs with some proven success, e.g. black-footed ferret (Howard, Marinari, and Wildt 2003), Arabian oryx (Stanley Price 1989b), and golden lion tamarin (Kleiman and Rylands 2002), demonstrate that a captive breeding program is a feasible conservation option. For species globally extinct in the wild, using a captive population for reintroduction is the only option, e.g. Pére David's deer, *Elaphurus davidianus* (see Gordon 1991), and Przewalski's horse, *Equus caballus przewalskii* (see Slotta-Bachmayr et al. 2004), and captive facilities may act as a refuge for a population while conservationists address the causes of extinction in the wild.

Individuals from captive populations in accredited zoos can have advantages as a source for reintroductions. The data on individuals in zoo collections are especially comprehensive for mammals, including age, sex, reproductive history, and pedigrees, and these data are maintained in standard electronic species databases (i.e. studbooks). Population managers routinely monitor, analyze, and adjust the demographic and genetic characteristics of these populations to meet defined objectives (Ballou and Foose 1996; Ballou et al., chap. 19, this volume). These data and analyses give managers unique control over the choice of individuals for release. Additionally, the intense management of captive populations provides more control over disease risks, source population size, and source population structure. While conservation biologists may agree that captive breeding and reintroduction are not an *ideal* means to create viable wild populations of endangered or threatened species, they can serve as one component of a multifaceted conservation plan (Lacy 1994; Miller, Reading, and Forrest 1996; Morrison 2002).

THE ROLE OF ZOOS IN REINTRODUCTIONS

A managed captive population includes individuals of a single species held by multiple zoos that agree to collaborate in its management. While all captive populations can benefit from a scientific management approach, populations intended for release into the wild, in particular, merit sound genetic and demographic management to improve their conservation prospects. This management requires an especially high level of cooperation among participants. When AZA developed Species Survival Plans (SSPs) in the early 1980s, one goal was conservation of endangered or threatened species in the wild, and reintroductions were considered one of the best options for zoo contribution to *in situ* conservation (Foose et al. 1986; Wiese and Hutchins 1994). Yet, in 2004, less than 20% of all SSP programs included reintroduction of the species as a program objective (AZA ReintroSAG 2005). While a conservation goal still exists and reintroduction can be successful for some mammal populations, population managers recognize that captive breeding programs and reintroductions are not a panacea for species recovery (Kleiman 1996; Miller, Reading, and Forrest 1996; Frankham, Ballou, and Briscoe 2002).

The zoo community may contribute to a reintroduction program in various ways, e.g. by providing animals for release (or for an *in situ* breeding program that will release offspring), but zoos may also provide funding and expertise in husbandry, animal transfers, veterinary protocols, and population management (Beck 1995; AZA ReintroSAG 2005; WAZA 2005; Zimmermann, chap. 23, this volume). The diverse and complex character of reintroductions often leads zoos to form partnerships with other agencies (Beck et al. 1994; Kleiman, Stanley Price, and Beck 1994; Reading and Miller 2001). An early and admirable example of such collaboration was the golden lion tamarin reintroduction project, led by the Smithsonian Institution's National Zoological Park in partnership with Brazil's federal agency, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA—formerly IBDF). The Smithsonian's commitment spans more than 30 years and has included providing personnel with expertise in ethology, population biology, veterinary care, education, and administration as well as considerable financial support from the zoo, the Smithsonian, and the Friends of the National Zoo (Kleiman and Rylands 2002). Zoos can make notable contributions to reintroduction programs, because their areas of expertise (including infrastructure and population management) address some of the principal needs of such efforts (Stanley Price 2005).

DEVELOPING SUSTAINABLE CAPTIVE POPULATIONS AS A SOURCE FOR REINTRODUCTIONS

Population management should be a basic focus when initiating a captive breeding program with the intent of a future reintroduction. To serve as a source, the captive population should represent, to the degree possible, the genetic composition present in the wild population at the time of initial capture and will need to provide a suitable number of animals for harvest and release. In the process of developing a sustainable captive population, growth proceeds through 3 typical stages (Ballou and Foose 1996):

1. A founder stage, in which individuals are brought into captivity
2. A growth stage, when births exceed deaths and the population size increases
3. A self-sustaining stage, in which the population is maintained at a desired population size

These 3 stages will be discussed in the context of reintroductions and relative to population biology theory and applications.

STAGE 1: CAPTURE OF WILD ANIMALS TO FOUND A CAPTIVE POPULATION

Capture of individuals from the wild to initiate a captive population can create conflicting demographic costs and benefits for the 2 populations. If the species is restricted to one location with only a single, small wild population, capture of individuals increases the population's vulnerability to catastrophic loss and increases the risk of species extinction, because small populations are more likely to become extinct (O'Grady et al. 2004). With a large wild population, capturing many individuals for founders may have no species impact. Of course, managers are more likely to need to capture animals from vulnerable small wild populations, because threatened and endangered species tend to exist in small numbers. Because a key objective is the viability of each population, identifying how many individuals to capture may pose a dilemma.

Using a computer model, Tenhumberg et al. (2004) simulated the trade-offs of different wild and captive population sizes with different levels of risk to identify optimal strategies; the authors assumed that a captive breeding program would succeed and that a stable captive population could ultimately benefit the recovery of the species in the wild. While no strategy was universal, the study found that some actions were more likely to result in the long-term persistence of the species: (1) as threats to the wild population increase, more individuals should be captured; (2) if the wild population declines to the level of <20 females, all remaining wild individuals should be captured; and (3) as population sizes in the wild and in captivity become smaller, the proportion of wild individuals that should be captured for a captive program increases (Tenhumberg et al. 2004). These results suggest that delaying capture of individuals from a small, declining population could be a risky strategy, especially if the species is limited to one population.

The number of animals captured from the wild affects the amount of genetic variation in the new captive population. In general, as the number of individuals captured increases, the gene diversity (i.e. expected heterozygosity [Allendorf 1986; Lacy 1995]) and probability of capturing rare alleles will also increase (Frankham, Ballou, and Briscoe 2002). Ten or 25 founders of a captive population can retain 95 and 98%, respectively, of the gene diversity (Allendorf 1986). Beyond 20 individuals, the additional benefit from more founders accrues more slowly.

Conventional practices which assume that founding individuals are unrelated may overestimate the effective allelic diversity (Allendorf 1986; Lacy 1994; Frankham, Ballou, and Briscoe 2002), because individuals from small wild populations are more likely to be related than those from large populations. As an example, molecular identification of relatedness among captive Guam rails, *Rallus owstoni*, revealed that some founder birds assumed to be unrelated had a high probability of relatedness even though the birds were collected from different nests (Haig, Ballou, and Casna 1994). Thus, pro-

TABLE 22.1. Population metrics from 7 Species Survival Plan (SSP) programs that have stated reintroduction is a goal of the program

Species	*N*	Lambda	% GD	No. of Founders	FGE	Dates of capture	*T*	Year of analysis
Black-footed ferret	309	1.80	86.99	7	3.84	mid-1980s	1.6	2005
Mexican wolf	307	1.12	82.41	7	2.84	1960s	5.4	2005
Red wolf	168	1.03	89.84	12	4.92	1970s	5.6	2005
Arabian oryx	111	1.06	92.30	13	6.47	1960s	6.3	2005
Addax	194	1.16	84.00	16	3.13	1960s	5.7	2005
Scimitar-horned oryx	243	1.14	96.04	32	12.64	1960s	5.3	2004
Bongo	171	1.13	94.20	33	8.66	1960s	6.3	2004

Source: Data are taken from breeding and transfer plans posted on the AZA Web site, 2006.

Note: *N* = captive population size as of analysis year; Lambda = potential population growth rate; GD = % gene diversity retained relative to the founding population; No. of founders = wild-caught animals with living descendants in the captive population; FGE = Founder Genome Equivalents; Dates of capture = a general range; *T* = mean generation time in years.

grams may need to capture a larger number of animals from a small population (Foose et al. 1986), increasing the cost/benefit conflict between captive and wild populations.

The numbers of wild-caught individuals that survive, reproduce, and have living descendants in the captive breeding program (termed founders) will be fewer than the number captured (Lacy 1994). The red wolf, *Canis rufus*, program was very successful at maximizing the number of surviving and reproductive individuals after capture. The red wolf breeding program applied genetic, demographic, and husbandry expertise from the initiation of the program, and 12 of the 14 initially captured individuals became founders (AZA Conservation and Science 2006). By contrast, of 422 cheetahs brought into captivity for the SSP program (where reintroduction was not an objective), there were only 83 founders in the population as of 2004 (Gerlach, personal communication). Retention of gene diversity in a captive population varies even when numbers of founders are similar, because founder genes can be retained in different frequencies (table 22.1). Inequalities in the number of descendants from founders, number of elapsed generations, and population size contribute to genetic differences in population programs (Ballou and Foose 1996). For example, the addax, *Addax nasomaculatus*, SSP population had more founders ($N = 16$), but as of 2005 had retained less gene diversity than the Arabian oryx SSP population with fewer founders ($N = 13$) (table 22.1).

STAGE 2: GROWTH OF THE CAPTIVE POPULATION

For a population to grow (i.e. the number of births exceeds the number of deaths), conditions must be suitable for the species in the captive environment. Zoos and aquariums usually (but not always) have sufficient expertise to create conditions under which a population can change from the founder to the growth stage. This expertise includes knowledge of husbandry, i.e. providing the proper environment and social grouping, veterinary care to minimize mortality at all stages of life, and nutrition to provide a diet appropriate for health and reproduction. Despite the best husbandry practices, however, population growth may not occur; this has been a challenge for a few captive mammal populations (e.g. southern black rhinoceros [*Diceros bicornis minor*] [Wiese, Farst, and Foose 2000] and drill [*Mandrillus leucophaeus*] [Earnhardt and Cox 2002]). Some captive populations that eventually grow may do so slowly, until husbandry techniques are perfected. Long-term population growth requires that the offspring born in captivity consistently survive and reproduce. Because rapid growth retains more gene diversity over the long term than slow growth, managers should pursue high reproductive rates (Lacy 1994). During the growth stage, captive individuals cannot be harvested for release without slowing the captive population's development toward stage 3 (ibid.).

STAGE 3: MAINTAINING A SELF-SUSTAINING CAPTIVE POPULATION DURING HARVEST OF ANIMALS

For any captive breeding program, harvesting individuals for release changes the size and the demographic and genetic structure of the captive population. Managers can control these changes, because most captive populations can be monitored. Like the initial capture of individuals for a captive population, harvest strategies produce competing costs and benefits between genetic and demographic structure and between captive and released populations. Identifying the trade-offs and the most effective harvest strategies can be based in population biology practices, but the decisions will also depend on a reintroduction program's specific objectives. Typically, the goal is to maintain a self-sustaining captive population during harvest for reintroduction.

COMPUTER MODELS FOR RESEARCH AND PLANNING

Computer simulation models can be valuable as a research and planning tool for reintroduction programs. These models require comprehensive data for quantitative simulation of events, and most captive mammal populations have the necessary data. Rather than conducting actual experiments with animals from an endangered or threatened population, models can simulate different management strategies and can project outcomes 10, 50, or more years into the future. Because reintroductions are costly and risky, models (e.g. population viability analysis) can provide quantitative evaluation *before* an actual release and inform managers about the most effective strategies to achieve their program objectives (Miller, Reading, and Forrest 1996; Bustamante 1998; Seigel and Dodd 2000; Morris and Doak 2002; Slotta-Bachmayr et al. 2004; Seddon, Armstrong, and Maloney 2007).

The IUCN/SSC RSG guidelines (1998) propose using models to assess the optimal number and composition of individuals to be released per year and to assess the number of years necessary to promote establishment of a viable release population. As an example, Steury and Murray (2004) constructed alternate models for the reintroduction of lynx, *Lynx canadensis*, to assess the total number to be released, the optimal number of releases, and the timing of releases. In a similar exercise, Saltz and Rubenstein (1995) used models to determine a maximum sustained yield from "breeding cores" and to project the growth of reintroduced populations of Persian fallow deer, *Dama dama mesopotamica*, and Arabian oryx in Israel. The simulations predicted that it would take 8 to 11 years to complete the fallow deer reintroduction and 6 to 10 years to complete the oryx reintroduction.

In a study on bearded vultures, *Gypaetus barbatus*, Bustamante (1998) used computer simulations to show that expanding the project to other European mountains would dangerously deplete the captive population, and that the most effective way to increase the release rate without increasing the captive population size was by improving hatching success in captivity. Models can thus integrate diverse factors affecting population dynamics typical of reintroduction programs; they can produce outcomes that are difficult for managers to predict solely through intuition.

STRATEGIES FOR HARVEST

In the following sections, I discuss those issues that affect captive population dynamics during harvest and that can be best evaluated using models. When developing strategies to harvest animals, managers need to consider

- when the captive population is large enough to sustain a suitable harvest,
- how many animals can be harvested while sustaining the captive population, and
- what demographic (e.g. age and sex) and genetic traits should be selected for the harvested animals.

WHEN IS THE CAPTIVE POPULATION LARGE ENOUGH TO HARVEST ANIMALS?

Allowing a captive population to increase in size produces benefits, e.g. more offspring for harvest and a less vulnerable captive population. In the hypothetical example presented in table 22.2, a population of 50 individuals produced only one individual for harvest while sustaining its captive population size, whereas a population of 300 individuals with the same reproductive and mortality rates produced 7 offspring for harvest each year. However, a larger captive population costs more to maintain.

Populations will differ in how long it takes to attain a specific population size, because generation time varies across species. The longer a species' generation time (i.e. the average age of first reproduction), the longer it will take before attaining a defined population size; e.g. the population of Mexican wolves, with a longer generation time, will increase more slowly than the black-footed ferret population (table 22.3).

Similar to the demographic trade-offs, genetic costs and benefits accrue when the time before harvest increases in length. Larger populations should retain more genetic diversity (Ballou and Foose 1996); however, as already described, the more generations in captivity, the greater the risk of genetic change. Thus, managers must balance these genetic trade-offs (ibid.; Miller, Reading, and Forrest 1996; Ostermann, Deforge, and Edge 2001).

HOW MANY CAPTIVE ANIMALS CAN BE HARVESTED FOR RELEASE?

Releasing a large number of individuals during a reintroduction program correlates with greater success (Griffith et al. 1989; Beck et al. 1994; Wolf, Garland, and Griffith 1998; Fischer and Lindenmayer 2000). However, programs that release a larger number of individuals may also be well funded, have greater community support, and conduct releases over a longer time frame, also factors correlated with success. In general, a small number of individuals is more vulnerable to random forces (i.e. demographic, genetic, and environmental stochasticity), and the released population is less likely to persist (Soulé 1980; Foose 1991; Caughley 1994; O'Grady et al. 2004).

Harvesting a large number of individuals for a release can present a challenge for managers, because most captive population sizes are small. If managers harvest more individuals than can be replaced through population growth in a given time frame, the population will not be self-sustaining. The RSG cautions against jeopardizing the future of a captive population that is the source of individuals for release (IUCN/SSC RSG 1998). Table 22.4 indicates that doubling an annual harvest from 12 to 24 individuals can reduce a captive population size from 100 to 27 animals within 5 years. How-

TABLE 22.2. Interaction of captive population size and number of offspring produced for harvest in a hypothetical population

Population	If population size is	No. of offspring produced annually		No. surviving one year		No. needed to sustain captive population (i.e., replacement)	No. available for harvest	
		Litter = 1	*Litter = 3*	*Litter = 1*	*Litter = 3*		*Litter = 1*	*Litter = 3*
1	50	4	11	3	8	2	1	6
2	100	8	23	5	16	3	2	13
3	200	15	45	11	32	6	5	26
4	300	23	68	16	47	9	7	38

Note: Breeding females equal 25% of the population, the birth rate of those females is 30%, first-year mortality is 30%, and all other mortality is 3%. Surviving offspring replace the animals that died. These calculations use one-time step and fixed values. Output values are rounded to integers.

TABLE 22.3. Examples of the relationship between a species' mean generation time (T) in captivity (based on data extracted from the SSP breeding and transfer plans, AZA 2006), the number of generations in a specific time frame, and the population size at 10 years using a lambda of 1.1

		Generations			
Species	T (years)	In 10 years	In 50 years	N_0	N_{10}
Black-footed ferret	1.6	6.25	32.26	100	181
Mexican wolf	5.4	1.85	9.26	100	119
Bongo	6.3	1.59	7.94	100	116
Black rhinoceros	15.9	0.63	3.14	100	106

TABLE 22.4. Impacts on the captive population size after 5 years of harvesting different numbers of individuals using population 2 from table 22.2 and a litter size of 3

No. harvested annually	N_{initial}	$N_{\text{at 5 years}}$
12	100	105
14	100	92
16	100	79
18	100	66
20	100	53
22	100	40
24	100	27
26	100	15
28	100	2
30	100	Extinct

TABLE 22.5. Demographic characteristics related to the life history patterns of fast and slow species

Species type	Reproduction	Life stage	Longevity	Population growth—most sensitive parameter
Fast	Large litters	Early maturity	Short-lived	Fecundity
Slow	Single or few offspring	Delayed maturity	Long-lived	Survival

Source: Heppell, Caswell, and Crowder 2000; Oli and Dobson 2003.

ever, a harvest of 26 individuals could be sustainable when the population size is 200 (table 22.2).

The number harvested for release may need to be adjusted based on other factors as well; for example, behavior has an impact on survival and reproductive rates. McPhee and Silverman (2004) developed a calculation termed a release ratio that increased the number of individuals to be released as a compensation for reduced survivorship among individuals with maladaptive behavioral traits. For example, a release of 130 to 150 captive-bred mice, which were less cautious than wild mice, was deemed equivalent to the release of 100 with wild-type behaviors (McPhee 2004).

WHICH CAPTIVE ANIMALS SHOULD BE HARVESTED?

Harvesting individuals with specific traits alters the composition of the remaining captive population, its vital rates, and its future population growth. In turn, the characteristics of released individuals influence the future growth of the wild population. Individuals for harvest can be selected based on demographic, genetic, and behavioral characteristics or a combination. Demographic (e.g. age and sex) and genetic (e.g. genetic relatedness and inbreeding coefficients) data on individuals are readily available in studbook databases for captive populations and can be the basis for decisions on which captive animals should be harvested.

The life stage of an individual (e.g. whether it is an infant, juvenile, or adult) interacts with the species' life history (e.g. age at reproductive maturity, life span, litter size) and behavioral (e.g. dispersal, learning) patterns to affect strongly the individual's contribution to future population growth. For some species, the release of adults in contrast to juveniles may fuel more rapid growth of the release population. From life history theory, mammal species can be characterized as "slow" or "fast" species (Heppell, Caswell, and Crowder 2000; Oli and Dobson 2003) (analogous to r- and K-selected species: Pianka, 1970). In a "slow" species where the infant and juvenile stages are of long duration (table 22.5), adults fuel more population growth because, they contribute (i.e. reproduce) immediately (Sarrazin and Legendre 2000; Oli and Dobson 2003). If the proximate objective is further growth of the captive population, managers should retain adults, but if the proximate objective is the growth of the released population, managers should release adults to promote wild population growth. Sarrazin and Legendre (2000) demonstrated this principle with a demographic model that assessed relative efficiency of releasing juvenile or adult griffon vultures, *Gyps fulvus*, a species with a "slow" life history. When only demographic considerations (e.g. not genetic) were incorporated into the model, it was most efficient for the reintroduction to release adults. Seigel and Dodd (2000) question the wisdom of reintroducing any species with a slow life history, because recruitment may take too long for a reintroduction to be successful.

Environmental differences in longevity may make decisions about which life stage to harvest even more complex. Because individuals commonly live longer in captivity than in the wild, adults may be more valuable in a captive population, where overall reproductive life span would be greater than in the wild. When adult behaviors differ from juveniles, these differences may be a factor influencing population growth. If adults are more philopatric than younger individuals and remain in the release area rather than dispersing, they might survive better and therefore promote a more successful reintroduction. Ostermann, Deforge, and Edge (2001) found that survival of bighorn sheep, *Ovis canadensis*, released as adults (which display lower dispersal rates) was significantly higher than yearlings.

While adults may be a preferred life stage in some species, juveniles may be more crucial to population growth in others. In "fast" species that have earlier reproductive opportunities and produce more offspring, harvesting juveniles may retard captive population growth but will promote growth of the released population. As a basic principle, the eventual population will be larger when the initial population comprises age classes with higher reproductive value (Caswell 1989). Additionally, younger individuals are more abundant in growing populations, and thus more individuals are available.

When behavior of juveniles improves their survivorship, the release of younger animals, regardless of reproductive value, may be more beneficial to a program. For example, in species where learning experience during development is important, younger individuals may acclimate more rapidly and thus have higher survival and reproductive rates after release into the wild (Gordon 1991; Stoinski and Beck 2004). Kleiman et al. (1991) found that in releases of captive-born golden lion tamarins, survival was higher for younger than for older individuals. Similarly, in a study of adult female Asiatic wild ass, *Equus hemionus*, released in Israel, Saltz and Rubenstein (1995) hypothesize that release of adults probably delayed population growth, because older females produce a male-biased birth sex ratio and have less reproductive success due to stress caused by capture, transport, and release procedures. They concluded that release of younger subadult female asses would therefore be better. Because the scope of contributing factors varies and the stage of individuals harvested for release consists of trade-offs, harvest/release strategies should be designed with experimental approaches to identify the most suitable protocols.

Genetic characteristics of released individuals (e.g. origins, adaptation to captivity, genetic variation, and inbreeding) also affect the probability of creating a viable wild population (Frankham, Ballou, and Briscoe 2002), and the interaction between genetic characteristics, behavior, and vital rates can elevate the relative importance of genetics within a program. Because individuals can adapt to local environmental conditions, guidelines suggest that the genetic origins of individuals for release match those of individuals formerly at the target site (Kleiman 1996; IUCN/SSC RSG 1998), with individuals from lineages with fewer captive generations being preferred (Ballou and Foose 1996).

Releasing highly inbred individuals is considered inadvisable, because inbreeding depression (i.e. deleterious effects from breeding between close relatives) can reduce reproduction and survival rates. In a reintroduction study that released inbred and noninbred mice from a captive population, Jiménez et al. (1994) found that (1) inbred mice suffered higher mortality than noninbred and (2) the mortality rate of inbred mice was more severe in the wild than in captivity. Similarly, Miller (1994) found that inbreeding depression was more severe under conditions of environmental stress (e.g. conditions encountered by animals released into a novel wild habitat).

Table 22.6 presents a simple contrast of 2 strategies that exemplifies the conflict between the captive and release populations (Ballou [1997] and Earnhardt [1999] provide discussions of additional genetic strategies). With captive breeding data that identify parentage, managers can calculate an individual's specific relationship to the founding and current population (Ballou and Foose 1996; Miller, Reading, and Forrest 1996). In strategy A, individuals that are highly related in the captive population are chosen for harvest (table 22.6). Because some lineages leave more descendants and are therefore overrepresented, harvest of these offspring can promote a more equal founder representation in the captive population. However, releasing highly related individuals can increase the probability of encountering and breeding with a close relative in the wild (i.e. inbreeding) and thus reduce genetic variation and adaptive potential in the release population. In contrast, in strategy B, individuals from lineages with fewer descendants are chosen for harvest. This strategy has potential negative impacts, since it may compromise future equalization of founder lineages in captivity; and if the released individuals die without producing offspring, the opportunity to capture their genes is lost. In general a population of individuals with the greatest genetic variation (i.e., equivalent to the founders) can enhance survival, since variation provides the released population with the evolutionary potential to adapt in the wild environment (McDougall et al. 2006).

Some reintroduction programs have used a combination of these strategies; for example, strategy A may be used during the beginning phase, when survival after release is uncertain, and strategy B may be switched to later, when survival and reproduction are more certain (e.g. golden lion tamarin: Ralls and Ballou 1992; black-footed ferret: Russell et al. 1994). Because the relative genetic costs and benefits are not consistent across all populations, the trade-offs should be considered for each population under investigation (Haig, Ballou, and Derrickson 1990; Ballou 1997; Earnhardt 1999). To make the identification of harvest strategy even more complex, selection of individuals based on genetic objectives may need to eclipse demographic objectives or vice versa.

POSTRELEASE MONITORING

Regardless of the traits selected, postrelease responses of animals are never certain and can only be known through reliable, long-term, postrelease monitoring of individually identified animals (Saltz and Rubenstein 1995; Miller, Reading, and Forrest 1996; Ostermann, Deforge, and Edge 2001; Stoinski and Beck 2004). Because the survival and reproduction of released animals are critical to success, postrelease monitoring is one of the most powerful tools available for managers of reintroductions. Evaluations of harvest/release

TABLE 22.6. Trade-offs in 2 genetic strategies to harvest animals from a captive population for release to the wild

Genetic strategy	Description of strategy to harvest individuals	Captive population		Released population	
		Benefits	*Costs*	*Benefits*	*Costs*
A	Individuals most related to the captive population	Smaller loss of gene diversity	—	Greater number available for release	Greater risk of inbreeding and less evolutionary potential
B	Individuals least related to the captive population	—	Greater loss of gene diversity	Smaller risk of inbreeding and more evolutionary potential	Smaller number available for release

protocols, welfare, and behavioral competence as well as reproduction and survival rates are considered essential to program management (Chivers 1991; Kleiman 1996; IUCN/SSC RSG 1998). Monitoring data can provide managers with vital rates for analysis and interpretation: e.g., is the observed mortality rate greater than expected, greater than in captivity, greater for males or females, greater for adults or juveniles, greater than wild conspecifics, or greater than births? Monitoring can identify causes of death (e.g. age, predation, starvation, conflict, or disease), essential information for managers who may want to change release protocols and improve management (Chivers 1991; Kleiman 1996; IUCN/SSC RSG 1998). Because the use of captive populations as a source for release animals is associated with less successful reintroductions (Griffith et al. 1989), postrelease monitoring is even more valuable for these reintroductions.

Postrelease monitoring can also provide data on the behavior of individuals to assess their competence in the wild (McDougall et al. 2006). The organization HELP (Habitat Ecologique et Liberté des Primates) released 34 chimpanzees, *Pan troglodytes*, from a sanctuary into an area with a remnant chimpanzee population (Goossens et al. 2005). Farmer, Buchanan-Smith, and Jamart (2006) found that the activity budgets and diets of released chimpanzees became similar to wild individuals, indicating that the released animals had adjusted to the wild, at least with respect to these behaviors. Similarly, Boyd and Bandi (2002) used activity budgets to assess adaptation by released Przewalski's horses and determined that they successfully acclimated to the wild. Postrelease monitoring data from captive-bred swift foxes, *Vulpes velox*, showed that individuals characterized as having low fear levels in captivity prerelease were less likely to survive in the wild, thus suggesting that such individuals are less suited for release (Bremner-Harrison, Prodoho, and Elwood 2004).

Postrelease monitoring can also be used to evaluate animal welfare, although the primary objective of a reintroduction program is population-level conservation, not individual welfare (Stanley Price 1991). Many people believe that animal welfare will improve with the opportunity to live in a complex wild environment, and that when the behavior of released animals resembles their wild conspecifics, their welfare will be satisfactory (Carlstead 1996; also see examples in previous paragraph).

However, there may be conflict between the welfare of an individual and the objectives of a reintroduction program (Beck 1995). Animals released into the wild may be exposed to risks that are rare or absent in captivity, e.g. predation, challenging environments, lack of food, inability to find a mate, and hazardous encounters with conspecifics. Indeed, risks may be greater for captive animals than their more experienced wild counterparts, thus generating concern about their welfare (ibid.; Mathews et al. 2005).

Kleiman (1996) recommends that each program develop guidelines governing when intervention is appropriate for those released animals whose welfare is in serious jeopardy. In the HELP project, observations collected on released male chimpanzees identified when they were attacked by resident conspecifics, thus provoking veterinary intervention to save individuals' lives (Goossens et al. 2005).

SUMMARY

Establishing captive or release populations is essentially an experiment in population biology, because we do not know the exact combination of factors governing the growth and persistence of specific populations. The experiment becomes more complex when the goal is establishing and maintaining 2 interdependent populations (i.e. source and release) simultaneously. The characteristics (e.g. age, sex, genetic background) of individuals in these populations vary, and thus population sizes and structures vary, creating unique interactions between the source and release populations. In this context, managers of captive breeding and reintroduction programs must frequently decide what level of risk is acceptable to the captive population as a trade-off against the opportunity to establish a successful reintroduced population.

Computer simulation models are a powerful tool that allows managers to test their assumptions and hypotheses as they weigh the trade-offs for population management in reintroduction programs. These investigations are best done before a release of animals to provide information for managers as they define their goals and objectives.

While this chapter has focused on captive mammal populations in a reintroduction program, the principles described here can also apply to other types of populations that serve as a source and to other taxa. Managers need to plan for a long-term commitment to the source population, since a successful reintroduction program may involve multiple releases over time and require many additional animals. Even when the wild population appears to be viable, managers may maintain the captive population as a safeguard against future catastrophic declines in the wild. The criteria used to decide on the future maintenance of a captive population once a wild population is self-sustaining are appropriately defined in the planning phase of the reintroduction program. The interdependency of source and release population may likely continue far into the future.

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The Role of Zoos in Contributing to *In Situ* Conservation

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INTRODUCTION

The Yunnan box turtle, *Cuora yunnanensis*, has not been recorded since 1906 despite intensive searches, and none are in captivity. The buff-nosed kangaroo rat, *Caloprymnus campestris*, was last seen in 1935; for this species also, none are in captivity. The last Carolina parakeet, *Conuropsis carolinensis*, died at Cincinnati Zoo in 1918, and the last thylacine, *Thylacinus cynocephalus*, at Hobart Zoo, Tasmania, Australia, in 1936. A further 782 species crowd the ominous IUCN (International Union for Conservation of Nature) Red List category of Extinct. A select few other species have been more fortunate: the Mauritius kestrel, *Falco punctatus*, California condor, *Gymnogyps californianus*, and Père David's deer, *Elaphurus davidianus*, were once on the brink of extinction but are now recovering, thanks largely to zoos. Yet paradoxically, while the mountain gorilla, *Gorilla beringei*, is Critically Endangered but not found in any zoo, there are more Amur tigers, *Panthera tigris* spp., in zoos than in the wild. In short, the *ex situ* conservation rationale of zoos is inconsistent. Captive breeding might help the axolotl, *Ambystoma bombypellum*, but for the Sumatran rhinoceros, *Dicerorhinus sumatrensis*, it is irrelevant and for grey whales, *Eschrichtius robustus*, impossible. And yet there is nothing stopping zoos and aquariums from ensuring the survival of axolotls, Sumatran rhinoceros, and grey whales. It is only a question of a paradigm shift, i.e. a major attitudinal and behavioral change. This chapter outlines the challenges and opportunities that zoos face in the implementation of their conservation role worldwide.

THE EVOLVING ROLES OF ZOOS

We have become so used to the pressure on zoos to commit to missions of conservation that it is almost difficult to imagine that this role is a relatively recent development in the evolution of zoos. The history of keeping wild animals for display is as old as our records of advanced civilizations: in 1490 BC, Queen Hatshepsut of Egypt kept a number of wild animals; circa 1000 BC the Chinese emperor Wang founded a large menagerie; the Greeks built menageries to study animal life; and King Henry I created what was possibly the first menagerie in Britain in the thirteenth century (Anonymous 1998). Zoos resembling our modern definition of the word began to appear in the eighteenth and nineteenth centuries, notably Schönbrunn (1752), London (1826), and Philadelphia (1859) (see Hancocks, chap. 11, this volume).

The keeping of wild animals is therefore undeniably part of human social history, feeding an ancient and indefatigable fascination with animals the world over. Even when the first natural history television films and documentaries created "armchair wildlife watching," the popular interest in zoos did not wane. For a child, seeing an elephant or a tiger from a close distance in a zoo is still an entirely different, and important, experience compared to the TV screen. What has changed, however, is an increased sympathetic attitude toward the well-being of the animals we see, as well as the public's perception of standards of acceptable animal keeping. While such standards vary interculturally, there is a general trend that captive animals—fellow mammals above all—will be well cared for in captivity (see Kagan and Veasey, chap. 2, this volume).

More recently, inundated with messages of environmental destruction and the plight of ever more vanishing species, an awareness of zoos' global responsibilities is appearing among these perceptions. Ask the average zoo visitors what makes a zoo a good zoo, and they will most often cite good animal welfare as their first reply and contributions to conservation as their second (Zimmermann 2000).

Conservation activities of zoos are not new. Conservation thinking began to sprout in a few select, forward-thinking zoos as early as 1945 (Baratay and Hardouin-Fugier 2002), and by the 1960s a number of zoos were portraying themselves as Noah's Arks—breeding and caring for endangered species while the world outside deteriorated. Pioneers among the conservation-minded zoos included Jersey Zoo, Channel Islands, United Kingdom, and its trust (now Durrell Wildlife

Conservation Trust), the Zoologische Gesellschaft Frankfurt, the New York Zoological Society (now Wildlife Conservation Society), the Zoological Society of London, the Smithsonian's National Zoological Park in Washington, DC, and a few more. Calling for a definition of the role of zoos in the conservation movement during the first World Conference on Breeding Endangered Species in Captivity in 1972, Jersey Zoo founder Gerald Durrell advocated the need to link zoos' *ex situ* activities to conservation needs (Durrell and Mallinson 1999). Many other zoo leaders followed the calling, with various degrees of commitment and resources, but a major change in thinking had begun; and in 1993, in the wake of the Earth Summit, the International Union of Directors of Zoological Gardens (then IUDZG, now the World Association of Zoos and Aquariums) wrote its first *World Zoo Conservation Strategy* (IUDZG/CBSG 1993).

HOW ZOOS CAN SUPPORT CONSERVATION

Around half the world's population lives in cities (Miller et al. 2004), so zoos offer an important connection to an element of the natural world. The number of people who visit zoos each year is enormous—in the United States, for example, AZA (Association of Zoos and Aquariums) institutions attracted 136 million visitors in 2000, a figure that exceeds the combined number of people going to professional baseball, basketball, hockey, and football games in that country in a year (Miller 2002). The World Association of Zoos and Aquariums (WAZA) estimates that around 600 million people visit zoos annually around the world (WAZA 2005). The potential, and indeed the responsibility, of zoos to educate and influence millions of people is therefore huge. In recent years the primary challenge for zoo-based educators has been to move beyond pure knowledge-oriented education to generate widespread awareness about conservation and the environment, and eventually to inspire masses of people to make fundamental changes in their behavior (Monroe and DeYoung 1993; Delapa 1994; Routman, Ogden, and Winsten, chap. 12, this volume).

Unfortunately, several attempts to evaluate the success of conservation education in zoos have shown poorer results than we would intuitively like to believe. Although acknowledging the difficulty of measuring learning in zoos, the independent studies that have been carried out have shown minimal impacts—studies at the National Aquarium in Baltimore, the American Museum of Natural History in New York City, and several British zoos have found that while some uptake of information takes place at the zoo, the impact on behavioral changes was lacking (Adelman, Falk, and James 2000; Giusti 1999; Balmford et al. 2007). Similarly, a visitor study at Hamilton Zoo, New Zealand, found that visitors were mostly concerned with viewing animals and not particularly interested in learning about them (Ryan and Saward 2004).

The overall role of zoos in conservation is a complex one. The main activities that zoos provide *ex situ* are the breeding of threatened species in captivity, their reintroduction, the maintenance of genetically managed insurance populations, the power to educate and influence large numbers of adults and children, and the ability to carry out essential basic research and to develop veterinary medicine using a vast range of otherwise inaccessible animals. Research within zoos, such as behavioral studies, animal biology, genetics, reproduction, and nutrition, is most often carried out with the aim of improving animal welfare, husbandry, veterinary knowledge, and population management, and thus contributing to the development of successful breeding programs as well as basic knowledge. However, such research can also have benefits for conservation and research in the wild, most often as a platform for researchers to test methodologies or gain experience.

Critics and advocates of zoos alike often cite the importance of fostering linkages between the zoo and the wild, *ex situ* and *in situ* conservation (e.g. Conway 1999; Hutchins 1999; Byers and Seal 2003). Specific linkages can take a variety of forms, including extrapolation of knowledge acquired from research in zoos, transfer of skills, testing of methodologies, and education on specific conservation issues. For example, most elephant reproductive biology research has been done in zoos—knowledge which is used in wild contexts as well (Smith and Hutchins 2000), and infrasonic communication in elephants, first discovered in captive animals, is now used in understanding how wild elephants coordinate their movements over great distances (Payne, Langbauer, and Thomas 1986). Wild jaguar, *Panthera onca*, surveying methodologies in Belize have been tested in the United Kingdom, using the footprints of the known zoo jaguars as control samples against unknown jaguars from the wild, and testing various noninvasive ways of collecting samples of jaguar hair by installing brushes and tape in their enclosure at Chester Zoo (P. Howse, personal communication). At Zurich Zoo, the construction of a major Madagascar-themed exhibit, the Masoala Hall, was designed with direct links to education and ecotourism opportunities for the visiting public; as a result, Swiss tourism to the Masoala region has doubled (Hatchwell and Rübel 2007).

While these contributions are enormously valuable not only to conservation in the wider sense but also to the sociology of our own species, their benefits to conservation are mostly indirect, and many zoo-based scientists now consider the addition of a portfolio of *in situ* activities a prerequisite for a zoo to call itself a conservation organization or a conservation-missioned zoo. To understand the importance of the contribution of zoos to *in situ* conservation, we first need to review the limitations of *ex situ* conservation.

THE LIMITATIONS OF *EX SITU* CONSERVATION

Among the mammals alone, there are 5416 known species, 20% of which are known to be threatened (IUCN 2004). A few species have benefited from *ex situ* conservation, but mammals, more than any other taxonomic group, make the limitations in the conservation value of captive breeding self-evident: First, space for captive breeding is limited—not all threatened species could be kept in genetically viable *ex situ* "insurance" populations in the world's zoos (Conway 1986; Soulé et al. 1986; Rahbek 1993). Second, the cost of captive breeding and *ex situ* conservation measures is high; e.g. one estimate calculated an average cost of $6546 for each native Australian animal bred for reintroduction (Perth Zoo 2000), while the animal food bill for very large zoos such as Chester Zoo is over $700,000 per year (NEZS 2005).

While the notion of rearing endangered animals in zoos and releasing them into the wild is appealing, the number of species that can ever be reintroduced into the wild is extremely low. Apart from the fact that reintroductions of higher vertebrates can be notoriously expensive, running at up to $500,000 per year per species (Derrickson and Snyder 1992), reintroductions also require a rigorous set of procedures and assessments. Reintroductions can only be considered if there is availability of suitable habitat under sustainable protection and in which the original cause of decline for the species has been identified and brought under control, along with a list of socioeconomic, legal, veterinary, and postrelease monitoring requirements (Kleiman, Stanley Price, and Beck 1994; IUCN/SSC RSG 1995). Reintroductions are therefore not frequently recommended in conservation action plans for mammals (see Earnhardt, chap. 22, this volume).

Yet despite these clear limitations of reintroduction, captive breeding is recommended for 64% of the species listed in the recovery plans in the United States (Tear et al. 1993). This paradox is explained by the concept of "insurance populations"—*ex situ* populations of animals that are unlikely to be reintroduced in the foreseeable future, but for which a Red List status of EW (Extinct in the Wild) is preferable to EX (Extinct).

However, even the extinction insurance concept has come under scrutiny. If zoos wish to use this line of argument, then, surely, their collections should reflect a clear prioritization in the species that they choose to keep. A controversial yet important critique of this notion emerged in a series of analyses that examined the choices zoos make in which species to keep. Balmford, Mace, and Leader-Williams (1996) presented the argument that if zoos claim to contribute to conservation through captive breeding of endangered species, there would logically follow a cost-benefit rationalization of which species they choose to keep. Gathering data on maintenance costs of animals in captivity, they found that annual per-capita costs increased greatly with body mass (from invertebrates to large mammals), and this was also true just within mammals themselves—small mammals being significantly cheaper for a zoo to keep than large ones. Reproductive rate of animals increased inversely with body size, so zoos could achieve higher rates of population growth if they concentrated on breeding small-bodied species (ibid.). Captive breeding is thus most appropriate for small-bodied taxa with a conservation need. For example, captive insurance populations have been recommended as a priority action for a large number of amphibian species in the recent Amphibian Conservation Action Plan of the Global Amphibian Assessment (DAPTF 2005; Anonymous 2005). Leader-Williams et al. (2007) have shown that 10 years after Balmford et al. (1996), there has only been a slight improvement in the number of coordinated breeding programs for smaller-bodied species, and the potential for reintroduction as a criterion remains weak.

CAPTIVATING RATIONALIZATIONS

Those who accept these arguments can then remind us that a zoo without an elephant, a tiger, or a giraffe is to most visitors "not much of a zoo." The public has expectations, and zoo directors are faced with a suite of demands different from directors of nonprofit, nongovernmental conservation organizations. So zoos may have these "charismatic" animals that bring in visitors, but still do little directly for their conservation. It is the public that pays, and the public that can become enthusiastic about animals and about conservation.

Most zoos, therefore, believe they need the large charismatic species to draw the attention of the public and generate income. Clever zoos were quick to argue that this income, in turn, could be used to fund more direct conservation work. "Ambassadors," they called these large species for which pure *ex situ* conservation arguments were difficult to find. The elephants at zoos are not there to breed for eventual reintroduction, nor are they part of insurance populations in the event of a sudden mass extinction where the cheaper option of translocation is not possible. These zoo elephants are the representatives of their kind, the comfortable martyrs flying the ambassadorial flag of their species. See them in the zoo, learn about the fate of our wild brothers, and donate money to conservation field projects—so goes the message.

In brief, there are many means to the end, and various zoos use different combinations of these to fulfill their mission of conservation. If zoos have such missions—and 90% of zoos in one international survey say that they do (Zimmermann and Wilkinson 2007)—then the question becomes one of accountability to their mission. A zoo that claims to contribute to conservation should be held accountable to that endeavor (Miller et al. 2004), and in many people's minds this means a serious contribution to conservation work where it matters most: *in situ*.

FUND-RAISING

The most straightforward way for zoos to contribute to *in situ* conservation is through financing, and the sums spent on conservation by zoos are significant. For example, a review of British and Irish zoos (for the years 1997–2000) showed that over £5 million (approx. USD $3 million) was spent by zoos on field conservation (WAZA 2005). Collaborative fund-raising can yield even more impressive results. The European Association of Zoos and Aquaria (EAZA) coordinates annual awareness and fund-raising campaigns, in which its members collectively raise over $300,000 per year for each themed campaign (e.g. Atlantic Rainforest campaign: €280,000, Tiger campaign: €750,000 over 2 years, Shellshock campaign €370,000; EAZA 2006).

Many zoos, especially large ones, have an advantage over nonzoo nonprofit organizations in public and corporate fund-raising, yet a slight disadvantage in winning grants from scientific trusts and foundations. The dilemma here is that often donors are more interested in *ex situ* facilities than *in situ* conservation. The high costs of exhibit construction perplexes some nonzoo conservation scientists: London Zoo's Millennium Commission–funded Web of Life exhibit cost £4.8 million (Miller 2002), Chester Zoo's Jaguar Cars–funded Spirit of the Jaguar cost £1.8 million, the Bronx Zoo's Tiger Mountain cost $8.5 million, and the latter's Congo Forest cost a staggering $43 million. Such costs cause field conservationists to lament that such money would be better spent on a given species' conservation in the wild. While most of us would intuitively agree with that idea, the reality is that not all funds or funders are flexible. Corporate donors often want a visible return for their philanthropy. A zoo offers a simple way for creating such visibility: a spot of sponsorship advertising in a zoo may be viewed by millions over several years. Indeed, in one recent case at a UK zoo, the donor wished to provide funding for tigers *only in the zoo*, despite zoo staff explaining the need for *in situ* tiger conservation funding. By contrast, however, zoos sometimes find it difficult to raise funds for "bricks and mortar" alone. Some donors expect the promise of a conservation project to go with an in-zoo development. So, just as the balance of animal welfare in the zoo versus focus on conservation outside the zoo is a challenge, so is the balance of fund-raising for projects within and outside the zoo.

Some zoos contribute reasonably large proportions of their income to conservation, but a study of AZA conservation expenditure in 1999 showed an average expenditure of only 0.1% of their operating budget (median 0.3%), and in this calculation was included captive research, field conservation, and staff time (Bettinger and Quinn 2000). While there is debate over how much of their income zoos *should* contribute to *in situ* conservation, and some authors (e.g. Kelly 1997) suggest 10% of operating income should be devoted to research and conservation, there are 2 considerations that would limit such a zoowide expectation. First, each zoo balances its priorities differently: some zoos subscribe to a conservation-oriented mission more than others. Setting a standard expectation could compromise welfare improvements in some zoos, while in others the share contributed may be well below the zoo's potential. Second, it is extremely difficult to define which expenditures in a budget should be included when calculating an *in situ* contribution level. Direct financing of *in situ* work is easily measured by adding up the outgoing payments to field projects. But the measurability may become almost impossible when a zoo integrates *ex situ* and *in situ* efforts. An equation involving salary and time can capture the value of the contribution of a zoo veterinarian spending part of her time advising on conservation projects in Africa, but quantifying the value of a DNA analysis of a zoo tiger to develop techniques for censuses in the wild goes beyond the mathematical expertise of most zoo people.

CAPACITY BUILDING AND TRANSFERABLE SKILLS

Zoos have a significant and as yet underexploited role in *in situ* conservation in providing technical skills and capacity building. Zoos employ people with a tremendous variety of skills, from keepers adept in breeding and rearing the most delicate and precious of threatened species, to biologists with an encyclopedic knowledge of nutritional needs of wild animals, to electricians who know how to design almost invisible wiring to keep animals where we want them, not to mention veterinarians, educators, and experts in marketing, fund-raising, public relations, and finance. These are all skills that can be of use to conservation projects, especially those that do not benefit from the umbrella of another large nonprofit nongovernmental organization.

The in-kind provision of zoo advice and/or equipment can be of enormous value to conservation work. Examples include Wildlife Conservation Society's Field Veterinary Program or Chester Zoo's keeper outreach scheme, through which zoo staff takes short sabbaticals to apply their skills hands-on to conservation projects in the wild. In a similar vein, there is a large role for zoos in training conservation scientists. The models of the International Training Centre at Jersey Zoo or the National Zoological Parks' Conservation and Research Center have produced professional conservation scientists for several decades, many of whom work on *in situ* conservation projects. One key area in which zoos need to focus, however, is the recruitment of professional field conservation scientists onto their staff; zoos need to be seen by conservation graduates as attractive places to work (Hutchins and Smith 2003; Zimmermann and Wilkinson 2007).

THE SHIFT TO THE WILD SIDE

The acceptance of the limitations of *ex situ* conservation has led many zoos to focus efforts directly into the wild. The primary motivator for this shift seems to be dedication to a defined mission, but in some countries legislation also requires it. In Europe, the European Union Council Directive 1999/22/EC relating to the keeping of wild animals in zoos was given force of law in 2003 by the United Kingdom, which, along with education, welfare, record-keeping, and safety requirements, requires zoos to contribute to conservation via either research, training, information exchange, or *ex situ* conservation. However, it does not explicitly require, or even advocate, direct *in situ* conservation by zoos. *In situ* contributions, therefore, remain the voluntary prerogative of zoos. Through peer pressure, however, *in situ* conservation contributions have become a widely accepted hallmark of a "good zoo." In the United States, the Fish and Wildlife Service now expects that zoos seeking endangered species permits will contribute to *in situ* conservation.

Living up to a mission of conservation is more than a question of money. Many zoos are limited in their in-house capacity to lead conservation projects. While more and more zoos now have conservation scientists on staff, the shift from donating to other peoples' projects to being in charge of their own initiatives is still a challenge, and one which blurs the threshold between a zoo that contributes to conservation and a conservation organization that runs a zoo (Zimmermann and Wilkinson 2007). There is a major distinction between being a stakeholder and being a leader, and the hierarchy goes roughly from *funding* conservation to *helping* conservation to *leading* conservation.

INTO THE FIELD

The *World Zoo and Aquarium Conservation Strategy* "calls on all zoos and aquariums to increase their work in support of conservation in the wild" (WAZA 2005, 19). Many zoos have already taken this recommendation much further, and have moved to the *leading* stage. In one international survey of zoos' *in situ* activities, the majority (81%) of respondents felt that all zoos should contribute to conservation in the field. At the same time, a majority (67%) also felt that their institution could be doing more for conservation than it presently was, and that *in situ* conservation ranked among the less-developed skills of their institution (Zimmermann and Wilkinson 2007).

While there is clearly still room for improvement, the growth of input and effort in recent years is very positive. The AZA reports that in 1992 American zoos and aquariums supported 325 projects, and that number had doubled by 1999 (Conway 1999). In Europe, BIAZA (British and Irish Association of Zoos and Aquariums) reported support of 177 projects in 2000, an increase of 65% from 1995. Of course, "support" in zoo jargon can mean anything from providing pure financial support, to giving technical/advisory support, to managing their own conservation projects. What is important here, however, is the general trend.

Are *in situ* projects only the realm of the financially privileged zoos in countries whose gross domestic product is high? Not necessarily. While the ability to spend a proportion of a zoo's income on conservation is a limiting factor to an extent, one of the most encouraging developments in recent years is the fact that zoos in developing countries are also carrying out *in situ* conservation work. Such examples are particularly encouraging and a sign that the paradigm shift is global.

A review of Latin American and Caribbean zoos' contributions to *in situ* conservation shows an impressive amount of involvement in such projects. For example, a 2001 WAZA workshop about *in situ* conservation involvement at Simón Bolivar National Zoo in San José, Costa Rica, showed that 16 zoos were participating in 56 *in situ* projects in 11 different countries (Matamoros Hidalgo 2002). Similarly, the Belo Horizonte Zoo in Brazil, which has a history of breeding maned wolves, *Chrysocyon brachyurus*, conducted field research on the ecology and behavior of wild maned wolves, combined this with *ex situ* behavioral studies, and carried out a conservation education program, using the wolf as a flagship and partnering with a corporation for in-kind help (Leite-Young, Coelho, and Young 2002). The Indian-based Zoo Outreach Organisation works to link zoos and rescue centers with *in situ* conservation organizations throughout much of South Asia (ZOO 2005).

As institutions managing *ex situ* collections as well as committing to conservation, zoos face challenging limitations in how much they can deliver to conservation in the field. With demands on their funds from so many directions, e.g. more education, better welfare, and more conservation, many zoos are simply not able to employ staff to focus solely on *in situ* conservation work. Fewer than half the 190 zoos surveyed in Zimmermann and Wilkinson's study (2007) had staff members dedicated to conservation.

Zoos, however, have become good collaborators in conservation. There are approximately 10,000 zoos worldwide, of which about 1000 belong to geographically arranged, acronym-rich associations such as WAZA, EAZA, AZA, ARAZPA, PAAZAB, BIAZA, VDZ, AMACZOOA, SEAZA, and DAZA (cf. WAZA 2005 for full names; Bingaman Lackey, appendix 3, this volume), with well-developed mechanisms for communicating about *ex situ* issues and the management of small populations. More recently, zoos have also become members of conservation governing bodies and associations such as IUCN. Apart from the conservation partnerships that zoos form individually with other conservation organizations, there are also a few multizoo conservation alliances, one excellent example of which is the Madagascar Fauna Group, an independent consortium of more than 30 zoos that pools resources and skills for conservation of Malagasy species (Sargent and Anderson 2003).

THE MISSION AHEAD

This chapter has given a broad outline of the types of contributions that zoos make to *in situ* conservation. Although there is a hierarchy of levels of involvement, a zoo involved in conservation solely through funding the projects of other organizations is not a less valuable contributor than one that is a leader with several of its own field projects. Rather, the question is one of the appropriate use of resources and capacity. As Miller et al. (2004) point out, zoos need to be accountable to their mission, and to evaluate frequently their methods and the impact of their activities.

Evaluating the impact of zoos on species and habitat conservation is a challenge still ahead. There have been many calls for zoos to measure their contribution to conservation (Bartos and Kelly 1998) so as to balance the critics who argue that zoos' conservation activities are public relations stunts (Scott 2001), and that their conservation efforts are superficial and ineffective (Hewitt 2000). One first attempt to develop a method to measure the impact and quality of conservation projects pursued by zoos has shown that it is possible to do so (Mace et al. 2007).

A handful of zoos have already made the leap from being a zoo that does conservation to being a conservation organization that runs a zoo. Most still have a way to go. We can thank zoos, at least in part, for the survival of the California condor, *Gymnogyps californianus*, Mauritius kestrel, *Falco punctatus*, black-footed ferret, *Mustela nigripes*, and Guam rail, *Rallus owstoni* (Snyder et al. 1996), all species that were extinct in the wild. However, in the future, if zoos want to share the credit for saving humpback whales, controlling wildlife trade, studying emerging diseases, or mitigating human-wildlife conflicts, they need to make that paradigm shift. To become true conservation organizations, zoos need to balance objectively the *ex situ* and *in situ* priorities for a species with its exhibition value, contribute significant proportions of their incomes and/or technical skills to good *in situ* conservation work, attract conservation scientists into their employment, and communicate their conservation work to their visitors as well as their nonzoo conservation peer organizations.

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24

Research Trends in Zoos

Terry L. Maple and Meredith J. Bashaw

INTRODUCTION

In her review "Current Research Activities in Zoos," published in the first edition of *Wild Mammals in Captivity*, Hardy (1996) documented a variety of promising advances in research conducted in zoological institutions. Many had been anticipated by Conway (1969), who noted significant changes to the collective zoo vision more than 30 years ago. Our approach derives from 3 decades of professional experience conducting and publishing research on mammals exhibited in zoological parks in the United States. In a broader context, we believe that research trends in the United States are highly similar to those in other regions of the world, and we have sampled information derived from other international sources in order to test this assumption. While a detailed comparison of world and U.S. zoo research trends is beyond the scope of our assignment, clearly, the challenges and opportunities that scientists face in conducting research are common to all zoos and aquariums throughout the world.

TOPICS OF ZOO RESEARCH

AREAS OF STUDY

One way to calculate the direction of zoo research is to monitor contributions to the journal *Zoo Biology*, published by Wiley/Liss in New York since 1982. Two reviews of its contents have been conducted since 1996. In their review of the first 15 years of *Zoo Biology*, Wemmer, Rodden, and Pickett (1997) confirmed earlier findings (e.g. Lindburg 1989; Kleiman 1992; Hosey 1997) that approximately one-third of the journal's contents consisted of behavioral studies, with another one-third devoted to the subject of reproductive biology. Other prominent (and growing) fields represented within the journal included nutrition, infectious disease, molecular genetics, population genetics, and environmental enrichment. Anderson, Kelling, and Maple (2008) evaluated research articles published during *Zoo Biology*'s first 2 decades and determined that most were on nonexperimental, applied, behavioral, and reproductive topics. In addition, most of the studies cited used inferential statistics or sophisticated biological analyses. A growing interest in methodology is illustrated by the "Commentary" contribution of Kuhar (2006, 351), who argued: "By continuing to develop guidelines for appropriate study design and use of statistical techniques in these unique captive populations we can increase the scientific rigor of the studies being conducted in zoos and aquariums worldwide." A review of a recent volume of *Zoo Biology* (vol. 26, 2007) found the contents to be about equally distributed among reproductive biology, behavior, and nutrition.

In addition to publishing in *Zoo Biology*, there is an increasing trend toward publishing zoo and aquarium science in other biological journals. To capture some basic information about research that appears in other journals, we conducted a search of the BasicBIOSIS database (provided by OCLC FirstSearch, accessed via the Franklin & Marshall College library) on September 28, 2005. We searched for "Zoo," "Zoological," and "Conservation Society" in the institutional affiliation of first authors publishing in indexed scientific journals between 2001 and the most recent update, September 1, 2005. We found 251 manuscripts whose first authors were affiliated with a zoological facility. Each of these articles was assigned a primary (and secondary, when applicable) research topic based on its abstract and keywords. Sixty-seven (27% of the total) were primarily or secondarily studies of behavior, the most popular topic. Conservation and ecology were also prominent; each described 62 articles (25%).

The results from other journals are generally consistent with those from *Zoo Biology*. Behavior is most strongly represented, and reproductive biology, genetics, and veterinary medicine are also prominent topics. Interestingly, the strong emphasis on conservation and ecology in the BasicBIOSIS search is not apparent in *Zoo Biology* publications. This is likely a result of the deliberate emphasis of *Zoo Biology* on work conducted in zoos and aquariums, rather than in the field. As a result, conservation and ecology studies are more likely to be published in journals specific to their content area, and therefore less likely to be submissions to *Zoo Biology*. For example, scientists based at the Bronx Zoo (Wildlife Conservation Society), New York City, are committed to field conservation and medicine, so their publications are more likely to appear in journals such as *Conservation Biology* (nutrition is an exception). Of the 108 articles with conservation and/or ecological content, 30 were published in journals with *conservation* in their titles (primarily *Conservation Biology*), and 11 were published in ecology journals (primarily *Behavioral Ecology and Sociobiology* and *Journal of Animal Ecology*). In addition, 21 appeared in taxon-specific journals like *Herpetological Review* and *Journal of Mammalogy*. Journals focused on these fields may provide alternative outlets for publication of conservation and ecology work that better reach their target audience than *Zoo Biology*.

TAXA STUDIED

The trend toward a disproportionate number of studies of mammals in *Zoo Biology* has continued throughout the journal's 25-year publication history. Hardy (1996) found that 82% of the articles published in the journal's first 11 years had mammalian subjects. The analysis of Wemmer, Rodden, and Pickett (1997) identified a 73% mammalian bias, which they explained as a function of the historical focus of zoo collections, but of course, ornithologists and herpetologists working in zoos have an excellent publication record in specialty avian and herpetological journals. We do not know why scientists working with zoo birds and reptiles submit so few manuscripts to *Zoo Biology*.

If it is true that the mammalian bias is more prevalent in *Zoo Biology* than in the rest of the published literature, we might overestimate the mammalian bias by monitoring only this journal. However, our search of biological abstracts on BasicBIOSIS is consistent with a strong bias toward the study of mammals, although many other taxa are represented (see figure 24.1).

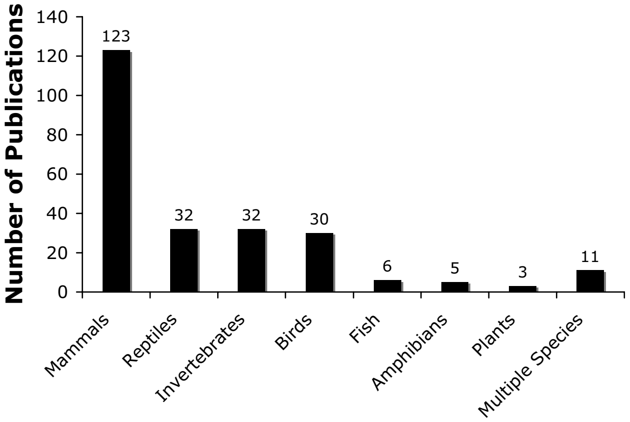

Fig. 24.1. The number of publications in each taxonomic category found in a *BasicBIOSIS* search for articles in which the first author was affiliated with a zoo or zoological institution.

Within mammals, both the BasicBIOSIS search and the *Zoo Biology* data describe nonhuman primates and carnivores as the most popular taxa studied, encompassing 60% of published papers combined. However, while the *Zoo Biology* data reveal the largest proportion of papers devoted to nonhuman primates (with carnivores second; see figure 24.2), the BasicBIOSIS data indicate that the largest proportion of papers is devoted to carnivores (35%), while the second largest is devoted to nonhuman primates (25%). For both data sets, Artiodactyla (11%) is the third most popular order and the only other order to account for more than 10% of manuscripts. The remaining orders from the BasicBIOSIS data are Chiroptera (7%), Perissodactyla (6%), Rodentia (6%), Cetacea (3%), Lagomorpha (3%), and Proboscidea (1%). In ad-

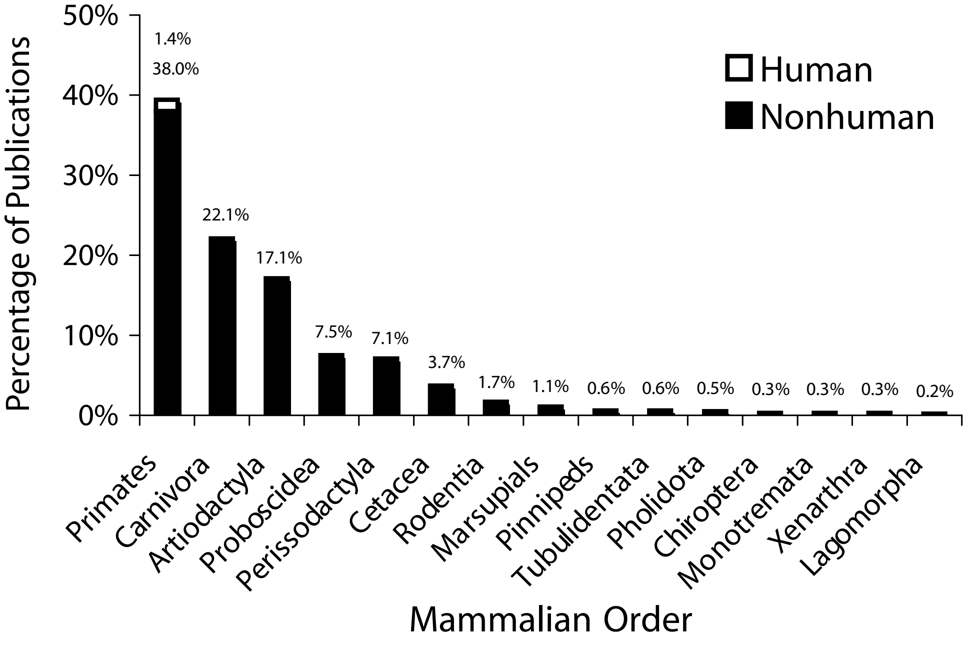

Fig. 24.2. Mammalian orders represented in research articles published in the journal *Zoo Biology* from 1982 to 2001. (After Anderson et al. 2008.)

dition, humans were studied in 5% of the articles. Although several publications have reported a perceived bias toward studies of zoo primates (Lindburg 1989; Stoinski et al. 1998), this bias may have been overemphasized by focusing on *Zoo Biology* as the primary source of information about zoo research. Using additional sources suggests that nonhuman primates and carnivores share the distinction of being the most commonly studied.

Although the data sets from *Zoo Biology* and the BasicBIOSIS search were not collected in the same way and therefore cannot be directly compared, the recent publications reflect some shift in research attention from nonhuman primates toward carnivores. The *Zoo Biology* data include publications from 1982 to 2002 with a greater primate bias, while the BasicBIOSIS data are from 2001 to 2005 and there is a bias toward carnivore studies. The increasing support for *in situ* conservation by zoos may be driving the larger research investment in carnivores, because large carnivores are often used as umbrella species to indicate the health of entire ecosystems. Similarly, increasing research on environmental enrichment may also have emphasized captive carnivores, because the development of undesirable behaviors, including stereotypy, is widespread in this order (Carlstead 1998; Clubb and Mason 2003).

A bias toward mammalian species is also evident in other journals that serve zoo professionals. For example, volume 40 (2006) of the *International Zoo Yearbook* (*IZY*) included 16 contributions on the biology and behavior of elephants and rhinoceroses. An additional 5 papers with scientific themes also featured mammalian subjects. Similarly, in volume 39 of this journal, 55% of the subjects featured in published papers were mammalian. *IZY* is primarily concerned with exhibit design, husbandry, and management of zoo and aquarium taxa and has only recently begun to use outside peer referees. The German journal *Der Zoologische Garten* has also not provided a comparable process of peer review for most of its history, so it is difficult to compare these publications with *Zoo Biology*. The European journals tend to include more applied studies, although *Zoo Biology* has also published a significant number of articles devoted to the applied specialty of environmental enrichment.

APPLICATIONS OF RESEARCH IN ZOOS

Two particular areas of recent endeavor, "environment and behavior" and "behavioral management," provide examples of the potential benefits deriving from a mutual exchange between scientists and animal managers. The origin of these fields arose from active research collaboration between academic scientists and architects/designers, on the one hand, and similar collaborations with laboratory colony managers, veterinarians, and psychologists.

ENVIRONMENT AND BEHAVIOR

The combination of animal behavior research and theory and naturalistic design led to a revolution in the construction of zoo animal facilities in the late twentieth century (see Hancocks, chap. 11, this volume; Coe and Dykstra, chap. 18, this volume). Among the first scientists to contemplate the social psychology of zoos, Robert Sommer characterized zoo architecture as either "hard" or "soft." Sommer observed that American zoos in the 1970s were predominantly hard in form and function (Sommer 1973, 1974), and that hard architecture and social deprivation were producing catatonic animals with a persistent repertoire of bizarre behavior patterns. He noted that hard zoos were teaching the public all the wrong things about animal behavior.

In 2005, addressing the membership of the Environmental Design and Research Association, Sommer compared the pace of change in zoos and other hard institutions that he studied (e.g. airports, prisons, and mental hospitals) and found that zoos had changed profoundly, morphing into soft architecture in the 3 decades since publication of his book *Tight Spaces* (1974). He attributed this change to a profession enlightened by exposure to the findings of zoo and field biologists, and a growing willingness to apply the findings of behavioral research to the facade and the function of the zoo. We are encouraged that zoo designers are eager to collaborate with wildlife experts whenever they begin to program a new, naturalistic exhibit.

Although modern zoo architecture derives from a dialogue between designers, animal managers, and scientists, scientific study could assess and improve its effectiveness. Post-occupancy evaluations (POEs) allow zoos to measure how well new exhibits are working by collecting data from one or more of the relevant user groups: animals, animal care staff, and visitors. Unfortunately, the science of POE in the zoo has not kept pace with the architecture, so we know precious little about how innovations in exhibit design actually work. There have only been a few POE studies conducted to date, with several being published in *Zoo Biology* (e.g. Wilson et al. 2003). POEs are the next step in the development of truly innovative zoo design, as they allow designers to improve new exhibits by emphasizing aspects of the environment that effectively accomplish their goals and correcting those aspects that fail. Animal welfare cannot be advanced in the zoo if we are not truly objective about our exhibits and facilities (see Kagan and Veasey, chap. 2, this volume).

BEHAVIORAL MANAGEMENT

Zoos have historically been dedicated to both the physical and psychological well-being of the animals they house, but ways to improve psychological well-being have garnered much attention in the latter half of the twentieth century (Erwin, Maple, and Mitchell 1979; Markowitz 1982; Shepherdson 1998, chap. 6, this volume). *Environmental enrichment* has been defined as "an animal husbandry principle that seeks to enhance the quality of captive animal care by providing the environmental stimuli necessary for optimal psychological and physiological well-being" (Shepherdson 1998), through both innovation in exhibit design and the addition of interactive elements in existing exhibits.

The development of enrichment occurred with varying degrees of scientific involvement. Markowitz and colleagues successfully applied the principles of behavioral analysis to develop technology associated with food delivery (e.g.

Markowitz and LaForse 1987; Markowitz, Aday, and Gavazzi 1995). Food delivery was contingent upon behavior: when animals interacted with the enrichment device, they activated an automated food delivery system. Hutchins and colleagues opposed the use of operant conditioning paradigms like these as overly simplistic, and instead proposed that enrichment be based on modeling the natural environment of animals (Hutchins, Hancocks, and Crockett 1984). Forthman-Quick (1984) published an excellent review and resolution of this controversy. However, the perceived need for enrichment in zoos led animal care staff to implement enrichment procedures of both types rapidly, without systematic evaluation of their effectiveness. In many cases, these enrichment devices and procedures were able to make dramatic but short-lived changes in behavior (e.g. Line, Morgan, and Markowitz 1991; Wells and Egli 2004). As the zoo world's commitment to enrichment grew, scientists and animal care staff alike began to see a need for both short-term and long-term evaluation of the effectiveness of enrichment (Bloomsmith and Maple 1997). In 2002, the American Zoo and Aquarium Association (now the Association of Zoos and Aquariums—AZA) added enrichment standards to its *Accreditation Guide and Standards*. The 2005 version of these standards recommends

> a formal written enrichment program . . . which promotes species-appropriate behavioral opportunities for appropriate taxa. [AC-39] Explanation: It is recommended that an enrichment program be based on current information in behavioral biology, and should include the following elements: goal-setting, planning and approval process, implementation, documentation/record-keeping, evaluation, and subsequent program refinement. (AZA 2005, p. 42)

The inclusion of the evaluation of enrichment in these standards indicates the priority of feedback between enrichment and science in the zoo community. Evaluation of enrichment has increasingly become a scientific endeavor, with full-length scientific studies conducted (e.g. Powell 1995) as well as the development of rapid assessment techniques by scientists to be used in everyday evaluation of enrichment efforts.

Although there is no single theoretical perspective that provides the basis for all enrichment research (Tarou and Bashaw 2007), several scientific viewpoints have been successfully applied to the enrichment literature (Swaisgood and Shepherdson 2007). Markowitz and colleagues (1987, 1995), Forthman and Ogden (1992), and most recently Tarou and Bashaw (2007) have used behavior analysis and operant conditioning paradigms from psychology; Hutchins, Hancocks, and Crockett (1984) have used a naturalistic approach most closely linked to ecology; and Hughes and Duncan (1988) have focused on the animal's behavioral needs base (an ethological approach), while both Mason (1991) and Carlstead (1998) have placed primary emphasis on stress and abnormal relationships between animals and their environments. Each of these conceptual approaches has contributed to designing effective enrichment programs. A recently published meta-analysis found no difference in success rates of enrichment studies based on the approach used (Swaisgood and Shepherdson 2007). We believe that the use of scientific methodology, including testing falsifiable hypotheses, is critical both to creating a better science of enrichment and to improving the effectiveness of enrichment techniques (Bloomsmith and Maple 1997). Enrichment therefore provides another example of a field in which zoo managers, keepers, and scientists can work hand in hand to enhance both application and theory.

The benchmark volume *Second Nature* (Shepherdson, Mellen, and Hutchins 1998), based on a world conference hosted by Portland's Washington Park Zoo (now Oregon Zoo), provided a global, comprehensive review of the subject, and guidelines for implementation of enrichment tactics. In both zoo and laboratory settings, specialists in "applied behavior analysis" have provided their input with techniques developed for institutionalized human populations (Bloomsmith, Marr, and Maple 2007). Behavioral management programs now combine all known training and enrichment techniques to improve the lives of individuals subjected to contingencies and control (see also Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume; Mellen and MacPhee, chap. 26, this volume).

CONSERVATION PSYCHOLOGY

Another promising research trend is the emerging, multidisciplinary field known as conservation psychology (e.g. Brook 2001; Saunders 2003), which promises to connect the fields of environmental psychology, social psychology, cognitive psychology, and human ecology to investigate the attitudes, behaviors, and emotions of a diversity of people, and how these constructs contribute to the well-being and very survival of wildlife. The potential interconnections are vast and we cannot predict how zoos and aquariums will use these findings, but they will surely benefit in tangible ways if studies of human beings (zoo visitors) become a major research topic within the field of zoo biology. Conservation psychology research will also link field studies of user groups (e.g. indigenous people and ecotourists) to attitude and behavior research conducted in aquariums, zoos, botanical gardens, and museums. Scientists at the Brookfield Zoo, Brookfield (Chicago), Illinois, in collaboration with academic psychologists launched this field of research and continue to contribute to its expansion throughout the world. A list of 31 journals (found on the Worldwide Web) synergistic to conservation psychology research presents opportunities for scientists working in this field. However, the field is still not clearly defined, nor is it sufficiently differentiated from the work of environmental psychologists working in a broader domain. If journals are as responsive as the associations embracing the construct, conservation psychology research appears to have a bright future. A comprehensive review by Rabb and Saunders (2005) examined the zoo's unique role in shaping conservation behavior by exposing people to close-up experiences with captive wildlife. The opportunity to connect wildlife and humanity to promulgate "caring" and commitment is profound but poorly understood. By focusing on the future of zoos as conservation centers, the authors also suggest future research that may serve to evaluate the effectiveness of our efforts.

SUPPORT FOR RESEARCH IN THE ZOO

Hardy (1996) provided evidence from other published studies (e.g. Finlay and Maple 1986; Wemmer and Thompson 1995) that zoo administrators were eager to support research in their institutions. We have identified relevant key support variables that may determine the success of research programs.

FINANCIAL SUPPORT

Kurt Benirschke (1996) strongly recommended that zoos establish dedicated research departments and provide a congenial work climate for scientific personnel in a variety of fields. He observed that American industry typically devotes 3%–5% of its operating budget to research and development, in contrast with lower investments evident in our zoological parks and aquariums. Research is not an option, according to Benirschke, but a necessity if we are to succeed in creating "self-sustaining populations" of endangered wildlife in the zoo. The number of dedicated scientific facilities and programs associated with zoos and aquariums is only a few, and they are generally focused, but they are well-funded, brimming with expertise, and highly effective. These facilities enhance the credibility of institutions with the vision to build and endow them. Among the best known are the department of Conservation and Research for Endangered Species (now the Institute for Conservation Research) of the Zoological Society of San Diego, the Audubon Center for Research on Endangered Species, the Center for Research on Endangered Wildlife at the Cincinnati Zoo, the Hubbs-Sea World Research Institute, the Smithsonian National Zoological Park's Department of Zoological Research and Conservation and Research Center (now united as the Conservation and Science Department), and the Wildlife Conservation Society of New York. Collectively, they have expended annually as much as $75 million on conservation and research (data derived from 2000–2005 sources; Anderson, Kelling, and Maple 2008).

The use of endowments to fund conservation and research projects (many of them in distant locations around the world) is a promising opportunity, as the public has consistently demonstrated a passion for conservation, education, and science. It is standard investment policy that programs funded from endowments should not exceed 5% of the corpus, but this figure would still meet the funding standard advocated by Benirschke. As conservation has become a higher-priority goal in aquariums and zoos, some experts (Miller et al. 2004) have recognized a need for larger allocations as a percentage of the operating budget. For example, the Wildlife Conservation Society expends more than 25%, which the authors regarded as the preferred benchmark for the profession. Conservation tends to be based on research, so any increases in conservation expenditures will likely affect research personnel and priorities.

In addition to endowments and internal funding, zoo professionals and their university collaborators increasingly depend on external funding to carry out research. Although these sources are exceedingly competitive and difficult to obtain, many U.S. federal, state, and local agencies and numerous private foundations and organizations have provided research support to zoos.

Over the past 20 years of its publication history, most authors publishing in *Zoo Biology* have acknowledged external sources of funding. Although the breadth of external zoo research funding is impressive, most zoos that conduct research have supported it with modest levels of in-house funding. Enhanced levels of extramural support will be required if the volume of zoo and aquarium research is to grow. For zoos, the greater sources of this support will likely come from private foundations and donors (Maple 2006) rather than government.

INFRASTRUCTURE SUPPORT

The participation of academic personnel who willingly shared expertise and technology led zoos down a path that required new skills and additional commitments. For example, zoos that are supported by federal research funding now must establish an Institutional Animal Care and Use Committee (IACUC) or use the services of existing committees at cooperating colleges and universities. Since IACUCs at universities are typically not familiar with the zoo as a research venue, each institution must adjust to the unique requirements and expectations of the other. The trend toward a more organized, complex, and regulated zoo research process is inevitable as liability, safety, and accountability issues loom ever larger in the realm of science. Further, in a recently published guide (Silverman, Suekow, and Murthy 2007, 469) to IACUC protocols, Bayne wrote on the subject of environmental enrichment: "The institution should not take a minimalist approach to implementing the enrichment program(s) and the IACUC should take a proactive role in its oversight." Zoo biologists have carried out meaningful research in this area, and the science of enrichment is likely to be a factor in future assessments of psychological well-being at the federal level, another reason why zoos and aquariums need to be prepared to conduct, monitor, and interpret scientific findings relevant to their mission.

STAFF SUPPORT

Zoos across the United States structure research within their institutions in different ways. Although this means no single model has become the standard, institutions can select a preferred institutional model when they begin investing in a research program (see table 24.1). In a recent survey, those responsible for zoo research regarded (1) support of the chief executive and (2) dedicated scientific staff as the 2 most important factors in successful research programs (Anderson, Bloomsmith, and Maple, forthcoming). Therefore, an affirming interest by zoo executives and the attainment of a critical

TABLE 24.1. Options for research programs in zoos and aquariums

- Centralized research leader
- Centralized research coordinator
- Decentralized, curator initiated
- Outsourced to collaborators
- Nested in a subordinate center/institute
- Nested in an autonomous center/institute
- *Ad hoc* collaborations

mass of dedicated scientists should be an aspiration of all zoological parks. A unique example of how much scientists value zoo leadership is the recent naming of a new mouse lemur, *Microcebus simmonsi*, to honor the Omaha Henry Doorly Zoo director, Lee Simmons, for his institution's sponsorship of the field research that led to this discovery (Louis et al. 2006).

INSTITUTIONAL MANDATES

The historical commitment by AZA to Species Survival Plans (SSPs) was a driving force to establish scientific programs and collaborations. For example, AZA's board of directors voted to affiliate with *Zoo Biology* and the *Journal of the American Association of Zoo Veterinarians*, demonstrating its commitment to a profession based on scientific inquiry, debate, and discovery. In 1999 the AZA board of directors established the Conway Chair in Conservation and Science, an endowed staff position named for William G. Conway, former general director of the New York Zoological Society/Wildlife Conservation Society and the Bronx Zoo/Wildlife Conservation Park (New York City). In addition, a committee of scientists within and outside the AZA community established a scientific book series (Smithsonian Institution Press, now defunct) that examined such topics as animal welfare, animal management, behavioral enrichment, and environmental ethics (e.g. Norton et al. 1995; Shepherdson, Mellen, and Hutchins 1998).

Adding to aspirations from within AZA to participate in science, new U.S. federal laws require documented participation in conservation programs for an endangered species before a zoo or aquarium can legally import that species. Throughout the world, other regional associations have engaged in scientific work to enhance management, facilities design, conservation, and education. The World Conservation Strategy promulgated by the World Association of Zoos and Aquariums (WAZA) is an evidence-based document of considerable influence and relevance, and WAZA meetings and programs reflect a growing commitment to the scientific foundation of zoo biology, conservation, and public education. However, while conservation programs enjoy considerable international cooperation, research within zoos tends to operate independently, with little collaboration across regions.

SCIENTIFIC PARTNERSHIPS

Several of the options for research models emphasize collaboration as an effective way to alleviate some of the financial, infrastructure, and staff burdens of zoo-based research. Such collaborations are increasing. Over a 20-year span of *Zoo Biology*, collaborative authorship has grown, accounting for nearly half the published research articles. Similarly, in our search of zoo-related articles in the BasicBIOSIS database between 2001 and 2005, the mean number of coauthors was 3.5 (median = 3). The mode was 2 authors: 25% of papers were written by a pair of individuals. Publications ranged from one to 18 authors, but 83% of the 251 publications had multiple authors.

In addition to collaborations among the research staff at different facilities, an increasing number of zoos and aquariums are providing strictly financial support for researchers employed by other institutions. This strategy has been encouraged by the U.S. regulations mentioned above that require involvement in conservation efforts for a species, before members of that species can be imported. If an institution wants to import multiple species, supporting research efforts of outside collaborators on that species may be a cheaper option than funding a large research department within the institution. One risk of adopting this approach is lack of control of the quality and productivity of outside researchers, so zoos and aquariums should carefully assess project quality and researcher qualifications. Because our BasicBIOSIS search included only affiliations of first authors and not acknowledgments or affiliations of later authors, our search would have omitted these projects. The identities of collaborators in zoo research can be measured by examining affiliations of the first authors of research articles published in *Zoo Biology*. The large number of university scientists appearing as first authors on these articles indicates the strength of academic interest in doing research in zoos and suggests that university collaborations are a feasible model for zoos wishing to be involved in research but unable to afford a qualified, dedicated scientific staff. Direct assessment of the extent to which zoos and aquariums provide financial support to outside researchers and the productivity of these efforts is needed to produce a cost-benefit analysis of internal and external research efforts.

UNIVERSITY-ZOO RELATIONSHIPS

The impediments of size and scarce resources can also be overcome if small zoos establish focused, behavioral research programs (Kleiman 1992), typified by their lower cost and lesser impact on daily animal management requirements. Small zoos can also elect to delegate research responsibilities to credible university collaborators and their students, providing only the setting and the subjects for conducting zoo research. We are surprised that more small zoos are not actively engaged in such partnerships, since they are highly correlated with discovery and research productivity (Finlay and Maple 1986). Small zoos that can share the cost of a trained scientist with a partnering university department can initiate a research program with a cost-effective investment. In our experience, college and university deans and department chairs generally welcome such collaborations, recognizing an opportunity for students to experience the fascination of working with exotic wildlife guided by expert supervision. A modest investment by each entity provides compensation and benefits to recruit a highly qualified assistant or associate professor/director of conservation and science, with accountability to both institutions. We believe that nearly every zoo in a developed country could afford to make this investment, and would benefit greatly from the joint program of research produced through collaboration with local colleges and universities. For example, the Web site of the Denver Zoo (Colorado) reveals an impressive list of scientific projects by Denver Zoo scientists and their university collaborators. Moreover, Denver Zoo scientists helped to create a new major in Ecology, Evolution and Conservation Biology at the University of Denver, a relationship which includes both teaching and graduate student supervision.

COLLABORATIONS AMONG ZOOS

Smaller zoos can also collaborate among themselves or with larger institutions by collecting group data. Conservation and Science grants issued through AZA's Conservation Endowment Fund have emphasized collaboration in recent years, as zoos have shared access to their collections and pooled human and financial resources to accomplish mutual research and conservation objectives. Recent examples of multi-institutional studies include Carlstead and colleagues on black rhinoceros, *Diceros bicornis*, reproduction (Carlstead, Mellen, and Kleiman 1999a, Carlstead et al. 1999b) and Stoinski and colleagues (2004) on all-male lowland gorilla, *Gorilla gorilla gorilla*, groups. The latter collected observational data for 80 young male gorillas exhibited in 7 AZA zoos, a study that required both cooperation and planning. The participating zoos gained the benefits of training from one of the project coordinators in the collection of behavioral data and more detailed knowledge about the behavior of their own and other gorilla bachelor groups, while Stoinski and colleagues were able to increase their sample size and assess more accurately whether bachelor groups were an effective way to house surplus male gorillas in zoos. Carlstead et al. (1999a, 1999b) were able to pinpoint certain environmental and husbandry characteristics negatively affecting black rhinoceros reproduction.

Similarly, Dierenfeld et al. (2005) gathered frozen plasma or serum samples from individual black rhinoceroses in cooperating AZA institutions from 1982 to 2000 to quantify mineral concentrations and establish baseline nutritional assessment criteria for the Rhinocerotidae. Petersen et al. (2004) recently published in *Zoo Biology* another good example of scientific and logistic collaboration among aquariums and universities, this time in transporting massive Scleractinian corals.

PUBLICATION OF ZOOLOGICAL RESEARCH

ZOO BIOLOGY

The journal *Zoo Biology*, now formally affiliated with AZA, has published continuously since 1982. The journal has an independent editorial board, selects its own editor-in-chief, and manages its affairs like any other autonomous scientific publication. *Zoo Biology* is the first scientific journal devoted to the zoo and aquarium profession that provides peer review and favorable publication latencies. Although published in the United States, the journal welcomes contributions from zoo biologists around the world. In addition to U.S. contributors, a recent volume of the journal (vol. 25, no. 4, 2006) included authors from Germany, Denmark, Switzerland, and Taiwan.

From 1982 to 2001, the journal published 584 research articles, 165 book/video reviews, 104 brief communications and reports, 64 proceedings and symposia, 60 editorials and commentaries, 35 technical reports, 5 review articles, and 11 other publication types, including introductions, forewords, discussions, and memorials. Research articles during this period comprised some 6824 pages of material. By any measure, *Zoo Biology* has facilitated research productivity among zoo biologists, an outcome envisioned by its founding editors. Hardy (1996, 531) observed that the journal was "an important vehicle for publication and dissemination of the results of scientific studies at zoos," and Wemmer, Rodden, and Pickett (1997) recognized the journal's key role in providing a refereed publication outlet for zoo professionals and their collaborators.

OTHER PEER-REVIEWED JOURNALS

Lindburg (1989), Chiszar, Murphy, and Smith (1993), and Hosey (1997) independently concurred that the fundamental purpose of *Zoo Biology* is to provide an outlet for zoo-based research to reach colleagues working in zoological institutions. The need for such an outlet is illustrated by Hosey's (ibid.) finding that the journal *Animal Behaviour* contained only 3 zoo-based studies over 2 volumes (1993–94) surveyed. Moreover, Ord et al. (2005) found no zoos represented among the 25 most published American institutions in 25 animal behavior journals. This finding amplifies 2 generalizations about zoo research: (1) collectively, zoo professionals are not yet publishing at a high rate in specialized journals, and (2) zoos differ from universities in their degree of emphasis on research productivity. Publication in a diverse array of peer-reviewed journals and greater emphasis on output by publication may be indicators that zoo research is becoming a more sophisticated enterprise. Furthermore, as zoo administrators learn to recruit, reward, and retain scientists, research productivity is likely to advance.

While it is difficult to assess the latter, the BasicBIOSIS database search we conducted suggests that the first of these indicators may be moving in a positive direction. We found zoo-based first authors as a group published an average of 58.25 peer-reviewed articles per year in Biosis-indexed journals for each full year examined (2001–4). The 251 articles identified came from 68 different journals, ranging from the *Journal of Wildlife Diseases* (26 articles) to *Folia Primatologica* (6 publications), and included both *Science* (4 publications) and *Nature* (8 publications). Perhaps zoo scientists are not published at a higher rate in animal behavior journals due to the variability in types of research conducted in zoos and the number of different journals now available for publication of their work. Another factor is the very existence of the specialized journal *Zoo Biology*: journal editors have rejected zoo studies and recommended submission to *Zoo Biology* instead. There may also be a systematic editorial bias that works against the publication of zoo-based research.

The profile of scientific zoo biology was elevated briefly in 1975 when the National Academy of Sciences published a collection of papers based on a 1974 meeting on zoo and aquarium research held in conjunction with the AZA (then AAZPA) zoo conference in Houston (ILAR 1975).

NONSCIENTIFIC DISSEMINATION OF DATA

In addition to academic publications, science conducted in zoos is also frequently published in newsletters and other sources subject to minimal or no peer review. This type of publication has both advantages and disadvantages. Many people prefer to read newsletters rather than scientific journals, enabling research to reach a diverse target audience.

However, without scientific peer review, the work presented may be of questionable scientific accuracy. In addition, these publications are rarely indexed in search engines or maintained in library collections, so it may be difficult to access the information. Scientists need to publish in peer-reviewed journals to maintain or improve the credibility of zoo science, but they should consider publishing brief summaries of their work in newsletters to alert potentially interested readers of their findings. *Giraffa*, published by the International Giraffe Working Group, is one example of a newsletter dedicated to publishing summaries of recent peer-reviewed publications and ongoing research. Increasingly, zoos and aquariums are featuring concise versions of scientific work on their Web sites and calling attention to publications of greater depth.

CHALLENGES, IMPEDIMENTS, OPPORTUNITIES

The national and regional conferences of AZA have occasionally stifled rather than encouraged the objectivity, criticism, and open debate that characterize other scientific societies. Too frequently, we believe, zoo professionals discuss important topics in closed-door sessions. Although many of the public debates surrounding animal welfare and animal rights have lacked civility, careful planning will provide opportunities for zoo professionals to discuss these and other issues in constructive public symposia, workshops, and lectures accessible to the wider membership. We hope to see a trend of greater openness at professional zoo meetings, since the scientists within the zoo community will not flourish without it. We believe that scientific conferences are actually improved by some degree of managed conflict and controversy, an approach demonstrated by a "point-counterpoint" debate format at the 1996 AZA conference stimulated by the publication of *Ethics on the Ark* (Norton et al. 1995).

Zoo collections are ideal for a variety of scientific studies, and while zoos have broadened the scope of *Zoo Biology*, there are still possibilities for expanding the taxa and topics studied. The current focus on mammals, and especially carnivores and primates, does not adequately reflect the diversity of zoo collections or the need for greater study of species for which minimal ecological, behavioral, or physiological data are available. Although behavior research has likely become prominent because it is minimally invasive and relatively inexpensive to conduct, zoos are also well suited to and conduct research on physiology, morphology, taxonomy, reproduction, environmental conditions, and veterinary medicine. Zoo professionals collect a wealth of data on many of these subjects during the daily care of animals, and with a relatively small investment of time could make more information available to others through publication. Simply by publishing data gleaned from animal records, zoos can provide information to their colleagues in an accessible form, address gaps in knowledge, and test hypotheses derived from biological and psychological debate (e.g. Bercovitch et al. 2004). Collaborations in which outside scientists are given access to zoological records in exchange for a publication coauthorship is a mutually beneficial opportunity to explore new research ideas on understudied taxa.

In *Zoo Biology*'s first 25 years of publication, Anderson, Kelling, and Maple (2008) found that only 25% of AZA zoos were represented in the affiliations of first authors, and only 6 zoos accounted for the majority of zoo-based research articles. In our BasicBIOSIS search, we identified 41 institutions with at least one publication in an indexed journal between 2001 and 2005. The number of institutions publishing each year was relatively constant, between 16 and 20 over the 4 full years included (2001–4). Out of these 41 institutions, however, 162 (65%) of their papers had a first author affiliated with one of 5 institutions: the Wildlife Conservation Society (54, USA), the Department of Conservation and Research for Endangered Species of the Zoological Society of San Diego (30, USA), the Institute for Zoo and Wildlife Research (29, Germany), the Zoological Society of London (28, UK), and the Smithsonian National Zoological Park (21, USA). The mode for number of publications by institutions was 1, with 21 of the 41 represented institutions publishing only a single indexed paper between 2001 and mid-2005. Clearly, larger, well-funded institutions are accomplishing the "heavy lifting" in zoo research. Similarly, an examination of the AZA's *Annual Report on Conservation and Science* (2005) reveals through self-report that the National Zoological Park and the San Diego Zoo were far ahead in publications. Only Disney's Animal Kingdom and the St. Louis Zoo reached double-digit figures in a list of other zoos that published frequently, but there are an increasing number of zoos that are publishing. Unfortunately, we cannot escape the conclusion that few zoos have adequately funded research, nor have they participated in research to their full potential. We agree with Benirschke's (1996) assertion that zoos

> will not manage [animals] adequately genetically, behaviorally, or nutritionally, let alone reproduce them at will, without more knowledge. (p. 537)

Benirschke (1996) has also argued for a dedicated critical mass of top scientists within the zoo, and for strong affiliations with universities and the larger research community. In the recent past, we believe that zoos have been reluctant to identify with research that involves experimentation, fearing the wrath of antivivisectionists and other foes of biomedical research. By contrast, Benirschke's expectations are worthy of emphasis:

> Being an optimist, I believe the zoo will catch up, not by doing all of the research themselves, but by becoming an integral part of the entire research community. (p. 544)

Zoo scientists may need to organize in order to advocate effectively for zoo research to become a higher priority. Using established principles of science enabled the growth of AZA's SSP programs when demography and population biology dominated the management landscape (Ballou and Foose 1996). Many compelling arguments have circulated to promote a higher profile and priority for research, but we fear they have not come to the attention of decision-making executives and boards in the majority of AZA zoos. Also, support for research may be competing with support for conservation, as the latter emerges as the zoo profession's highest funding priority (Miller et al. 2004). However, as zoos hire conservation leaders they have an opportunity to hire people with strong scientific credentials. Building research programs to support both *in situ* and *ex situ* conservation provides team-building opportunities throughout the organization.

PERCEPTIONS OF RESEARCH IN ZOOS

In part, the success of research in zoos can be evaluated by examining prestigious honors, awards, and prizes presented to scientists working in zoos or collaborating with them. Although the presentation of these awards is difficult to track systematically, several notable examples may indicate a growing acknowledgment that zoo biology is gaining respect for its increasing rigor and its relevance. Two behavioral scientists affiliated with zoos for much of their careers have been honored with membership in the prestigious National Academy of Sciences: Jeanne Altmann of Princeton University and formerly the Brookfield Zoo, and Frans de Waal (Emory University), who spent many years conducting research at Arnhem's "Burgher Zoo" in the Netherlands. In addition, Katherine Ralls has received the Merriam Award from the American Society of Mammalogists and the LaRoe Award from the Society for Conservation Biology (SCB), and Devra Kleiman has received an SCB Distinguished Achievement Award, both of them for scientific and conservation research accomplished at the Smithsonian's National Zoological Park. Interestingly, for 3 terms in a row, zoo-based individuals were elected president of the Society for Conservation Biology (Deborah Jensen, Woodland Park, Seattle; John Robinson, WCS; Georgina Mace, Zoological Society of London).

Awards presented outside academia or scholarly societies have also recognized zoo scientists. According to Rolex's Web site, zoo-affiliated scientists have won 3 highly competitive Rolex Awards for Enterprise. In 1978, Bill Lasley, a reproductive biologist, was named a Rolex Laureate. Although Lasley is now an emeritus professor at the University of California at Davis, he was honored for his work on developing procedures to sex endangered birds and thereby facilitate their breeding while at the Zoological Society of San Diego. In 1996, Norberto Luis Jácome, working at Buenos Aires Zoo, was named an Associate Laureate for his efforts to stockpile genetic material from endangered and rare species, particularly the Andean condor. Most recently, in 2002, WCS affiliate José Márcio Ayres (deceased) was named a Laureate for protecting a large corridor of rainforest habitat in Brazil by involving local people. WCS has also provided support to Rolex Award Laureate Rodney Jackson's work on snow leopards and Rolex Award Laureate Nancy Lee Nash's efforts to increase awareness of and support for conservation in Asia and worldwide using Buddhist teachings about the environment.

In addition to outside awards, zoos have taken it on themselves to recognize exceptional contributions in conservation science. The Zoological Society of San Diego awards medals each year to individuals who have had a significant impact on conservation by increasing our knowledge of animal and plant species, and directly promoting the reproduction or preservation of animals and their habitats or raising public awareness of conservation. In 1989, its centennial year, the Smithsonian National Zoological Park presented a Centennial Medal to Donald G. Lindburg for his career contributions to the science of zoo biology. In 2004 Lindburg was also honored by the American Society of Primatologists with its Distinguished Primatologist Award. Recently, the David Packard Medal was presented by the Monterey Bay Aquarium Institute to David Karl of the University of Hawaii for his "achievements and leadership" in the study of ocean microorganisms.

We hope to see the emergence of awards and prizes to honor distinguished scientific advances in the field as zoo biologists approach a critical mass. Currently, Wiley/Liss (the publisher of *Zoo Biology*) and AZA provide an annual $1,000 prize for the best published paper in the journal, but there is no dedicated award from AZA that recognizes scholarship or career achievement in science, although AZA's highest honor, The Marlin Perkins Award, has been presented to 2 scientists who met the criteria for the award (usually presented to zoo directors) in part because of their strong professional leadership. Ulysses S. Seal, whose leadership of the IUCN/SSC (International Union for Conservation of Nature/Species Survival Commission) Conservation Breeding Specialist Group brought the science of population biology to the forefront of zoo management, won the award in 1991. Kurt Benirschke, founder of the Zoological Society of San Diego's Center for Research on Endangered Species and an internationally known scholar in zoological medicine and pathology, received the award in 1998. Recently, the Indianapolis Zoo established the world's largest individual monetary award for animal conservation, the $100,000 Indianapolis Prize, to be given every other year to "an individual who has made significant strides in animal conservation efforts." George Archibald received the inaugural prize in 2006. The recipient of the 2008 Indianapolis Prize was George B. Schaller, a distinguished naturalist who has spent much of his career with the Wildlife Conservation Society. While this award does not necessarily recognize scientific achievement, the criteria include quality of science and synergistic relationships with education and public relations programs.

CONCLUSIONS

The zoo profession has far to go in its commitment to scientific research; too few zoos actively participate in or support it. It may be that many zoos have not found a way actively and sufficiently to support research, but there are many cost-effective options for establishing a research program and enough experts working in established zoo research departments to mentor others. Ignorance is not preventing a proliferation of scientific programs; it is more likely a lack of institutional commitment. Since zoos and aquariums need well-trained, high-achieving scientists, these institutions must become more competitive to recruit top scientific talent. Furthermore, they need to encourage productivity through competitive research funding and publication in peer-reviewed journals, and greater visibility for conservation and science programs. Leadership is a key component to research success; thus, institutional chief executives must shoulder the burden of strengthening and expanding zoo and aquarium research programs.

The type of research conducted in zoos is relatively stable, as we primarily conduct nonexperimental, behavioral, nutritional, genetic, and reproductive biology research on mammalian subjects. The scope of zoo research may be broadening, and today's zoo research is better designed and more accurately executed, and includes more advanced statistical techniques. This trend to more sophisticated research designs and larger subject populations permits greater generalization. Better research will surely lead to more publications in highly competitive scientific journals, and a greater share of external research funding. All this is possible because many institutions are recruiting doctoral-level talent from the nation's best universities. We must continue to strengthen our conservation and science vision in order to recruit, retain, and reward scientific talent, and to stoke the passion they bring to the workplace.

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Part Six

Behavior

Introduction

Katerina V. Thompson

For zoos to achieve their full potential in conservation and education, ensuring the mere survival of zoo specimens is not sufficient. We must also strive to preserve behavioral diversity among the animals in our care. If captive animals fail to exhibit normal reproductive and parental behavior, then captive propagation efforts will be futile; if animals fail to develop normal behavioral repertoires, then reintroduction attempts are doomed. Preserving behavioral diversity is a challenge for zoo managers, since the captive environment differs, in ways both obvious and subtle, from the habitats in which wild mammals evolved. This section provides an overview of aspects of behavior that have particular relevance to captive management and shows how the social and physical environments can be optimized to preserve behavioral diversity. It concludes with an introduction to behavioral research techniques, in the hopes of stimulating further research that will help inform future decisions regarding captive management.

Despite the recent emphasis on designing naturalistic exhibits to promote behavioral well-being in captive animals, the captive environment can never fully duplicate the habitats of wild mammals. These differences can have both immediate and cumulative effects on the behavior of captive mammals, and over many generations can cause the behavior of captive-bred mammals to diverge from that of their wild counterparts. In chapter 25, McPhee and Carlstead review how the captive environment affects behavior. They make the case that preserving

Female gorilla with her infant at the Smithsonian's National Zoological Park, Washington, DC. Photography by Mehgan Murphy, Smithsonian's National Zoological Park. Reprinted by permission.

natural behaviors in captive animals is key to maintaining their well-being, facilitating successful reintroduction efforts, and instilling in zoo visitors an appreciation for conservation of the natural world.

Animals in zoos are neither "wild" nor truly domesticated. There is a long tradition of training to increase tractability in some species, e.g. elephants and marine mammals, but the broad applicability of training programs to captive mammal management is a relatively new endeavor. There is now increasing recognition that training can be used to accomplish procedures that once required anesthesia, e.g. blood collection, hoof trimming, and semen collection. In addition, training programs provide cognitive and social stimulation for mammals that may contribute to their well-being. In chapter 26, Mellen and MacPhee provide an overview of how animals learn, and show how the basic principles of learning theory can be applied to improve captive management and enhance the welfare of captive mammals. They conclude with advice on establishing a self-sustaining husbandry training program.

Swaisgood and Schulte, in chapter 27, provide an overview of mammalian social behavior and communication as it relates to captive management. Wild mammals display an astonishing diversity of social organizations, from solitary to highly gregarious. The social organization of a given species, and therefore an individual animal's tolerance of conspecifics, is somewhat flexible and is influenced by both the environment (e.g. food, space) and the social milieu (e.g. age and sex of conspecifics). Mimicking a species' natural social organization is a useful starting point, but Swaisgood and Schulte stress that it is critical for captive managers to define their objectives (e.g. education, captive breeding, reintroduction), because adjustments to the natural social organization may be necessary to optimize these factors in the zoo environment.

Chapter 28, on pregnancy and parturition, by Thomas, Asa, and Hutchins, and chapter 29, on parental care and behavioral development, by Thompson, Baker, and Baker, provide an introduction to the physiological and behavioral aspects of these activities in mammals. It is critical to recognize typical behavioral parameters and provide appropriate captive conditions for the expression of normal reproductive and parental behavior. It is likewise essential to understand normal developmental trajectories, because early development has a strong influence on the behavioral and reproductive competence of mammals in adulthood. Future conservation efforts will depend on coordinated *in situ* and *ex situ* activities. Thus, we must ensure that captive populations do not simply retain genetic diversity, but also retain appropriate behavioral repertoires. Careful attention to behavioral needs will permit the expression of more normal behavior in both captive and reintroduced mammals.

While emphasizing behavioral research, Crockett and Ha's chapter on data collection and analysis (chapter 30) provides a recipe that can be applied to any discipline. It emphasizes the importance of formulating research questions, designing protocols for collecting data, choosing appropriate data recording techniques, and conducting statistical analyses. All too often, zoos do not collect systematic data or test alternative hypotheses when trying to explain a given behavior pattern or biological phenomenon. This lack of scientific rigor makes it impossible to generalize the results of many zoo research projects, while more careful attention to experimental design and analysis will enhance our collective efforts to improve captive husbandry and well-being.

25

The Importance of Maintaining Natural Behaviors in Captive Mammals

M. Elsbeth McPhee and Kathy Carlstead

INTRODUCTION

Behavior, like morphology and physiology, evolves in complex environments to increase an individual's survival and reproductive success in its native habitat. Captive mammals, however, are living in environments widely different from that in which they evolved. In response, they adjust their behavior to cope with their environment, potentially resulting in genetic and phenotypic divergence between captive and wild populations (Darwin 1868; Price 1984, 1998; Lickliter and Ness 1990; McPhee 2003a, 2003b, 2004).

These responses can occur on 3 levels. First, an individual can change its behavior to meet an immediate specific need, e.g. conforming to feeding schedules or conspecific groupings. Second, growing up in a captive environment that is more restrictive than the wild can alter how an animal learns and change how it responds to future events. These changes occur within an individual, but build as the animal develops. The third level of response comprises many individual changes, but is expressed across a population. Within a captive population, certain behaviors will confer greater survivorship on the individuals who express them, e.g. greater tolerance of loud noises. These behaviors will be passed on genetically from generation to generation, resulting in a distribution of traits within the captive population that is distinct from distributions observed in wild populations.

Maintaining natural behaviors in captive-bred mammals is a top priority for zoo biologists, because all 3 levels of change may compromise *ex situ* and *in situ* conservation efforts for endangered mammal species. For an individual animal, the presence of normal, species-specific behaviors, similar to those observed in the wild, is one potential indicator that its needs are being met, its captive environment is optimal, and it has good health and well-being. In exhibited animals, natural behavior is also a signal to the zoo visitor that the animal is a viable representative of its wild counterparts. Visitors who witness captive animals displaying abnormal behaviors are more likely to perceive those animals as "unhappy" (McPhee et al. 1995, unpublished data), and increased aberrant behaviors can detract from the educational message of the exhibit (Altman 1998). Such negative experiences with captive animals can potentially cause visitors to reject the concept that zoos are authorities in the preservation of that species and of biodiversity in general.

In addition, formation of natural species-specific behaviors during growth and development is necessary for successful reproduction. Reproductive behaviors, such as mate choice, courtship, mating, and rearing of offspring, are significantly influenced by the captive environment (see Swaisgood and Schulte, chap. 27, this volume; Thompson, Baker, and Baker, chap. 29, this volume). For many mammal species, development of natural reproductive behaviors requires normal learning experiences during early development and appropriate socialization throughout development. Therefore, to maintain sustainable captive populations, the effects of captive conditions on the development of behavior must be given serious consideration in all captive breeding programs (Kleiman 1980; Carlstead and Shepherdson 1994).

Finally, for captive populations to represent their wild counterparts accurately, overall trait distributions must be similar. Captive populations are exposed to selective pressures that, over generations, shape behaviors adaptive to the captive environment. These pressures alter behavioral expression and trait distribution within a population, resulting in captive populations that are behaviorally and morphologically distinct from wild populations. The captive population may thus evolve toward one lacking individuals able to survive in a wild environment, severely limiting the ability of captive populations to contribute to the recovery of wild populations.

In this chapter we will discuss the importance of addressing all 3 levels of behavioral change within the contexts of individual animal well-being, development of natural reproductive behavior, and behavioral diversity of captive populations, and how these relate to *in situ* and *ex situ* conservation efforts.

ANIMAL WELL-BEING

An ethical and operational imperative of every zoo is to optimize an animal's well-being (see Kagan and Veasey, chap. 2, this volume). Psychological well-being is an individual-level phenomenon, for it depends on how an animal perceives its own ability to respond to changes in its environment and react to its constraints. Dawkins (2004, 2006) suggests that determining whether the welfare of animals is good or bad requires answering 2 questions: is the animal healthy, and does it have what it wants? Poor physical health is an obvious sign of poor well-being, but other measures of health are less straightforward, such as reduced food intake or depressed immune function. Behavioral scientists are increasingly interested in studying stress responses of captive animals in order to link animal well-being to animal health.

IS THE ANIMAL HEALTHY? STRESS ASSESSMENT

To keep an animal physiologically and behaviorally healthy, the demands of stress must be kept within a tolerable range. Chronic stress is an undisputed cause of poor welfare in captive mammals (Broom and Johnson 1993). Prolonged periods of high levels of hypothalamic pituitary-adrenal activity in response to repeated or chronically present stressors may have costly biological consequences, such as immunosuppression and disease, atrophy of tissues, decreased reproductive function, or maladaptive behavior (Engel 1967; Henry 1982; Bioni and Zannino 1997; Blecha 2000; Elsasser et al. 2000; Whay et al. 2003). Stress can be good or bad for an animal depending on how long the stress lasts, how intensive it is, and how many options the animal has for responding to its situation (Ladewig 2000; McEwan 2002; Wielebnowski 2003).

There are few zoo studies, however, that relate actual measurements of stress to consequences for animal health; stress is often presumed rather than measured, based on coincidental occurrence of precipitating events. For example, Cociu et al. (1974) reported that Siberian tigers, *Panthera tigris altaica*, at the Bucharest zoo developed gastroenteritis due to a failure to adapt to unfamiliar quarters. Also, a persistent high noise level lasting several months caused by repairs in an adjacent courtyard was thought to induce gastroenteritis in some of the tigers. There is more recent direct evidence for a correlation between elevated corticoids and biological costs among some zoo-housed species. Carlstead and Brown (2005) provide evidence that mortality in black rhinoceroses, *Diceros bicornis*, and reproductive failure in white rhinoceroses, *Ceratotherium simum*, are associated with high variability in the secretion of stress hormones (glucocorticoids) from the adrenal cortex. They interpreted high variability in fecal corticoids over a one-year collection period as indicating an inability of some rhinoceroses to adapt or maintain homeostatic levels of adrenal activity.

There is also an association of high average glucocorticoid concentrations with hair loss in polar bears, *Ursus maritimus* (Shepherdson, personal communication), and with conspecific trauma, neoplasia, renal disease, and adrenal cortical histopathology in clouded leopards, *Neofelis nebulosa* (Terio and Wielebnowski, personal communication).

To address the causes and reduce the deleterious effects of stress on well-being and health, measurement of stress in zoo animals is necessary. How do we assess stress? A definition of chronic, or "bad," stress is "when *environmental demands* tax or exceed the *adaptive capacity of an organism*, resulting in *psychological and biological changes* that may place a person or animal at *risk for disease*" (Cohen, Kessler, and Underwood Gordon 1997, 3). Thus, to measure stress in zoo animals we must assess and integrate at least 3 factors: (1) environmental conditions and changes, (2) physiological and behavioral responses to these changes, and (3) biological consequences to health, reproduction, and disease processes. In zoos today, stress assessment is a rapidly growing field that necessitates the integration of these biological data collected sequentially on individual animals, for individuals perceive stressors differently as a function of their age, sex, background, personality, or reproductive condition (Benus, Koolhaas, and van Oortmerssen 1987; Suomi 1987; Mason, Mendoza, and Moberg 1991; Cavigelli and McClintock 2003).

The environmental and social events that cause stress in captive mammals vary depending on the species. Morgan and Tromborg (2007) provide an admirable review of factors that elicit stress responses in captive mammals. These include sound and sound pressure, olfactory stimulation from predators and chemicals, and space restriction (see also Kagan and Veasey, chap. 2, this volume). Unstable social groups (DeVries, Lasper, and Detillion 2003) or unnaturally high group densities, denied concealment, removal of scent marks, induced feeding competition, or forced proximity to zoo visitors also cause problems (Glatston et al. 1984; Hosey and Druck 1987; Chamove, Hosey, and Schaetzel 1988; Thompson 1989). In a multi-institutional study of 74 clouded leopards, Wielebnowski et al. (2002) found that public display, proximity of predators, frequent changing of keepers, and lack of enclosure height are environmental factors associated with high levels of fecal corticoids and aberrant behavior. Similarly, black rhinoceroses in enclosures with a large percentage of the perimeter exposed to public viewing had higher fecal glucocorticoids than those in enclosures with more restricted viewing (Carlstead and Brown 2005).

Responses to stressors may include various combinations of protective or defensive behaviors and neuroendocrine responses, depending on the stressor (Matteri, Carroll, and Dyer 2000; Moberg 2000). Physiological stress responses may occur transiently in response to normal situations such as courtship, copulation, or routine husbandry events, or they may be more sustained or variable as a result of more difficult challenges. A primary avenue for measuring stress, therefore, is to pair changes in behavior with changes in physiological measures, and then examine the precipitating environmental and/or social events. Measurement of glucocorticoids in feces and urine has become the primary means of studying stress responses in zoo animals and wildlife, because the collection method is noninvasive and represents a pooled sample of corticoid output over a period of several hours (Whitten, Brockman, and Stavisky 1998; Möstl and Palme 2002; Hodges, Brown, and Heistermann, chap. 33, this volume). In contrast, sampling blood for corticoid measurement needs to be conducted more frequently under rigidly controlled conditions in order to control for the naturally pulsatile excretion of corticoids and for circadian rhythms. This makes measuring basal levels and changes associated with environmental stressors more difficult.

Behavior is the animal's "first line of defense" in response to environmental change; it is what animals do to interact with, respond to, and control their environment (Mench 1998). Therefore, behavioral changes must be monitored when assessing stress in zoo animals. The increased occurrence of repetitive pacing, aggression, excessive sleep or inactivity, or fear behaviors can be indicative of stress. In a group of socially housed captive gorillas, *Gorilla gorilla gorilla*, periods of social instability were indicated by elevated glucocorticoids, aggressive displays, and fighting (Peel et al. 2005). Wielebnowski et al. (2002) found that elevated glucocorticoids in clouded leopards correlated with fur plucking, extensive pacing, and hiding behavior. A singly housed male orangutan, *Pongo* spp., had higher glucocorticoid levels on days when the keepers recorded his temperament as being "upset" and he refused to shift between enclosures (Carlstead 2006, unpublished data). In a zoo-housed giant panda, *Ailuropoda melanoleuca*, there was a positive association between glucocorticoids, locomotion, and door-directed scratching behavior and loud noise levels (Owen et al. 2004).

Conversely, the frequent occurrence of positive and/or natural behaviors may indicate low levels of stress and, presumably, good welfare. Leopard cats, *Felis bengalensis*, living in virtually barren cages had chronically elevated glucocorticoids and high levels of stereotypic pacing that decreased dramatically when they were given the opportunity to hide or conceal themselves in newly provided complex furnishings and vegetation. They also increased the amount of time spent exploring their cages (Carlstead, Brown, and Seidensticker 1993). Falk (personal communication) reported that, at one zoo, opening the shift doors for polar bears and giving them the choice to go inside or outside greatly reduced stereotypic pacing. Individual white rhinoceroses that keepers assess as being most adapted to their captive environment based on how "friendly" they are toward the keeper have lower mean glucocorticoids than conspecifics who seem less relaxed around keepers (Carlstead and Brown 2005).

DOES THE ANIMAL HAVE WHAT IT WANTS?

In zoos, absence of stress and abnormal behaviors are, by themselves, insufficient criteria to ensure animal well-being. Animals are motivated to perform behaviors (see Shepherdson, chap. 6, this volume), and animal welfare science seeks to identify which behaviors the animal wants/needs to do most (e.g. hunting, foraging, swimming). Captive mammals should also be active at levels similar to those in the wild (Kagan and Veasey, chap. 2, this volume). Thus, they need to be able to carry out highly motivated behaviors, especially those that result in a level of behavioral proficiency that supports the goals of the program for which they were raised (e.g. reintroduction, social living, captive breeding, program animal docile to humans, or exhibit animal displaying normal behavior). Motivations change with the season and reproductive condition; e.g. an American black bear, *Ursus americanus*, had a seasonal pattern of stereotypic pacing where the pacing changed temporally and spatially depending on whether it was the mating season or the prewintering season. Carlstead and Seidensticker (1991) interpreted this result to indicate a change in what the bear wanted—mating or foraging opportunities.

Two of the most common approaches to determine whether an animal has what it wants are (1) using environmental modifications and enrichment to reduce experimentally negative behaviors such as stereotypy, aggression, and excessive inactivity, and to increase activity levels and behavioral diversity, and (2) choice tests through which animals may indicate which behaviors they are most highly motivated to perform. One explanation for negative behaviors such as stereotypies is that appetitive motivation to seek something missing in the environment causes the animal to channel motivation toward repetitive locomotion (reviewed in Mason and Latham 2004; see Shepherdson, chap. 6, this volume). In other words, the animal cannot find an outlet for its desired behavior. As an example, feeding in the wild constitutes a large portion of some species' activity budget. Foraging and hunting are processes that include searching, acquiring (harvesting or capturing and killing), and consuming food items (Lindburg 1998). Captive animals, however, rarely have opportunities to do anything but consume, and often that is a compromised experience, as food is reduced from a complex (e.g. an intact prey item) to an overly simple form (e.g. preprocessed meat). In such cases, enrichment in the form of provisioning with whole carcasses increases handling time of food and reduces time spent in stereotypic pacing (ibid.; McPhee 2002).

Choice tests can suggest what the animal "wants" to be doing for pleasure, comfort, or satisfaction and have demonstrated that animals usually prefer challenges and engagement over passive rewards (Mench 1998). Animals of many species prefer to work for food, such as running a maze or pushing a lever, as opposed to getting food for free. Likewise, they prefer to explore novel environments and objects.

Modifications to animals' environments or changes in feeding methods frequently reduce negative behaviors and increase activity and behavioral diversity (for a review, see Swaisgood and Shepherdson 2005 and Shepherdson, chap. 6, this volume). Wiedenmayer (1996) hypothesized that stereotypic digging develops in captive Mongolian gerbils, *Meriones unguiculatus*, because the stimuli that normally cause the animal to cease digging were lacking in the captive environment. He kept young gerbils on a wood-chip substrate with access to an artificial burrow and found less digging behavior than in gerbils that were able to dig in a dry, sandy substrate which was incapable of supporting a burrow.

In many captive species, stereotypies occur mainly before feeding time, when the animal is motivated to perform food acquisition behaviors such as foraging or hunting. Winkelstraeter (1960) describes a female ocelot, *Leopardus pardalis*, that ran in a circular path before feeding. Similarly, Geoffroy's cats, *Felis geoffroyi*, paced for 2 to 4 hours before feeding time (Carlstead 1998). Stereotypic behaviors in large felids decrease with the provisioning of intact prey items, while food-handling time and other consumptive behaviors increase (e.g. crouch, stalk, pounce, leap, swipe, bite, hold, eat) (McPhee 2002; Bashaw et al. 2003). An American black bear paced less and explored/foraged more before feeding time when food was scattered throughout its enclosure (Carlstead, Seidensticker, and Baldwin 1991). Gould and Bres (1986) had some success in reducing regurgitation behavior in captive gorillas by feeding browse, which increased time spent handling and ingesting food. Such studies can be interpreted as meaning that animals benefit from the opportunity to "work" for their food (Markowitz 1982).

Another fundamental question is whether an animal has as much space as it wants or needs in a zoo enclosure. For carnivores and other wide-ranging species, home range size predicts the level of pacing in captivity (Clubb and Mason 2003). With primates, generally the smaller the cage, the more some individuals perform stereotypies (Paulk, Dienske, and Ribbens 1977; Prescott and Buchanan-Smith 2004). By increasing the size of the area available to an animal, the behavior can sometimes be eliminated or altered (Draper and Bernstein 1963; Clarke, Juno, and Maple 1982).

Exactly how much space an animal needs is unclear, particularly because the critical factor for well-being is often the quality of the space (Berkson, Mason, and Saxon 1963). Polar bears have the largest home ranges of all carnivores in the wild and presumably need the most space in zoos—more space, in fact, than can be provided by any zoo. Shepherdson's recent multi-institutional study of polar bear stereotypy found that enrichment and training is highly negatively correlated with time spent in stereotypy, implying that giving bears something to do continually can be compensation for lack of space (Shepherdson, personal communication). Perkins (1992) and Wilson (1982) found that cage size was not as important for stimulating higher levels of activity in groups of zoo-housed great apes (gorillas and orangutans) as was the number and type of furnishings. Odberg (1987) compared the behavior of bank voles, *Myodes glareolus*, in small, rich environments and in large, sparse ones, and found less stereotypic jumping in the former. Similarly, spatial confinement was not a causal factor of stereotypies in Mongolian gerbils (Wiedenmayer 1996). Such evidence lends credence to Hediger's (1964) statements that the quality of a confined animal's space is more important than the quantity.

Choice tests are common in animal welfare research of intensive farming practices to determine how much effort animals are willing to expend to achieve access to opportunities for preferred activities. Dawkins (1990) has used a consumer demand model derived from economic theory that requires animals to work to acquire commodities. For example, Mason, Cooper, and Clarebrough (2001) found that mink, *Mustela vison*, expend more energy pressing a weighted door to acquire access to a swimming pool than to gain access to toys, novel objects, or alternative nest sites. When deprived of pool access they exhibited corticoids elevated to a level similar to the corticoid response when they are food deprived. The authors concluded that farmed mink are still highly motivated to perform aquatic activities despite being bred in captivity without access to pools of water for 70 generations.

Choice test experiments are not commonly used with zoo animals, because standardizing environments sufficiently to offer 2 equal choices is difficult. However, studies of space utilization that divide enclosures into grids can assess animal preferences to some degree, particularly when behavior is also assessed. For example, Mallapur, Qureshi, and Chellam (2002) found that almost all 14 leopards, *Panthera pardus*, in Indian zoos used the edge zone of their enclosure for stereotypic pacing and the "back" zone, farthest from visitors, for resting.

Of additional interest for future research are the individual differences when using operant conditioning to train captive animals: learning and performing behaviors could be an indication of willingness to work for food rewards or social interaction with the keeper (see Mellen and MacPhee, chap. 26, this volume). Certainly, there are individuals who choose not to be trained, or do so only for their most highly valued rewards.

BEHAVIORAL DEVELOPMENT AND REPRODUCTION

Maintaining natural reproductive behaviors in captive-bred animals is vital to the establishment of self-sustaining captive populations and maintaining genetic diversity within those populations. Historically, however, many captive mammals have reproduced with difficulty or not at all (Wielebnowski 1998). Common problems include inability to court and choose mates, copulate successfully, or rear viable offspring, often due to a lack of normal species-specific interactions with the environment as an animal matures. As with animal welfare, such developmental problems are observed at the individual level.

Interactions between the developing organism and its environment start before birth, since the hormonal state of the mother affects the uterine environment of the growing fetus. There are numerous reports of the effects of stress experienced by mothers during pregnancy on the behavior of their offspring, including increases (Ader and Blefer 1962) or decreases (Thompson, Watson, and Charlsworth 1962) in emotionality in a novel environment (open field), alterations of exploratory behavior in rats (Archer and Blackman 1971), and reductions in attack and threat behavior in male offspring in mice (Harvey and Chevins 1985). Male offspring of mother rats stressed daily in the last week of gestation showed reductions in attempted copulations and ejaculation responses as adults (Ward 1972). Such studies imply that prenatal stressors specific to a captive environment can cause postnatal behavioral changes that reduce reproductive viability of offspring.

In most mammals, the mother-infant relationship is critical to the future development of offspring, affecting future defensive responses and reproductive behavior (Cameron et al. 2005). Subtle aspects of the parent-infant or juvenile-peer relationship may affect later sexual preferences and competence, and researchers speak of an extended period of socialization occurring during infant and juvenile stages (Aoki, Feldman, and Kerr 2001). A disturbed mother-infant relationship may deprive the young animal of specific stimulation essential for the development of normal emotional regulation, social interaction, and complex goal-directed behaviors, in particular, maternal and sexual behaviors. Deprivation of maternal licking when pups are young has been shown to affect the timing of sexual behavior patterns in male rats when grown; intromissions were more slowly paced and the rats took longer to ejaculate (Moore 1984).

Relationships with peers are also important, especially for great apes. Maple and Hoff (1982) found that young gorillas maintained with little or no conspecific contact are often sexually dysfunctional as adults. Captive female chimpanzees, *Pan troglodytes*, are better mothers when they have social experience with nonrelated infants or other mothers with infants (Hannah and Brotman 1990).

As an animal matures in captivity, many elements influence it that are unique to the captive environment. Close contact with humans can produce a range of behavioral characteristics not found in a wild-reared animal, depending on when it occurs during the animal's development and how long it is sustained. The most significant effects of human contact on overall behavior likely occur as a result of contact early in life in lieu of caregiving by the natural mother (i.e. hand rearing) (see also Thompson, Baker, and Baker, chap. 29, this volume). In a study of western lowland gorillas, Ryan et al. (2002) found that mother-reared females had more offspring and were more likely to become successful mothers than hand-reared females.

Early socialization with humans can affect species-specific social skills in both positive and negative ways. Among ungulates with precocial young, filial imprinting, in which the young learn to follow the mother (rather than objects and individuals that do not resemble the mother), occurs within the first day or two of life (for reviews see Bateson 1966; Hogan and Bolhuis 2005). Guinea pigs, *Cavia porcellus*, also exhibit characteristics of filial imprinting (Sluckin 1968; Hess 1973). Removing a young animal from the mother during this sensitive period may result in following responses being elicited by human caregivers, as is commonly seen in sheep and goats, but has also been reported in the American bison, *Bison bison*, zebra, *Equus* spp., African buffalo, *Syncerus caffer*, mouflon, *Ovis musimon*, and vicuña, *Vicugna vicugna* (see Hediger 1964). Mellen and MacPhee (chap. 26, this volume) recommend caution in training young male ungulates, because as they mature they tend to show aggression toward humans. Ideally, captive-born mammals should be socialized with humans only to the point where they have minimal fear of humans (tameness) but still recognize them as heterospecifics.

Many reproductive deficiencies derive from an inappropriate developmental environment, while others occur through lack of opportunities in captivity. In the wild, many mammals can choose their mate based on cues ranging from chemical odors to complicated courtship displays. Based on such cues, wild individuals tend to choose a mate such that inbreeding is decreased, pathogen resistance is increased, and ultimately, survival and reproductive success of offspring are maximized (Grahn, Langefors, and von Schantz 1998). Many species have evolved mechanisms by which they choose mates that are genetically dissimilar, which reduces the risk of inbreeding (Blouin and Blouin 1988) and increases the ability of offspring to resist disease. House mice, *Mus musculus*, prefer mates that are genetically dissimilar at the major histocompatibility complex (MHC), a suite of genes responsible for immune function, thus conferring increased immune response and disease resistance in their offspring (Penn and Potts 1999). Grahn, Langefors, and von Schantz (1998) suggest that allowing greater mate choice in captive animals might increase disease resistance in captive populations through increased diversity of the MHC. Specifically, they suggest allowing captive males to display for females and using female reactions to guide breeding decisions.

Captive mammals, however, are not usually given the opportunity to assess multiple potential mates and ultimately choose an individual suitable to them. Indeed, little is known about how mate preferences develop or are lost in captive populations. For example, species differ in whether familiarity is a good or a bad feature, and in some, the introduction of an unfamiliar individual as a mate results in high levels of aggression. Yamada and Durrant (1989) found that clouded leopards need to be paired while still sexually immature; in pairs established later, males show extreme aggression toward females, often resulting in serious or fatal injuries. Female kangaroo rats, *Dipodomys heermanni arenae*, were less aggressive toward and more responsive to familiar males with whom they had prior experience (Thompson 1995). By contrast, cheetah, *Acinonyx jubatus*, and white rhinoceroses are anecdotally known to be more likely to breed with newly introduced, unfamiliar mates.

BEHAVIORAL DIVERSITY

Animal managers must also be aware of how small, individual changes affect behavioral trait expression at the population rather than the individual level. Selection in captivity can affect the expression of behavioral traits in multiple ways; however, the selective pressures associated with captivity are vastly different from those in the wild environments in which species have evolved (Hediger 1964; Price 1970; Frankham et al. 1986; Soulé 1986; Soulé et al. 1986; Price 1998; Seidensticker and Forthman 1998). Captivity can thus impose novel selective pressures—either intentionally or inadvertently (Price 1970, 1998; Endler 1986)—and, over generations, result in changes in important life history and behavioral traits that affect functional relationships between behavioral, morphological, and physiological traits (McDougall et al. 2006). Understanding and identifying the ultimate mechanisms behind behavioral change can be difficult, because different selective pressures do not occur in isolation of one another. One trait may experience relaxed selection, while another experiences directional. The overall expression of traits is therefore the result of complicated synergistic effects. For the purposes of this chapter, we will focus on directional and relaxed selection.

Directional selection occurs when the expression of traits at one end of the distribution is favored (Endler 1986). In this case, mean trait expression will shift, but variance around the mean will not necessarily change (fig. 25.1a). For example, time spent foraging is a trade-off with predator avoidance for many wild species. More time foraging means more food, but it also means higher predation risk. On the other hand, reduced foraging time might decrease probability of predation, but the animal will have fewer resources than its bolder counterparts. In the captive environment, that trade-off does not exist. Some animals that are given foraging opportunities may increase the amount of time spent foraging—and as a result have healthier offspring and higher reproductive success than individuals who continued to balance foraging and vigilance. In this case the trait *foraging time* has been pushed in an increasing direction.

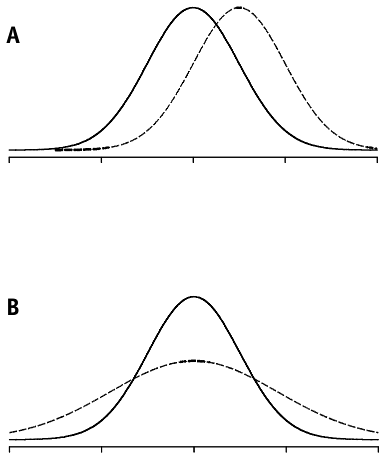

Fig. 25.1. Directional and relaxed selection. The solid curve represents the original distribution of a trait; the dashed curve represents how the distribution changes due to either directional (*A*) or relaxed (*B*) selection. With directional selection, the mean shifts, but the shape of the distribution does not change; with relaxed selection, the mean remains the same, but the distribution flattens out, including more values at either extreme.

Relaxed selection can occur when captive conditions permit expression of certain behavioral traits that otherwise would have been selected against in the wild, resulting in an increase in genotypic and phenotypic trait variability (Endler 1986; fig. 25.1b). Consider the time necessary to respond to a predator. In the wild, animals have limited time to detect a predator and flee. In a captive environment, however, there is typically no predation and individuals can respond immediately, or never, to perceived threats with no effect on reproductive success. In this case, relaxed selective pressures in the captive environment result in an increase in variance in response time.

In one of the few investigations of population-level behavioral processes affecting captive mammals, McPhee (2003a, 2003b, 2004) tested for directional and relaxed selection in captive-bred oldfield mice, *Peromyscus polionotus subgriseus*, and found that behavioral and morphological divergence from the wild population increased with generations in captivity, primarily due to relaxed selection. Trait variance increased significantly for burrow/refuge use, activity level, response time to predators, and skull shape. To our knowledge, this is the only explicit test of these hypotheses in mammals. We recommend more research in this area to identify interspecific and trait-specific patterns, as well as linkages between traits.

Initially, these increases in behavioral trait variance may seem counter to the large body of literature that shows that, with generations in captivity, genetic variance decreases. Two views can potentially resolve this difference. First, phenotypes may be the primary trait on which selection acts (West-Eberhard 2003), and minor genetic changes can result in profound phenotypic changes, which are then selected for (or not). Second, reduced genetic variance resulting from inbreeding is not natural selection—it is the reduction of genetic variance based on what genes are available. Selection then acts on the phenotypic expressions that result from inbreeding, a process that may ultimately appear to reduce genetic variance.

Artificial selection, be it directional or relaxed, can be intentionally or inadvertently imposed. The most common form of intentional artificial selection is domestication (Price 2002). Humans have attempted, but failed, to domesticate many species. Not all animals are amenable to domestication, because certain behavioral characteristics are more favorable for domestication than others. Easily domesticated species generally live in large, hierarchical social groups in which the males affiliate with female groups, and mating is promiscuous. Young are precocial and experience a sensitive imprinting period during development. They are also generally adapted to a wide range of environments and dietary habits rather than to highly specialized conditions (ibid.).

Species targeted for domestication are subjected to strong selective pressures designed to produce a certain outcome, e.g. increased milk production in dairy cows or long, pointed snouts in rat-hunting dogs; but many behavioral changes in domesticated populations are the indirect consequence of selection for other morphological and/or physiological attributes. For example, in Belyaev's famous selection experiments with silver fox, *Vulpes vulpes*, animals selected over generations exclusively for tameness also exhibited a shift from one to 2 annual estrous cycles (Belyaev and Trut 1975) as well as phenotypic traits such as floppy ears and curly tail that are typical of domesticated dog species (Trut 1999). Although nondomestic captive populations do not undergo such strong intentional selection, they do experience unintentional selective pressures. For example, temperament in captive mammals is likely shaped by directional selection (Arnold 1995; Frankham et al. 2000; McDougall et al. 2006). In captivity, docile individuals are easier to handle, transport, and medicate than their more aggressive counterparts. In a human-controlled environment, docility might translate into better survival and reproduction, which could lead to unconscious artificial selection for docility and tractability in mammals—selection that may eventually make captive populations divergent from wild populations. On the other hand, Kunzl et al. (2003) compared behavior and physiological responses of domestic guinea pigs, *Cavia aperea f. porcellus*, wild-caught cavies, and captive-bred cavies, *Cavia aperea*, bred with no purposeful selection. There were no significant differences between the wild-caught animals and those bred in captivity for 30 generations, suggesting that purposeful selection for specific traits may be necessary to produce domesticated animals.

CONSERVATION IMPLICATIONS

Maintaining natural behaviors in captive-bred animals is vital to the success of conservation efforts that rely on those animals, such as zoo education and reintroduction of captive-bred animals into their native habitat.

VISITOR EXPERIENCE

Maintaining good animal welfare is important for not only the individual animal, but also the zoo visitor. Zoos often justify the exhibition of exotic species by highlighting the zoo's and the species' educational value. A zoo is likely the only opportunity most people have to see such animals live, and most of a visitor's education while at a zoo comes from watching the exhibited animals (see Routman, Ogden, and Winsten, chap. 12, this volume).

Zoo visitors often base their evaluation of an animal's health and "happiness" on observed behavior (Wolf and Tymitz 1981). In general, visitors tend to be more engaged in front of an exhibit with an active animal (Altman 1998; Margulis, Hoyos, and Anderson 2003). When that activity is the display of obviously repetitive and abnormal behaviors, however, visitors perceive animals to be "unhappy" and "bored" (McPhee 1995, unpublished data).

Through nature documentaries and other media sources, visitors are coming into zoos with more background information than ever before, e.g. knowledge of how animals in the wild behave. This knowledge, however, can create false expectations. Nature programs often show carnivores capturing and killing prey. Yet, when visitors see a captive carnivore, it is often sleeping (a very natural behavior), and they may think it is "bored" and has "nothing to do" (Wolf and Tymitz 1981; McPhee 1995, unpublished data).

Exhibit type also influences visitor perceptions of natural behavior. McPhee et al. (1998) surveyed over 800 Brookfield Zoo (Brookfield [Chicago], Illinois) visitors in front of 4 exhibits—an outdoor barren grotto, an outdoor vegetated grotto, an indoor immersion exhibit, and an outdoor traditional cage—and found that visitors were more likely to perceive animals observed in more naturalistic enclosures as behaving naturally and thus being "happy," compared with animals in traditional cagelike enclosures. Perceptions of animal well-being also strongly affected the educational power of a zoo exhibit. Visitors that observe behaviorally healthy animals are more likely to walk away with an appreciation for that species' biological significance and need for conservation. These data suggest that, ultimately, an animal's behavior is the most powerful communicator of that individual's health and well-being as well as its natural history and conservation value.

REINTRODUCTION

Though most zoo animals will spend their entire lives as captive representatives of their wild counterparts, a very small percentage of individuals are targeted for release into their native habitat. Due to changes in important life history and behavioral traits, however, individuals from an established captive population are often at a disadvantage upon reintroduction. Evaluation of reintroduction programs indicates that many deaths of reintroduced animals are due to behavioral deficiencies (Kleiman 1989; Yalden 1993; Miller, Hanebury, and Vargas 1994; Biggins et al. 1999; Britt, Katz, and Welch 1999). When golden lion tamarins, *Leontopithecus rosalia*, were first reintroduced into the coastal rain forests of Brazil, captive-born animals had deficient locomotor skills; they could not orient themselves spatially; and they were unable to recognize natural foods, nonavian predators, and dangerous nonpredaceous animals (Kleiman et al. 1990; Stoinski and Beck 2004). Similarly, in Madagascar, reintroduced black-and-white ruffed lemur, *Varecia variegata variegata*, failed to avoid predators, find food, negotiate a complex arboreal environment, and recognize appropriate habitat (Britt, Katz, and Welch 1999). In 1985, all known wild black-footed ferrets, *Mustela nigripes*, were brought into captivity for breeding and eventual release of offspring. The initial releases of captive-bred ferrets resulted in high mortality due to predation, suggesting antipredator deficiencies (Reading et al. 1997).

Since many of these problems stem from the fact that the animals developed and matured in a captive environment, such behavioral problems might be eliminated by training animals targeted for reintroduction for certain skills before release. Most work in this area has been done with predator response behaviors. For juvenile prairie dogs, *Cynomys ludovicianus*, prerelease training consisted of exposure to either a live black-footed ferret, a live prairie rattlesnake, *Crotalus viridis*, or a mounted red-tailed hawk, *Buteo jamaicensis*. All exposures were coupled with the appropriate conspecific alarm call, but there was no aversive stimulus associated with the predator presentation. This training was sufficient to enhance survival for at least the first year postrelease (Shier and Owings 2006). Similarly, captive-bred Siberian polecats, *Mustela eversmanni*, exposed to predator models (e.g. great horned owl, *Bubo virginianus*, and badger, *Taxidea taxus*) coupled with mildly aversive stimuli, exhibited heightened antipredator responses (Miller et al. 1990). McLean, Lundie-Jenkins, and Jarman (1996) trained hare-wallabies, *Lagorchestes hirsutus*, to be cautious in the presence of new predators. Prerelease training, especially in orientation and locomotor behavior, for golden lion tamarins was not as effective as hoped in increasing survival (Kleiman 1989; Beck 1994; Beck et al. 2002). However, pairing captive-bred individuals with experienced wild-caught animals did increase the reintroduced animals' survival rate (Kleiman 1989).

Prerelease training can also be used to establish hunting and foraging behaviors. For example, red wolves, *Canis rufus*, were exposed to carcasses and live prey before release, and swift foxes, *Vulpes velox*, were given natural foods in the form of road-killed prey (ungulates and beavers) and chicks from a local hatchery (USFWS 1982 and Scott-Brown, Herrero, and Mamo 1986, as cited in Kleiman 1989). Black-footed ferrets that had prerelease conditioning with prey were more efficient at locating and killing prey than those without prey experience (Vargas and Anderson 1999).

At the population level, understanding how selection has altered the distribution of key behavioral traits within the population may allow reintroduction biologists to compensate for the observed changes. If the distribution of a trait or traits has shifted significantly, the proportion of individuals in a population that exhibits natural behaviors will also shift. Mortality will then increase in the release population, because fewer individuals will exhibit behaviors adapted for the wild environment. If a program's goal is to release 100 individuals, the question becomes how many need to be released such that 100 individuals will fall within the natural behavioral range? To address this question, McPhee and Silverman (2004) developed the concept of the release ratio, a calculation that uses trait variances in release and wild populations to determine the number of release individuals needed such that the targeted number of individuals exhibits natural behaviors.

For example, McPhee's (2003a, 2003b, 2004) behavioral and morphological measurements of oldfield mice showed that various traits, such as time to burrow and time in a refuge after having been exposed to a predator, exhibited significant increases in variance. Thus, if a representative sample of the captive population were released into the wild, there would be more individuals in the tails of trait distributions than would be seen in a wild population, resulting in a higher mortality rate than would otherwise be expected. Based on these data, McPhee and Silverman (2004) calculated release ratios of about 1.5 for the oldfield mouse, which means that for every 100 mice targeted to exhibit wild-type behaviors, 150 individuals need to be released.

CONCLUSION

In this chapter we highlighted 3 areas in which understanding and maintaining captive mammals' natural behavior is key to the success of propagation programs. We commonly see behavioral change in captive and captive-bred mammals, and these changes can occur on a number of levels. First, individuals adapt their behavior to captive conditions. Chronic or repeated stress due to inappropriate environmental conditions may result in poor health for a captive mammal. In addition, animals need to be able to carry out a diversity of species-appropriate behaviors. Thus, zoos and aquariums have a responsibility to promote a range of natural behaviors through appropriate exhibit design, husbandry, and enrichment programs. Second, as an individual develops and matures, behaviors emerge that are the result of interactions between the individual's genetic makeup and its captive environment. In some cases, such changes can have strong negative effects on an individual's ability to reproduce successfully, thus affecting the probability of maintaining a sustainable *ex situ* population. Finally, captivity can exert directional or relaxed selective pressures on behaviors that will affect the frequencies of those behaviors in future generations. Therefore, as individual behavior shifts, the distribution of traits within a population will also shift over generations.

One of the primary missions of zoos is conservation education through animal exhibitry, outreach programs, on-site tours and courses, and exhibit graphics (Hutchins, Willis, and Wiese 1995; Routman, Ogden, and Winsten, chap. 12, this volume). Behaviorally healthy captive-bred animals enhance *in situ* conservation primarily by educating the public about and instilling an appreciation for the importance of conservation. For many visitors, the zoo setting will be their only opportunity to see most species of wildlife. What that visitor takes away from the experience in terms of appreciation for the species and understanding of its natural history is largely dependent on what the visitor experiences—an animal in a barren cage displaying aberrant behavior or a behaviorally healthy animal in a naturalistic enclosure, doing what it does naturally in the wild.

Another conservation imperative of zoos is providing viable animals for reintroduction into native habitat. If captive breeding is to be a successful conservation tool, we must understand how captivity affects behavior developmentally and genetically, and how we can counter those effects if they are deleterious. More immediately, however, we need to maintain natural behaviors in captive animals because it is ethically imperative from the perspective of animal well-being.

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26

Animal Learning and Husbandry Training for Management

Jill Mellen and Marty MacPhee

TRAINING AND WELFARE

Training is one of many tools that an animal care staff uses to enhance the welfare of the animals under its care. Historically, animals have been trained to shift on and off exhibit, providing opportunities to examine them closely, offer individual diets, and create an environment that facilitates enhanced care. By training this and other behaviors, the number of physical captures and handlings can be minimized, reducing safety hazards to both animals and caretakers. Animals can be trained to participate voluntarily in their own medical care. Additionally, training can facilitate research on zoo and aquarium animals; results from these studies can enhance our abilities to understand and care for animals. Presumably, training provides a level of cognitive stimulation for animals (Hediger 1950) and thus may be enriching to the animals as well.

What follows is a description of how animals learn, an overview of husbandry training, and a framework for designing and implementing a training program at a zoo or aquarium.

ANIMAL LEARNING

All animals appear to be capable of learning. For example, mammals in the wild learn what foods to eat or avoid, where to find water, and how to find safe havens. *Learning* can be broadly defined as a change in behavior resulting from practice or experience (Dewsbury 1978); when that practice or experience is defined by humans, the process is called training. Generally, it is thought that animals can exhibit 4 types of learning: habituation, classical conditioning, operant (or instrumental) conditioning, and complex learning.

TYPES OF LEARNING

Habituation is the waning of a response due to repeated presentations of the eliciting stimulus. For example, an impala, *Aepyceros melampus*, may show a startle response to trees newly planted in its exhibit. Over time, the impala's startle response decreases, i.e. it habituates to the presence of the new trees. When animal caretakers actively manipulate the animal's environment to encourage habituation, it is termed desensitization, i.e. the act of pairing a negative or aversive event with a positive reinforcement until the animal's response to the aversive stimuli wanes.

Classical conditioning occurs when a neutral event initially incapable of evoking a physiological response acquires the ability to do so through repeated pairing with other stimuli that are able to elicit such responses. The most familiar example of classical conditioning involves studies by Pavlov (1927) on dogs. A dog is given some meat powder (unconditioned stimulus, or US) and salivates (unconditioned response, or UR). A bell is repeatedly sounded (conditioned stimulus, or CS) just before the food is presented, i.e. the CS and the US are paired. After repeated pairing of the taste of food and a bell, the sound of the bell alone (CS) can elicit salivation even without the taste of food. The dog salivating after hearing the sound of the bell is then exhibiting a conditioned response (CR).

What does classical conditioning look like in a zoo setting? A young sand cat, *Felis margarita*, initially may not respond to a visitor holding a camera (the camera here is the unconditioned stimulus—US). However, if the camera's flash goes off in close proximity to the sand cat, startling the animal, it may associate the camera with a startling flash (cat's behavior here is an unconditioned response—UR). After repeated pairings of visitors aiming cameras at the sand cat and the flash going off, the initially neutral camera (US) becomes a conditioned stimulus (CS), and the startle reaction to the sight of a camera a conditioned response (CR). Over time, the sand cat may show a startle response to visitors holding cameras—even those cameras that do not flash. A crucial characteristic of classical conditioning is that the sequence of events is in no way affected by the behavior of the animal. Regardless of whether or not the sand cat startles at the sight of a camera-wielding visitor, the unsuspecting visitors aim their cameras at the sand cat.

In contrast with classical conditioning, operant or instrumental conditioning is highly dependent on the behavior of the animal. Operant conditioning is a type of learning in which behavior is determined by its consequences. It is called operant conditioning because the animal "operates" on the environment, leading to the desired outcome. A behavior is strengthened if followed by reinforcement (positive or negative) and diminished if followed by punishment (see table 26.1 for definitions). For example, a mandrill monkey, *Mandrillus sphinx*, can be trained to enter a specific holding area by initially placing food in that holding area. Eventually, the monkey learns that if it moves into that specific holding area when the animal caretaker opens the door, it will receive a food reward. The monkey's behavior (entering a specific holding area) is instrumental in the monkey's receiving a reward. The monkey can also be trained by the use of punishment; e.g. if the monkey enters the wrong holding cage, it can be squirted with water. Punishment *decreases* the rate of responding (here, entering the wrong holding cage); reinforcement *increases* the rate of responding (entering the correct holding cage). While presumably both positive reinforcement and punishment can be used to shift animals,

TABLE 26.1. Training terms and definitions

Approximation	One small step in a series of progressive steps that leads to the behavioral goal; see Shaping by Successive Approximation.
Behavioral criterion	The level or behavioral response that must be met to earn reinforcement.
Bridging stimulus	A stimulus that pinpoints the exact moment that the behavioral criterion (for that approximation) is met. The "bridge," as it is often referred to (often a clicker, whistle, or word), communicates to the subject that it has performed correctly and often signals that additional reinforcement is on the way. It "bridges" the gap between the time the correct response is given and the time the additional reinforcer is delivered. It is a stimulus that can act as both an S^D (see Discriminative Stimulus, or Cue) and a secondary reinforcer.
Capture (Scan)	The process of placing a behavior that is limited by the subject under stimulus control by reinforcing the behavior as it spontaneously occurs.
Classical conditioning	A basic form of learning in which a neutral event initially incapable of evoking certain responses acquires the ability to do so through repeated pairing with other stimuli that are able to elicit such responses. This type of conditioning does not involve any voluntary choices by the animal; the response or reaction is reflexive (e.g. blinking or salivating) and not dependent on operant learning.
Conditioned stimulus (CS)	An initially neutral stimulus that will elicit a specific response as a result of repeated pairing or learned association between that stimulus and that response. A discriminative stimulus (S^D), or cue, is a conditioned stimulus.
Continuous reinforcement	A schedule of reinforcement in which the desired or correct responses are reinforced every time they occur. Animal caretakers typically use a continuous reinforcement schedule when the animal is in the process of learning a new behavior.
Desensitization	The act of pairing a negative or aversive event with a positive reinforcement until the event loses its aversive quality. The resulting behavior can be maintained through the use of positive reinforcement.
Discriminative stimulus (S^D), or Cue	A stimulus that precedes a behavior, signaling that a specific response will be reinforced if emitted correctly. The result is that the stimulus will consistently elicit only that particular response.
Extinction	A method of eliminating a behavior by no longer reinforcing it.
Extinction burst	A short-term increase in the frequency and intensity of a response during the extinction process due to lack of reinforcement.
Generalization	The lack of discrimination between two stimuli. An animal that has been conditioned to respond to a specific stimulus may offer the same response in the presence of a similar stimulus.
Habituation	The declining or waning of a behavior as the result of repeated presentation of the stimuli that initially caused the behavior; the process of gradually getting an animal used to a situation that it normally reacts to (i.e. avoids or reacts adversely to) by prolonged or repeated exposure to that situation.
Incompatible behavior	A behavior that is impossible to perform at the same time as another specific behavior.
Intermittent reinforcement	A schedule of reinforcement in which not every correct response is reinforced. Any schedule of reinforcement that is not continuous (i.e. variable ratio, variable interval, fixed ratio, fixed interval).
Jackpot or bonus	A positive reinforcer that is much larger than usual and usually unexpected.
Magnitude of reinforcement	The size and duration of the reinforcement following a behavior.
Negative reinforcement	A process in which a response increases in frequency due to the removal of an aversive stimulus from the animal's environment.
Observational learning	A type of learning in which one animal learns from observing the behavior and consequences of another's actions.
Operant conditioning	A type of learning in which behavior is determined by its consequences. A behavior is strengthened if followed by reinforcement (positive or negative) and diminished if followed by punishment. The animal "operates" on the environment, leading to the desired outcome.
Primary reinforcer or Unconditioned reinforcer	A reinforcing event that does not depend on learning or previous experience to achieve its reinforcing properties (e.g. biological need: food, water, warmth, sex).
Positive reinforcement	The process of following an action or response with something that the subject wants, thereby causing an increase in the frequency of occurrence of that behavior.

(*continued*)

TABLE 26.1. continued

Punishment	The application of stimulus or the removal of a stimulus that occurs *after* a behavior it is meant to affect, and causes a *decrease* in the frequency of that behavior.
Regression	The state of a conditioned behavior reverting to a previous stage in the learning process.
Reinforcer	Anything (either the application of a stimulus or the removal of a stimulus) that occurs in conjunction with a behavior that tends to increase the likelihood that the behavior will occur again.
Schedule of reinforcement	The conditions or parameters under which reinforcement is delivered; see continuous reinforcement and intermittent reinforcement.
Secondary reinforcer or Conditioned reinforcer	An object or event (stimulus) that initially may mean nothing to the animal but becomes reinforcing through pairing with a primary reinforcer or other conditioned/established reinforcer.
Selective or differential reinforcer	The act of reinforcing specific criteria for desirable responses to shape a specific behavior; the reinforcing of selected responses of higher quality to improve performance.
Shaping by successive approximations	An operant-conditioned method of taking an action or tendency and shifting it, one approximation, or step at a time, toward the final behavioral goal; building of a behavior by dividing it into small increments or steps and then teaching one step at a time until the desired behavior is achieved. Steps become a series of intermediate goals.
Stimulus	Anything that elicits a physiological or behavioral response; see Conditioned Stimulus.
Stimulus control	A behavior is said to be under stimulus control if it meets 3 conditions: (1) it is immediately offered following the S^D; (2) it is offered only when preceded by the correct S^D; (3) it is not offered in the presence of another S^D.
Superstitious behavior	A behavior that the animal offers during the training of another behavior but is unrelated to the behavior being trained. Because the unrelated behavior is inadvertently reinforced with the desired behavior, the animal perceives it as a necessary component of the behavior being trained, and therefore necessary to receive reinforcement.
Time-out	A mild type of punishment in which the opportunity to obtain reinforcement is removed immediately following an inappropriate or undesirable response; it is generally short in duration.

Source: Sources of definitions include Blasko et al. 1996; Dewsbury 1978; Kazdin 1994; Mellen and Ellis 1996; Pryor 1995, 1999; Ramirez 1999; Reynolds 1975; Wilkes 1994. This list of terms was developed by the Association of Zoos and Aquariums' Behavior Advisory Group and the Training Committee of the American Association of Zoo Keepers. It is a teaching tool in the following AZA courses: Principles of Elephant Management, Managing Animal Enrichment and Training Programs, and Advances in Animal Keeping in Zoos and Aquariums. Used by permission.

most animal care professionals advocate the use of positive reinforcement over punishment; in most cases, it is more effective and seems to facilitate a positive relationship between the animal and its caretaker.

Behavioral scientists initially thought that all learning could be categorized as one of the types discussed above. However, it eventually became apparent that other types of learning were taking place that could not be classified using the existing descriptions. The term *complex learning* is used to describe learning behavior in which the animal appears to develop strategies incidental to the learning task itself. Harlow (1949) called this "learning to learn." He found that rhesus macaques, *Macaca mulatta*, that had been taught to solve one type of problem learned to solve similar problems more quickly than inexperienced monkeys. Other examples of complex learning are latent learning and observational learning. In latent learning, experience or familiarity with a situation facilitates the learning of a task. For example, rats allowed to play in a maze can run later trials in that maze faster than naive animals. Observational learning involves an animal learning a task simply by observing another individual executing that task. At Sea World in Orlando, Florida, a young killer whale, *Orcinus orca*, learned to perform many different behaviors, apparently by observing its mother and other adults housed in the same pool. Observational learning has also been observed in infant bottle-nosed dolphins, *Tursiops truncatus* (L. Cornell, personal communication).

TRAINING TERMINOLOGY

Modern animal training has its roots in experimental and comparative psychology. Within this psychology literature are descriptions of how animals learn: through habituation, classical conditioning, operant/instrumental conditioning, and complex learning. The literature also provides insights into schedules of reinforcement and the roles of positive reinforcement, negative reinforcement, and punishment in learning and training. We think it is important here to remind the reader that in the laboratory, these concepts seem very clear cut and unambiguous. However, in a more "real world" situation, when watching an animal learn how to shift into and out of a barn, it is much more difficult to ascertain which types of learning are involved or whether positive reinforcement, negative reinforcement, or punishment played a role in the learning of that behavior. In all likelihood, an animal is learning in a multitude of ways and receiving a combination of reinforcement types. Many new animal caretakers seem to get bogged down by the terminology. We suggest that caretakers focus on understanding the broad concepts, the most important of which is that training is a process where animals are making associations. The job of an animal caretaker is to facilitate the animal's making those associations.

To add to the confusion, animal caretakers who work in an environment much more complex than the laboratory have developed an additional set of terms that are used to describe nuances of training. A list of the basic terminology associated with learning and training is given in table 26.1. We suggest here that understanding the *concepts* of training is more important than the specifics of each and every term, definition, and related jargon.

The concepts of reinforcement and punishment are integral to an understanding of learning and training theories. Reinforcement (both positive and negative) refers to an event that occurs as the result of a behavior and *increases* the likelihood that a behavior will occur again. A positive reinforcer (like food) is an attractive stimulus that is sought or added to the environment. A negative reinforcer is an aversive stimulus that is avoided or removed. If an animal comes into a holding area (the behavior requested) and is provided with a desired food item, we are using positive reinforcement to train the animal to enter the holding area. If an animal comes into a holding area because the animal caretaker hoses the outdoor exhibit (the animal is avoiding the water spray), we are using negative reinforcement. Both methods increase the rate of responding (entering the holding area).

Punishment differs from reinforcement in 2 ways: first, punishment occurs after the undesired behavior, and second, punishment decreases/suppresses the frequency of the undesired behavior. In this example of asking an animal to come into a holding area, the animal caretaker may want the animal to come always into stall A and never into stall B. With punishment, the caretaker might squirt an animal with water if it entered stall B. The animal has already "made the mistake," i.e. entered stall B; presumably by then squirting the animal with water, the caretaker has decreased the probability that the animal will enter stall B another time. Although we provide an example here of using punishment in the training of an animal, punishment can deteriorate the relationship between animal and caretaker and can even result in animal aggression.

It is common to hear people say that they only use "positive reinforcement" techniques when they train. However, it is unlikely that this training technique is the only one used. When used properly, negative reinforcement and punishment are effective tools. For example, animal caretakers often "walk" an animal into the barn, i.e. use the animal's flight distance to encourage it to move away from the animal caretaker (and into the barn). This is an example of using negative reinforcement. The animal is moving away from a mildly aversive stimulus (animal caretaker entering within the animal's flight space) and increasing the rate of responding (entering the barn). Similarly, animal caretakers may use a "time-out" (i.e. no reinforcement available) when an animal shows aggression during a training session. This is an example of punishment. The animal has directed aggression at the animal caretaker (the undesirable behavior); after the fact (the "misdeed" has occurred), the animal caretaker responds by removing all opportunity for reinforcement. Presumably, this time-out decreases the occurrence of caretaker-directed aggression during a training session.

Typically, during initial stages of training, the desired behavior is continuously rewarded (positively reinforced) every time it occurs. For example, when an elephant lifts its foot upon request, it receives praise or a carrot. However, reinforcement does not have to be given each time the response occurs. The elephant could be rewarded every fifth time it correctly lifts its foot. This is called a fixed-ratio schedule of reinforcement: the behavior is reinforced after a fixed number of responses. In another type of reinforcement schedule, termed a fixed interval schedule, the first correct response after a given time interval is reinforced. In both reinforcement schedules, the interval or ratio is "fixed" by the animal caretaker.

Schedules of reinforcement can also be intermittent or variable. An intermittent- or variable-ratio schedule of reinforcement might involve rewarding the elephant after the fifth correct response, then the third, then the twentieth. A variable interval schedule might involve rewarding the animal for the first correct response after 2 minutes, then 5 minutes, then 1 minute, and so forth.

Of the 4 schedules of reinforcement, the variable-ratio schedule produces the faster rate of learning, and more important, is best for maintaining the behavior. Behaviors learned using a variable-ratio schedule are also the most resistant to extinction. Extinction is the decrease in the rate or magnitude of response that occurs when the behavior is no longer reinforced. Animals that learn a behavior when variable schedules of reinforcement are utilized tend to persist in performing the behavior longer than those learning a behavior when a fixed schedule of reinforcement is used. Behaviors learned under variable-reinforcement ratios resist extinction for several reasons. Animals learn to persist in responding when faced with some nonreinforced responses during training, and there is less difference between variable reinforcement and no reinforcement than between continuous reinforcement and none (Drickamer and Vessey 1986).

Reinforcers such as food, water, or warmth are called primary reinforcers, because their capacity to reinforce is based on immediate biological consequences (i.e. the animal needs no previous experience with a primary stimulus for it to be reinforcing). If a stimulus such as a whistle is repeatedly paired with a primary reinforcer such as a food item, that stimulus becomes a conditioned or secondary reinforcer. For example, marine mammal trainers often use a whistle or an underwater tone when training. Immediately upon completion of a desired behavior, the animal caretaker sounds the whistle or tone (secondary reinforcer), and the animal returns to the animal caretaker for food (primary reinforcer). In training, the sound of a whistle or other secondary reinforcer is often called a bridging stimulus or bridge, because it bridges the gap between the time the desired behavior occurs and when the primary reinforcer is delivered.

When using positive reinforcement, negative reinforcement, or punishment, the animal caretaker needs to track the progress he/she is making. It is possible that the caretaker could be using the technique in an ineffective manner. For example, if the caretaker is using a time-out (punishment) to decrease aggression, he/she may need to use time-outs frequently over an extended period of time. If the animal is demonstrating the same level of aggression, there is a good chance that the time-outs are not being used effectively. Other techniques to decrease the behavior or training-incompatible behaviors may need to be investigated.

Some workers in the field of animal learning (e.g. Levine 1972) have discussed animals' "motivation" as if motivational differences affected ability to learn. However, the term *motivation* became an explanation in and of itself and yet offered no additional information about the learning process. Motivation explains why a stimulus has different effects in different situations and why behavior seems to be goal oriented, but it must be kept in mind that the term *motivation* is simply a label and not an explanation for variability in rates of learning. Examples of how an understanding of an animal's motivation influences training will be provided below.

SPECIES-SPECIFIC CONSTRAINTS ON LEARNING

For about 50 years, most American psychologists considered habituation and classical and operant conditioning the only forms of learning to take place in all organisms. This view also assumed that the processes involved in these types of learning were identical in all species. During the 1960s, however, a number of critical studies began to dispel this misconception. As more and more species were studied, it became apparent that not all animals are capable of learning the same things. Rather, each individual brings certain predispositions to the learning/training situation that can have powerful effects on its learning process. Breland and Breland (1961), students of B. F. Skinner's, demonstrated this in their attempts to use operant techniques to create animal attractions for carnivals. They taught chickens to "play" baseball and raccoons, *Procyon lotor*, to deposit coins in a "bank." Initially, these animals performed as planned, but eventually the chickens began to peck at the ball instead of hitting it; the raccoons, instead of depositing the coins, began to rub them together in a "miserly" fashion. The Brelands called this phenomenon "instinctive drift," because the animals were exhibiting behaviors they typically used in nature.

Two general influences, or constraints, on learning that can directly affect training merit discussion. Both involve biological predispositions brought to the training situation by the animal. First, a concept called preparedness (Seligman 1970) suggests that certain genetic predispositions make an animal prepared, contraprepared, or unprepared to learn particular things—whether in nature or in a training situation. An animal is generally *prepared* to learn tasks that include species-typical behaviors, i.e. tasks that are biologically relevant. For example, a killer whale can be easily trained to breach on cue, because this behavior is part of the species' natural repertoire. Behaviors that an animal is *contraprepared* to learn are exceptionally difficult to master, because they run counter to the species' natural history. In applying these concepts, the ease with which a particular animal can be trained to enter a small crate depends in part on its natural behavior. A denning species like an ocelot, *Leopardus pardalis*, is more easily trained to enter a small, dark space (i.e. a crate) than is a Thomson's gazelle, *Eudorcas thomsonii*, whose main defense strategy is to flee. We might say that a Thomson's gazelle is "contraprepared" to enter a crate, while an ocelot is "prepared" to enter a crate. Behaviors that an animal is *unprepared* to learn are neither easy nor exceptionally difficult to master but can be learned with moderate effort. Balancing a ball on its nose is not part of the normal behavioral repertoire in sea lions, *Zalophus californianus*, but can be learned with reasonable effort because it incorporates the extension of the animal's vibrissae, which are normally used to investigate new objects in the environment. For any particular learning task, an animal's ability to learn lies at a point along a continuum from preparedness to contrapreparedness that reflects the species' natural behavioral tendencies.

A second constraint on learning involves the sensory world, or *Ümwelt* (von Uexküll 1934), of animals. An animal's environment is made up of the particular stimuli that the individual perceives. An animal may not be able to perform a particular task because it is not able to interpret the stimuli involved. For example, color obviously is not a good choice for a cue to elicit a behavior from an animal that cannot see color. In order to be effective, all stimuli must be readily perceptible within the sensory limitations of the animal being trained. Temple Grandin's 2 books (Grandin 1995; Grandin and Johnson 2005) provide insightful descriptions of how domestic cattle perceive their environment and how those perceptions differ from those of humans. She describes cattle being fearful of seemingly (from a human's perspective) small changes in the environment (a rattling chain, clothing hung on a fence, a small object on the floor), and encourages animal care staff to take a "cow's eye view" of the animals' environment.

Thus, in training animals, it is imperative to keep in mind that each species is preadapted to learn certain behaviors and unable to learn—or able to learn only with great difficulty—other behaviors due to its natural history, including morphological, sensory, or other species-specific adaptations.

HUSBANDRY TRAINING

EVOLUTION OF HUSBANDRY TRAINING: FROM LABORATORY TO POOL TO BARN

In the early 1900s, E. L. Thorndike (1911) published a study on trial-and-error learning in which he described cats and dogs escaping from puzzle boxes. His work demonstrated the role of reinforcement in learning, and he became the first of many animal psychologists who influenced animal training. Pavlov's work on dogs in a laboratory (1927) characterized classical conditioning. B. F. Skinner's work (1938) on rats in "Skinner boxes" added to our knowledge of operant conditioning. Eventually, application of these concepts began to "creep" outside the laboratory. Heini Hediger, often considered "the father of zoo biology," recognized that training engaged animals at the cognitive level. Hediger (1950, 1969) believed strongly that simple training exercises were a form of "occupational therapy" for animals, reducing boredom in captivity. His use of the term *training* referred mainly to nonhusbandry-related behaviors; he perceived this type of behavior as "disciplined play." Breland and Breland (1961) used operant techniques to train a wide range of species, from marine mammals to animal attractions for carnivals. Learning and cognition of marine mammals were studied in university, laboratory, and aquarium settings in the 1960s and 1970s; operant conditioning was used to conduct this research (e.g. Turner and Norris 1966; Herman and Arbeit 1973). In the 1970s, oceanariums and the U.S. Navy used operant techniques to train dolphins and other marine mammals (see Defran and Pryor 1980). Hal Markowitz (1982) used operant conditioning techniques to train zoo animals in the use of a range of devices; these "behavioral engineering" devices both added to our knowledge of how animals learn and provided enrichment to the animals. By the mid-1980s, training techniques used primarily in the management of marine mammals were being applied to an ever-growing number of taxa.

Examples of this application follow. A gorilla, *Gorilla g. gorilla*, at Disney's Animal Kingdom, Orlando, Florida, injured its hand. Animal caretakers built on existing trained

Fig. 26.1. Western lowland gorilla (*Gorilla g. gorilla*) being trained in an off-exhibit area for a radiograph of his hand. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

behaviors to teach the gorilla to position its hand on a portable X-ray machine. The animal's hand was x-rayed without the need for immobilization (see figure 26.1). Giraffe, *Giraffa camelopardalis*, have been chute trained to allow long-term management of hoof problems (Kornak 1999; Burgess 2004). In situations where animals are fed in groups, aggression can result when animals compete for the food items. As an alternative, animals were trained to feed cooperatively near one another (Bloomsmith et al. 1992).

It is important to reiterate that training is just one of many tools used in the day-to-day management of captive animals. If an animal fails to shift off exhibit, the "problem" may not be as simple as the animal's having been trained inadequately. An animal may refuse to come into a barn because of aggression from a dominant animal, because there is insufficient space for it, or because it is ill or injured. A careful review of the issues surrounding a management problem typically identifies multiple concerns with multiple solutions, one of which may involve husbandry training (see Ramirez 1999 or Colahan and Breder 2003 for details on problem-solving models).

WHAT IS HUSBANDRY TRAINING?

Whether we are aware of it or not, as animal caretakers, we influence what animals in zoos and aquariums learn. In other words, as caretakers, we are teaching or training animals under our care all the time. In fact, Ramirez (1999) simply defines *training* as "teaching." Sometimes we are aware of what we teach or train; we make conscious efforts to "train" animals to exhibit a variety of behaviors for husbandry, education, research, and entertainment purposes. However, sometimes we influence (train) animals' behavior inadvertently through our actions, our husbandry routines, or other stimuli present in the captive environment. In effect, animal care staff is always training and needs to be aware of that fact. Training is all about associations. The key to an optimal captive environment is to facilitate an animal's opportunity to make associations that enhance its well-being.

As various applications for animal training are being developed and as training methods are being applied to an increasingly diverse number of species, it is important to discover what methods are appropriate and most successful for each species. There is a popular, and possibly misleading, philosophy among some animal caretakers that "training is training." That concept comes from the behaviorist psychology literature related to learning theory. Early in the twentieth century, psychologists (e.g. Skinner 1938) suggested that the mechanisms of learning were the same in all animals ("learning is learning"). However, as comparative psychologists and ethologists studied learning throughout the twentieth century in a broad range of species, they discovered that while the basic concepts associated with learning were very similar, the natural history of an animal strongly influenced how that animal learned. As discussed earlier, this was called "constraints on learning" or "preparedness to learn" (Dewsbury 1978).

COMPONENTS OF EFFECTIVE TRAINING

In order to select the most effective and appropriate techniques to train behavior, we need to consider a number of factors: the animal's natural history, its individual history, its function or role in the collection, exhibit constraints, and safety. Animal trainers must "do their homework" as part of their training preparation and planning. A successful animal trainer uses knowledge of natural history, individual history, the animal's role in the collection, facility design, and an awareness of safety issues in developing and implementing a training plan. Knowing what is reinforcing or aversive to an animal, knowing the time of day when it is most receptive to learning, and understanding and recognizing the stress-related and comfort behaviors of the species are all critical in setting up the animal and its caretaker for success.

Natural history. We should consider the natural history of the animal for which we prepare a training plan and know which behaviors the animals are most prepared to learn. Animal caretakers tend to fall into the trap that animals are infinitely flexible and "available" for learning. For example, at a recent gathering of animal trainers, a participant commented that animal caretakers are inadvertently "training" animals like Thomson's gazelle to be flighty, and that, through desensitization, it would be possible to eliminate the flight response. However, Thomson's gazelles *are* flighty! They are a prey species and as such have evolved a set of behaviors that includes fleeing perceived danger. It is neither reasonable nor appropriate to assume that we can "train out" a flight response that is so ingrained in the species. Habituation or desensitization might reduce the flight distance and, in essence, make the animal less flighty.

Training is a tool for animal management. To that end, we must understand how to set appropriate behavioral goals and expectations with respect to an animal's natural behavior, and not inadvertently endanger animals (or staff) with our actions in an attempt to train behaviors that an animal is "contraprepared" to learn.

A number of animal management and animal training programs have recently been developed that embrace philosophies and techniques which are rooted in an understanding

Fig. 26.2. Knowledge of natural history, such as using an elevated area for training, facilitated training a pouch check of a Matschie's tree kangaroo, *Dendrolagus matschiei*. (Photography by Jim Schulz, Chicago Zoological Society. Reprinted by permission.)

of the animal's natural history, thus applying its natural behavior. For example, John Lyons (1991), one of several trainers known as a "horse whisperer," uses techniques for training horses that involve the animal caretaker's learning how to read the subtle cues of the horse, and the caretaker's using body language that the horse can "read." Similarly, Temple Grandin has designed handling systems for livestock based on an understanding of the psychological and physical needs of these animals. These facilities are considered among the most humane (Grandin 1995; Grandin et al. 1995).

The selection of species-appropriate training techniques is also important. For example, caretakers at the Brookfield Zoo, Brookfield (Chicago), Illinois, while training Matschie's tree kangaroo, *Dendrolagus matschiei*, initially used a standard training clicker as a bridging stimulus. The first time the clicker sound was made, the initially calm tree kangaroo fled to the highest areas of the exhibit. Further investigation revealed that the clicker sound closely mimicked the alarm call of the species. After removing that specific aspect of the training protocol, the caretakers successfully trained the tree kangaroo. In addition, the caretakers learned that when they trained this arboreal animal in an elevated area, the training sessions were much more productive (fig. 26.2).

A series of questions about natural history as it may relate to training are listed in appendix 26.1. We suggest that gathering this information (i.e. answering the questions) will help during the process of developing a training plan.

Individual history/collection constraints. An animal's early rearing experience, its social rank, and its history greatly affect its response to the environment and readiness to learn new behaviors. Animals that are hand reared versus parent reared may have very different reactions to their animal caretakers. In some cases, having a hand-reared animal to train may facilitate the training goals (e.g. the animal caretaker can get close to the animal without triggering a flight response). Or, hand rearing may be a hindrance to achieving goals: some hand-reared individuals, when sexually mature, may become aggressive or bond inappropriately with an animal caretaker. Other individual history factors that may affect a training plan include social status within the animal's group, previous training experience, previous experience with a facility or part of a facility, and previous experience with people (e.g. animal caretakers, veterinarians, etc.).

Also, the animal's function or "role" in the collection may influence the type of training as well as the animal caretaker's level of interactions with that animal. Trainers and animals need not always be in close proximity or have physical contact for training to occur. Frequently, trainers work animals remotely through barriers. Animals that are part of a Species Survival Plan (SSP) or other breeding program may be trained remotely or less intensively than an animal for which there are no plans for propagation. Animals that are allowed to roam free with caretakers/visitors may be worked very differently than animals that are contained by a barrier.

Knowing the details of the individual animal's history and its function in the collection can assist animal caretakers in providing the best environment. Appendix 26.1 also contains questions about the animal's individual history that can facilitate the gathering of information for developing training plans.

Facility design and safety. A properly designed animal facility will (1) be safe for the animals, caretakers, and visitors (see also Rosenthal and Xanten, chap. 14, this volume); (2) encourage species-appropriate behaviors and allow the animal to move easily and comfortably; (3) facilitate animal care, including cleaning, feeding, enrichment, and training; and (4) allow the visitors a good view of the animal (Coe 1992; Coe and Dykstra, chap. 18, this volume; Laule 1995). Figures 26.3a and 26.3b illustrate a specially designed crate that facilitates animal caretakers' ability to train large cats safely for a variety of husbandry and medical behaviors.

A facility that works well for the animal and for the caretaker has a positive effect on a training program. Training in a facility where the animal feels comfortable takes much less time, and the behaviors are much easier to maintain. For example, Disney's Animal Kingdom's group of Colobus monkeys, *Colobus guereza kikuyuensis*, shifted much more readily once the following components were added to the holding facility: an overhead transfer chute, increased space for subordinate animals, additional perching, and additional visual barriers.

An animal caretaker who feels safe in a well-designed facility is less likely to reinforce charging or aggressive behavior inadvertently by flinching in response to the animal's rapid approach. By contrast, an animal caretaker working with an ape through a large-gauge mesh barrier may be understandably wary and react when the animal moves suddenly, thus actually encouraging the animal to be grabby and aggressive.

Many animal facilities were not designed to facilitate safe interaction between an animal and an animal caretaker. Facility modifications may be necessary when training begins and can range from simple and inexpensive to complex and expensive. A few examples: (1) a panel of smaller-gauge mesh can be attached over larger-gauge mesh, thus creating a safe

Fig. 26.3. (*A*) Specially designed crates for large cats (*Panthera*) in an off-exhibit area. (*B*) Small "flap" door allows safe access to cat's hindquarters for administering hand injection, taking rectal temperature, and drawing blood. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

training area.; (2) a crate or restraint device can be added to allow the animal caretaker to have safe access to the animals; and (3) small doors or openings can be added to a crate to allow the animal caretaker safe access to a particular part of the body (see figures 26.3a and 26.3b).

In her book *Thinking in Pictures*, Grandin (1995) describes how even well-designed facilities can be misused if the animal caretaker is not sensitive to an animal's behavior and needs. Animal caretakers who think that working with animals is a contest or a test of wills, or that there are "winners" and "losers" during the training process, do not maximize the potential for a good training program or provide the best care possible for those animals.

HOW TO TRAIN

Historically, training of mammals has focused on marine mammals and elephants (see Mellen and Ellis 1996 for a review). As we have illustrated in this chapter, training techniques have now been applied successfully to a wide variety of mammalian species. What follows is a description of the steps a caretaker takes to train a behavior. First, we describe the "tools" a caretaker needs to begin training. We then provide an example of training a husbandry behavior by describing one approach used in training a tiger to enter a crate at the request of the caretaker.

HOW TO TRAIN: TOOLS/TECHNIQUES USED IN TRAINING

Before an animal caretaker begins a training session, he/she must have a substantial background in and a key understanding of the components of effective training. These include knowing how to develop a training plan, knowing how to develop a positive relationship with an animal, and understanding the concepts of baiting, desensitization, successive approximations, shaping, and targeting.

Creating an environment that is both safe and comfortable for caretaker and animal is a critical first step to the successful training process. Many older facilities were not designed for training sessions, but some newer exhibits include an area designed specifically for this purpose. In fact, some facilities (e.g. Denver Zoo, Colorado, and Bronx Zoo, New York) have designed husbandry training areas into the exhibit, providing opportunities for visitors to view training sessions.

Many animals may have made positive associations with their caretaker and approach them readily. In some cases, however, an animal may have an initial tendency to flee when approached by humans. Teaching the animal to accept food from the caretaker can surmount this tendency. Alternately, an animal can be trained to go to a particular location (away from the caretaker) to receive a food reward. In order to train an animal effectively, the trainer needs to find a positive reinforcement that the animal is motivated to receive. Food items are most commonly used, although other reinforcement can work; e.g. rhinoceroses are often reinforced during a training session by rubbing/scratching the belly area. When food is used, usually the animal receives a portion of its daily diet or the daily diet in its entirety (divided into many portions) in the form of rewards. Sometimes it may be necessary to change the presentation of a food item (e.g. meat chunks instead of ground meat) or add special items to the diet (e.g. chicken). Food that is consumed by the animal must be factored into its overall balanced diet and not result in an animal that is overweight or a diet that is nutritionally incomplete.

If the behavior that is being trained requires precise timing or if, due to limited access to the animal, there is a delay in the delivery of reinforcement, it may be necessary to condition a bridging stimulus (process described earlier). The type of bridge selected should be something that is distinct, consistent, easy for the caretaker to use, and appropriate for the species.

In all training, a goal behavior must be selected and clearly defined. Once the aim of a training exercise is selected, progress is accomplished in a series of small steps toward the goal behavior. Correct responses, usually successive approximations toward the goal behavior, are selectively reinforced, while incorrect responses are ignored or punished. Once the animal performs an approximation without hesitation, the caretaker moves on to the next approximation. This process is also referred to as "shaping." We recommend that the caretaker write down his/her intended approximations, i.e. create a training plan. The training plan is a guide for the shaping process. Unfortunately, since animals do not read the training plan and the process does not always follow the trainer's initial intended path, trainers must be willing to modify their training plans to accommodate the animal. Also, an animal may "skip" a step or stay at a particular approximation for a long period of time. This variation is what makes training interesting to some people and frustrating to others. The most important thing is for caretakers to be flexible, prepared, and focused on what behavior they are reinforcing.

Various training techniques can be used to encourage an animal to offer a desired behavior. One popular method is using food to lure an animal to a desired location. This technique is called baiting. Another is initially teaching an animal to touch a part of its body to an object. The object can then be moved to encourage the animal to move in a certain direction or held still to encourage the animal to hold in a steady position. When used in this manner, the object is referred to as a "target." Targets can take on many forms, from a spot painted on the wall/floor, a pool float on a stick, or a caretaker's hand or foot (fig. 26.4).

Fig. 26.4. Asian small clawed otter (*Aonyx cinerea*) being trained in an off-exhibit area using a target. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

As training progresses, the animal begins to exhibit the desired behavior and offers that behavior in response to some sort of stimulus. The stimulus could be the presentation of the target, the sight of the caretaker, or a certain location in the enclosure where training typically occurs. The current stimulus, or "cue," for the behavior may be sufficient, or a new cue may need to be trained. In order to change the cue for a trained behavior, the new cue must precede the old one. After a number of repetitions, the animal begins to associate the new cue with the behavior being trained, and the old cue then is gradually removed, or "faded." Once the requested behavior is exhibited reliably in response to the cue, the behavior is considered under "stimulus control" (see table 26.1 for details).

The completion of a behavior is not the end of the training process. Typically, multiple caretakers need to be able to request the behavior of the animal. We suggest that a particular behavior is not truly trained until a number of caretakers can successfully request a behavior. Training additional people can be as challenging as the task of training the animal in the first place. In some cases, the new caretaker may have to spend some time just creating positive associations with the animal. The key to using multiple trainers is consistency. New caretakers need to provide a cue that is the same as that used by the initial trainer and reinforce the correct behavior criteria. It is during these times of adding new caretakers to the training process that a trained behavior may be at risk to regression. Regression is when a conditioned or trained behavior reverts to a previous stage in the learning/training process. If anticipated, the regression can be short-lived and manageable. The caretakers need to communicate with one another and observe each other during training sessions to achieve the consistent environment that is necessary for success.

An animal's motivation can also influence the success of a training session. A monkey that may have accepted raisins at the beginning of a session may begin dropping them and wait for a different reinforcement by the middle of a session. Dolphins that generally are very attentive may completely ignore a trainer for a period of time during a particular session, if it coincides with the breeding season. Using a secondary reinforcement, such as scratching or rubbing, will depend on the relationship the animal has with a caretaker. For example, a rhinoceros may be responsive to scratching from one caretaker, but not another.

The size or value of reinforcement is also a factor. This is termed magnitude of reinforcement (see table 26.1). An animal's performance of a certain behavior may either decline or be enhanced if the quantity or type of the reinforcement is changed. Caretakers always need to be aware of the signals that an animal may be sending them and to evaluate whether the reinforcement offered is "worth it" to the animal.

EXAMPLE OF TRAINING: TIGER VOLUNTARILY ENTERS CRATE ON CUE

Training a tiger, *Panthera tigris*, to enter a crate voluntarily on cue starts with creating an appropriate working environment (see above). The training scenario described here is in a "protected contact" setting, meaning that there is a physical barrier such as a welded-wire-mesh screen between the animal and the caretaker. The animal caretaker begins by spending time with the cat, and creates a positive association between them by feeding the tiger and providing enrichment.

Eventually, the cat associates the animal caretaker with the positive events and begins approaching the caretaker, i.e. moves toward the mesh door when the caretaker is standing there. The caretaker then begins feeding the cat by dropping small chunks of meat through or under the mesh door. With the caretaker in a crouched position at the mesh gate, the cat eventually stays at the cage front and calmly eats multiple pieces of meat.

The caretaker then introduces a meat stick, a 0.6-m length of fiberglass rod; chunks of meat are speared on the end of the stick and safely passed through the mesh to the tiger. Once the cat takes chunks of meat from the meat stick without hesitation, the caretaker passes meat through the mesh gate at multiple locations. Eventually, the caretaker stands up and expands the areas on the mesh gate where meat is passed to the tiger. To shape the desired behavior, the caretaker then uses the meat stick with a chunk of meat to lure the cat to walk to various locations. During the phase when the animal is learning a behavior, the caretaker reinforces every correct response (continuous schedule of reinforcement). After the cat has mastered that behavior, it does not have to be reinforced every time (intermittent schedule of reinforcement).

The next step in training is for the caretaker to train the cat to enter a crate (see figures 26.3a and 26.3b for illustrations of a well-designed crate). The crate's primary function is to facilitate safe access to the cat. To encourage the tiger to enter the crate, the caretaker begins feeding it near the entrance to the crate and then tosses meat into the crate. (Again, all this training is done with a stout mesh barrier between cat and caretaker.) When the cat begins eating multiple pieces of meat that were tossed into the crate and stays in the crate even momentarily, the caretaker begins standing in front of the crate and uses the meat stick to deliver meat directly to the cat. At this point in the training, the caretaker's goal is for the cat to enter the crate on cue with its whole body. A next step is to close the guillotine door on the crate. In order to close this door, the caretaker begins with the cat outside the crate, reinforcing the cat for calm behavior by opening and closing the door. The cat is then asked to enter the crate with the guillotine door partially closed. The cat is reinforced for remaining calm inside the crate and for allowing the door to be opened completely. This technique allows the cat to experience door movement without being closed in. Next, the cat is reinforced for remaining calm while the door is completely closed. If it becomes nervous, the caretaker releases the cat by opening the door. The goal here is for the cat to be very relaxed while the door is closed.

MISUSE AND OVERUSE OF TRAINING

Like any tool, training can be misused and overused. While many behaviors can be trained, each animal caretaker should evaluate whether a particular behavior is appropriate to train. For example, extensive husbandry training of juvenile male hoofstock may result in these males imprinting on their human caretaker. At sexual maturity, these males may direct significant aggressive behavior toward humans as a result of that early training (J. Kalla, personal communication).

Moreover, some species of hoofstock are extremely flighty, are housed in large groups, or are difficult to access safely due to the facility design. Caretakers may need to evaluate the costs and benefits of taking the time to train one of these animals when injured or ill to cooperate in a procedure versus using physical or chemical immobilization (e.g. darting the animal). They also need to evaluate the relative value of training hoofstock to stand for yearly vaccinations (i.e. voluntary hand injections) versus using more traditional physical methods of capture. Every husbandry and medical procedure has inherent costs and benefits associated with it as well as multiple solutions. Training is just one of many tools that can be considered as a solution. It may be in the animal's best interests *not* to be trained for all situations.

Animals involved in training programs can sometimes be overfed if too many additional or high-calorie items are added to the diet as reinforcers. An animal's total intake should be evaluated so as to provide a complete and balanced diet. Animal caretakers may reduce an animal's diet in order to motivate it for training, but the animal's nutritional needs and body composition need to be considered. Using food as reinforcement is appropriate; creating stressed or underweight animals is not. In fact, most animals do not need to be food deprived to increase motivation. Use of preferred diet items usually suffices.

Caretakers need to be aware of and take responsibility for the behavior the animals are learning. In some cases, caretakers may inadvertently reinforce an undesirable behavior; e.g. throwing a flake of hay to an elephant that is banging on a door may result in the elephant's stopping the door banging, but it has learned that door banging is followed by a flake of hay. In this example, both animal and caretaker are being unintentionally trained.

Training as a management tool is most effective when well integrated into other components of animal care. The Association of Zoos and Aquariums (AZA) Animal Welfare Committee has focused on 7 components of animal care: veterinary care, nutrition, husbandry, habitat, research, enrichment, and training. If an institution has progressive programs in each of these areas *and* each of these programs is integrated with others (i.e. the nutritionist works with the curator, the curator with the veterinarian, etc.), the welfare of the animals at that institution is enhanced. The key here is effective partnerships and communication among the animal care teams (Barber and Mellen 2004).

DEVELOPING A SELF-SUSTAINING HUSBANDRY TRAINING PROGRAM

If asked the question, "Do you have a training *program* at your facility?" a zoo or aquarium director might remember a diabetic monkey that has been trained to take insulin injections and thus answers, "Yes, we have a training program." But what happens if the animal caretaker who trained that monkey leaves the zoo? Does the ability to inject the monkey leave with that caretaker? If a director were asked to characterize his/her training program, what would that include?

The point here is that isolated training *events* do not constitute training *programs*. Similarly, simply identifying a staff *position* (e.g. Enrichment and Training Coordinator) does not constitute a *program*. In contrast with training, other programs, such as veterinary care or nutrition, are not implemented in a haphazard way. Veterinary care and nutritional plans are integrated programs, and there is an expectation at the director, curator, and animal caretaker levels that animals will be medicated and fed in a prescribed and consistent manner (Shepherdson and Carlstead 2000). Most zoo training programs, however, are not yet integrated or self-sustaining; i.e. they are dependent on a few highly motivated animal caretakers. And finally, some current training programs lack strong leadership or direction (i.e. "What is our goal?"). Zoos and aquariums that have small sectors with successful training do not have successful *programs*. A successful program is goal-oriented, self-sustaining, and integrated into daily management of the animals—just as veterinary care and adequate nutrition are integrated into daily management. We believe that a successful husbandry training program is dependent on 3 important components: a solid framework, staff training, and, perhaps most critically, strong leadership (MacPhee and Mellen 2000).

When designing training programs, it is important to follow a process that provides a map to the destination. A process or framework that can be used to create and maintain a training program at a zoo/aquarium is described below. The goal of this framework is to provide these facilities with various concepts to consider in developing a training program. All programs include different species, staffing, and facility design. There is no simple standardized approach to training; each facility needs to design a process that works best for it. This framework is taught as a key component of the AZA course Managing Animal Enrichment and Training Programs.

FRAMEWORK

Described below is a framework (fig. 26.5) that can be used to develop and maintain a successful (goal-oriented, self-sustaining) husbandry training program. It can serve as a potential model for institutions to review, refine, and modify to fit their own needs. We call this the SPIDER model or framework, because the first letter of each component spells out the word *spider* (see MacPhee and Mellen 2002 for details).

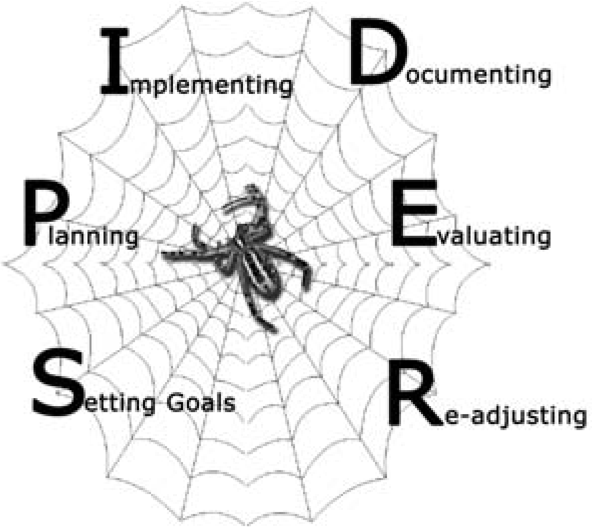

Fig. 26.5. Framework for developing and maintaining a husbandry training program. This framework is sometimes called a SPIDER framework, because the first letters of each component spell the word *spider*. (Courtesy of Disney's Animal Kingdom. Reprinted by permission.)

Setting goals for training animals. Given limited time and resources, an important first step in developing a training program is for key decision makers to prioritize the institution's training needs. An initial focus may be to get animals to shift reliably on and off exhibit. A next step might be to focus on creating a list of medical procedures animals can be trained to accept. When Disney's Animal Kingdom was opening, the animal care staff (curators, zoological managers, animal caretakers, behavioral husbandry team, and veterinarians) developed a "top 10" list of animals they hoped, due to difficulty with anesthesia, they would not need to immobilize for husbandry or medical procedures (e.g. elephants, okapi, giraffe, hippopotamuses, rhinoceroses, crocodiles, and several bird species). The "top 10" list enabled staff to prioritize husbandry behaviors to be trained for these species and to identify roles and responsibilities among the staff in developing training plans. Examples of specific training goals included training animals to stand on scales for weighing, targeting to allow for body inspections and injections, and targeting to allow for collection of blood, saliva, and urine for medical tests and physiological studies. The first gorilla born at Disney's Animal Kingdom received all her infant inoculations while being held by her mother; her mother had been trained to hold the infant close to the mesh and to allow the injections.

Planning for training animals. A training program must have an agreed-on process for developing and approving training plans. Animal caretakers are the staff members who typically initiate these plans, which include describing a behavior to be trained (and why that behavior is being trained), outlining the specific steps to shape that behavior, including necessary resources (e.g. targets, clickers), and providing a description of cues and criteria. In an effective plan, the training techniques selected are appropriate for the species, the plan is written with safety in mind, and the jump from each approximation makes sense to the animal. Caretakers then typically distribute the written plan to area managers, who review and approve it. Area managers can facilitate the training process by assuring that time is allotted for training sessions and that there are clear role assignments for staff.

Implementing training. Since a primary consideration in actual training is consistency, a key component of a training program is a process by which the roles and responsibilities of all involved staff are detailed. Ideally, a single animal caretaker works on a particular behavior throughout the behavior acquisition process. Once trained, multiple animal caretakers then can maintain the behavior. Since some animals can tolerate multiple trainers, while others cannot, good communication among multiple animal caretakers is critical to success, e.g. having written descriptions of cues and criteria for the trained behaviors. Also important are records of the status of each behavior being trained and of the successes and challenges.

Documenting training. Many zoos and aquariums have processes in place for planning and implementing training sessions. However, they are not as consistent in documenting the outcomes of each training session or in assessing the general success of the training program.

Having a written account of the training process is important, in terms of tracking both the animal's and the animal caretaker's progress. A written record becomes an "institutional memory" of the training process. It also helps animal caretakers make decisions about reinforcers used, time of day to train, and specific techniques used (e.g. baiting, shaping). If a trained behavior has regressed, then the training plan and session documentation can be used as a guide for training the behavior again or in determining why the behavior was extinguished. Training documentation may be a resource for other animal caretakers training the same or similar behaviors, and the animal's training history can be shared if it moves to a new facility.

The format for training session records depends on what information is necessary to evaluate training progress over time. Documentation should include time of day training occurred, name of animal caretaker, description of the animal's performance during that training session, description of any aggression toward animal caretaker, record of latency to respond (i.e. amount of time between presentation of cue and behavior performed), record of reinforcement used, and assessment of progress toward the training goal (for samples of training documentation, see Ramirez 1999 and MacPhee and Mellen 2002).

Evaluating training. The evaluation of training involves the routine discussion of progress toward goals with team members and managers. It also involves looking at the daily documentation and seeking trends in the records of an animal's performance over time, including progress toward goals, changes in aggression, whether patterns of aggression are associated with particular animal caretakers, and how long it takes to train a particular behavior. The goal of evaluation is to obtain a clearer idea of what the issues are, as well as potential solutions for improving future training sessions.

Readjusting training. Based on a review of the training plans and documentation, and an evaluation of trends in the records, it may be necessary to readjust a training plan. Key issues include determining whether there are any safety concerns and progress toward the goal. Programs that are very work intensive for the staff or require many resources may not be cost effective. After reviewing the documentation for trends over time (evaluation), training plans are then fine-tuned (i.e. readjusted), and the cycle continues (setting new goals, developing revised plans, implementing new training, etc.).

On a broader scale, we recommend that animal caretakers and managers routinely review and assess an area's training program. Some good questions for such a review include:

- What are our specific training goals?
- Which of these goals have been achieved?
- Which have not been achieved?
- For those goals that have been achieved, what has been the key to success?
- Are there any commonly occurring roadblocks to success?

Area supervisors play a critical role. Managers who believe in the value of training as an animal management tool and have a clear understanding of the technical skills required are key to the success of a husbandry training program.

The result of using this framework is a program that is proactive and holistic. The process is cyclical, facilitates sustainability of the program over time, and allows the program to evolve. This framework can work for any institution regardless of size, but the specific methods of how a particular element is achieved may differ.

STAFF TRAINING

Even with a framework in place, a training program will not be successful without a skilled staff to implement it. There is a plethora of written material about learning theory, and many organization courses and volumes of written materials describe species-specific training plans and discuss the training of specific behaviors. However, reading, attending conferences, and watching DVDs on how to train may not provide animal care staff members with all the tools they need to be successful trainers. Animal training is a technical skill that requires opportunities to practice, access to skilled coaching, and feedback on progress. As discussed previously, if done poorly, animal training can be detrimental to an animal's well-being.

Leaders should not direct inexperienced staff to train animals without proper instruction and support. New trainers need an open learning environment that encourages them to continue to improve their skills and to have a positive attitude toward the animal's success in being trained. Even in an established training program, a process for integrating new trainers into a team is critical for the program's integrity over time. Care needs to be taken to transfer information about training plans to new staff members so that the "institutional memory" will not be lost. An inconsistent team may lead to inconsistent animal responses and behavior, which may in turn result in inconsistency in the animal's training performance.

Many zoos and aquariums contract with consultants to facilitate the integration of training into their institutions. The training framework presented above can be a useful tool to assist directors in determining where their program is in most need of assistance. The framework can serve as a "needs assessment" to make the best use of a consultant's expertise. For example, with a framework in place, the consultant may be directed to focus not only on a particular training project and the animal's progress toward the training goal, but also on the development of the staff and its knowledge and skills in regard to training techniques. Most important, the framework provides a foundation within which consultants can work to assure that their efforts will be sustained over time and that their fee is of value to the institution (MacPhee and Mellen 2000).

CONCLUSION

The effect of training on animal welfare is still speculative and a source of continued debate. Future research may be able to assess the impact of training styles on cortisol levels, behavior, and reproductive function, traditional methods of assessing welfare in captive animals. The results of such studies could lead to improved selection of behaviors to be trained and improved approaches to training those behaviors.

Most institutions continue to increase their focus on using husbandry training as part of the daily care of their animal collection. The behaviors trained and the species being trained continue to grow and evolve. The goal of many institutions is to promote training as an integral tool for daily animal care. However, husbandry training, while a critical tool in animal management, is only one of many tools we use to manage captive animals and to enhance their welfare. Solving animal management problems may include anything from capture or restraint, to full voluntary cooperation of the animal, to creative exhibit design. A future goal for managing animals in captivity may include providing animal care staff with problem-solving skills as well as animal management skills so they may more effectively choose appropriate animal care tools from their repertoire of animal management techniques.

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APPENDIX 26.1

Using Natural History and Individual History to Develop Training Plans

Understanding the natural history and individual history of an animal is the first step in developing a training program for a particular animal. These questions about natural history, individual history, staffing, and facility design are meant to assist in compiling information about the animal to be trained. This list (from the Web site www.animaltraining.org) is not exhaustive, but the answers to these questions will help enable an animal caretaker to identify and develop the most appropriate goals and training methods for a particular animal.

1. What is this animal's history? Was this individual parent-raised or hand-raised? Does this animal have any behavioral problems or behavior peculiarities? Has this animal been trained to perform any previous behaviors? Describe the cues, criteria, bridging stimuli, reinforcements (both food and nonfood), and reinforcement schedules that are used. If possible, describe techniques that were used to train previous behaviors. *The answers to these questions will provide the animal caretaker with some guidance in selecting the most appropriate training goals and training methods for an individual animal.*

2. Does the species inhabit primarily arboreal, terrestrial, or aquatic environments, or does it switch between them at times? *This answer will provide the animal caretaker with an idea of how an animal moves through its environment, where it is most comfortable, and some potential constraints in selection of behavior to be trained* (*e.g. a tree kangaroo* [*arboreal animal*] *may be more easily trained to station off the ground*).

3. How does the animal behave in response to changes in temperature and weather? What is the optimal temperature for this animal? *This answer will provide the animal caretaker with an understanding of what these behaviors* (*i.e. responses to cold, heat*) *look like and allow animal caretaker to interpret and respond appropriately to the animal's behavior.*

4. In the wild, when is this species most active (diurnal, nocturnal, crepuscular)? Are there times of the day when this animal seems most receptive to the animal caretaker? *When the animal is most active and receptive to the animal caretaker may be the best time of day to train, especially at the start of your program. As the animal becomes more consistent in its behavior and responsive to the animal caretaker, the session times can be manipulated.*

5. What does it look like when this animal is comfortable/calm? What do fearful behaviors look like in this species? How does this animal respond when stressed? *This answer will help the animal caretaker to be able to interpret the animal's behavior and react appropriately. A situation where this understanding is most helpful is when an animal caretaker is habituating an animal to new stimuli. Knowing what the animal looks like when stressed, frightened, or calm will allow the animal caretaker to be able to make judgments about whether an animal is ready to move to the next approximation in a training process.*

6. What are its primary sensory modalities (e.g. sight, sound, smell)? *Answers to this question can help animal caretakers in the selection of their cue, bridge, target, and other training tools by making the most appropriate choices for a species* (*e.g. an auditory cue may be more effective for a rhino* [*with relatively poor eyesight*] *than a visual cue*). *In some cases, habituation/desensitization may be necessary when introducing a new cue. Some auditory cues or visual cues may be frightening to some animals.*

7. Is the animal naturally social or solitary in the wild? Is the animal managed in a social group or as an individual? What are this species' primary social behaviors, and what do they look like (e.g. aggression, courtship, affiliative behavior)? Can the animal be easily separated from the social group? How does the animal behave when

separated? How does the rest of the group behave when that animal is separated? *Understanding the social structure and how the animal caretaker fits into the structure can assist the animal caretaker in understanding and responding appropriately to a variety of responses by that animal and in the selection of different training techniques. For some animals, training them with other animals will increase their comfort level and possibly facilitate progress; for other animals, having conspecifics with them could cause distractions and possibly slow down their progress.*

8. How does this animal currently respond to its caretaker (both during animal caretaker–solicited interactions and outside of planned interactions)? To new staff members? To veterinarian? To visitors/guests/strangers? Is there any noticeable reaction to a particular gender (men versus women)? *Understanding how an animal currently responds to the animal caretakers and other people that work within the area can provide information on how you can leverage the relationship that currently exists in your program. If an animal has a positive relationship with caretakers, this may assist in achieving some goals. Some relationships may first need to be built in order to make progress in training a particular behavior.*

9. What does the species feed on in the wild? How does this species procure and process its food? What is this individual animal's normal diet? What are the food items that seem to be the most desirable to this individual? What is the feeding routine for this animal? *Understanding how an animal responds to food and how it processes food can assist animal caretakers in interpreting and responding appropriately to the behaviors that the animal displays. Knowing what food items are more favorable can provide insight into what food items may make good positive reinforcement.*

10. What is the animal's primary function in the collection (e.g. breeding, exhibition, or educational programs)? What is this animal's normal daily routine? What are the routine husbandry procedures that are desirable for this animal to be able to do? *Knowing the primary function the animal has in the collection can assist animal caretakers in developing appropriate behavior goals and utilizing the most appropriate training techniques. Animals whose primary function is breeding may not be great candidates for some training methods that require a lot of hands-on work. Knowing the daily routine can help animal caretakers determine what behavioral goals would be good to train, to have the animal cooperate with day-to-day care. Knowing what the animal's routine is can assist the animal caretaker in understanding what the animal's expectations are, where those expectations can assist in achieving a training goal, and where those expectations may hinder achieving a goal.*

11. Are there any medical conditions common to this species that need to be monitored? Could training facilitate this monitoring? What procedures are necessary for an annual exam? Does this individual animal have any medical problems or area on the body that is particularly sensitive to touch? How often will procedures need to be done (e.g. daily insulin injections versus yearly vaccine)? *The answers to these questions will assist the animal caretaker develop husbandry goals, train behaviors that potentially could allow medical procedures to be performed without relying on heavy restraint and immobilization, and create program goals that are responsive to individual animal's needs.*

12. Are there specific pieces of equipment/facility design considerations that are necessary to perform procedures? Describe all aspects of the equipment (what does the equipment look, sound, smell, feel like?). *The answers to these questions can allow the animal caretaker to prepare for any additional training approximations that are necessary. These approximations could be related to the facility and/or be necessary for habituation to equipment used for a procedure (e.g. if an animal is being trained to accept an ultrasound procedure, training should involve habituation to the equipment and personnel that will be present for the actual procedure*).

Facility considerations: many of our facilities have not been constructed with our training goals in mind. Questions 13–17 can assist in developing a facility design or facility modification that is the most functional for a training project, or the development of a training plan that takes the facility design into consideration.

13. Is there a space that is safe for the animal caretaker, veterinarian, and animal to interact? Is this a space that the animal can have easy access to?

14. Does the design of the facility cause encroachment into the animal's personal space? *Some animals may initially be very sensitive to the close proximity of an animal caretaker. If the initial training is done in a space in which the animal is more comfortable, the training may be more successful. Eventually, sessions can usually be moved to other areas.*

15. Does the facility allow animals to be easily separated from one another or moved easily?

16. Is the location of cage furniture a hindrance/help to the training process?

17. Is the facility designed in such a way that an animal has the opportunity to habituate to potentially frightening areas or equipment (e.g. acclimate to squeeze chutes, working panels)? Are there ways to limit unpredictable distractions (e.g. high-traffic areas)?

Staffing considerations: questions 18–20 can assist in the development of a staffing plan that will support your training program.

18. Who will be doing the training? How many people does it take to conduct a training session? How often will the training sessions take place? When will the training sessions occur?

19. How will the staff be trained, and how will new animal caretakers be integrated into the training team?

20. In addition to the staff in the area, will additional assistance be necessary for the training (veterinarians, veterinarian technicians, or interns)? If so, how often?

Any other considerations?

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27

Applying Knowledge of Mammalian Social Organization, Mating Systems, and Communication to Management

Ronald R. Swaisgood and Bruce A. Schulte

INTRODUCTION

Understanding mammalian social organization is not a simple matter. Casual observations in nature often overlook the subtle behavioral interactions that give away the true organization and complexity of social dynamics (Kleiman 1980, 1994; Wielebnowski 1998). A species can express a variety of forms of social organization that are dependent on prevailing ecological, social, and demographic conditions (Lott 1991), leading to numerous questions regarding captive animal management. Which one of these forms should captive managers emulate? How can we be sure that we know the various social systems that occur in nature, especially when we know so little about what many zoo-bred species do in nature? Should the goal always be to look to nature for guidance, or are there circumstances where nature can be "improved on" to meet captive breeding goals? Is maximizing reproduction always the best goal? What about the needs for animal welfare, conservation education, and public perception? Can one management plan fit all these conflicting needs?

Numerous excellent reviews characterize the evolution and ecology of social organization (Terborgh and Janson 1986; Lott 1991; Berger and Stevens 1996), and we will not duplicate those efforts here. Instead, we focus on practical aspects of problem solving, and managing mammals' social environment in captivity. We start with the presumption that mimicking nature—or at least understanding it—is important, but do not recommend adopting the simplistic philosophy that "everything wild" is best (see also Veasey, Waran, and Young 1996). Even if we wanted to follow this model blindly, "the wild" is not monotypic but instead is characterized by exceptional diversity and social flexibility. Indeed, this flexibility provides the raw material for animals to adapt to various social circumstances in captivity, e.g. becoming more or less social as the need arises (Berger and Stevens 1996). Moreover, the form that optimal management takes also is dependent on the goals that need to be identified when devising management strategies.

Knowledge of behavioral patterns and "needs" in the wild is frequently used to guide enrichment and breeding programs, with the aim of optimizing welfare and reproduction. Captive breeding contributes to *in situ* conservation when captive-born individuals are successfully reintroduced into the wild. Establishing baseline knowledge about species that are poorly understood and difficult to study in nature also can play a role in *in situ* conservation management. No matter what the goal, however, behaviorists working in captive breeding programs need to draw on their experience with experimental design and hypothesis testing. Although many have advocated a greater emphasis on this approach (Wielebnowski 1998; Swaisgood 2004), controlled studies that systematically rule out alternative hypotheses are notably lacking. Until this approach is adopted wholeheartedly, many management strategies will rely on speculative conclusions, and improvements will accumulate incrementally through trial and error.

GOALS OF CAPTIVE BREEDING PROGRAMS

The selection of a certain form of social organization for a species under captive management is the outcome of several considerations. First, the goal is often to minimize aggression or maximize well-being. Second, the goal may be to maximize breeding, e.g. find the right combination of sex and age classes that get animals breeding. Third, public perception and conservation education goals can affect social housing decisions. For example, a naturalistic social organization may convey a better conservation message, because it displays the animals in a more wildlike state and encourages the animals to perform their natural behavioral repertoire. By contrast, aggression levels may be too high under such natural management, e.g. in the case of multimale groups. In this case negative public perception or welfare concerns may offset the conservation education or other goals. Fourth, the goal may be to retain natural social organization(s) if the animals are to be released back into the wild. Finally, the social organization may simply be the result of logistical or financial constraints, such as the availability of animals or space—although this may often run counter to both animal welfare and education goals, and should be avoided if zoos of the future are to become more than menageries for human entertainment.

The crucial first question to be answered by animal managers is, what is the purpose for maintaining this population in captivity? At one extreme, the animals may be housed for the express purpose of restocking wild populations. Such individuals are a genetic reservoir for reintroduction into areas where the species was extirpated or as augmentation of existing populations that are below carrying capacity due to anthropogenic factors (IUCN 1998). At the other extreme, zoos and aquariums house individual animals in naturalistic groups for long-term display and propagation of the species. These individuals serve as ambassadors for their wild counterparts, providing scientific, educational, and entertainment benefits to humans. Captive management of social organization may be completely different depending on which objective is preeminent. In short, retaining natural behaviors is the *sine qua non* of captive management if the goal is captive release (Rabin 2003), but deviations from the norm(s) in the wild may be necessary to maximize captive reproduction or welfare.

If the objective of maintaining a species in captivity is to establish a viable captive population, then the first obstacle to surmount is to get the animals to mate and bear and rear offspring. Getting them to "do what comes naturally" can be a real challenge, and in some cases—when behavioral husbandry fails—zoo managers must resort to assisted reproduction techniques such as artificial insemination (see Spindler and Wildt, chap. 32, this volume). A secondary, but absolutely necessary goal is to facilitate breeding with the right partners to maintain an optimal level of genetic diversity, necessary to sustain a captive or wild population (see Ballou et al., chap. 19, this volume). In some cases genetic diversity can be augmented by further importation from wild populations, but for rapidly declining populations such removal can compromise population viability. Captive breeding programs today rely on genetic management of the existing captive population to ensure sufficient genetic diversity for the future genetic health of the population (e.g. Species Survival Plans). In practice, this means that managers need to be careful not to rely too heavily on a few "proven breeders" and try to get relatively equal genetic representation from most of the founding population. Breeding in zoos is often meticulously managed to ensure optimal outbreeding (i.e. mating between individuals that are not too closely related), although this is all too often done without regard to behavioral compatibility of chosen partners (Lindburg and Fitch-Snyder 1994; Wielebnowski 1998; Swaisgood 2004). Moreover, studbook-driven breeding management—based solely on mean kinship—may not always lead to optimal genetic compatibility. For example, recent empirical evidence has demonstrated that when animals are given "free mate choice," they may select partners that maximize the genetic viability of their offspring (Wedekind 2002; Drickamer, Gowaty, and Wagner 2003).

MANAGING THE SOCIAL ENVIRONMENT FOR REPRODUCTION

Social organization is the emergent outcome of the patterns of social interactions between individuals (Lott 1991). In practice, categories of social organization are convenient labels for various observed grouping patterns defined by such parameters as the number of adult males and females (e.g. single-male, multifemale groups), the kin structure of members of a group (e.g. matriarchal), retention of offspring (e.g. family groups such as cooperative breeders), distribution of individuals in space (e.g. territoriality), type of social relationships (e.g. dominance), and so forth. Social organization often is considered an attribute of a species, but this broad generalization, ranging from solitary to highly social, belies the intraspecific variability that may be critical to captive management (Kleiman 1980, 1994; Lott 1991). Mating systems—a subcategory of social organization—are considered below.

Several aspects of social behavior and organization are important for captive management, including social density, sex ratio, age-sex composition, and kin structure. A best first approach to captive social environments is often to mimic the social organization(s) found *in situ*. Without a doubt, many captive breeding successes have been realized because information about the social organization in the wild was sought and applied (Kleiman 1980, 1994; Lindburg and Fitch-Snyder 1994; Wielebnowski 1998). For example, zoos are reluctant to house males with dangerous weaponry together in the same enclosure, but there are species where this is appropriate—even desirable—if their males live together in the wild in peaceable coalitions (e.g. male cheetahs, *Acinonyx jubatus* [Caro 1993]). By contrast, female cheetahs are solitary in the wild, and controlled studies have shown that females housed socially with other females display more aggression and behavioral indices of agitation and suppressed ovarian activity (Wielebnowski et al. 2002). Insights from the wild can be crucial for reversing poor captive reproduction. For instance, elephant shrews kept in groups were suffering poor reproduction, until field studies indicated that they were probably monogamous. When managers adopted pair housing, successful reproduction followed (Kleiman 1994).

A long-known principle in the social ecology of animals, the Allee effect (Allee et al. 1949), has simple and far-reaching consequences for captive breeding, but the concept has played a surprisingly small role in animal management for reproduction. The Allee effect states that there is an optimal degree of aggregation of individuals for population growth. Both under- or overcrowding can have adverse effects on reproduction. Most discussions of the Allee effect focus on the benefits of sociality, which, through several mechanisms, gives rise to the phenomenon of conspecific attraction (where animal settlement patterns do not conform to an "ideal free" distribution with regard to resource distribution, and animals actively prefer to settle near conspecifics) (Courchamp, Clutton-Brock, and Grenfell 1999; Stephens and Sutherland 1999). Because the Allee effect influences distribution of animals on the landscape, it also plays a strong role in determining social organization, in particular mating systems.

The application of the Allee effect for captive breeding is straightforward; for each species, we need to find the optimum social density and maintain the animals in the appropriate social environment. Experimental hypothesis-testing approaches to this question are notably lacking in captive breeding programs, although a few retrospective analyses have been illuminating. One of the best of these studies was undertaken with relatively solitary species of lemurs (Hearne, Berghaier, and George 1996). Mongoose lemur, *Eulemur mongoz*, pairs housed near other pairs or males had a 500% higher reproduction rate than those housed in facilities without other conspecifics. Similar, albeit less robust effects were found for black lemurs, *E. macaco*. Of course, the disadvantage of retrospective studies based on studbook breeding records is that we do not know which cues—e.g. olfactory or visual—were responsible for the Allee effect. The now-classic study showing that introducing mirrors can increase courtship in flamingoes underscores the advantage of the experimental approach (Pickering and Duverge 1992).

Some factors affecting social organization may be beyond our control in captivity. The social grouping of many primates has evolved under the forces of predation and competition, notably within- and between-group competition (Pazol and Cords 2005). Most facilities are unlikely to house multiple groups of a species that can interact, go through fission and fusion, and disperse to found new groups. How such species respond to alterations in competitive interactions (e.g. less intergroup and perhaps more intragroup interactions in captivity) may have implications for not only captive housing but management of wild populations facing dwindling habitat. Many mammals show a degree of sexual segregation (Ruckstuhl and Neuhaus 2005). In winter, male bison feed on more abundant foods compared to females and thus forage in different areas (Mooring et al. 2005). Such seasonal variation in social structure for the same proximate reasons is difficult to replicate in captivity, but the same outcome can be achieved (i.e. males and females can be separated at relevant times of the year). Disentangling mechanism from outcome in captive settings can provide a rich arena for scientific study and have potential applications for captive and wild management.

While numerous studies demonstrate that nature is often a successful model for captive breeding, there are also times when we may not wish to follow the example of the wild. For example, naturally occurring reproductive suppression may be undesirable in captive settings where the goal is to attain breeding from as many individuals as possible to maximize reproductive potential and genetic diversity (Anthony and Blumstein 2000). Suppression can be an obligate strategy common in species with advanced sociality (Blumstein and Armitage 1998) or can be facultative, e.g. in response to limited resources (Goldizen 1988, reviews in Solomon and French 1996). In either case, some animals forgo reproductive opportunities in the presence of other, usually dominant, conspecifics. The mechanism can be either behavioral (e.g. mating interference) or physiological (e.g. gonadal activity is shut down), mediated by several mechanisms, including "social stress" and chemical signals. Thus, resources and rank often interact to cause suppression. For example, reproductive success in females can be related to resource availability, since dominant females can often monopolize limited resources that affect their ability to reproduce successfully (Clutton-Brock 1989). Dominant female reindeer had higher reproductive success attributed to greater access to food over winter (Holand et al. 2004). For a breeding program, variation in breeding success is generally unwanted, given the goal of equalizing genetic contributions by members of a small population; thus, alleviating the linear hierarchies may be desirable. In animals with breeding limited mostly to dominant pairs, such as wolves, *Canis lupus* (Mech 1999, 2000), and callitrichid monkeys (French 1997), separating subordinates (usually offspring) from the suppressive effects of dominants will yield more equitable reproduction than replicating the social structure typical in the wild. In addition to these "natural" examples of suppression, suppression also can be the byproduct of unusually high social density. In contrast with the view we express here, others advocate managing the social environment to mimic naturally occurring reproductive suppression despite its effects on genetics and reproductive potential (Ganslosser 1995). Our counterargument is that the rule of nature should be followed only when it fits the goals of the captive breeding program.

Another problem with following the example of the wild too closely is that we often have only limited insights into what takes place in the wild. Ignorance of these nuances can lead to inappropriate captive management, especially for solitary mammals, which are commonly misunderstood and notoriously difficult to breed in captivity. For example, in the lemur case study discussed above, the majority of institutions held mongoose lemurs in the suboptimal single-pair arrangement (Hearne, Berghaier, and George 1996). Why? Field studies suggested that monogamy is common in this species, so single pairs became the standard housing arrangement. Apparently, however, the fact that wild lemurs live in pairs did not mean that they should be housed as *isolated* pairs. While housing solitary or monogamous species in highly social environments is not usually desirable, we often underestimate the degree of communication and contact that occurs among conspecifics in nature. Indeed, *solitary* does not mean "asocial" (Yoerg 1999), and behaviorists are discovering that many subtle but important processes bring solitary animals together. Many territorial vertebrates, for example, prefer to settle and live next to other conspecifics rather than carve out a new territory in isolation from others (Stamps 1988, 2001). Thus, most solitary species live in communities where they know and interact with their neighbors. Managers of captive mammals, therefore, should beware of simplistic interpretations of what *solitary* means. In practice, managers must discover species-specific housing and husbandry practices that yield an optimal level of contact, ideally through controlled studies manipulating both spatial and temporal aspects of interanimal contact. Several examples follow in this chapter, including the management of giant pandas and kangaroo rats, *Dipodomys heermanni*, for mating.

Sometimes the rationale for diverging from wild social organization is less clear, and is arrived at by trial and error. For example, rufous mouse lemurs, *Microcebus rufus*, appear to breed best in pairs despite possessing a promiscuous mating system in nature (Wrogemann and Zimmermann 2001). Is there something that we do not fully understand about lemur mating patterns in the wild, or is this an example of a flexible mating system adapting to the constraints of confinement? Further research would be helpful to clarify the relationship between social organization in the wild and optimal social organization in captive settings.

Often there is more than one way to breed an endangered species. Take the case of the giant panda, *Ailuropoda melanoleuca*: breeding success was achieved via 2 methods, one that mimicked nature and another that diverged from circumstances in the wild (Swaisgood et al. 2006). Giant pandas are relatively solitary in nature, rarely encountering one another outside the brief annual mating season (Schaller et al. 1985). Using this model of social interaction and communication, managers at the Wolong breeding facility in Sichuan, China, developed a management strategy wherein giant pandas were kept alone in separate enclosures and given controlled, episodic opportunities for communication (see below). In contrast, managers at other facilities have successfully bred giant pandas in much more social housing arrangements, where the pair was housed together most of the time (Kleiman 1984; Hoyo Bastien, Schoch, and Tellez Girón 1985). This latter strategy appears successful with individuals of gentle temperament, but can result in excessive and injurious aggression in some animals (Swaisgood et al. 2006). It is worth noting that Wolong, using the more "natural" strategy, has the most successful panda mating program in the world: most animals now mate naturally and the population has expanded exponentially, with approximately 5 to 15 surviving cubs in a given year (Swaisgood et al. 2003; 2006). This indicates that the "mimic nature" model is perhaps best for giant pandas, but the best management strategy varies with species. For example, females of the more social Egyptian buffalo show greater sexual interest in males and increased reproductive performance when held continuously with a bull than when given only brief daily access (Abdalla 2003). Yet, management at the species level often is too broad. As illustrated by the variation in giant pandas, strategy can and should be modified to suit individual animals and circumstances.

MATING SYSTEMS AND MATE CHOICE: EFFECTS ON GENETIC MANAGEMENT

For captive breeding programs, the mating system is a critical component of social organization. Mating systems are determined either by the number of mates per sex (e.g. monogamy, polygyny, or polyandry), by the genetic relationships between mates (e.g. random mating, inbreeding, or outbreeding), or by the combination of the two (see Shuster and Wade 2003 for their 12 categories, p. 368). In small populations—wild or captive—understanding the mating system is of vital importance for conservation (Parker and Waite 1997; Blumstein 1998; Creel 1998; Anthony and Blumstein 2000; Møller 2000; Wedekind 2002). The most significant implication is that mating patterns have a profound effect on effective population size (N_e) and maintenance of genetic heterozygosity (see Ballou et al., chap. 19, this volume). Population size (N) approximates N_e in an ideal population where all individuals mate and partners are chosen at random. When reproduction is skewed in favor of a few successful individuals and other individuals fail to breed, N_e can be a fraction of the actual N. Reproductive skew tends to be least in highly promiscuous systems, moderate in monogamous mating systems, and greatest in polygamous systems (N_e declines dramatically) (Parker and Waite 1997). Consequences of small N_e can be severe for genetic diversity and population persistence. As heterozygosity is lost, the effects of inbreeding depression increase, usually resulting in lower population viability and increased population susceptibility to environmental variation.

Knowledge of mating systems in nature can be important for conservation management. The mating system is often thought of as a species attribute (Emlen and Oring 1977), but a single species can in fact exhibit several types of mating systems under varying social and ecological situations (Lott 1991). This flexibility is good news for *in situ* and *ex situ* management, because these influencing factors can be manipulated to encourage mating systems that will equalize reproductive contributions by individuals or meet some other conservation goal. A more direct way to reduce reproductive skew in small populations is to remove those individuals that are winning more than their share of reproductive opportunities. At the metapopulation level, studbook managers can remove these overrepresented individuals from breeding recommendations, while at a single facility, dominant individuals can be removed from a group (Alberts et al. 2002).

Within mating systems, both males and females can pursue different mating strategies, which can be loosely defined as the behaviors employed to find, choose among, and win access to potential mates. In nature a major determinant of mating strategies is the spatial and temporal distribution of receptive females (Emlen and Oring 1977). Generally, males compete directly for females that live in social groups and have predictable estrous periods (Clutton-Brock 1989). Male dominance hierarchies are common where this strategy prevails. However, when females are relatively solitary and widely dispersed, searching and "scramble competition" often characterize the male mating strategy (Schwagmeyer 1995). In such species at least 2 factors influence male mating success: (1) occupying a large home range may provide access to estrous females, and (2) fighting ability (e.g. body size) may determine which males able to locate estrous females actually obtain matings (Sandell 1989; Fisher and Lara 1999). Spatial defense and female defense strategies, however, lie on a continuum, and both territoriality and dominance interactions can be at play simultaneously in determining the mating strategy (Lacey and Wieczorek 2001). Resident males may have an advantage, but other males at times may compete and win access to the female. The existence of male-male competition for access to females does not nullify any active role the female may play in choosing her mate. She may passively accept the winning male as her mate, or she may choose to reject one male in favor of another. There is also the possibility of indirect choice (Wiley and Poston 1996). For example, a female may advertise her reproductive state to recruit males and incite competition, ensuring that she mates with the best available male without actively having to choose among them (Cox and Le Boeuf 1977; Lott 1981).

Most mammals are polygynous; thus, females tend to be the choosier sex (Andersson 1994). Females of some species may procure important nongenetic resources from mating partners, such as nuptial gifts or paternal care, but in mammalian species this is not usually the case (Clutton-Brock 1991; Andersson 1994). Thus, genetic benefits have played a major role in the evolution of mate choice mechanisms. Genetic benefits may be based on arbitrary female preferences that confer advantages to offspring because they are attractive to the opposite sex, but have no effect on survival or other measures of fitness (Fisher 1930). By contrast, the "good genes" hypothesis suggests that female preferences are for heritable male traits correlated with viability (Hamilton and Zuk 1982; Andersson 1994; Zahavi and Zahavi 1997). In support of this hypothesis, female preferences often are based on condition-dependent traits, which are expressed in more exaggerated form in males in better condition, e.g. tail length and plumage color in birds, comb size in jungle fowl, and antler size in cervids. Maintenance of these static displays is energetically costly, preventing low-condition males from bluffing higher levels of viability. The expression of such viability signals may indicate a male's ability to extract resources efficiently, ability to win access to resources in contests with other males (competitive ability), or level of resistance to local pathogens. Thus, condition-dependent signals that are correlated with overall health and vigor are likely the result of many interacting factors, including the male's genetic makeup and prevailing local conditions. To the extent that these traits are heritable, female preferences for males with exaggerated condition-dependent signals may confer enhanced viability to offspring.

Mate choice can have important consequences for conservation breeding, because it can reduce breeding altogether, in addition to exacerbating reproductive skew. The exact nature of the problem depends on how females (or, less frequently, males) go about selecting a mate. If females have threshold criteria for certain male qualities, they may forgo breeding entirely if none of the available males meet these criteria (Anthony and Blumstein 2000; Møller 2000). By accident of sampling error, small founding populations may be composed of females that have above-average thresholds or males that have below-average attractiveness. If male cues are condition dependent, the captive environment may not provide the needed resources for their full expression, worsening the problem. Also, females may use a "best of *N*" sampling rule, choosing to mate with the best male after they have sampled a certain number of males. Under this scenario, females in captivity may be exposed to too few males to carry out their sampling regime and choose not to mate, regardless of the quality of the available male(s). Unknown is the extent to which these choice mechanisms may contribute to the frequent mate "incompatibility" found in captive environments. Generally speaking, the more intensely sexually selected the species (e.g. as evident in sexual dimorphism or dichromatism), the greater the impact, and the larger the founding population will need to be (Møller 2000).

When female mate preferences are similar, a few males that score high for preferred female traits will obtain most of the matings, which will further reduce N_e. This is the case for condition-dependent traits correlated with overall vigor, where all females should prefer the same males—those with the most exaggerated sexually selected signals. However, female choice also may be based on genetic compatibility, wherein certain allelic combinations yield higher fitness in offspring (Grahn, Langefors, and von Schantz 1998; Wedekind 2002). The simplest case is inbreeding avoidance, which promotes heterozygosity and attendant positive consequences for fitness and lessens the probability that deleterious recessive homozygous alleles will be expressed (Frankham 1995). Heterozygosity at the major histocompatibility complex (MHC), which controls pathogen resistance, appears to be the specific target of some mate preference decision rules (Penn 2002). Females of several species prefer to mate with males that differ from them at MHC loci, and offspring that are MHC heterozygotes attain higher fitness. Because different females select different males based on genetic compatibility, reproductive skew is not nearly as pronounced as when all females have identical preferences.

As is so often the case in conservation behavior, practical application lags far behind the development of theoretical implications (Swaisgood 2007). While there is a long history of manipulating mate choice to test behavioral ecological hypotheses (Andersson 1994), there are perhaps only 2 examples of manipulating choice for conservation breeding. In one example chemical signals for mate choice were manipulated in the threatened pygmy loris, *Nycticebus pygmaeus*, to encourage females to mate with specific males chosen on the basis of optimal outbreeding by studbook managers (Fisher, Swaisgood, and Fitch-Snyder 2003b). Theory suggested that females should prefer familiar-smelling males, because in nature females of this relatively solitary species could assess male quality by frequently encountering a particular male's scent. Only males with high competitive ability will be capable of excluding intruders from their territories, monopolizing the area and saturating it with their own scent, making this important assessment cue unbluffable (Gosling and Roberts 2001). Thus, familiarity with a male's odor may be the proximate mechanism by which females choose a high-quality male. A corollary of this hypothesis is that females should prefer males that countermark another male's scent marks, which, while less impressive than complete monopolization, still indicates higher competitive ability than those males who cannot partially exclude, patrol, and countermark a rival's odors (Rich and Hurst 1999). Using this theory, Fisher, Swaisgood, and Fitch-Snyder (2003b) found that female lorises showed nearly a tenfold sociosexual preference for males whose odors were made familiar experimentally, and approximately a twofold preference for top-scent over bottom-scent males (Fisher, Swaisgood, and Fitch-Snyder 2003a).

In a similar study with female harvest mice, *Micromys minutus*, Roberts and Gosling (2004) used male odor cues to increase female familiarity with male odors, which enhanced pair compatibility and increased female preferences in this conservation breeding program. However, we do need to be careful not to force pairings between individuals that may not be genetically compatible (Wedekind 2002). Indeed, giving animals free choice to select mates can result in more viable offspring (Ryan and Altmann 2001; Gowaty, Drickamer, and Schmid-Holmes 2003), but this may be a price we have to pay when dealing with very small populations where preservation of genetic diversity in the founders may outweigh the costs of lower individual fitness. For conservation, the mean population fitness over the long term matters most.

Finally, 2 rather old—even commonsense—ideas about mating strategies have been subject to a recent resurgence in interest and new understandings. One of those is that "beauty is in the eye of the beholder" (Widemo and Saether 1999), meaning that individual, sometimes idiosyncratic, preferences are relatively common in nature, despite the influence of many general, uniform preference rules (e.g. for condition-dependent traits). Those of us involved in conservation breeding programs have witnessed inexplicable incompatibility problems when trying to get animals to breed. To the extent that these failures result from such individualistic preferences, we may have little recourse other than to keep trying different pairs until a compatible match is found. Another realization is that sexual conflict is inherent in mating behavior. The traditional view is that "this temporary union . . . [is] a harmonious affair, where males and females, after a period of courtship, join in the shared goal of producing offspring that carry their genes" (Arnqvist and Rowe 2005, p. 44). These authors go on to detail the prevalence of highly antagonistic behaviors between the sexes, the behavioral discord driven in part by differing consequences for fitness costs and benefits to the male and female. For example, male harassment in the face of female resistance can lead to injury and even death (LeBouef and Mesnick 1991). Giant panda courtship involves escalated aggression before and immediately after copulation, both in captivity (Swaisgood et al. 2006) and in the wild (Z. Zhang and R. Swaisgood, unpublished data). This inherent sexual conflict may mean that it is even more difficult for animals to "do what comes naturally" than we once believed. It is not hard to see why mating so often fails even under optimal conditions, much less the compromised situation in captive environments. Yet, as we have seen, these kinds of obstacles can be overcome with experimentation and application of behavioral ecological theory.

COMMUNICATION SYSTEMS AND CAPTIVE MANAGEMENT AND PROPAGATION

It is impossible to discuss social and mating behavior without reference to communication. The combination of signaling behavior and the perceivers' response is how most animals negotiate many aspects of sociality. Through signaling behavior, territories are defended, threats made, fighting ability probed and assessed, conflict resolved, mates located and chosen, reproductive condition advertised and evaluated, social partners recognized, movement coordinated, group cohesion achieved, and a myriad of other functions served (Bradbury and Vehrenkamp 1998; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). Signaling behavior has evolved to capitalize on all known sensory modalities: acoustic, visual, olfactory, gustatory, tactile, proprioceptive, vibrational, and electroreceptive. Signals began their evolutionary history as cues. Perceivers, by extracting information from these cues, generate the selective pressure for cues to be ritualized for communication to serve the signaler's own self-interest (Guilford and Dawkins 1991; Owings and Morton 1998). Signals need not be honest and individuals may bluff abilities and intentions, but bluffing is held in check by skeptical assessment.

While undervalued to date, monitoring the natural communication systems between mammals in captivity could facilitate their care and breeding. Condition-dependent sexually selected signals, which are sensitive to nutritional status, stress, and overall condition, may serve as indicators of the physical well-being of animals (McGregor, Peak, and Gilbert 2000). For example, dull colors or small weaponry may be an early warning sign of a looming problem. Signals also can be honest signals of emotional state (Maestripieri et al. 1992; Weary and Fraser 1995), allowing researchers to monitor well-being and identify potential stressors noninvasively in zoo settings. Both males and females of most species use signals to advertise reproductive condition and sexual motivation, and such signals can be used to determine the female's fertile period (Aujard et al. 1998; Wielebnowski and Brown 1998) or if a mating introduction is likely to be successful (Swaisgood et al. 2006). Changes in agonistic signaling can portend escalated aggression, indicating that intervention may be necessary. For example, female giant pandas when paired with males often begin with predominantly affiliative vocalizations, but as time passes males usually begin to exert more physical control over the female. She may first show ambivalence by emitting both aggressive and affiliative signals before escalating to higher levels of aggressive threat and ultimately contact aggression (Kleiman and Peters 1990). A decision tree, based largely on vocalizations, has been developed to guide managers through these changes and determine when to separate animals before the risk of injury grows too great (Swaisgood et al. 2006). Similarly, aggressive signals can be monitored to predict incipient birth or aggression outbreak in destabilized social groups (Koontz and Roush 1996).

Communication has featured rather prominently in some efforts to get captive animals to breed. Kangaroo rat pair compatibility is enhanced if given long-term opportunity to communicate through cages with neighboring opposite-sexed individuals (Thompson, Roberts, and Rall 1995). As discussed earlier, mouse lemurs breed better when they are near, and presumably communicating with, conspecifics (Hearne, Berghaier, and George 1996). Of course, for species that prefer their privacy, a lack of communicatory potential might be better (Lindburg and Fitch-Snyder 1994; Koontz and Roush 1996). Unfortunately, few studies in a zoo context use signal "playback" methodology to ascertain the role of various sensory modalities and signal sources in stimulating reproduction or other relevant parameters.

Chemical communication is well established as a major behavioral mechanism for facilitating all kinds of reproductive processes, and it can be used to prime individuals for sexual activity (Lindburg and Fitch-Snyder 1994). Chemosignals speed up puberty onset (Vandenbergh 1983), stimulate ovulation and improve sperm transport in the female reproductive tract (Rekwot et al. 2001), signal female reproductive condition to males (Doty 1986; Taylor and Dewsbury 1990), and stimulate sexual motivation in both sexes (Brown 1979; Johnston 1990; Rasmussen and Schulte 1998), to name just a few functions. It is no surprise, then, that the use of chemosignals plays a significant management role in stimulating reproduction in mammalian agricultural species (Rekwot et al. 2001). This role is only just beginning to be tapped systematically in zoo species.

A potential problem in captive environments that is perhaps underrecognized is that perception of important signals might be masked by background stimuli, compromising mating and courtship and other functions served by signals (Koontz and Roush 1996). The captive environment likely contains—from the animal's perspective—many sources of noise, light, and odor pollution. Insecticides can impair chemical communication, disrupt mate choice, and reduce reproduction in newts (Park, Hempleman, and Propper 2001). In swordtail fish, mate choice mechanisms for species recognition break down in the presence of agricultural and sewage runoff, and these fish consequently hybridize with a congeneric species (Fisher, Wong, and Rosenthal 2006). Mammals, a highly olfactory-oriented taxon, also must be susceptible to chemical pollutants. Overzealous cleaning can eliminate odors, which may be important signals to others (e.g. for mating) or for self-regulation. For example, some animals mark their home area, creating an odor field of self, which if removed or masked could be a source of stress (Eisenberg and Kleiman 1972). Light conditions are known to affect signal assessment in a variety of taxa (Endler 1992). UV-deficient light conditions can elevate stress levels and influence mate preferences in some bird species (Morgan and Tromborg 2007), and artificial night lighting may have far-reaching consequences for the conservation of an array of species (Rich and Longcore 2005). Ambient noise levels have significantly influenced the evolution of signal design for efficient transmission (Bradbury and Vehrenkamp 1998). Captive animals are exposed to, detect, and respond aversively to a variety of noises (Morgan and Tromborg 2007). Apparently, little is known about how noise in captive environments may hinder communication, but it has been suggested that noise may impede signal detection in marine mammals and other species (McGregor, Peak, and Gilbert 2000). The great tit (*Parus major*) sings at a higher pitch in urban compared to rural environments, apparently to combat the problems of signal detection in a noisy environment (Slabbekoorn and Peet 2003). Future research may reveal that "background noise" in all sensory modalities seriously compromises welfare and reproduction in captive mammals.

MANAGING THE SOCIAL ENVIRONMENT FOR WELFARE

The welfare of the animals stands out as an overarching concern when deciding on appropriate management strategies in captivity. In their exhaustive review of stress and welfare in captivity, Morgan and Tromborg (2007, p. 275) conclude that the evidence indicates "a variety of sensory elements in the environments of captive animals—including the quantity, quality, and periodicity of light, the presence or absence of particular odors, the pitch, frequency, and sound pressure level of sounds, and the heat indices, slickness, softness, and manipulability of substrate—have potential as sources of chronic stress." Measuring, understanding, and striving to enhance welfare are decidedly difficult tasks fraught with many complexities and caveats (Mason and Latham 2004; Swaisgood and Shepherdson 2005, 2006; Kagan and Veasey, chap. 2, this volume), so this topic is beyond the scope of our present purposes. For example, glucocorticoids—the most common measure of stress—are not always an adequate and straightforward measure of stress (Hofer and East 1998; Cook et al. 2000; Sapolsky, Romero, and Munck 2000; see also Hodges, Brown, and Heistermann, chap. 33, this volume). Behavioral measures that indicate potentially diminished well-being (e.g. heightened aggression, Kuhar et al. 2003) may not be associated with some physiological measures of stress. An interesting example is that female cheetahs do not demonstrate a glucocorticoid response to social housing, yet suffer from impaired ovarian function and behavioral indicators of agitation (Wielebnowski et al. 2002). Seasonal effects on glucocorticoid secretion also can be a confounding factor compromising the value of this endocrine measure of stress (Owen et al. 2005). Stereotypies—another common measure of welfare—may indicate either current problems or a scar from past suboptimal conditions (Mason and Latham 2004; McPhee and Carlstead, chap. 25, this volume). Enrichment is undoubtedly the best way to tackle these welfare problems, but there are surprisingly few zoo-based studies that adequately test the effects of enrichment (Swaisgood and Shepherdson 2006; Mason et al. 2007; see also Shepherdson, chap. 6, this volume; Cipreste, Schetini de Azevedo, and Young, chap. 15, this volume). Although we still have a way to go before we fully understand "what works and what doesn't," providing for animal welfare remains a major concern in zoo environments.

As with reproduction, managers of captive mammals often look to nature for guidance when considering welfare, seeking to replicate the social environment observed in the wild, often with success. Indeed, abnormal social grouping is one of the major factors negatively affecting well-being in captive mammals (Young 2003; Morgan and Tromborg 2007). Some of the worst cases occur when naturally social animals are held in isolation from other conspecifics. Social housing in appropriate groups can reverse some of these problems. Bloomsmith, Pazol, and Alford (1994) found that chimpanzees, *Pan troglodytes*, raised in mixed age and sex groups, reflecting natural group composition, displayed more diverse behavior typical of that seen in the wild. Species-typical behavioral diversity itself is often seen as an index of psychological well-being (Wemelsfelder et al. 2000; Rabin 2003). One also needs to consider that social housing can have different results for males and females. For example, socially isolated female laboratory rats are highly motivated to reestablish social contact, whereas males seem to treat social isolation as a natural consequence of territorial organization (Hurst et al. 1998). The presence of familiar conspecifics can even buffer social species against other potentially stressful perturbations in the environment (Mendoza 1991; Schaffner and Smith 2005). By contrast, the close proximity of conspecifics in more asocial species is also a potential source of stress and compromised well-being (Lindburg and Fitch-Snyder 1994; Wielebnowski 1998).

However, because of the vastly different environment in captivity compared to the wild, the natural social structure may not always ensure the best welfare for the captive individuals. Placing animals together in a group that reflects typical age and sex distributions does not mean that the group will function as an appropriate unit if environmental factors greatly differ from those in the wild. Veasey, Waran, and Young (1996) make a similar point, arguing that there are many aspects of nature that should not be replicated in captivity because of welfare concerns. In some cases, captive studies do not mirror the results of ones in the wild, indicating that extrapolation from wild to captive is not a simple matter.

McLeod et al. (1996) found that glucocorticoid levels—a potential indicator of stress—were associated with social rank in captive wolves, but in a way substantively different from wild wolves. Because captivity can reduce the ability to escape conflict, the wild social structure may be inappropriate. In captivity, managers may be able to create a social structure that permits high benefits (fecundity) with relatively low costs (competition), which may enhance animal welfare.

Excessive aggression can be a significant obstacle to the well-being of captive mammals. Behavioral research can provide a better understanding of the functions and mechanisms and suggest ways to minimize aggression. For example, female sable antelope, *Hippotragus niger*, form dominance hierarchies that are maintained through frequent aggressive behavior (Thompson 1993). Unfamiliar animals introduced to the group are the target of apparently unending aggression (e.g. one female was excluded from the group until her death a year later). One solution is to introduce new females to the group during seasonal periods when aggression is low. Another might be to familiarize residents with newcomers through cues (such as odors) before the introduction (Koontz and Roush 1996; see also Powell, chap. 5, this volume). Where management cannot alleviate aggression problems sufficiently, pharmacological treatment may be a solution. This situation is common when surplus males are removed from breeding groups and held in "bachelor groups." For example, fringe-eared oryx, *Oryx gazella*, bachelor groups show heightened aggression, which can be mitigated with a synthetic progestin such as melengestrol acetate (Patton et al. 2001).

In many cases, the same management strategy will enhance both well-being and reproduction, but in others these goals will run counter to each other. The relative costs and benefits to each of these important goals—as well as others—need to be weighed when deciding on a course of action (see also Bradshaw and Bateson 2000).

CASE STUDIES OF SOCIAL MANAGEMENT

THE ROLE OF CHEMICAL COMMUNICATION IN THE MANAGEMENT OF GIANT PANDA REPRODUCTION

The giant panda makes an interesting case study, highlighting the potential role of chemosignaling in conservation breeding programs. A solitary animal in nature, giant pandas visit scent-mark stations, where they pass scent messages back and forth to one another (Schaller et al. 1985). In the absence of regular face-to-face encounters, giant pandas appear to use odors and sounds to communicate during the breeding season. However, in captive breeding centers such as Wolong in China, more than half the mating introductions failed because the pandas were indifferent to one another or excessively aggressive (Zhang, Swaisgood, and Zhang 2004). This problem characterizes many solitary mammals, which need to transition from the aggression and avoidance that prevails throughout most of the year to affiliative and mating behavior during the brief reproductive season (1 to 3 days per year for giant pandas) (Lindburg and Fitch-Snyder 1994). Swaisgood et al. (2004) hypothesized that the problems with the panda breeding program (unsustainable on a worldwide basis) were the result of reproductive failure related to poor scent communication management.

A series of studies at the Wolong breeding center examined the functional and motivational bases of panda chemosignals (urine and anogenital gland secretions) by using variations on discrimination tests. These studies revealed that giant pandas possess a sophisticated chemical communication system. They can distinguish individuals using chemosignals (Swaisgood, Lindburg, and Zhou 1999) and are able to differentiate how long the scent has been left in the environment (Swaisgood, unpublished data). Giant pandas also can recognize the signaler's age (White, Swaisgood, and Zhang 2003), female reproductive condition (Swaisgood et al. 2000; Swaisgood et al. 2002), and sex (Swaisgood et al. 2000) (but are only able or motivated to discriminate sex during the breeding season; White, Swaisgood, and Zhang 2004). White, Swaisgood, and Zhang (2002) suggest that males even use a handstand posture to signal their competitive ability. For each of these chemosignals, the response was dependent on the age-sex class and reproductive condition of the receiver, as well as the context in which the chemosignal was detected.

But perhaps the most important function that panda chemosignals serve is priming the animals for sexual relations: males become sexually aroused by female odors, especially from estrous females, and females become sexually aroused by male odors. These odors also mitigate aggressive motivation in males. Capitalizing on these priming effects, managers at the Wolong breeding center began to manage the olfactory environment of the pandas, sending "scent postcards" back and forth between the males and females or swapping them in and out of each other's temporarily unoccupied enclosures, exposing them to a suite of odors (Swaisgood et al. 2004). Caretakers begin this procedure as soon as a female begins to show signs of estrus, thus providing a few days to a few weeks of olfactory familiarization before mating introductions. Due in part to this management, but also because of other changes such as an enrichment program (Swaisgood et al. 2001; Swaisgood et al. 2005), the Wolong breeding center now claims the best natural mating record of any panda breeding facility (Swaisgood et al. 2006).

SOCIAL PROCESSES IN RHINOCEROS BREEDING PROGRAMS

Rhinoceros species make for a good case study of the role that social processes can play in captive breeding programs. Black rhinoceroses (*Diceros bicornis*) are a relatively asocial species according to observations in the field, whereas white rhinoceros (*Ceratotherium simum*) females form both long-lasting and short-lived attachments with subadults and other females (Owen-Smith 1988). How do these differing social tendencies affect captive breeding and management? For black rhinoceroses the presence of other females tends to have a suppressive effect on female reproduction, leading to the recommendation that members of this species be held in male-female pairs (Carlstead et al. 1999; Carlstead and Brown 2005). Unlike some highly social species that have reproductive suppression in nature, reproductive suppression appears to be an artifact of captivity in black rhinoceroses, most likely related to the high social density. By contrast, white rhinoceros females reproduce *better* if they are kept in groups including one or more other females (Rawlings 1979; Lindemann 1982; Fouraker and Wagener 1996; Wielebnowski 1998; Swaisgood, Dickman, and White 2006). Despite our understanding of these basic species requirements for reproduction, neither species is self-sustaining in captivity. Some combination of disease, nutrition, and stress appears to contribute to high mortality in captive black rhinoceroses (AZA 2004), and dominance interactions between male-female pairs are important in determining pair compatibility and reproductive success (Carlstead et al. 1999). Moreover, constant forced proximity within a pair, a situation greatly divergent from the wild, is associated with higher levels of aggression and stress. Thus, for optimal reproduction, the male and female should be kept in separate enclosures and placed together during the female's fertile period. These social factors appear to interact with other aspects of the captive environment, such as exposure to zoo visitors, to influence both welfare and reproduction and even increase mortality risk (Carlstead and Brown 2005). From this case, we see that attention to social organization *in situ* and further evaluation of the specifics of captive management can make inroads into better captive management.

The reasons for failure in the white rhinoceros conservation breeding program are even more enigmatic. Many of the founding population (F_0 generation), given appropriate husbandry and management, reproduced well, but reproduction among captive-born (F_1) females has been extremely sluggish (Emslie and Brooks 1999; AZA 2004). Most of the F_0 females that formerly drove population growth have died or reached reproductive senescence in the past decade, leading to a crisis that can be abated only by further importation from the wild or resolution of the F_1 problem. Despite considerable effort, this problem remains intractable. Several endocrine studies have identified anomalies in the reproductive cycle that influence reproductive success, but there is no evidence that these problems are more prevalent among the F_1 generation (Schwarzenberger et al. 1998; Patton et al. 1999; Brown et al. 2001). Behavioral studies of 5 F_1 and 6 F_0 females at the San Diego Zoo's Wild Animal Park and an international questionnaire survey of holders of 68 white rhinoceroses indicated that F_1 females showed normal signs of behavioral estrus and reproductive behavior, comparable to or better than F_0 females (Swaisgood, Dickman, and White 2006). Similarly, males showed no sociosexual preferences for F_0 females. However, among females known to copulate with males, the birthrate was much higher in the F_0 generation, indicating that the F_1 problem is postcopulatory. These data also directly contradicted the prevailing hypothesis of white rhinoceros managers—that mothers or the older F_0 females behaviorally or physiologically suppress reproduction in younger F_1 females. Indeed, the presence of F_0 females significantly facilitated reproduction in F_1 females. By comparing F_1 females with F_0 females living in the same enclosures, Swaisgood et al. (ibid.) determined that the only factor that differed between the groups was the rearing environment, thus strongly implicating the captive environment during development as the ultimate causal factor. While testing these hypotheses has helped define the social processes that do and do not influence F_1 reproduction, future research will need to explore the developmental processes, including the social environment, that seem to be the root cause of F_1 reproductive failure.

MANAGEMENT OF ELEPHANTS IN CAPTIVITY

Captive elephants in North America are housed in a way that reflects social organization in nature, but there exist marked differences (Schulte 2000). Captive elephants are generally housed in small female groups, with only a few, often unrelated adults. While true matriarchs rarely exist in captivity, matrilineal dominance still is evident and commonly determined by size and temperament (Freeman, Weiss, and Brown 2004). Adult males are relatively rare in captivity in North America and are maintained separately from females except to breed. In most zoological facilities, breeding has not been highly successful, and calves, the core of female society in wild populations, are not common. Furthermore, significant calf mortality from endotheliotropic herpesviruses is a major concern (Richman, Montali, and Hayward 2000; Ryan and Thompson 2001). Historically, captive populations have never been self-sustaining (Sukumar 2003b). Unless breeding rates increase dramatically in North America, elephants will not be maintained through breeding (Olson and Wiese 2000; Wiese 2000; Hermes and Hildebrandt 2004).

Ideally, captive elephants would exhibit a relatively normal behavioral repertoire and set of social skills, with family units of appropriate size and composition for the species (Fernando and Lande 2000; Vidya and Sukumar 2005) and sufficient space and enriched environment (Stoinski, Daniel, and Maple 2000) to maximize physical and psychological well-being, as well as reproduction (Sukumar 2003a). In India, the interaction of tame and wild elephants provides enrichment for working elephants, but this is not a viable alternative in nonrange state regions (Sukumar 2003b). In captivity, the social environment can be changed to achieve more ideal group composition, but while enriching, social change is potentially disruptive. One protocol for introductions that mitigates stress and conflict involves a sequential method in which baseline hormone levels and behaviors are documented, and then contact is increased incrementally until full introduction (Burks et al. 2004). Schmid et al. (2001) at the Muenster Zoo showed that changes in behavior and cortisol levels are relatively short-lived (a few months) when introductions are performed with care (see Powell, chap. 5, this volume). Because of the limited number of viable, breeding males in captivity for each species, one of the sexes may be moved to the other's location for mating. However, with the recent success of artificial insemination, moving sperm rather than individuals has become more desirable (Brown et al. 2004a).

One of the most significant obstacles to breeding captive elephants is the prevalence of acyclicity (also called flatlining) in female Asian, *Elephas maximus*, and more prominently African elephants, *Loxodonta africana* (Brown 2000; Freeman 2005). Reproductive tract pathologies may explain some of the acyclicity, especially in older individuals (Brown et al. 2004b), but social organization and behavioral issues also may play a role (Freeman 2005). In general, acyclicity is most prevalent in the older, more dominant females (Freeman, Weiss, and Brown 2004; Freeman 2005). Although kin structure might be important for maintaining African ele-

Fig. 27.1. Female Asian elephant and calf at Ringling Bros. and Barnum & Bailey Center for Elephant Conservation, Polk County, Florida. (Photograph courtesy of Ringling Brothers and Barnum & Bailey Center for Elephant Conservation. Reprinted by permission.)

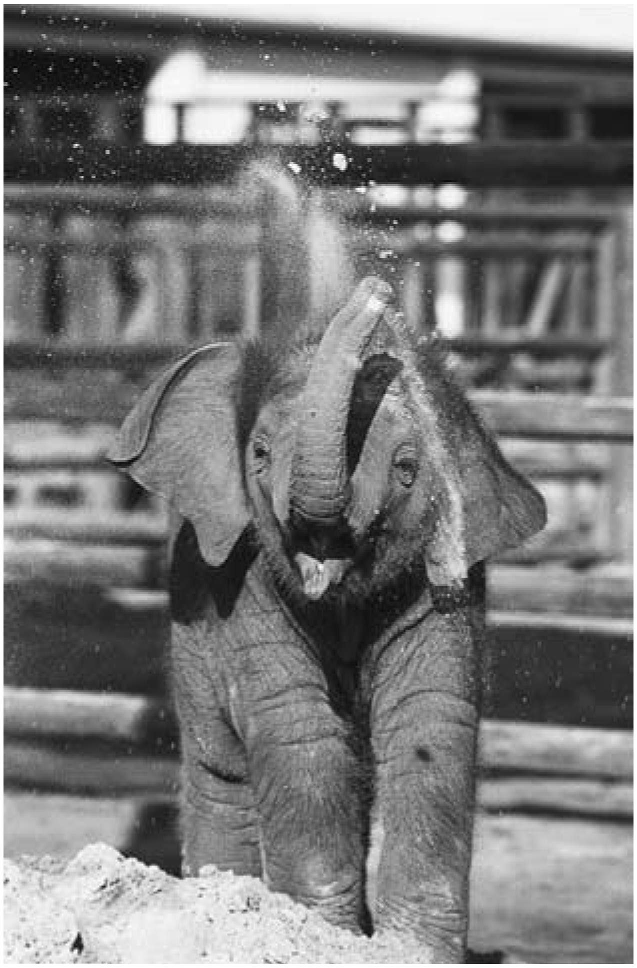

Fig. 27.2. Asian elephant calf born at Ringling Bros. and Barnum & Bailey Center for Elephant Conservation, Polk County, Florida. (Photograph courtesy of Ringling Brothers and Barnum & Bailey Center for Elephant Conservation. Reprinted by permission.)

phants in captivity, Archie et al. (2006) found that female hierarchies were structured around age and size, not genetic relatedness. Hence, the housing of elephants in unrelated social groups may be less of an issue than ensuring breeding early in life (10 to 15 years of age) and, when possible, maintaining exposure to adult males or at least cues from males, such as odors and vocalizations (Schulte et al. 2007).

From its opening in 1995 through 2005, 18 Asian elephant calves have been born through natural breeding at the Ringling Bros. and Barnum & Bailey Center for Elephant Conservation in Polk County, Florida (figs. 27.1 and 27.2). Traditionally, African elephants have experienced lower breeding success in captivity, but assisted reproductive techniques (e.g. Indianapolis Zoo), natural breeding (Riddle's Elephant and Wildlife Sanctuary, in the Ozark Mountain foothills), and a mix of the two (e.g. Disney's Animal Kingdom, Orlando, Florida) have yielded success in recent years (Riddle 2002; Hermes et al. 2007). Demographic analysis for Asian elephants suggests that maintaining or increasing the captive population in North America would require an increase in birthrate, with assistance from other management strategies such as reducing calf mortality and altering the birth sex ratio (Faust, Thompson, and Earnhardt 2006)

SOCIAL MANAGEMENT OF CAPTIVE MAMMALS FOR REINTRODUCTION

The majority of captive mammals will not be returned to the wild, yet many breeding programs are in place as a safeguard against extinction in the wild or as a genetic reservoir should wild populations need augmentation. Captive management should be structured to allow successful reintroduction if needed, even when reintroduction is not an explicit goal.

Ultimately, the genetic and experiential consequences of captive breeding will determine the suitability of captive-bred animals to play a role in *in situ* conservation. Compared to the wild, the captive environment creates a different set of selective pressures and developmental consequences that can depress essential survival skills (Beck 1991, 1995; Hediger 1964; Price 1984, 1999; McPhee and Silverman 2004; see also McPhee and Carlstead, chap. 25, this volume; Earnhardt, chap. 22, this volume). This kind of unintentional domestication should be avoided for any species that may eventually be returned to the wild. A captive population of animals ill-prepared for life in the wild will make a poor reservoir for reestablishing wild populations, should the need for this conservation action arise.

Social organization is an essential component in this scenario. It not only affects access to mates and mating strategies, but has been shaped by natural selection to optimize resource extraction, deal with predation pressure, and address other aspects of ecology that dramatically affect survival. As an illustration, large group size may be beneficial for antipredator vigilance or to locate ephemeral, highly patchy but locally abundant resources (Pulliam and Caraco 1984). Captive animals maladapted for group living (e.g. because of social deprivation) may not form or join larger groups, and pay the consequences. Social effects on survival have been found to be especially profound when animals are dealing with a novel environment. For example, black-tailed prairie dogs, *Cynomys ludovicianus*, survived at 5 times the rate if a group of familiar individuals was captured and translocated to a new site together than if release groups were selected at random (Shier 2006).

The role of sociality in the development of antipredator behavior in captivity can also be crucial for postrelease success. For instance, captive black-tailed prairie dogs trained with predators in the presence of an adult "demonstrator" developed much more proficient antipredator behavior and demonstrated increased survival postrelease than those trained without a demonstrator (Shier and Owings 2007). However, possession of specific socially facilitated survival skills is sometimes not enough to ensure postrelease success. Watters and Meehan (2007) have reviewed evidence suggesting that captive-reared animals in release groups should be comprised of individuals that perform different social roles. Groups made up of a mix of different social behavioral types (e.g. aggressive and submissive) may be more stable and attain higher mean population fitness postrelease. Thus, a goal of captive rearing should be to provide the appropriate physical and social environments for developing different behavioral types, as well as maintaining the genetic diversity that underlies these predispositions. These examples highlight the need for managers of captive mammals to consider numerous dimensions of social organization if those animals are intended for release into the wild.

CONCLUSIONS: HOLISTIC MANAGEMENT OF CAPTIVE MAMMALS

Multiple social processes impinge on the management of captive mammals. Social management does not occur in a vacuum, and other aspects of the captive environment need to be considered carefully in an integrative, holistic way. Enclosure design, enrichment programs, and other means of enhancing well-being are a prerequisite to breeding animals, and they interact synergistically with social management (Carlstead and Shepherdson 1994; Morgan and Tromborg 2007; Swaisgood 2007). Whether the objective of maintaining animals is to aid the species in the wild through education, appreciation, and science or to restock the wild directly, an enriched environment can improve the psychological landscape of captive animals. The management strategy should be tailored for the requirements of the species and the particular suite of individuals at a given facility, to reflect the specific objectives for their management in captivity. In developing management strategies, we should draw from behavioral ecological theory, which is rich in predictions regarding what behavioral mechanisms can be manipulated for conservation or welfare purposes.

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28

The Management of Pregnancy and Parturition in Captive Mammals

Patrick Thomas, Cheryl S. Asa, and Michael Hutchins

INTRODUCTION

One of the requisites for a successful captive breeding program is knowledge of a species' reproductive biology and behavior (Kleiman 1975, 1980; Lasley 1980; Eisenberg and Kleiman 1977). One of the most critical periods in mammalian reproduction extends from conception to birth. The purpose of this chapter is to review physiological and behavioral factors related to pregnancy and parturition in mammals. Rather than attempting to review these processes in the entire class, we will describe some of the similarities and differences that exist among its various members and focus on issues relevant to zoo animal management and propagation.

PHYSIOLOGY OF PREGNANCY AND PARTURITION

Knowledge of the physiological aspects of pregnancy can be important in captive animal management (Kleiman 1975; Lasley 1980), but, unfortunately, most studies have focused on humans, laboratory rodents, and domestic ungulates and carnivores. However, information on basic aspects of pregnancy in a wide variety of nondomestic animals is provided by Hayssen, Van Tienhoven, and Van Tienhoven (1993), and Lamming (1984). In addition, general information about pregnancy and parturition can be found in 2 comprehensive references (Knobil and Neill 1988, 1998).

For the purposes of this discussion, conception, or fertilization of the ovum, constitutes the initiation of pregnancy. In most mammals, the major events that follow fertilization include transport of the fertilized ovum, or zygote, to the uterus; maternal recognition of pregnancy, with ensuing maintenance of the corpora lutea (CL); implantation of the zygote in the uterine lining; and placentation. Following a species-typical period of development, gestation ends with parturition, or expulsion of the fetus from its uterine environment.

Among mammals, the most divergent reproductive pattern is found in the Monotremata. The duck-billed platypus, *Ornithorhynchus anatinus*, lays eggs that are incubated in a nest. Another monotreme, the echidna, *Tachyglossus aculeatus*, incubates its eggs first for 2–4 weeks in utero, then in an external pouch (Griffiths 1984).

Marsupials differ from both monotremes and eutherian mammals in that the embryo spends a relatively short time in utero. The extremely small neonate (range 5 mg–1 g), which is born at an early stage of development relative to eutherian mammals, climbs into the pouch and attaches itself to a teat without maternal assistance (Tyndale-Biscoe 1973, 1984; Shaw 2006).

MATERNAL RECOGNITION OF PREGNANCY

If conception does not occur at the time of ovulation, most female mammals begin another ovulatory cycle or enter a quiescent phase (anestrus). The CL that form as a result of ovulation may regress spontaneously or, in some species, transient prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$) may cause CL demise (Hendricks and Mayer 1977). If conception does occur, CL production of steroid hormones, particularly progesterone, must continue to maintain pregnancy. Thus, the maternal system must receive a signal that fertilization has occurred, and the obvious source of such a signal is the newly formed zygote or conceptus.

The earliest message yet detected appears in maternal blood serum as little as one hour after fertilization (Nancarrow, Wallace, and Grewal 1981). A substance released by the zygote (Orozco, Perkins, and Clarke 1986; Nancarrow, Wallace, and Grewal 1981) stimulates production of this early pregnancy factor (EPF) by the maternal oviduct and ovaries (Morton et al. 1980). The immunosuppressive action of EPF suggests its involvement in preventing rejection of the embryo by the maternal immune surveillance processes (Morton et al. 2000).

Not only does the presence of EPF in maternal serum confirm fertilization, but its subsequent disappearance during the first half of pregnancy signals embryonic or fetal loss

(Morton, Rolfe, and Cavanagh 1982). The rosette inhibition test (RIT), the first assay for EPF, although accurate is not practical for routine use. An alternative EPF assay, called ECF for early conception factor to distinguish it from the RIT, also measures EPF but by a different process (Gandy et al. 2001). However, its tendency to produce false positives makes it unreliable.

Following maternal recognition of pregnancy, a number of gonadotropic hormones may be responsible for maintaining the CL, including luteinizing hormone (LH), follicle-stimulating hormone (FSH), prolactin (PRL), and chorionic gonadotropin (CG). However, there is great variation among species. In domestic ruminants (cattle, sheep, and goats) interferon-tau, produced by the trophectoderm between days 10 and 21 to 25, is the factor that prevents lysis of the CL so that progesterone secretion can be maintained (Spencer and Bazer 2004). However, in the pregnant pig, estradiol secreted by the conceptus, not interferon-tau, is the agent that prevents CL regression (ibid.). Instead, porcine trophoblastic interferons play a role in implantation.

IMPLANTATION

The embryo develops from a one-cell zygote to the blastocyst stage, which results in the generation of 2 tissue types, one that will grow into the fetus and the other, the trophectoderm, that establishes contact with the maternal environment. Following blastocyst stage development, the embryo hatches from the zona pellucida and becomes capable of attachment. In species with delayed implantation, the blastocyst is held at this stage and fails to implant until the proper signal is received. At the point of contact with the uterine wall, the trophectoderm proliferates, forming the syncytiotrophoblast that secretes enzymes to disrupt the uterine epithelium, allowing the blastocyst to embed itself in the uterine wall (Burdsal 1998). The time of implantation varies greatly by species but commonly occurs between 1 and 4 weeks postfertilization. In many species, gonadotropic hormones such as CG increase or first appear at or near the time of implantation.

At least in primates, CG may stimulate secretion of relaxin, a hormone most associated with the relaxation of pelvic ligaments in preparation for parturition. However, its role in early pregnancy includes preparing the uterine endometrium for implantation (Hayes 2004). All species require progesterone for implantation, but estradiol, either from the ovary or from the blastocyst itself, also is necessary in others (Paria, Song, and Dey 2001). Blastocyst development must be synchronized with uterine development, so that the uterus is prepared to receive the blastocyst at the species-appropriate time, which may be as brief as 24 hours (e.g. mouse).

GESTATION

In most mammals, the estrogens and progestins that support pregnancy are supplied primarily by the ovaries, although more recent evidence indicates that the blastocyst of some species can secrete estradiol. In many species, only the ovarian CL are necessary for steroid hormone production during pregnancy (e.g. domestic cow, goat, pig, dog, cat, mouse), whereas in others the feto-placental unit supplements or in some cases replaces the ovaries as a source of steroid hormones (e.g. horse, sheep, primate) (see Amoroso and Finn 1962; Van Tienhoven 1983). There is a great deal of species variation in patterns of steroid secretion and excretion throughout pregnancy; progestins typically dominate in early pregnancy and estrogens in later stages.

Although ovarian activity during pregnancy is commonly restricted to CL function, some species show follicular growth during this period. These follicles may ovulate before forming accessory CL or may luteinize spontaneously. The fertilization of another ovum or set of ova during the latter stages of pregnancy has been described in several species (Rollhauser 1949; Scanlon 1972; Martinet 1980).

EMBRYONIC LOSS

Obviously, not every copulation results in fertilization, but even when fertilization is successful, embryo loss can be surprisingly high. Pregnancy detection soon after fertilization has revealed that most losses occur in the first days or weeks, before pregnancy can be diagnosed by more conventional methods (e.g. ultrasound). Estimates for embryo loss throughout pregnancy vary considerably by species and by method of measurement. Reasons include high environmental temperatures (Ryan et al. 1993; Wolfendon, Roth, and Meidan 2000), large litters (Perry 1954), age of mother (Maurer and Foote 1971), age of sperm (Martin-DeLéon and Boice 1985), genetic abnormalities (Murray et al. 1986), and immune response (Erlebacher et al. 2004).

PARTURITION

Gestation ends with parturition, a series of events that are probably initiated by a signal from the fetus, although this signal has not been identified in most species. Most thoroughly investigated in the rhesus macaque, *Macaca mulatta*, sheep, and goat, a fetal pituitary release of adrenocorticotropic hormone (ACTH) stimulates the release of adrenal cortisol, which acts on placental steroid metabolism to suppress the production of progesterone and enhance that of estrogen. This estrogen, passing into the uterus, stimulates $PGF_{2\alpha}$ release, which causes secretion of posterior pituitary oxytocin. Together with oxytocin, $PGF_{2\alpha}$ stimulates contractions of the uterine muscles (First 1979; Fuchs 1983; Challis and Olson 1988). In marsupials, a transient elevation of prolactin, and perhaps $PGF_{2\alpha}$, precedes the decline in progesterone necessary for the initiation of labor (Tyndale-Biscoe, Hinds, and Horn 1988).

LENGTH OF GESTATION

Gestation length is species specific (Holm 1966), but even within a species, breeds may have slightly different gestation lengths. Among kangaroos, *Macropus* spp., interspecific hybrids have pregnancy durations that are intermediate to the mean lengths of the 2 parental species, which also implies a strong genetic component (Poole 1975).

Forces other than genotype, however, can act to modify the inherent pattern (Racey 1981; Kiltie 1982). Time of conception during the breeding season, for example, can affect pregnancy duration. In sheep, early breeding results in longer pregnancies, and in horses, spring breeding results in longer pregnancies than does fall breeding (Campitelli, Carenzi, and Verga 1982; Van Tienhoven 1983). Male fetuses tend to be carried longer than female fetuses in some species (Jainudeen and Hafez 1993). In others, older dams tend to have longer pregnancies than younger dams (Jainudeen and Hafez 1993). Increasing litter size is correlated with shorter gestation length in some mammals. Experiments with laboratory rabbits suggest that the effect of litter size on gestation length is a function of uterine volume (Csapo and Lloyd-Jacobs 1962).

The level of nutrition in the diet has been associated with both shorter (Terrill 1974) and longer pregnancies (Riopelle and Hale 1975; Verme and Ullrey 1984; Silk 1986). In some heterothermic bats (Racey 1973; Uchida, Inoue, and Kimura 1984), warmer temperatures accelerate and colder temperatures retard embryonic growth and thus advance or delay parturition, respectively.

The most commonly recognized phenomenon that influences gestation length is delayed implantation, or embryonic diapause. Widespread in rodents, mustelids, and kangaroos, it also occurs in some bats, carnivores, and pinnipeds, as well as a few other disparate species. Factors that affect diapause vary by species and include lactation, season, and nutrition. The specific hormonal control of diapause has not been elucidated in all species, but estrogen, progesterone, and prolactin are commonly involved (Renfree and Shaw 2000). Obligate diapause, the type most often found in higher mammals, is a quiescent period of blastocyst development that occurs in every pregnancy. In contrast, facultative diapause is a quiescent period that may occur under nutritionally stressful conditions, such as lactation (Wimsatt 1975; Renfree and Calaby 1981; Van Tienhoven 1983).

Embryonic diapause is especially prevalent in macropod marsupials (Shaw 2006), in which it can be either obligate or facultative (Renfree 1981). In most kangaroos, fertilization occurs at a postpartum estrus, although estrus may be prepartum in some species (Sharman, Calaby, and Poole 1966). Following conception, development of the embryo is delayed by the suckling stimulus of the newborn, and its development resumes late in the pouch life of the older sibling. Birth is accompanied by yet another ovulation and potential conception, and this new embryo will then undergo facultative lactational diapause in turn. Thus, a female can have 3 offspring simultaneously: one that is becoming independent of the pouch but may continue to suckle for several months, one that is firmly attached to a teat in the pouch, and one in embryonic diapause. Each mammary gland produces milk of the proper composition for the needs of the suckling young at various stages of growth. If pouch young are lost at any time, embryonic development proceeds without further delay (Renfree 1981; Stewart and Tyndale-Biscoe 1983).

There are several variations on this theme. Some marsupials experience an additional obligate seasonal diapause. In others, ovulation is suppressed during gestation until late in the pouch life of the most recent offspring, and diapause of the embryo continues during suckling. Embryonic diapause is known to be absent in only one macropod species, the western grey kangaroo, *Macropus fuliginosus* (see Poole 1975). However, Tyndale-Biscoe (1968) contends that the embryos of all marsupials experience diapause, but that in nonmacropods the period is very brief. Furthermore, Renfree (1981) and Vogel (1981) suggest that all mammalian embryos are capable of some degree of diapause. Diapause may also allow some marsupials to respond more quickly to favorable conditions in an unpredictable environment (Low 1978).

Another form of pregnancy prolongation is delayed or retarded development, described most extensively in heterothermic bats (Bradshaw 1962; Fleming 1971). In these species, the lower metabolic rate associated with hibernation results in slower embryonic or fetal growth. Bernard (1989) suggested that the principal effect of this phenomenon is to lengthen the reproductive cycle so that gametogenesis is initiated in the middle of summer, and parturition and lactation occur in the following summer, when food is abundant. Retarded development may also occur in the hedgehog, *Erinaceus europaeus* (see Herter 1965).

Female mammals maintain considerable control over the actual timing of birth by being able to prolong the initial stage of parturition if disturbed. Thus, behavioral factors can have minor influences on pregnancy duration (see "Timing of Birth" and "Prepartus Phase" below).

INTERBIRTH INTERVALS

A species' life history strategy places some constraints on its reproductive potential (Pianka 1970), which for many captive mammals is determined not only by gestation length but also by interbirth interval (IBI). A variety of factors can influence IBI (see table 28.1). Not all species respond in the same way to these factors, and there may be some intraspecific variation as well. For example, studies have shown that poor physical condition of the female can either prolong (Clutton-Brock, Guinness, and Albon 1982) or shorten (Berger 1986) IBIs.

Although lactational anovulation has been documented in a variety of mammals (Loudon, McNeilly, and Milne 1983), primatological studies provide the best data on the effect that suckling offspring have on IBIs. According to Altmann, Altmann, and Hausfater (1978), primate IBIs consist of 3 major phases: (1) a period of postpartum amenorrhea, (2) a period of cycling, which consists of one or more estrous cycles, and (3) a period of gestation. The postpartum anovulatory phase is apparently due to both the residual effects of pregnancy and the suckling stimulus. For example, female yellow baboons, *Papio cynocephalus*, that lose young infants begin cycling within one month and typically conceive by the second estrus. In contrast, females with surviving offspring experience 12 months of postpartum amenorrhea, and typically do not conceive until their fourth estrous cycle (Altmann 1980). Burton and Sawchuk (1982), however, found no relationship between infant loss and IBI in Barbary macaques, *Macaca sylvanus*.

In New World monkeys the relationship between IBI and lactation is even more equivocal. Howler monkeys, *Alouatta* spp., show an effect of lactation on IBI similar to that in Old World monkeys (Glander 1980). In contrast, the owl monkey, *Aotus trivirgatus* (Hunter et al. 1979), and marmosets (Poole and Evans 1982) appear to be unaffected by lactation and have an IBI similar to the gestation length. However, French

TABLE 28.1. Factors influencing interbirth intervals in selected mammals

Factor	Species	Reference
Seasonal and/or environmental factors	Beaver, *Castor canadensis*	Patenaude and Bovet 1983
	Mountain goat, *Oreamnos americanus*	Hutchins 1984
Physical condition	Horse, *Equus caballus*	Berger 1986
	Olive baboon, *Papio anubis*	Bercovitch 1987
	Red deer, *Cervus elaphus*	Clutton-Brock, Guinness, and Albon 1982
Lactational anovulation	Chimpanzee, *Pan troglodytes*	Nadler et al. 1981
	Cotton-top tamarin, *Saguinus oedipus*	French 1983
	Crab-eating macaque, *Macaca fascicularis*	Williams 1986
	Hanuman langur, *Semnopithecus entellus*	Harley 1985
	Howler monkey, *Alouatta* spp.	Glander 1980
	Lesser galago, *Galago senegalensis*	Izard and Simons 1986
	Mountain gorilla, *Gorilla beringei*	Stewart 1988
	Red deer, *Cervus elaphus*	Loudon, McNeilly, and Milne 1983
	Stump-tailed macaque, *Macaca arctoides*	Nieuwenhuijsen et al. 1985
Loss of previous offspring	Binturong, *Arctictis binturong*	Wemmer and Murtaugh 1981
	Greater one-horned rhinoceros, *Rhinoceros unicornis*	Laurie 1979
Sex of previous offspring	Dorcas gazelle, *Gazella dorcas*	Kranz, Xanten, and Lumpkin 1983
	Red deer, *Cervus elaphus*	Clutton-Brock, Guinness, and Albon 1982
	Rhesus macaque, *Macaca mulatta*	Simpson et al. 1981
Age at first breeding	Caribou, *Rangifer tarandus*	Adams and Dale 1998
	Dall sheep, *Ovis dalli*	Heimer and Watson 1982

(1983) reported an effect for cotton-top tamarins, *Saguinus oedipus*.

In the case of highly endangered species, early removal of infants can be used as a management strategy to reduce IBIs and increase reproductive output. However, the early removal of offspring is not a viable strategy if it deprives infants of learning experiences necessary for their own reproductive success (i.e. socialization).

MATERNAL AND FETAL NUTRITION

Allen and Ullrey (2004) provide an excellent overview of the relationship between nutrition and reproduction in wild animals. The most comprehensive information available on the nutritional and metabolic aspects of pregnancy comes from domestic ungulates, laboratory rodents, and humans (Metcalfe, Stock, and Barron 1988). In general, gestation requires a larger quantity or quality of the normal ration, particularly during the last trimester. A review of the energy costs of pregnancy in selected mammals is provided by Randolph et al. (1977, table 3, p. 40).

Deficiencies of particular vitamins and minerals can affect pregnancy maintenance and fetal development as well. For example, too little vitamin A, beta-carotene, iodine, or manganese may result in abortion or fetal deformities in domestic cattle (Gerloff and Morrow 1980). Similarly, low reproductive success in felids has been attributed to deficiencies in dietary taurine, an essential amino acid (Sturman et al. 1986). Supplementation of folic acid has resulted in increased birth weight in squirrel monkey neonates (Rasmussen, Thene, and Hayes 1980).

Undernourishment during pregnancy is known to lead to fetal resorption or abortion in many species (Van Niekerk 1965; Thorne, Dean, and Hepworth 1976). For sheep and goats, in particular, undernourishment in late pregnancy, especially with twins, often results in ketosis or pregnancy toxemia (Pope 1972; Lindahl 1972; Church and Lloyd 1972). Figure 28.1 outlines some of the potential effects of maternal diet and body condition on the fetus.

Overfeeding can have detrimental effects, however, including a suppression of reproduction. Although a high caloric intake or continuous, unlimited feeding increases ovulation rates among sheep and swine (Pryor 1980; Flowers et al. 1989), embryonic mortality prior to implantation also increases (Hafez and Jainudeen 1974). In addition, pregnant female bovids and caprids, especially those with multiple fetuses that are overfed in early pregnancy, are subsequently susceptible to pregnancy toxemia in late pregnancy (Bruere 1980; Pryor 1980). The apparent paradox of the deleterious effects of both high and low planes of nutrition can perhaps be explained by the finding that maximum conception rates are associated with moderate progesterone levels. Because progesterone concentration is inversely related to nutrition level, only a moderate feeding level will optimize conception (Parr et al. 1987).

Leptin, a hormone produced primarily in adipose tissue, was first described for its role as a modulator of feeding behavior and adipose stores. More recently, leptin has been found to integrate the mother's energy requirements for pregnancy and lactation. In addition, leptin, which also can be produced by the placenta, may regulate fetal and placental growth and development. Leptin levels affect not only appetite but energy metabolism and distribution of nutrients in both the mother and neonate.

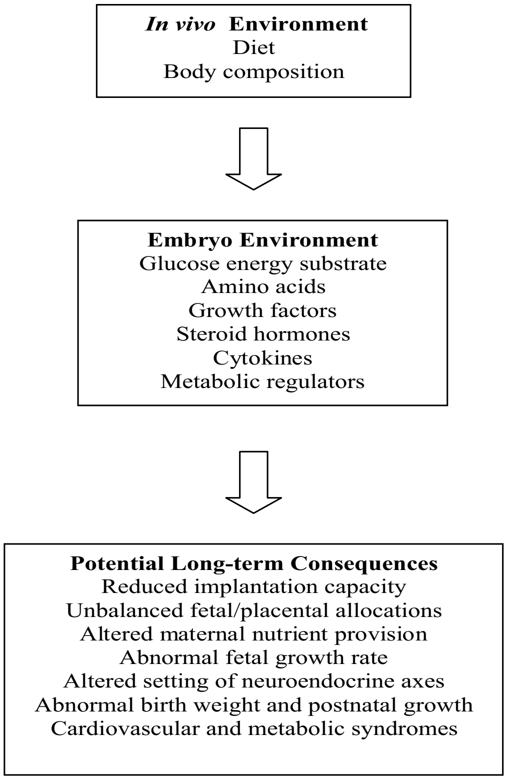

Fig. 28.1. Potential effects of maternal diet and body composition on the embryo, with possible long-term consequences. (Adapted from Fleming et al. 2004. Reprinted by permission.)

The plane of maternal nutrition can affect sex ratio in at least some species (Rosenfeld and Roberts 2004). Trivers and Willard (1973) hypothesized that in polygynous species only the larger, more aggressive males are likely to reproduce, whereas most females, regardless of body condition, reproduce. A corollary is that mothers in the best body condition should produce more male offspring, reasoning that their sons would benefit most from a higher allocation of resources. Indeed, the hypothesis has been supported in a majority of studies of wild populations, with the notable exceptions of some primates in which inheritance of maternal rank may favor daughters more than sons (reviewed in Clutton-Brock and Iason 1986).

Insufficient water intake can result in decreased food intake and undernutrition. In addition, limited water intake can suppress gametogenesis independently from food intake (Nelson and Desjardins 1987).

PREGNANCY DIAGNOSIS

The ability to predict whether and when an animal will give birth is often important to zoo managers. For example, in those cases in which females should be isolated from the rest of the social group before parturition (see "Social Factors and Pregnancy Outcome" below), it is desirable to know precisely when births are going to occur. It is also helpful to be ready to provide medical support or shelter if necessary. Provision of shelter may be important because captive mammals do not always give birth at opportune times, especially subtropical or tropical species that lack strong seasonal peaks in reproduction. When these animals are transported to more temperate climates, births may occur at any time of year, including midwinter (Frädrich 1987). Since many mammals lack thermoregulatory mechanisms at birth, death can result from hypothermia. Early detection of pregnancies also makes it possible for curators and keepers to anticipate the need for dietary changes associated with pregnancy (see "Maternal and Fetal Nutrition" above).

In zoos, noninvasive methods of pregnancy diagnosis, such as analysis of fecal and urinary hormone metabolites, are usually preferred. Hormonal methods useful for pregnancy detection are reviewed by Hodges, Brown, and Heistermann (chap. 33, this volume). However, because these tests often require multiple samples collected for several weeks, procedures such as radiography or ultrasonography are sometimes more practical. In particular, ultrasound imaging, which has become much more widely available in zoos in recent years, can be used to determine not only whether a female is pregnant, but how many fetuses are present and perhaps even their gestational ages (see table 28.2). As with other methodologies, most investigations have involved domestic species, many of which can be used as models for closely related exotic species. Basic information on ultrasound imaging can be found in Ginther (1995a), with more specific material on horses (Ginther 1995b), cattle (Ginther 1998), pigs (Martinat-Botte et al. 2000), and dogs and cats (Barr 1990).

Hormonal changes offer some of the best early indicators of pregnancy in mammals, but sample collection or laboratory testing may not always be possible. In such cases, zoo managers may have to rely on other cues. In some instances, changes in the dam's external appearance can be used to detect pregnancy. For example, swelling of the labia or changes in labial pigmentation indicates pregnancy in some primates (Wasser, Risler, and Steiner 1988).

Other physical signs of pregnancy in its later stages include a swollen and distended abdomen and an increase in maternal body weight. In some cases, various portions of the fetus may be visible as they press against the uterine walls (Jarman 1976; Rothe 1977). Fetal movement is sometimes also detectable by visual examination (Estes and Estes 1979). Zoo managers can condition some animals to stand on scales to monitor weight increases. When animals can be handled or restrained, pregnancy can sometimes be confirmed by rectal or abdominal palpation (Bonney and Crotty 1979; Sokolowski 1980). Occasionally, the various stages of fetal growth can also be determined through palpation techniques, but these require practice (Mahoney and Eisele 1978).

X rays are another potential method of pregnancy diagnosis. In humans, chromosomal aberrations can result from repeated long-term exposure to X rays during medical and dental procedures. Lasley (1980) argues that they should therefore be avoided as a diagnostic tool for animals. Radiographs have, however, been used successfully for pregnancy detection in a number of species (Boyd 1971; Sokolowski 1980). In some cases, fetal age and weight can also be determined by using radiographic techniques (Ferron, Miller, and McNulty 1976; Ozoga and Verme 1985).

TABLE 28.2. Ultrasound diagnosis of pregnancy in wild mammals

Species	Reference
African elephant, *Loxodonta africana*	Hildebrandt et al. 2000
Arabian oryx, *Oryx leucoryx*	Vié 1996
Asian elephant, *Elephas maximus*	Hildebrandt et al. 2000
Babirusa, *Babyrousa babyrussa*	Houston et al. 2002
Badger, *Meles meles*	Macdonald and Newman 2002
Banteng, *Bos javanicus*	Adams et al. 1991
Beluga, *Delphinapterus leucas*	Robeck et al. 2005
Black rhinoceros, *Diceros bicornis*	Adams et al. 1991
Bottle-nosed dolphin, *Tursiops truncatus*	Lacave et al. 2004
Camel, *Camelus bactrianus*	Adams et al. 1991
Chimpanzee, *Pan troglodytes*	Hobson, Graham, and Rowell 1991
Clouded leopard, *Neofelis nebulosa*	Howard et al. 1996
Common marmoset, *Callithrix jacchus*	Oerke et al. 2002
Cotton-top tamarin, *Saguinus oedipus*	Oerke et al. 2002
Cynomolgous macaque, *Macaca fascicularis*	Tarantal and Hendrickx 1998
European hare, *Lepus europaeus*	Hacklander et al. 2002
Fennec fox, *Vulpes zerda*	Valdespino, Asa, and Baumann 2002
Ferret, *Mustela eversmanni*	Wimsatt et al. 1998
Giant panda, *Ailuropoda melanoleuca*	Sutherland-Smith, Morris, and Silverman 2004
Giraffe, *Giraffa camelopardalis*	Adams et al. 1991
Goeldi's monkey, *Callimico goeldii*	Oerke et al. 2002
Harbor seal, *Phoca vitulina concolor*	Young and Grantmyre 1992
Moose, *Alces alces*	Testa and Adams 1998
Okapi, *Okapia johnstoni*	Thomas, pers. obs.
Olive baboon, *Papio anubis*	Fazleabas et al. 1993
Red deer, *Cervus elaphus*	Bingham, Wilson, and Davies 1990
Reindeer, *Rangifer tarandus tarandus*	Vahtiala et al. 2004
Rhesus macaque, *Macaca mulatta*	Tarantal and Hendrickx 1998
Scimitar-horned oryx, *Oryx dammah*	Morrow et al. 2000
Southern black rhinoceros, *D. b. minor*	Radcliffe et al. 2001
Spotted hyena, *Crocuta crocuta*	Place, Weldele, and Wahaj 2002
Squirrel monkey, *Saimiri sciureus*	Brady et al. 1998
Sumatran rhinoceros, *Dicerorhinus sumatrensis*	Roth et al. 2004

A major drawback to the above techniques is that they generally require that the dam be immobilized or restrained, especially when dealing with large or dangerous species. Chemical immobilization and physical restraint entail risks to both the fetus and the dam; however, some managers have avoided this problem by training animals to submit to regular ultrasonic testing (see Cornell et al. 1987), and training is becoming much more common in zoos (Mellen and MacPhee, chap. 26, this volume).

PHYSICAL SIGNS OF IMPENDING BIRTH

In many mammals the mammary glands or nipples may become swollen or distended near the end of pregnancy. However, enlargement of the mammary glands or nipples is not always a reliable indicator of pregnancy or impending birth, especially in females that previously have had young. In some species, mammary engorgement is accompanied by changes in pigmentation (e.g. dik-dik, *Madoqua kirkii*: Hendrichs and Hendrichs 1971) or by free-flowing milk (Bonney and Crotty 1979; Styles 1982) or a clear secretion (Phillips and Grist 1975; Sloss and Duffy 1980). The appearance of a waxy material at the end of the milk canal (i.e. "waxing" of the nipples) may be a sign that birth is imminent.

Wild and domestic canids reportedly shed the hair on their abdomen for up to a week before parturition, thus exposing the nipples; Naaktgeboren (1968) suggested that this characteristic could be used to predict impending parturition. Such shedding can, however, occur during pseudopregnancy as well.

The vulvar region of the dam may become swollen and distended, or the vulva itself may become dilated, as parturition approaches; this is sometimes accompanied by a mucous discharge. However, there is much variation in this regard, and some species show little or no swelling until immediately before parturition. Just before parturition, the hindquarters of the bitch, cow, and mare may take on a noticeable "sunken" appearance, due primarily to a relaxation of the pelvic ligaments (Harrop 1960; Sloss and Duffy 1980; Waring 1983). Female elephants, chimpanzees, *Pan troglodytes*, and baboons reportedly expel mucous plugs from the aperture of the cervix within 24 hours of parturition (Lang 1967; Mitchell and Brandt 1975). In some rodents, onset of parturition can be predicted by a separation of the pubic symphysis (Naaktgeboren and Vandendriessche 1962, cited in Kleiman 1972).

In a variety of species, the amniotic sac may be seen protruding from the vulva shortly before parturition. Similarly, the sudden rupture of the allantochorion and passage of large quantities of fluid from the vulva (i.e. "breaking water") is a good indication that parturition is imminent. Table 28.3 lists some of the common physical signs of impending birth in select mammals.

TIMING OF BIRTH

Little is known about the factors influencing the actual times when births occur. Whereas some mammals (e.g. wildebeest, *Connochaetes gnou*: Estes and Estes 1979; impala, *Aepyceros melampus*: Jarman 1976) tend to give birth in the daytime, many others have a tendency to give birth at night or in the early morning—times when light levels are low and disturbances are greatly reduced. In some species the peak hours of births are highly variable, and are probably affected by weather, illumination, and behavioral stress as well (Alexander, Signoret, and Hafez 1974; see "Prepartus Phase" below). Time of parturition in laboratory rats is affected by both photoperiod and feeding schedules (Bosc, Nicolle, and Ducelliez 1986). There is evidence that the effect of photoperiod

TABLE 28.3. Physical signs of imminent parturition in selected mammals

Sign	Species	Reference
Swollen or distended nipples	African elephant, *Loxodonta africana*	Mainka and Lothrop 1980
	African wild dog, *Lycaon pictus*	Thomas et al. 2006
	Bats, various species	Racey 1988
	Bottle-nosed dolphin, *Tursiops truncatus*	Tavolga and Essapian 1957
	Giant panda, *Ailuropoda melanoleuca*	Kleiman 1985
	Horse, *Equus spp*.	Waring 1983
	Impala, *Aepyceros melampus*	Jarman 1976
	Lowland gorilla, *Gorilla g. gorilla*	Meder 1986
	Pig, *Sus scrofa*	Jones 1966
	White-tailed deer, *Odocoileus virginianus*	Townsend and Baily 1975
Mammary secretions	African elephant, *Loxodonta africana*	Styles 1982
	Cow, *Bos taurus*	Sloss and Duffy 1980
	Dog, *Canis familiaris*	Harrop 1960
	Mountain tapir, *Tapirus pinchaque*	Bonney and Crotty 1979
Swollen and distended vulva	African elephant, *Loxodonta africana*	Styles 1982
	African wild dog, *Lycaon pictus*	Thomas et al. 2006
	Bottle-nosed dolphin, *Tursiops truncatus*	Tavolga and Essapian 1957
	Cow, *Bos taurus*	Sloss and Duffy 1980
	Coke's hartebeest, *Alcelaphus buselaphus*	Gosling 1969
	Dog, *Canis familiaris*	Harrop 1960
	Mountain tapir, *Tapirus pinchaque*	Bonney and Crotty 1979
	Vampire bat, *Desmodus rotundus*	Mills 1980
Quantities of fluid from the vulva ("breaking water")	African elephant, *Loxodonta africana*	Styles 1982
	Cat, *Felis catus*	Hart 1985
	Dog, *Canis familiaris*	Hart 1985
	Horse, *Equus caballus*	Rossdale 1967
	Weddell seal, *Leptonychotes weddellii*	Stirling 1969
	Wildebeest, *Connochaetes gnou*	Estes and Estes 1979
Decrease in basal body temperature	Cow, *Bos taurus*	Ewbank 1963
	Dog, *Canis familiaris*	Concannon et al 1977
	Horse, *Equus caballus*	Cross et al. 1992
	Sheep, *Ovis aries*	Ewbank 1969
	Pig-tailed macaque, *Macaca nemestrina*	Ruppenthal and Goodlin 1982

on time of parturition may be mediated by melatonin, a substance produced by the pineal gland (Bosc 1987).

Nocturnal births present logistical problems for zoo managers in that personnel are not always available to monitor the animals. Jensen and Bobbitt (1967) describe methods for shifting parturition time from night to day in a laboratory colony of pig-tailed macaques, *Macaca nemestrina*, by reversing the light cycle and altering environmental noise levels and maintenance routines. Similar techniques might be applicable to off-exhibit breeding facilities in zoos. In addition, several studies have shown that daytime births in livestock can be increased by manipulating feeding regimes. For example, nighttime feedings increased the percentage of daytime births in cattle (Clark, Spearow, and Owens 1983), whereas morning feedings had a similar effect in sheep (Gonyou and Cobb 1986). The use of closed-circuit cameras and recorders can enable zoo managers to noninvasively monitor and record nocturnal births without disturbing the expectant dam.

BEHAVIORAL SIGNS OF IMPENDING BIRTH

Parturition can sometimes be predicted on the basis of known gestation lengths or physical changes in the dam (see "Physical Signs of Impending Birth" above). However, copulations are not always observed, and gestation lengths may vary, not only among species but also among individuals of the same species (Kiltie 1982). Similarly, physical indications of impending birth are not always present, or may be evident only during the latter stages of the process. Fortunately, many female mammals exhibit characteristic prepartum behavior, thus allowing managers to predict impending births with reasonable exactness (Fraser 1968). The form and frequency of these behaviors vary, however, depending on the species and sometimes on the individual in question. Table 28.4 lists some common behaviors associated with imminent parturition in mammals.

The accuracy of time-of-birth estimations depends on a

TABLE 28.4. Behavioral signs of imminent parturition in selected mammals

Behavior	Species	Reference
Restless or pacing	African elephant, *Loxodonta africana*	Styles 1982; Lang 1967
	African wild dog, *Lycaon pictus*	Thomas, pers. obs.
	Bats, various species	Wimsatt 1960
	Beaver, *Castor canadensis*	Patenaude and Bovet 1983
	Common marmoset, *Callithrix jacchus*	Rothe 1977
	Domestic dog, *Canis familiaris*	Hart 1985
	Giant panda, *Ailuropoda melanoleuca*	Kleiman 1985
	Hamster, *Mesocricetus auratus*	Rowell 1961
	Horses, *Equus spp*.	Waring 1983
	Lowland gorilla, *Gorilla g. gorilla*	Nadler 1974
	Mountain tapir, *Tapirus pinchaque*	Bonney and Crotty 1979
	White-tailed deer, *Odocoileus virginianus*	Schwede, Hendrichs, and McShea 1993
Lethargy	Deer mouse, *Peromyscus spp*.	Layne 1968
	Bottle-nosed dolphin, *Tursiops truncatus*	Tavolga and Essapian 1957
	Giant panda, *Ailuropoda melanoleuca*	Kleiman 1985
	Tree shrew, *Tupaia belangeri*	Martin 1968
Frequent genital grooming or rubbing	Brushtail possum, *Trichosurus vulpecula*	Veitch, Nelson, and Gemmell 2000
	Coke's hartebeest, *Alcelaphus buselaphus*	Gosling 1969
	Common marmoset, *Callithrix jacchus*	Rothe 1977
	Cat, *Felis catus*	Hart 1985
	Dog, *Canis familiaris*	Hart 1985
	Giant panda, *Ailuropoda melanoleuca*	Kleiman 1985
	Sifaka, *Propithecus verreauxi*	Richard 1976
	Laboratory rat, *Rattus norvegicus*	Rosenblatt and Lehrman 1963
	Red kangaroo, *Macropus rufus*	Tyndale-Biscoe 1973
	White-tailed deer, *Odocoileus virginianus*	Townsend and Baily 1975
Increased aggression toward and/or isolation from conspecifics	African wild dog, *Lycaon pictus*	Thomas, pers. obs.
	Black lemur, *Eulemur macaco*	Frueh 1979
	Bottle-nosed dolphin, *Tursiops truncatus*	Tavolga and Essapian 1957
	Coke's hartebeest, *Alcelaphus buselaphus*	Gosling 1969
	Hamster, *Mesocricetus auratus*	Wise 1974
	Horse, *Equus caballus*	Waring 1983
	Mountain goat, *Oreamnos americanus*	Hutchins 1984
	White-tailed deer, *Odocoileus virginianus*	Townsend and Baily 1975
Frequent urination and/or defecation	Bottle-nosed dolphin, *Tursiops truncatus*	Tavolga and Essapian 1957
	White-tailed deer, *Odocoileus virginianus*	Townsend and Baily 1975
Depressed appetite	Giant panda, *Ailuropoda melanoleuca*	Kleiman 1985
Nest building	Canids, various species	Hart 1985; Naaktgeboren 1968
	Giant panda, *Ailuropoda melanoleuca*	Kleiman 1985
	Hamster, *Mesocricetus auratus*	Daly 1972
	Pig, *Sus scrofa*	Jones 1966
	Rabbit	Ross et al. 1963
	Ruffed lemur, *Varecia variegata*	Petter-Rousseaux 1964
Labored, irregular, or rapid breathing	Black-footed ferret, *Mustela nigripes*	Hillman and Carpenter 1983
	Bottle-nosed dolphin, *Tursiops truncatus*	Tavolga and Essapian 1957
	Hamster, *Mesocricetus auratus*	Rowell 1961
	Mountain goat, *Oreamnos americanus*	Hutchins 1984

knowledge of the range of behavioral variation possible in a given species. For example, when a sow suddenly becomes inactive, lies on her side, and shows signs of abdominal contractions, she is likely to give birth within 10 to 90 minutes (Signoret et al. 1975). In contrast, pregnant bottle-nosed dolphins may strain and flex their body as if they were experiencing contractions for up to 3 months before parturition (Tavolga and Essapian 1957).

Unfortunately, some species (e.g. ring-tailed mongoose, *Galidia elegans*: Larkin and Roberts 1983; harp seal, *Phoca groenlandica*: Stewart, Lightfoot, and Innes 1981) appear to lack any overt signs of impending birth, and the process itself may be very rapid. In such cases, prediction must be based on other cues.

EVENTS OF PARTURITION

Several authors have attempted to classify the events that characterize parturition into different stages or phases, but the literature is far from being standardized. The discussion follows the classification of Kemps and Timmermans (1982), who divide parturition into 3 distinct phases: prepartus, partus, and postpartus. The prepartus phase includes the period extending from the first contractions to immediately before birth. The partus phase encompasses the birth itself, and the postpartus phase extends from birth to the severing of the umbilical cord and expulsion of the placenta.

PREPARTUS PHASE

Dams may adopt a variety of postures during labor (e.g. lying, sitting, hanging, or standing), depending on the species or individual. Abdominal straining is often evident, and dams of many species may assume a "squatting" or "crouching" posture similar to that used for urination or defecation. Both the frequency and intensity of uterine contractions generally increase as labor progresses. In bats, the contractions are arrhythmic, occurring in a series of 3 to 6 or more rapid spasms, followed by a variable rest interval of a few seconds to several minutes (Wimsatt 1960; Tamsitt and Valdivieso 1966). Contractions are sometimes accompanied by vocalizations suggestive of pain and by labored or rapid breathing (Hutchins 1984; Lawson and Renouf 1985).

Length of labor is highly variable among mammals and can be influenced by many factors, including the size and shape of the fetus, the number of young in a litter, complications during delivery (see "Abnormalities of Pregnancy and Parturition" below), and environmental factors. For example, with a few exceptions (e.g. elephant seals, *Mirounga angustirostris*: Le Boeuf, Whiting, and Gantt 1972), birth in phocid seals is a comparatively rapid process, perhaps owing to the shape of the fetus, which is fusiform or sausage-shaped (Stewart, Lightfoot, and Innes 1981). Average time to delivery in harbor seals, *Phoca vitulina*, from the onset of obvious contractions is only 3.5 minutes (Lawson and Renouf 1985). In contrast, normal labor can be a long process in polytocous species (i.e. those that typically give birth to multiple offspring). In dogs, for example, the time between the first and last deliveries may be as much as 16 hours, and in pigs, 24 hours (Pond and Houpt 1978; Hart 1985). Primiparous females may experience more difficult deliveries than multiparous females, perhaps owing to the relative size of the birth canal.

In many mammalian species, environmental disturbances causing fright or anxiety can interfere with the birth process (Bontekoe et al. 1977). For example, the presence of a strange conspecific during labor inhibits uterine contractions in some female canids (Bleicher 1962; Naaktgeboren 1968). Similarly, Newton, Foshee, and Newton (1966) found that time between second and third births was 64 to 72% longer in laboratory mice when dams were forced to give birth in an unfamiliar environment. Bontekoe et al. (1977) showed that stress associated with environmental disturbances may either stimulate or inhibit uterine activity in sheep and rabbits, depending on the stage of gestation. The authors speculated that inhibition of labor contractions in a stressful situation is adaptive in that it offers the mother a chance to move to a more favorable environment before giving birth.

Females of many species seek out a secluded, quiet, sheltered place in which to give birth and should be provided with suitable locations in captivity. To reduce behavioral stress, changes in feeding procedures, cleaning routines, and keeper staff should be avoided at this time. Closed-circuit television is recommended as a means for observing pregnant, parturient, or immediately postparturient females without having to disturb them.

PARTUS PHASE

The dam may adopt a variety of postures during parturition, depending on the species and individual in question. Many ungulates, such as elephants and giraffes, *Giraffa camelopardalis*, typically give birth while standing (Robinson et al. 1965; Styles 1982) (fig. 28.2), whereas others expel the fetus while reclining (Jones 1966), or may adopt either posture (e.g. mountain goat: Hutchins 1984). Canids and felids typically give birth while lying on their side, usually with the head oriented toward the hindquarters (Fox 1966; Hart 1985). Vespertilionid bats, which normally hang upside-down, reverse their normal position during parturition; the tail is recurved ventrally so that the uropatagial membrane forms a pouch-like receptacle into which the young is received (Wimsatt 1960). However, other bat species are known to give birth in their typical resting position (Mills 1980; West and Redshaw 1987). Some kangaroos give birth with the tail pulled forward between the legs and with the back propped up against a vertical support (Tyndale-Biscoe 1973). Many primates deliver in a squatting or sitting position (Rothe 1977; Kemps and Timmermans 1982; Beck 1984). Rodents typically assume a quadrupedal or bipedal crouching or "hunched over" position as the fetus emerges (Kleiman 1972; Patenaude and Bovet 1983).

The amount of assistance the dam gives to the emerging young also varies among species. Among kangaroos, for instance, the female offers no assistance to the infant as it leaves the birth canal and makes its journey to the pouch (Tyndale-Biscoe 1973). In some other mammals, the mother licks her infant vigorously, thus helping to free it from the amniotic sac. In some cases (e.g. primates: Hopf 1967; bats: Wimsatt 1960), the infant assists in its own birth by grasping portions of the mother's body and pulling itself out. Newborn kanga-

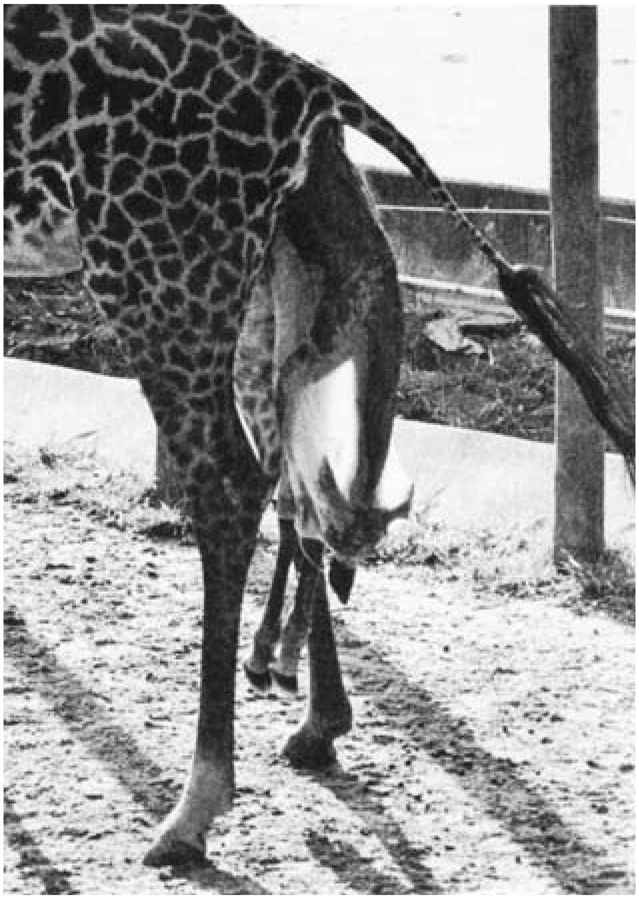

Fig. 28.2. Many ungulates typically give birth while standing. (Photography by Jessie Cohen, National Zoological Park. Reprinted by permission.)

roos emerge fully enclosed in the fluid-filled amnion; they free themselves from the membranes with the well-developed claws on their forelegs (Tyndale-Biscoe 1973).

POSTPARTUS PHASE

As it passes from the birth canal, the fetus begins its life outside the womb. It is not physically separated from the mother, however, until the umbilical cord is detached. In many cases, the umbilical cord is broken as part of the normal birth process. In other cases, the dam may actively sever the cord, usually by chewing through it with her teeth or by consuming it along with the placenta (Rothe 1977; Hart 1985).

A female mammal's initial reaction to her newborn is generally dependent on the behavior of the newborn: active, healthy newborns tend to stimulate maternal care, while stillborn, relatively inactive, or physically unhealthy infants may be ignored (see Rothe 1977). The vocalizations of infants may be particularly important in some species. Indeed, playbacks of recorded infant distress calls have been effective in eliciting maternal behavior in some species (e.g. black-footed cats, *Felis nigripes*: Leyhausen and Tonkin 1966; common marmosets, *Callithrix jacchus*: Rothe 1975). This approach deserves further exploration as a management tool to stimulate maternal care in dams that act indifferently toward their offspring.

Female mammals typically orient toward their infants and begin licking them thoroughly during or shortly after parturition (e.g. many carnivores: Ewer 1973; many ungulates: Lent 1974; many primates: Brandt and Mitchell 1971; many bats: Wimsatt 1960; rodents: Patenaude and Bovet 1983) (fig. 28.3). Maternal licking of neonates generally does not occur in aquatic mammals (Ewer 1973), and it is also reportedly absent in some terrestrial mammals (Lent 1974; Packard et al. 1987). Several functions have been proposed for this behavior. Maternal licking may be responsible for stimulating movement and initiating respiration in the newborn (Townsend and Baily 1975), and may also help to keep the neonate clean and dry, thus resulting in more efficient thermoregulation (Ewer 1973; Lent 1974). Furthermore, maternal licking, in conjunction with olfaction, is thought to be important in the development of the mother-offspring bond (Ewer 1973; Gubernick 1981), although evidence suggests that vaginal stimulation during birth may also contribute to the bonding process (Keverne et al. 1983). In some species, perineal grooming by the mother stimulates urination and defecation in the newborn, and in many mammals the female consumes

Fig. 28.3. Female mammals typically begin licking their infants during or shortly after parturition. This stimulation may serve several functions for the neonate. (Photography by Jessie Cohen, National Zoological Park. Reprinted by permission.)

her offspring's wastes, a behavior that may help to eliminate odors, thus reducing the probability of predation, or prevent fouling of the nest (Ewer 1973; Lent 1974).

With the possible exception of the monotremes, which lay eggs rather than giving birth to live young, most mammals pass birth fluids, fetal membranes, and the placenta during or after the expulsion of the fetus. Time from birth to passage of the placenta varies greatly. In some eutherian mammals, the afterbirth is largely ignored, whereas in others, it may be consumed. Eating of the placenta, or placentophagy, has been reported in a wide variety of species, including rodents (Patenaude and Bovet 1983), artiodactyls (Lent 1974), carnivores (Ewer 1973), bats (West and Redshaw 1987), and most primates (Brandt and Mitchell 1971). Placentophagy generally does not occur in aquatic mammals (Ewer 1973), although partial ingestion of a placenta has been reported in Hooker's sea lion, *Phocarctos hookeri* (see Marlow 1974).

Several functions have been proposed for placentophagy (Kristal 1980). Consumption of the placenta, fetal membranes, and birth fluids removes olfactory cues that might result in predation on the newborn (Ewer 1973; Lent 1974). The placenta may also have some nutritional value (Ewer 1973). In addition, it is filled with hormones, and there is some evidence that these may contribute to the letdown of milk (Kristal 1980). Furthermore, Kristal (ibid.) suggested that the placenta contains factors that prevent a mother from forming antibodies against fetal antigens that might act to inhibit subsequent pregnancies. It should be noted, however, that failure to consume the placenta does not seem to have any adverse effects on the mother.

BEHAVIOR OF CONSPECIFICS TOWARD PREGNANT AND PARTURIENT FEMALES AND THEIR INFANTS

Pregnant and parturient females may elicit different responses from other group members than do nonpregnant females because of their altered behavior, appearance, and odor. Of course, the range of responses is largely dependent on a species' social organization, as this will determine the number and types of conspecifics present during both pregnancy and parturition (see Eisenberg 1966; Spencer-Booth 1970; Caine and Mitchell 1979). For example, many of the relatively solitary carnivores do not typically interact with conspecifics at or near the time of birth (Ewer 1973), and encounters that do occur are likely to be antagonistic. Among social species, however, a pregnant female or newborn infant can stimulate a variety of responses, ranging from aggression to caregiving.

Among some social mammals, conspecifics are simply benign—though curious—bystanders, whereas in others, they may aid the pregnant female during labor or birth. Direct aid during the birth process appears to be rare, but it has been documented in several orders, including the Chiroptera, Pilosa, Primates, and Rodentia. Among rodents, for example, female spiny mice, *Acomys* sp., are known to exhibit "midwifery" behavior (Piechocki 1975). During parturition, other females gather around the mother, licking the infant as it emerges and helping to free it from the amniotic membranes. Similarly, in the monogamous prairie voles, *Microtus ochrogaster* (McGuire et al. 2003), and beaver, *Castor canadensis* (Patenaude and Bovet 1983), male and yearling offspring gather closely around the female and newborn, presumably aiding in thermoregulation, and also lick the infant shortly after birth. Among primates, male marmosets and tamarins (Callitrichidae) have been known to assist with the births of their offspring (see Langford 1963). Ullrich (1970) described a captive male orangutan that exhibited similar behavior; however, orangutans are relatively asocial animals (MacKinnon 1971), and this behavior was probably an artifact of captivity. McCrane (1966) describes several instances in which captive two-toed sloths, *Choloepus didactylus*, actively assisted during births, both by helping the infant to reach its mother's abdomen and by preventing it from falling (i.e. by blocking it with their body). Other colony members clustered around a parturient female vampire bat, licking fluids from her vagina and from the emerging fetus (Mills 1980).

In many social species (e.g. herd-forming ungulates), females seek isolation just before parturition. Isolation may help to reduce the incidence of accidental "adoptions" that could occur when females give birth in close proximity to one another. Newborn ungulates will approach any nearby female, and the potential for confusion is high (Lent 1974). The risk of predation may also be minimized by withdrawing from the herd so that birth can occur in a concealed or inaccessible area (ibid.; Jarman 1976; Hutchins 1984). While both of these factors are likely to be important, predation appears to have the strongest effect. Indeed, Lott and Galland (1985) found that female bison, *Bison bison*, inhabiting open terrain usually gave birth within the herd, whereas cows in habitat with cover usually gave birth alone. Alternatively, Hutchins (1984) suggested that females and infants are especially vulnerable to aggressive attacks by other conspecifics during and shortly after the birth process, and that by seeking isolation, dams may minimize this risk. Attacks by conspecifics on females and neonates have been documented among several ungulate species, both in captivity and in the wild (Styles 1982; Hutchins 1984; Packard et al. 1990).

Among primates, females and juveniles generally exhibit greater interest in newborns than do adult males (Caine and Mitchell 1979). Attempts to kidnap infants have been documented in a wide variety of species (Mitchell and Brandt 1975; Silk 1980). Similar behavior has been observed among other mammals and can result in aggressive interactions as females attempt to protect their newborns (Bullerman 1976; Thomas et al. 2006). The outcome of such interactions depends largely on the size and dominance status of the mother; the infants of subordinate females are at greatest risk. In some instances kidnappings may result in infants being left without maternal care (Alexander, Signoret, and Hafez 1974).

In some species, pregnant, parturient, and immediately postparturient females are harassed by males. Among ungulates (Manski 1982; Hutchins 1984), cetaceans (Tavolga and Essapian 1957; Amundin 1986), and primates (Rothe 1977; Wallis and Lemmon 1986), males court parturient or immediately postparturient females aggressively; this behavior may be triggered as a result of olfactory and visual cues resembling those of estrus (Manski 1982; Hutchins 1984; Wallis and Lemmon 1986). In some instances, the associated stress results in the female abandoning her offspring. The infant can also be injured by the male (McBride and Kritzler 1951). In such cases, it is advisable to isolate the female before parturition. However, the females of some species have an immediate postpartum estrus (e.g. large Malayan mouse deer, *Tragulus napu*: Davis 1965; pika, *Ochotona princeps*: Severaid 1950), and mating within a few hours after parturition is normal.

An important decision for the zoo manager is whether to isolate the pregnant female before parturition or allow her to remain in the social group. As a general rule, the species' natural social milieu at the time of birth should be simulated when possible (Kleiman 1980). In the case of relatively solitary species, it is probably best to isolate the female before parturition, as the presence of conspecifics may either disrupt the birth process or interfere with early postpartum maternal care. Similarly, the females of social species may require isolation to prevent aggression, harassment, or interference by other group members. For example, Izard and Simons (1986) showed that isolation before parturition significantly decreased neonatal mortality in 3 galago species. In the wild, female galagos normally sleep in groups during the day; however, they seek social isolation before parturition and for some time after their infants are born. Infanticide is relatively common among some mammals (Hausfater and Hrdy 1984), and newborns are always at some risk, especially under captive conditions where there is little opportunity for hiding or escape. However, pregnant females of highly social species may be stressed by isolation, which may have a detrimental effect on breeding success (Kaplan 1972).

ABNORMALITIES OF PREGNANCY AND PARTURITION

Most mammals commonly held in zoos go through pregnancy and parturition without difficulty, although complications do occasionally arise. While not all the elements influencing a dam and fetus during pregnancy are well understood, certain factors (e.g. improper nutrition, overcrowding, stress, inadequate cage design, injury, and illness) can have adverse effects on both mother and offspring (Benirschke 1967; Hafez and Jainudeen 1974). The following section outlines some of the more common problems associated with pregnancy and parturition (see table 28.5), and briefly summarizes management and clinical techniques used to avoid or correct such conditions.

BREECH BIRTH OR FAULTY POSITIONING OF THE FETUS

One of the more commonly encountered disorders of parturition is the "breech birth," or posterior presentation of the fetus. With the notable exception of certain species of insectivorous bats (Wimsatt 1960) and cetaceans (Essapian 1963; Tavolga and Essapian 1957), mammals normally give birth with the fetus in an anterior, longitudinal presentation, with the body fully extended in the birth canal. Among seals (Stewart, Lightfoot, and Innes 1981) and some other mammals (e.g. slender loris, *Loris tardigradus*: Kadam and Swayaamprabha 1980; various rodents: McGuire et al. 2003), cephalic and caudal (i.e. breech) presentations appear to be equally common.

Several factors can affect the positioning and delivery of the fetus and thus lead to a breech birth. Deformities in either the dam's birth canal or the fetus itself can hinder proper alignment (Hafez and Jainudeen 1974); so can excessive fetal movement just before parturition, or the death of the fetus before the onset of parturition (Sloss and Duffy 1980).

In most breech births, the dam is able to expel the fetus on her own, although the delivery may be protracted in comparison with normal births. In cases in which dystocia results from faulty positioning (see "Dystocia" below), human intervention may be required. In large mammals, the clinical procedures used in the removal of a fetus usually involve sedation or anesthesia. The easiest and safest method of delivering the fetus is by manual removal. With smaller mammals, this method is often impractical, and a cesarean section is the best alternative. If the fetus is already dead, a fetotomy (i.e. surgical sectioning and removal of the fetus) can sometimes be performed in lieu of a cesarean section.

DYSTOCIA

Dystocia is a prolonged or difficult labor, usually characterized by some functional defect or physical blockage of the birth canal. Along with breech births, it is among the most frequent complications of parturition. Several factors may be responsible for dystocia. First, faulty positioning of the fetus in the birth canal can result in a blockage that prevents normal birth. Another frequent cause of dystocia is fetopelvic disproportion, which occurs when the fetus is too large to pass through the pelvic girdle of the dam. One indication of fetopelvic disproportion is an expectant dam continuously straining with little or no sign of fetal expulsion. Often the vaginal area will be dry. The perineum can be palpated for the presence of a fetus; digital examination of the birth canal is generally also recommended to assess the degree of cervical dilation and to identify any congenital abnormalities that might be present (Bennett 1980). If the dam's condition is not differentiated from a typical labor, fetal death can occur, usually from suffocation or trauma. In cases of fetopelvic disproportion, removal of the fetus typically requires a cesarean section or fetotomy (Hubbell 1962; Sloss and Duffy 1980).

Ruptured uteri during late pregnancy can cause, or be the result of, dystocia. Uterine ruptures may result from trauma, fetal malformations, intrauterine pressure during parturition, or a variety of other factors (Sloss and Duffy 1980). If the uterus ruptures during labor, straining by the dam typically ceases. If the initial signs of labor are not detected, it is difficult to recognize signs of trouble.

Another cause of dystocia is ineffective labor. This can result from a variety of factors (e.g. nutritional deficiencies, toxemia, multiple offspring, excessive uterine load, an abnormally large fetus, or failure of the cervix to dilate: see Sloss and Duffy 1980; Saltet et al. 2000). It is often difficult to distinguish between ineffective labor and fetopelvic disproportion, but in most instances the dam would be treated in the same manner. Multiple offspring, especially in species that normally have a single offspring, can result in ineffective labor and dystocia. Uterine contractions may weaken or stop after the expulsion of one fetus, or 2 fetuses may be presented simultaneously (Williams, Mattison, and Ames 1980). Human intervention may be required to save the dam and offspring. In many instances, at least one fetus can be manually removed from the birth canal. Oxytocin can be

TABLE 28.5. Common abnormalities of pregnancy and parturition in mammals

Disorder	Species	Reference
Breech birth	Carnivores, various species	Law and Boyle 1983; Fox 1966
	Primates, various species	Brandt and Mitchell 1971
	Ungulates, various species	Norment 1980; Sloss and Duffy 1980
Dystocia	African elephant, *Loxodonta africana*	Hildebrandt et al. 2003
	Alpaca, *Lama pacos*	Saltet et al. 2000
	Asian elephant, *Elephas maximus*	Klös and Lang 1982
	California sea lion, *Zalophus californianus*	Klös and Lang 1982
	Cow, *Bos taurus*	Sloss and Duffy 1980
	Dog, *Canis familiaris*	Bennett 1980
	Gelada baboon, *Theropithecus gelada*	Hubbell 1962
	Giraffe, *Giraffa camelopardalis*	Citino, Bush, and Phillips 1984
	Grevy's zebra, *Equus grevyi*	Smith 1982
	Puma, *Felis concolor*	Peters 1963
Resorption or retention of the fetus	Bactrian camel, *Camelus bactrianus*	Mayberry and Ditterbrandt 1971
	Cow, *Bos taurus*	Sloss and Duffy 1980
	Horse, *Equus caballus*	Roberts and Myhre 1983
	Pig, *Sus scrofa*	Pond and Houpt 1978
	Primates, various species	King and Chalifoux 1986
Abortion	Bottle-nosed dolphin, *Tursiops truncatus*	Miller et al. 1999
	Chimpanzee, *Pan troglodytes*	Soma 1990
	Horse, *Equus caballus*	Roberts and Myhre 1983
	Lion-tailed macaque, *Macaca silenus*	Calle and Ensley 1985
	Little brown bat, *Myotis lucifugus*	Wimsatt 1960
	Lowland gorilla, *Gorilla gorilla gorilla*	Benirschke and Miller 1982
Stillbirths	Bottle-nosed dolphin, *Tursiops truncatus*	Amunden 1986
	Cow, *Bos taurus*	Sloss and Duffy 1980
	Geoffroy's cat, *Felis geoffroyi*	Law and Boyle 1983
	Lowland gorilla, *Gorilla gorilla*	Randall, Taylor, and Banks 1984
	Northern fur seal, *Callorhinus ursinus*	Bigg 1984
	Pig, *Sus scrofa*	Day 1980
	White-tailed deer, *Odocoileus virginianus*	Verme and Ullrey 1984

administered to the dam after the birth of the first fetus to help stimulate uterine contractions. Occasionally, a cesarean section is necessary.

RESORPTION OR RETENTION OF THE FETUS OR PLACENTA

Pregnancy may continue indefinitely when a fetus dies and is not expelled by the dam. Depending on gestational age, the embryo or fetus may undergo resorption, mummification, or maceration. Prenatal mortality can result from a variety of factors, including nutritional deficiencies, endocrine abnormalities, large litter sizes, thermal stress, lactation, immunological incompatibility, chromosomal aberrations, and inbreeding (Hafez and Jainudeen 1974; see also "Abortion" below). When an embryo or fetus dies, intrauterine liquids are quickly absorbed into the dam's body. The fetal tissues begin to decompose, and the process is considered enzymatic if no infection occurs. Among cattle and swine, if the fetus dies before the sixth week of gestation, resorption is nearly complete (ibid.; Sloss and Duffy 1980).

Fetal mummification has been documented in a variety of ungulates. It involves the retention of a dead fetus, resorption of the placental fluids, and subsequent dehydration of the fetal tissues. Usually there are no obvious signs of maternal illness, and in some species, mummified fetuses are frequently carried for many months or years beyond the normal gestation period without apparent harm to the dam (Hafez and Jainudeen 1974).

Fetal maceration is a more serious condition than mummification, because it involves a massive uterine infection. Maceration can be suspected when the condition of a pregnant female deteriorates rapidly and there is a fetid, bloody vaginal discharge (Sloss and Duffy 1980; Gahlot et al. 1983). Following the diagnosis of maceration, the entire uterus should be evacuated and thoroughly cleaned, and intrauterine medication administered. Long-acting antibiotics should be administered to lessen the risk of further infection.

In a formal sense, parturition is not completed until the fetal membranes, including the placenta, have been expelled from the dam's body. Placental retention occurs in a wide variety of mammals and can lead to infection or death (Jordan 1965; Sloss and Duffy 1980). There is a general tendency for membranes to be retained in older females and in instances in which gestation terminates prematurely or is abnormally prolonged. The retention of fetal membranes can sometimes be detected by observing a small portion of tissue hanging from the vulva. More frequently, however, there are no overt signs, as the tissue is retained entirely within the vagina or uterus, and diagnosis can be made only when the condition of the dam begins to deteriorate. When practical, manual removal of the membranes is the best solution. If this is not feasible, the administration of oxytocin can help promote expulsion (Fox 1966; Sloss and Duffy 1980).

ABORTION

The premature expulsion from the uterus of a dead fetus or a living fetus before it has reached a viable age is termed spontaneous abortion. Abortions may result from a variety of factors, including genetic abnormalities, developmental malformations, hormonal aberrations, infections, fatigue, trauma, drugs, litter size, behavioral stress, overcrowding, and inadequate nutrition (see Medearis 1967; Kendrick and Howarth 1974; Hafez and Jainudeen 1974; Johnston 1980; see also "Social Factors and Pregnancy Outcome" below and "Maternal and Fetal Nutrition" above). A phenomenon known as *abruptio placentae*, the premature separation of the placenta from the uterus, is known to cause fetal death and result in abortion in primates (Calle and Ensley 1985).

Leptospirosis is a bacterial disease that causes abortions in a wide range of species (Fowler 1993; Forrest et al. 1998). Zoo animals likely contract this disease by coming into direct contact with urine from infected animals or animals that carry the disease. There is a wide range of hosts, including many of the small carnivores and rodents. There are no clinical signs distinctive to this disease, and most abortions occur in the last 3 months of pregnancy. Animals that carry the disease can be successfully treated with antibiotic therapy if the disease is diagnosed early.

The factors surrounding the spontaneous expulsion of a fetus are still not well understood, even for domestic animals. Herrenkohl (1979) found that female rats subjected to prenatal stress had more spontaneous abortions upon reaching adulthood than did nonstressed rats. Other scientists have argued that abortions may be an adaptive response to unfavorable environmental conditions or to embryonic malformation (see Carr 1967; Bernds and Barash 1979). Still others have argued that social factors, especially those related to reproductive competition, may be involved (see "Social Factors and Pregnancy Outcome" below; Wasser and Barash 1983). Detection of early abortion in many mammals is difficult because the embryo is often eaten by the dam (e.g. primates: King and Chalifoux 1986). During the last trimester of pregnancy, however, abortions can sometimes be predicted in cattle by the appearance of a bloody vaginal discharge (Sloss and Duffy 1980). Since many cases of abortion also involve the retention of fetal membranes, it is important to treat the dam with antibiotics, although practical considerations may prevent this in some cases.

STILLBIRTH

Because most births are not actually witnessed, the term *stillbirth* (also called perinatal mortality) will be used here to describe any fetus that is found dead (having died before, during, or shortly after parturition). A wide range of internal and external factors acting on the dam or fetus at any time during pregnancy can lead to a stillbirth.

The occurrence of multiple births in species that typically have one offspring can result in stillbirths (Williams, Mattison, and Ames 1980). In certain polytocous species (i.e. those that typically have multiple fetuses), there is a positive correlation between the incidence of stillbirths and litter size (Pond and Houpt 1978). Stillbirths have also been attributed to nutritional deficiencies (Verme and Ullrey 1984); genetic factors, including inbreeding and congenital defects (Sloss and Duffy 1980); difficulties during parturition, including dystocia and abnormal fetal presentation (Randall, Taylor, and Banks 1984); premature expulsion of the fetus (Bigg 1984); ruptured umbilical cords (Day 1980); placental lesions caused by infarcts (i.e. areas of dead tissue caused by an obstruction of blood vessels) or premature separation (King and Chalifoux 1986); and maternal and fetal infections (ibid.). In some species, the incidence of stillbirths is related to the sex of the fetus, with male fetuses being stillborn more often than female fetuses (Sloss and Duffy 1980). Birth order has some effect on the incidence of stillbirths in pigs, with the frequency being highest in the latter third of the young born (Randall 1972).

FETAL MALFORMATION

Malformations are usually caused by abnormal development of the fetus during the embryonic period, and can be attributed to genetic and developmental aberrations, nutritional deficiencies, infections, trauma, or exposure to toxic substances (Fox 1966; Hutt 1967; Sloss and Duffy 1980). Many types of congenital defects have been identified in domestic, zoo, and wild animals (see Hutt 1967 and Leipold 1980 for a comprehensive review). In most instances, malformed fetuses do not survive, although minor deformities may not seriously hamper a young animal's development. One of the goals of the modern zoo, however, is the long-term maintenance of animal populations in captivity (Foose 1983). In some cases this requires the systematic elimination of traits deemed undesirable or potentially hazardous. Thus, malformed offspring may be humanely euthanized if the malformation is serious enough to hamper normal function.

PROLAPSED UTERUS OR VAGINA

Eversion or prolapse of the vagina or prolapse of the cervix through the vagina is a fairly common occurrence in domestic livestock (Fielden 1980; Sloss and Duffy 1980) and has been documented in a variety of mammals, including rodents, lagomorphs, and various ungulates (Wallach and Boever 1983). Diagnosis is readily made by visual examination: the prolapsed mass, sometimes including the bowel or bladder, can be seen protruding from the lips of the vulva

(Fielden 1980). Although this condition usually occurs in multiparous females during the later stages of pregnancy, there is some evidence that the tendency to prolapse can be inherited, as it has also been observed in primiparas (Sloss and Duffy 1980). Risk of recurrence in the affected animal is very high (Fielden 1980). Because most prolapses are experienced by multiparous females, frequent stretching of the vagina may predispose it to eversion.

Prolapses usually require veterinary intervention, because they seldom involute properly. In most cases, large mammals will need to be sedated or anesthetized before handling. All prolapsed tissues must be thoroughly cleaned before being repositioned. Antibiotics are administered, and the vagina is sutured into its correct position (Fielden 1980).

ADDITIONAL PROBLEMS

Environmental factors, such as temperature and humidity, are known to affect conception and pregnancy at several levels. Transient infertility due to heat stress has been most extensively documented in domestic cattle (Ingraham, Gillette, and Wagner 1974). Postfertilization hypothermia can also adversely affect fetal development and result in increased embryonic mortality in many species (Alliston and Ulberg 1961; Trujano and Wrathall 1985; Biggers et al. 1987). Reproductive rates in captive eastern rufous mouse lemurs, *Microcebus rufus*, were lower when humidity levels were low (Wrogemann and Zimmermann 2001). Captive mammals should therefore be maintained at temperature and humidity ranges that are appropriate for the species. Deviations from the norm may result in reproductive failure.

SOCIAL FACTORS AND PREGNANCY OUTCOME

Many social factors can influence pregnancy outcome (Wasser and Barash 1983). For example, among some social mammals, typically only the dominant female breeds while subordinate females, which are reproductively suppressed, help to raise her offspring. Wasser and Barash (ibid.) suggest the term *reproductive despotism* for this phenomenon. It has been reported in several group-living species, including callitrichids (Kleiman 1980; Carroll 1986; Savage, Ziegler, and Snowdon 1988), dwarf mongooses, *Helogale parvula* (see Rood 1980), African wild dogs, *Lycaon pictus* (see Frame et al. 1979), wolves, *Canis lupus* (see Rabb, Woolpy, and Ginsburg 1967), and naked mole-rats, *Heterocephalus glaber* (see Jarvis 1991). There are also many social species in which dominant females tend to have higher reproductive rates than subordinates (e.g. gelada, *Theropithecus gelada*: Dunbar 1980). Such differences are thought to be due to female-female competition (Dunbar and Sharman 1983).

Dominant females can suppress reproduction in subordinates through a variety of mechanisms, including estrous cycle disruption (Bowman, Dilley, and Keverne 1978; Huck, Bracken, and Lisk 1983), mating interference, and infanticide (see Hrdy 1979; Kleiman 1980). However, there is some evidence that dominant females may also interfere with normal pregnancies. Wasser and Barash (1983) suggest that the stress of living with dominant females can lead to fetal resorptions, abortions, and stillbirths in subordinate females.

The presence of strange males can also have a deleterious effect on pregnancy. In some mammals, such as rodents, implantation is inhibited and pregnancy is blocked when recently mated females are exposed to unfamiliar males (Bruce 1960). The effect is strongest when the male is dominant in his own social group (Huck 1982). Postimplantation termination of pregnancy after exposure to strange males has also been documented (Kenny, Evans, and Dewsbury 1977). Similarly, Pereira (1983) and Mohnot, Agoramoorthy, and Pajpurohit (1986) observed several cases of abortion in free-ranging troops of yellow baboons and Hanuman langurs, *Semnopithecus entellus*, respectively, in which circumstantial evidence suggested that the losses were due to the recent immigrations of aggressive, high-ranking males. Furthermore, Berger (1983) found a correlation between abortion frequency and male takeovers in feral horses. Pregnant females were forced to copulate with the new males, and their abortions were attributed to harassment or "stress imposed by changing social environments" (p. 60).

Pregnancy block and inducement of abortion have been interpreted as male reproductive tactics; a female that loses her fetus prematurely ovulates and becomes sexually receptive much sooner than one that carries her fetus to term (see Schwagmeyer 1979; Berger 1983; Pereira 1983). In contrast, pair-bond disruption immediately after mating can cause implantation failure in some rodents (Berger and Negus 1982; Norris 1985). The implications of these findings for zoo animal management are clear: care should be taken when introducing new animals into established groups, especially when one or more females may be pregnant.

In some cases, social factors have been shown to be important in stimulating or delaying parturition, and thus can have a bearing on pregnancy outcome. Among Northern fur seals, *Callorhinus ursinus*, for instance, parturition may be triggered by the social stimulus of large numbers of conspecifics. Such concentrations occur when females and males gather on their traditional breeding beaches (Bigg 1984). Bigg (ibid.) suggests that the high incidence of stillbirths and abortions seen in captive pinnipeds may be related to social factors. Indeed, the social milieu of captive animals rarely changes. Thus, the lack of appropriate cues to trigger parturition may result in premature births or abnormally long gestations—problems that are frequently exhibited by these species under captive conditions.

SUMMARY AND CONCLUSIONS

We have shown how knowledge of both the physiological and the behavioral aspects of pregnancy can contribute to the development of successful captive breeding programs. Of particular importance to zoo managers are (1) the use of hormonal, physical, and behavioral cues to detect pregnancy and estimate the time of birth, (2) the special nutritional and housing needs of pregnant females and neonates, (3) the possible influence of social factors and behavioral stresses on pregnancy outcome, and (4) the recognition and treatment of various abnormalities of pregnancy and parturition.

It is our hope that the information contained here will aid zoo managers in their efforts to propagate endangered wildlife. As Poole and Trefethen (1978, p. 344) have stated, "Knowledge is the essential prerequisite to making a management decision respecting a species, population, or group of wildlife. A decision made in the absence of information about a species or population, depending on the result, is, at worst, an act of ignorance, or, at best, a stroke of good fortune." Unfortunately, in reviewing our current state of knowledge, it is evident that there are glaring deficiencies in our understanding of mammalian reproduction. Indeed, many of the general principles outlined in this chapter are based on studies of domestic species and therefore may not be applicable to exotic mammals. There is a clear and urgent need for detailed information on the reproductive biology of a variety of exotic species.

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29

Parental Care and Behavioral Development in Captive Mammals

Katerina V. Thompson, Andrew J. Baker, and Anne M. Baker

INTRODUCTION

All mammal infants must receive some care in order to survive. How much care an infant receives, and from whom, is determined by developmental, social, and environmental factors, resulting in great diversity in parental care even among closely related species. Furthermore, behaviors that confer reproductive or survival advantages in one environment may not do so in another. This diversity underscores the need for managers to be familiar with the natural social structure of each species that they manage, to evaluate behaviors seen in captivity in the framework in which they evolved, and to adjust management practices accordingly.

The extent of parental care required is also influenced by the infant's degree of development at birth, which varies by species from extremely undeveloped, or altricial, to well developed, or precocial (table 29.1). Altriciality and precociality are, of course, endpoints in a continuum. Most mammalian species show intermediate degrees of development and are referred to as semialtricial or semiprecocial, depending on which traits predominate.

GENERAL PATTERNS OF PARENTAL CARE

MATERNAL CARE

Mothers are the primary caregivers in most mammalian species (Clutton-Brock 1991), in part because all infant mammals are nourished by maternal milk. Mothers may also build nests, clean young, stimulate urination and defecation, huddle with them to provide warmth, protect them from conspecifics, and defend them against predators. In a number of species, mothers continue to provide such care far beyond the time of weaning. For animals that live in stable social groups, mothers may play an important role in establishing their offspring's social position within the group (e.g. Cheney 1977) and buffering their interactions with other group members.

The onset of maternal behavior is triggered by distinct hormonal changes that occur shortly before parturition and prime the female to respond appropriately to the presence of young. Key hormonal changes include a sharp drop in progesterone just before parturition, a rise in prolactin, and sharp increases in intracerebral oxytocin that are first triggered by dilation of the cervix and later by suckling of the infant (Kendrick et al. 1991; Numan and Insel 2003). There is growing evidence that lack of vaginocervical stimulation during parturition (e.g. because of anesthesia and/or Caesarian delivery) interferes with oxytocin release and therefore may inhibit normal maternal behavior such as consumption of the placenta, licking of the infant, and maternal recognition of infants (Levy et al. 1992, 1995). First-time mothers show a less robust increase in oxytocin at parturition (Levy et al. 1995), which may account in part for the lower rearing success noted for first-time mothers in many species. In many mammals, this hormonal priming also results in lactational aggression, a generalized increase in female aggression in defense of their young. Even normally tractable females can become unpredictable when an infant is present; keepers and other individuals dealing with mothers and newborns should exercise special caution.

In most terrestrial placental mammals, mothers lick the neonate clean and consume the placenta. Licking dries the neonate's coat, thus aiding in thermoregulation, and provides tactile stimulation that initiates the onset of breathing (Ewer 1968), urination, and defecation (see Thomas, Asa, and Hutchins, chap. 28, this volume). The placenta and amniotic fluid contain substances that have analgesic effects on the mother (Corpening, Doerr, and Kristal 2000); consuming these substances may enable mothers to focus their attention more fully on providing care to their infants. Licking and consumption of birth fluids also provide the mother with gustatory and olfactory input that will later aid her in identifying her infant (Hepper 1987; Levy and Poindron 1987).

Maternal-offspring recognition through olfactory and/or auditory cues has been documented in a variety of species, including rodents (Elwood and McCauley 1983), bats

TABLE 29.1. Characteristics of altricial and precocial infant mammals

Altricial	Precocial
Hairless or sparsely furred	Fully furred
Sensory systems undeveloped, eyes and ears closed	Functional sensory systems
Incapable of coordinated locomotion	Capable of coordinated locomotion
Unable to maintain a stable body temperature independently	Able to thermoregulate
Complete nutritional dependence on mother	Able to eat some solid food shortly after birth
Examples	Examples
Spectacled bear, *Tremarctos ornatus*	Brindled wildebeest, *Connochaetes taurinus*
Red kangaroo, *Macropus rufus*	Common zebra, *Equus burchellii*
Oriental small-clawed otter, *Aonyx cinereus*	Patagonian cavy, *Dolichotis patagonum*

(Kleiman 1969; Yalden and Morris 1975), pinnipeds (Marlow 1975), and ungulates (Lent 1974; Carson and Wood-Gush 1983). Recognition mechanisms are common in social species that give birth to well-developed young capable of moving independently of the mother and are less common in species bearing undeveloped young that spend their early postnatal time being carried by the mother or in a secluded nest. Recognition generally develops within hours or days of parturition, during a period of intensive mother-infant contact. In some social species, parturient females seek seclusion from conspecifics during this time. Once the mother-infant bond has formed, a mother will usually drive strange young away; however, in captive ungulates, failure to isolate females that normally would leave the herd may result in attempted adoption or nursing interference by other females (Lent 1974; Read and Freuch 1980). Oxytocin release during parturition appears to be important for the development olfactory recognition (Levy et al. 1995).

Nursing begins any time from minutes to hours after birth, depending on the species. In species with multiple offspring per birth, the female sometimes will not suckle the first infant until the entire litter has been born, even though the interval may be a long one. While the onset of maternal care is governed largely by endogenous endocrine processes, the maintenance of maternal responsiveness to young is dependent on sensory stimulation provided by the young themselves (Rosenblatt 1967; Harper 1981). Suckling provides sensory stimulation that maintains lactation and helps ensure that milk production corresponds to the number and size of nursing young. Tactics used by infants to stimulate milk delivery include massaging of the mammary gland with the forepaws (as in kittens) and bunting, a forceful butting of the udder seen in ungulates (Ewer 1968, 1973). Even in highly altricial species such as rats, infants can control the amount of milk received by modulating the vigor with which they suck (Hall and Williams 1983).

Because of their high surface-area-to-body-weight ratio, many neonates do not have sufficient energy to maintain a constant body temperature and require an external source of heat. In most altricial mammals, and some precocial ones, frequent contact with one or both parents provides this heat. Contact with other young in the nest may serve to conserve body heat when parents are absent.

The initially strong bond between a mother and her infant weakens as the infant matures and begins to take an active interest in its surroundings. To a great degree the freedom an infant has to explore its surroundings is dependent on its mother's willingness to allow it this freedom. A mother's attitude toward her infant can be affected by both her parity and, in social species, her social rank (Altmann 1980). In general, primiparous mothers, once they have accepted and begun to take care of an infant, are much more protective of that infant than are multiparous mothers (Carlier and Noirot 1965; Shoemaker 1979; Amundin 1986). Primate mothers of low social rank may be more restrictive of their infants than are mothers of high social rank, possibly because they have little control over how an interaction between their infant and other members of the social group will progress (Altmann 1980).

PATERNAL CARE

All maternal infant care behaviors can also be exhibited by fathers, with the exception of lactation (but see Francis et al. [1994] for a report of lactation in fruit bats, *Dyacopterus spadiceus*). Paternal care encompasses those behaviors that have an immediate physical influence on young, such as feeding, carrying, grooming, protecting, and playing with infants (direct care: Kleiman and Malcolm 1981). It also includes acts performed in the absence of young that may nevertheless increase their likelihood of survival, such as shelter construction and maintenance, antipredator behavior, and provisioning of pregnant or lactating females (indirect care: ibid.).

While direct care by mothers is universal among mammals, direct paternal care is rare, occurring regularly in fewer than 5% of mammalian species (Kleiman and Malcolm 1981). Species with extensive paternal care exhibit several common characteristics. First, most have a monogamous social system, which limits male mating opportunities but allows them a higher certainty of paternity than in solitary or multimale polygynous systems (Kleiman 1977; Werren, Gross, and Shine 1980; Wittenberger and Tilson 1980). Second, most species with extensive direct male care bear altricial young; with altricial young, there is greater opportunity for male involvement to have a substantial effect on infant and maternal well-being. Paternal care is rare or absent in monogamous species bearing relatively precocial young (e.g. elephant shrews, *Elephantulus rufescens*: Rathbun 1979; Kirk's dik-dik, *Madoqua kirkii*: Komers 1996).

Paternal care is facilitated by prepartum association between the male and the female. Male Djungarian hamsters, *Phodopus sungorus*, are even active participants during parturition itself, licking birth fluids and consuming the placenta, which might have implications for the initiation of paternal behavior (Jones and Wynne-Edwards 2000). There are also pronounced changes in the male hormonal milieu in species with substantial paternal care, with decreased levels of testosterone and increased prolactin, the same hormone necessary for the maintenance of maternal behavior (Smale, Heideman, and French 2005; Ziegler 2000).

CARE BY OTHER GROUP MEMBERS

In many social mammals, individuals other than parents also provide care for neonates and infants (alloparenting: Spencer-Booth 1970). Alloparenting has been reported in callitrichid primates (Epple 1975; Box 1977; Hoage 1977), colobine primates (Hrdy 1977; McKenna 1981), elephants (McKay 1973; Lee 1987), canids (Mech 1970; Malcolm and Marten 1982; Moehlman 1986), and some bats (McCracken 1984), rodents (Sherman 1980; Hoogland 1981), cetaceans (Caldwell and Caldwell 1977), noncallitrichid/colobine primates (Fairbanks 1990), and noncanid carnivores (Rasa 1977; Rood 1978; Packer and Pusey 1983; Owens and Owens 1984). Alloparenting is less characteristic or unreported among monotremes, marsupials, edentates, elephant shrews, tree shrews, lagomorphs, insectivores, most rodent groups, pinnipeds, and ungulates (for reviews see Riedman 1982; Gittleman 1985).

The most extensive alloparenting is observed in species whose social organization typically consists of a single breeding pair and their offspring from one or more previous litters (callitrichids: Epple 1975; Box 1977; Hoage 1977; dwarf mongoose, *Helogale parvula*: Rasa 1977; Rood 1978; African wild dog, *Lycaon pictus*: Malcolm and Marten 1982). In these species, nonreproductive males and females ("helpers": Emlen 1984)—typically older offspring of the breeding pair—may participate in all infant care behaviors shown by mothers, including carrying, guarding, food sharing, and nursing, with specific behaviors observed varying by species. In social species with multiple females breeding, other mothers may also act as alloparents (e.g. African elephants, *Loxodonta africana*: Lee 1987; grivets, *Chlorocebus aethiops*: Fairbanks 1990; some bats: McCracken 1984; lions, *Panthera leo*: Schaller 1972; Packer and Pusey 1983; mice, *Mus musculus*: Manning et al. 1995).

Alloparents often are related to the young with whom they interact; by caring for a younger relative, the alloparent may increase the probability that genes it shares with the infant will be passed on to future generations (Hamilton 1964). Alloparenting may also provide "practice" that will increase the alloparent's chances of successfully rearing its own young in the future (Spencer-Booth 1970). Sometimes, though, nursing of nonoffspring young occurs inadvertently because of the difficulty in locating and recognizing offspring, particularly in species that breed in high densities (e.g. bats: McCracken 1984; northern elephant seals, *Mirounga angustirostris*: Riedman 1982; Riedman and Le Boeuf 1982).

While alloparenting is common in many species, it is important to recognize that apparent care behaviors are sometimes detrimental to young. Inexperienced females may handle young incorrectly. Among some ungulates and primates, "kidnapping" by adult females may be a form of competitive interference (Lent 1974; Mohnot 1980; Silk 1980) that decreases the probability that young will survive. Adult male cercopithecid primates may use infants as "buffers" against aggression from other males (Deag and Crook 1971; Packer 1980).

PROXIMITY TO CAREGIVERS

There is considerable interspecific variation in the spatial relationships that mothers and other caregivers maintain with the young. Some species maintain constant close contact with their offspring (fig. 29.1), while others leave offspring unattended for extended periods of time. Four basic groups of species can be identified: nesters, hiders, carriers, and followers. Nesting species leave their young in a protected den or nest. Young may be constantly attended at the nest by the mother, as in polar bears, *Ursus maritimus* (Kenny and Bickel 2005), or mothers may return at intervals to feed and care for them. Hiding, the predominant infant behavioral strategy among ungulates (Estes 1976; Ralls, Lundrigan, and Kranz 1987), involves intermittent mother-offspring contact but differs from the behavior observed in nesting species in that the hiding site is chosen by the infant (Lent 1974; Leuthold 1977) rather than being prepared by the mother. Carrier species maintain constant physical contact with their infants during early development, with infants typically clinging to the fur of the mother's back or belly (e.g. most primates, anteaters, sloths, some bats). In marsupials, carried infants are firmly attached to one of the mother's nipples during early postnatal life, then ride in the mother's pouch or on her back (in pouchless species). Following is characteristic of highly precocial species such as some ungulates (Lent 1974; Ralls, Lundrigan, and Kranz 1987) and many aquatic mammals (Ewer

Fig. 29.1. In some species, care of offspring involves constant cradling of young. (Photography by Jessie Cohen, National Zoological Park. Reprinted by permission.)

TABLE 29.2. Developmental, ecological, and social correlates of nesting, hiding, carrying, and following behavioral strategies

	Nesting	Hiding	Carrying	Following	References[a]
Degree of development at birth	Altricial	Precocial	Semiprecocial (e.g. primates) or highly altricial (e.g. marsupials)	Extremely precocial	1, 2, 3
Body size	Usually small, occasionally large	Small relative to followers	No obvious trend	Large	2, 4
Habitat	Terrestrial or arboreal	Terrestrial	Arboreal, flying, or terrestrial	Terrestrial or aquatic	1, 5
Availability of nesting or hiding sites	Present	Present	Absent	Absent	2, 6
Home range stability	Stable	Stable	Stable or nomadic	Nomadic	4
Litter size	Large	Usually one young	Usually one or two	Usually one	1, 7

[a] 1, Ewer 1968; 2, Lent 1974; 3, Nowak and Paradiso 1983; 4, Lundrigan, unpub.; 5, Jolly 1972; 6, Estes 1976; 7, Rosenblatt 1976.

1968). Follower infants are capable of independent locomotion and remain in close proximity to their mother throughout their daily activities.

Nesting, hiding, carrying, and following can be interpreted as different strategies for protecting vulnerable newborns from predators and accidents. The specific strategy used depends on a variety of ecological and social factors, as well as the degree of precociality of the infant (table 29.2). Most species adopt one strategy, but some species show a mixture of strategies, or show different strategies during different periods of development. For example, several prosimians that carry their young most of the time occasionally "park" them, leaving the young clinging to a tree branch unattended while the mother forages (Charles-Dominique 1977; Lekagul and McNeely 1977; Pereira, Klepper, and Simons 1987).

The behavioral strategy adopted by a species strongly influences the temporal distribution of parental care. The constant maternal contact provided by carrier and follower strategies allows greater flexibility and often results in more frequent suckling opportunities (e.g. every 10–15 minutes in newborn mouflon, *Ovis musimon*: Pfeffer 1967; 2–3 times per hour in infant chimpanzees, *Pan troglodytes*: Clark 1977). In contrast, hiding and nesting species can nurse only during mother-offspring reunion periods, which may be brief and infrequent. The most extreme pattern is shown by the tree shrews, nesting species in which the mother approaches the nest site only once every 48 hours to nurse the young (Martin 1968; Lekagul and McNeely 1977).

INFANTICIDE

In nature, animals often behave in ways that increase their individual reproductive success at the expense of that of conspecifics. Infanticide, the killing of immature conspecifics, may be a dramatic example of such a selfish reproductive tactic (Hausfater and Hrdy 1984). Cases of infanticide in captivity must therefore be interpreted with caution, since they do not necessarily reflect problems with the physical environment per se, but rather may be a predictable consequence of the social environment.

Infanticide in nature. Maternal infanticide in nature usually takes the form of mothers abandoning their dependent offspring. Evolutionary theory predicts that maternal abandonment should occur when the current offspring are unlikely to survive or when continuing to provide parental care for those offspring would jeopardize the survival of the mother (Packer and Pusey 1984). Abandonment enables the female to devote her limited resources to future offspring with potentially higher chances of survival. In some species that typically have multiple offspring, mothers abandon young or cease to lactate if litter size drops to one (New World marsupials: Hunsaker and Shupe 1977; lions: Packer and Pusey 1984; brown bears, *Ursus arctos*: Tait 1980).

Infanticide by females other than the mother may serve to eliminate individuals that might compete with the infanticidal female's own offspring in the future. In Belding's ground squirrels, *Spermophilus beldingi* (see Sherman 1981), and black-tailed prairie dogs, *Cynomys ludovicianus* (see Hoogland 1985), immigrant females attempt to usurp occupied territories by killing the pups of the residents. The death of a litter may precipitate abandonment of the territory, allowing the immigrant to establish herself there. Dominant females kill the offspring of subordinate females in a variety of social carnivores, including African wild dogs, wolves, *Canis lupus*, dwarf mongooses, and brown hyenas, *Hyaena brunnea* (reviewed by Packer and Pusey 1984). In several of these species the mother of the dead pups subsequently helps to care for the dominant female's young. Thus, the benefits to the dominant female are twofold: more resources are available for her litter, and an additional female is available to assist with their care. Other species in which females have been reported to kill nondescendant offspring include vampire bats, *Desmodus rotundus* (see Wimsatt and Guerriere 1961), and hamsters, *Mesocricetus* spp. (Rowell 1961).

Infanticide by males has been documented in a number of species in the wild, and often occurs when an intruder male ousts a resident male (Packer and Pusey 1984). Since females often do not return to estrus until their offspring are weaned, the killing of her dependent young may hasten a female's return to estrus and allow the immigrant male to mate with her more quickly. In Hanuman langurs, *Semnopithecus entellus*, for example, when the breeding male in a harem is replaced, the incoming male kills the recent offspring of the previous male (Hrdy 1977). Male infanticide has been reported in many mammalian species, including rodents (Hrdy 1979; Labov 1984), equids (Hrdy 1979), carnivores (Packer and Pusey 1984), and primates (Hrdy 1977; Butynski 1982; Crockett and Sekulic 1984; Leland, Struhsaker, and Butynski 1984; Collins, Busse, and Goodall 1984). Male infanticide can be easily averted in captivity by postponing introductions of new males until infants are past their period of vulnerability. In primates, for example, new males should not be introduced to groups with infants until the infants have outgrown their natal coat, and care should be taken in the process.

Infanticide in captivity. Instances of infanticide in captivity can often be traced to inadequacies of the captive social or physical environment. In some cases, its cause may be obvious (e.g. extreme overcrowding: Rasa 1979), but often infanticide appears to result from more subtle alterations in the social environment. In species that are solitary or live in single-sex groups in the wild, males present in the enclosure during infant rearing may become infanticidal (white rhinoceros, *Ceratotherium simum*: Lindemann 1982; Syrian hyrax, *Procavia capensis syriacus*: Mendelssohn 1965). In some species, the mere presence of a male in a nearby (but separate) enclosure may cause females to become infanticidal (e.g. spectacled bears, *Tremarctos ornatus*: Peel, Price, and Karsten 1979; Aquilina 1981). In monogamous species, *removal* of the male may predispose the female to maternal neglect or infanticide. For example, female bush dogs, *Speothos venaticus*, fail to rear young in the absence of the male (Jantschke 1973; I. Porton, personal communication).

Maternal infanticide may occur in response to disturbance in the physical environment. Captive female maned wolves, *Chrysocyon brachyurus*, often move young between dens when disturbed, and if alternative dens are not available, may kill young (Faust and Scherpner 1967; Brady and Ditton 1979). Other sources of disturbance that may provoke maternal infanticide include moving the parturient female to a new enclosure, excessive noise, and disturbance by human caretakers.

FACILITATING APPROPRIATE PARENTAL BEHAVIOR IN CAPTIVITY

Familiarity with a particular species' pattern of early behavioral development and parent-offspring proximity is essential to its successful management in captivity. Such familiarity allows the detection of deviations from the normal developmental pattern that may indicate problems. Followers that do not remain close to their mother, carrier infants that are found separated from their parents, and nester adults that constantly carry young are all cause for concern. Knowledge of a species' early developmental history allows exhibit designers to provide the necessary environmental features so that normal developmental behaviors can be expressed. For example, ungulates that are hiders frequently change hiding sites and thus need to have access to multiple potential hiding areas. Similarly, nesting species should be provided with a selection of appropriate nesting sites. Tree shrews are among the many species that require multiple nesting sites. Females rest separately from their young and, if provided with fewer than 2 nest boxes, often kill their offspring (Martin 1968). Knowledge of interspecific differences in early development allows informed management decisions when temporary separation of mother and young becomes necessary for medical treatment, neonatal examinations, or marking of the infant. In species with intermittent contact, the normal periods of mother-infant separation are an ideal time to gain access to the infants with a minimum of trauma. Separating infants from their mother in constant-contact species is necessarily more traumatic and disruptive.

Encouraging maternal competence can be one of the most challenging aspects of zoo animal husbandry, but it is essential for the development of self-sustaining captive populations and for the maintenance of genetic diversity within them. Rearing failures resulting from maternal neglect, abuse, or cannibalism are common in zoos for a variety of species (e.g. gorilla, *Gorilla g. gorilla*: Nadler 1975; cheetah, *Acinonyx jubatus*: McKeown, cited in Lee 1992; Laurenson 1993; aardvark, *Orycteropus afer*: Goldman 1986). Psychological stress is thought to be a primary cause of these maternal failures, perhaps because typical behavioral mechanisms for stress reduction in wild mammals are usually unavailable to zoo animals (e.g. flight) or generally ineffective in the captive context (e.g. aggression). The level of stress experienced by an individual will depend on the physical and social environment and on the individual's reaction to those conditions. Two individuals of the same species may experience different levels of stress in the same situation because of genetic or developmental differences (e.g. Joffe 1965; Suomi and Ripp 1983; see also McPhee and Carlstead, chap. 25, this volume). Zoo managers can maximize the probability of appropriate parental behavior by (1) providing each individual with the optimal social and physical environment at parturition and (2) providing each individual with a developmental environment that prepares it to deliver appropriate parental care and enables it to cope with the stressors routinely associated with zoo facilities.

Stability in both the social and physical environment during the period of parental care is often crucial. Changes in either, even if viewed as positive by zoo staff, can be experienced as at least transiently stressful by the animal. An African civet, *Civettictis civetta*, at the Philadelphia Zoo began frantically pacing following the introduction of a small pile of wood mulch into her tile-floored cage and did not stop until the mulch was removed (K. R. Kranz, personal communication). Moseley and Carroll (1992) noted extreme maternal agitation and subsequent rearing failure after the attempted periparturitional separation of a female spectacled bear and her 23-month-old male offspring. Changes in social groupings, husbandry procedures, and the physical environment—in particular, those changes required specifically for the birth (e.g. new nest boxes, removal of the male)—should be anticipated and implemented sufficiently before parturition to allow adjustment on the part of the expectant mother. All aspects of the physical and social environment should be reevaluated following any failure in parental care.

OPTIMIZING THE PHYSICAL ENVIRONMENT

It is important to provide materials that will allow for the expression of maternal behaviors. Nest boxes or dens are generally required for species bearing altricial young that are not carried with the mother (e.g. monotremes and some marsupials, carnivores, insectivores, lagomorphs, myomorph and sciuromorph rodents, pigs, aardvarks, and some prosimian primates). In some species, specific design characteristics of the nest box or den are important (e.g. overall dimensions, compartmentalization, entrance size, number of entrances, entrance tunnel), and it is critical that nest-building species be provided with the appropriate raw materials, such as leaves, straw, grasses, branches or twigs, paper towels, tissue, woodwool, or wood shavings. Multiple boxes or dens are recommended or required for some species, because adults sleep separately from infants or mothers move infants between nesting sites. Providing multiple nest boxes or dens and a variety of different nesting materials is the conservative approach and allows for choice by individuals, which can guide future changes in design and placement (reviewed by Baker, Baker, and Thompson 1996).

Human presence and activities are the most common external stressors in the captive environment, and even brief disturbances may have profound effects on parental care and offspring survival. Martin (1975) reported that a single testing of a 30-second alarm bell disrupted nursing patterns of tree shrews in his laboratory for a week and was associated with substantial increases in infant mortality in an adjacent rodent colony. Visitor presence has been shown to reduce affiliative behavior and increase agonism in some captive primates (Chamove, Hosey, and Schaetzel 1988; Fa 1989), but the paucity of data from nonprimate species makes generalization across mammalian species difficult (Hosey 2000). Regardless of a species' typical response to visitor presence, animals are likely to be less than normally tolerant of visitor disturbance after parturition. Cotton-top tamarins, *Saguinus oedipus*, on exhibit displayed higher levels of mother-young agonism and greater avoidance of offspring by parents than did individuals not on exhibit (Glatston et al. 1984). Giant pandas are particularly sensitive to ambient noise during lactation, which is thought to have had a detrimental effect on breeding success in some individuals (Owen et al. 2004). Substantial anecdotal evidence suggests that carnivores, in particular, are prone to exhibit excessive carrying behavior, neglect, and cannibalism if not offered a higher level of privacy than experienced at other times (Faust and Scherpner 1967; Roberts 1975; Brady and Ditton 1979; Peel, Price, and Karsten 1979; Paintiff and Anderson 1980; Aquilina 1981; Poglayen-Neuwall 1987; Blomquist and Larsson 1990; Hagenbeck and Wünnemann 1992). If secluded off-exhibit denning areas are not available, exhibits or buildings may have to be temporarily closed to the public after parturition (e.g. Roberts 1975).

The birth of infants, particularly in high-profile species, is also often accompanied by changes in usual caretaking routines and the increased presence in off-exhibit areas of zoo personnel who otherwise rarely visit. The following guidelines for the postpartum period can reduce the potential for stress caused by caretakers and other zoo personnel: (1) avoid changing caretaker routines in the period following parturition, except to increase the seclusion afforded the new mother; (2) avoid personnel changes in the caretaker staff; and (3) restrict or eliminate access to off-exhibit areas by nonessential personnel, especially those who are not regular visitors.

OPTIMIZING THE SOCIAL ENVIRONMENT

As a general rule, captive social environments should approximate those in the wild. Three basic aspects of social organization in the wild must be considered when planning and managing captive breeding groups:

1. Do females associate with other females during infant rearing?
2. Do males and females associate during infant rearing?
3. In social species, do parturient females seek isolation?

Sociality of females. In species in which females are generally solitary or monogamous, housing multiple females together may result in infanticide or poor reproductive success. For example, Demidoff's galagos, *Galago demidoff*, showed normal maternal care only when maintained as monogamous pairs; when housed in multifemale groups, females competed intensely for access to infants, and the infants had to be hand reared (Dulaney 1987). However, females of some species that are monogamous in the wild have bred successfully in multifemale groups when food and nesting sites were provided in abundance (e.g. dik-diks: Kleiman 1980). Conversely, females of social species may show inadequate maternal behavior when housed alone. This has been documented in a variety of captive primates, including gorillas (Nadler 1980), pig-tailed macaques, *Macaca nemestrina* (Wolfheim, Jensen, and Bobbitt 1970), and squirrel monkeys, *Saimiri sciureus* (Kaplan 1972). Separation of new mothers and infants from their social group does not appear to have the same negative effects in chimpanzees and orangutans, *Pongo pygmaeus* and *Pongo abelii*, species that typically give birth in isolation (Miller and Nadler 1980).

Extent of male-female association. In deciding whether the father should be permitted to remain in a captive family group during infant rearing, both the temporal and spatial aspects of association in nature are of critical importance. In general, if males and females are normally in close physical proximity during infant rearing in the wild, the father can be safely left in the captive social group. If females are solitary or live in single-sex groups in the wild, males should typically be separated from the female before parturition. Unfortunately, many mammalian species are small and nocturnal, and their social organization in the wild is poorly known or ambiguous.

Many mammalian species exhibit a social organization in which males and females have independent, but largely overlapping, home ranges. Males and females may share a home range without ever coming into close contact (as is common in felids and ursids). In these species, males are typically intolerant of young, even their own. In other species, males and females generally move independently but may encounter one another frequently. Males of these species may show a high degree of tolerance for infants in the wild, but may show inconsistent and unpredictable paternal reactions to infants in captivity. In some such species, individual males may be tolerant of infants, but the literature abounds with anecdotes of male infanticide and inadequate maternal care in the presence of the male (reviewed by Baker, Baker, and

Thompson 1996). No general pattern has emerged from published accounts that enables prediction of whether an attempt at leaving the male in will be successful; we recommend that, in the absence of compelling evidence that males are tolerant of infants, males be removed before parturition and reintroduced only when infants are large enough to be less vulnerable. When resources (e.g. space, resting areas, nesting areas) are much more limited in captivity than in the wild, it may be necessary, even for social species, to separate males from their mate and offspring, especially in those species in which males normally do not participate in parental care.

Seclusion of parturient females. If females normally isolate themselves from conspecifics for the period of time during and shortly after parturition, managers should consider short-term separation of expectant mothers. Mothers and new infants are sometimes separated from conspecifics in social ungulates, but in most cases it is possible to leave them with their herd mates, removing the mother-infant pair only if conspecific harassment is persistent.

Management strategies. Several things can be done to increase the likelihood that infants and other conspecifics (whether male or female) will be able to coexist peacefully. If a male is to be left in, it should be the father only. As described above, unrelated males are likely to be infanticidal, even in highly social species. Enclosures should be sufficiently large so that infants and new mothers are not forced into contact with other animals. For the same reason, enclosures should offer extra nest boxes (if appropriate for the species), visual barriers, and refuges for harassed animals. In all cases, the mother-infant pair should be watched closely for any signs of distress.

BEHAVIORAL DEVELOPMENT

Young mammals undergo profound physical and behavioral transformations between birth and the attainment of sexual maturity, changing from infants highly dependent on their mother for nourishment and protection to independently functioning adults capable of dispersal or integration into the social group. During this period of maternal dependence, young mammals are buffered from the demands of the adult world, and have the opportunity for protected growth and learning. These early experiences may greatly influence adult behavior and reproductive success. Current investigations of behavioral development clearly show that immature mammals, rather than being passive recipients of experiences that modify adult behavior, are active participants in the developmental process. Young mammals display an impressive array of behavioral strategies that appear to maximize their success and chances of survival through all stages of development (Galef 1981; Bekoff 1985).

Mammalian behavioral development is typically subdivided into 3 major periods based on the degree of maternal dependence and physical maturity (Jolly 1972). Infancy encompasses the interval from birth until weaning, and represents the period of maximal dependence on the mother. Following weaning, young animals are termed juveniles. While nutritionally independent, juveniles are frequently still dependent on their mother (or other members of the social group) for protection from predators, physical elements, and aggressive conspecifics. The final stage of development is adulthood, the period following the attainment of sexual maturity. During the transition from the juvenile period to adulthood, animals are termed subadults.

In placental mammals, early development of altricial infants primarily involves maturation of the sensory systems and development of motor coordination (Happold 1976; Rosenblatt 1976; Ferron 1981). The timing of the development of motor skills and sensory systems is closely associated with the demands of the environment, with species that inhabit more complex environments showing slower rates of maturation (Ferron 1981). Developmental landmarks for more than 400 mammalian species are tabulated in Brainard (1985) and Eisenberg (1981).

The infant's first critical tasks are initiating and sustaining suckling and, in some species, maintaining contact with nest mates (Rosenblatt 1976). At birth, altricial infants are most sensitive to thermal and tactile stimuli, which are used to locate teats and maintain contact with the mother and littermates. Infants respond to any temperature change or loss of contact with nest mates by vocalizing, which stimulates parental attentiveness (mice: Ehret and Berndecker 1986; pikas, *Ochotona princeps*: Whitworth 1984; rodents: DeGhett 1978), and by crawling in circles, which often reestablishes contact with nest mates. Heightened sensitivity to olfactory cues develops within days of birth, and the infant's responses to various situations become more specific. At this stage, infant rats learn to recognize the odors of their mother (Leon 1975), littermates (Hepper 1983), and the nest site (Carr, Marasco, and Landauer 1979).

The final stage of early development begins when the eyes open. This event typically coincides with hair growth and the ability to regulate body temperature. The infant then assumes an active role in initiating suckling, since it can detect the mother at a distance and approach her to nurse (Walters and Parke 1965). Vision permits greatly increased mobility, exploration, and interaction with littermates.

THE DEVELOPMENT OF INDEPENDENCE

Increasing maturity of the infant brings about changes in the quality of the mother-young relationship and a general trend toward decreased proximity. In species in which constant proximity was the rule early in development, the infant begins to wander farther away from its mother, and the mother's attempts to limit the infant's forays decrease (ungulates: Ralls, Lundrigan, and Kranz 1987; domestic horses: Crowell-Davis 1986; cotton-top tamarins: Cleveland and Snowdon 1984; baboons, *Papio anubis*: Nash 1978; yellow baboons, *Papio cynocephalus*: Altmann 1978; rhesus macaques, *Macaca mulatta*: Hinde and Spencer-Booth 1967). Infants of species with intermittent contact show an increased tendency to be active in the absence of the mother (white-tailed deer, *Odocoileus virginianus*: Nelson and Woolf 1987; pika: Whitworth 1984; roe deer, *Capreolus capreolus*: Espmark 1969). In both primates (Hinde 1977; Altmann 1978; Nash 1978; Hauser and Fairbanks

1988) and ungulates (Espmark 1969; Lickliter 1984), there is a gradual shift toward greater responsibility on the part of the infant for maintaining proximity.

Parent-offspring conflict. Conflict between mother and offspring during this period of growing independence is a normal and expected feature of behavioral development. This conflict arises because an offspring shares only half its genes with each parent, and therefore its interests cannot be expected to coincide completely with those of its parents (Trivers 1974). Clashes between parent and offspring arise over the amount and duration of parental care, with parents attempting to limit the total care provided to any particular offspring so that they are better able to care for other offspring.

The most widely reported manifestation of parent-offspring conflict is often termed weaning conflict, and involves disputes over the duration and frequency of individual nursing bouts and the age at which weaning occurs. Occasionally, weaning conflict is accompanied by increased maternal aggression toward her offspring (pikas: Whitworth 1984; bighorn sheep, *Ovis canadensis*: Berger 1979a; baboons: Nash 1978).

Weaning and the transition to adult feeding. The transition to adult feeding is perhaps the most critical milestone in early mammalian development. In some species, weaning is abrupt and highly predictable. For example, hooded seal pups, *Cystophora cristata*, which show the shortest period of suckling known among mammals, are completely weaned at 3–5 days of age (Bowen, Oftedal, and Boness 1985). For the vast majority of species, however, weaning is a slow, gradual process characterized by decreasing milk intake and a corresponding increase in the consumption of solid food (e.g. African elephants: Lee and Moss 1986; cervids: Gauthier and Barrette 1985; baboons: Nash 1978; Rhine et al. 1985).

Weaning is ultimately achieved through the efforts of both mother and young. Mothers may discourage suckling by adopting postures that make it difficult for the young to reach the nipples (tree shrews: Martin 1968), and often actively reject suckling attempts (vervet monkeys: Hauser and Fairbanks 1988; cervids: Gauthier and Barrette 1985; cotton-top tamarins: Cleveland and Snowdon 1984; baboons: Nash 1978). Additionally, mothers may promote independent feeding by bringing food items to the young (beavers, *Castor canadensis*: Patenaude 1983; golden lion tamarins, *Leontopithecus rosalia*: Hoage 1982; dholes, *Cuon alpinus*: Johnsingh 1982; cats: Leyhausen 1979). Young may contribute to the weaning process by decreasing their attempts to suckle and increasing their interest in alternative foods as they grow more able to provide for themselves (Roberts, Thompson, and Cranford 1988) and mother's milk becomes insufficient for maintaining their growth (Galef 1981).

Most infants are capable of adequately feeding themselves long before the complete cessation of suckling. African elephant calves, for example, normally suckle for about 5 years, but calves orphaned at only 2 years of age can survive on solid food alone (Lee and Moss 1986). Additionally, the timing of weaning appears to be sensitive to the availability of solid food in the environment (vervet monkeys: Lee 1984; bighorn sheep: Berger 1979a). In captivity, where food is plentiful, weaning may occur weeks or even months earlier than in free-ranging populations (Ewer 1973). Thus, the time at which infants first become nutritionally independent is difficult to pinpoint using behavioral indicators and often can be determined only through anecdotes or experimental means.

Making the transition from nursing to eating solid food is far more complex than simply substituting one type of food for another. The process can involve engaging in specialized behaviors that prepare the infant's digestive system for the digestion of solid food, learning to discriminate appropriate foods from potentially harmful ones, and developing complex food acquisition skills, such as hunting.

In herbivores, digestion of plant material depends on microorganisms living in the animal's gut. At birth, the digestive system is virtually devoid of these essential microorganisms (Eadie and Mann 1970), and young must inoculate themselves to enable their digestive system to assimilate plant material. Behaviors that may serve this purpose include licking the lips and tongue of the mother, which could result in the transfer of microbes in the saliva (Hungate 1968), feeding on plants that have maternal saliva remaining on them (elephants: Eltringham 1982), and eating the feces of the mother or other adults (domestic horses: Crowell-Davis and Houpt 1985; African elephants: Guy 1977). Koalas, *Phascolarctos cinereus*, have a specialized method for transferring digestive microbes from mother to offspring. At about 5 months of age, when the infant's teeth are beginning to erupt, the mother begins producing a special defecate composed of partially digested plant matter from the cecum, the organ in which microbial digestion occurs. The infant koala receives feedings of this material at 2- to 3-day intervals for 1–6 weeks, after which it is capable of feeding independently (Martin and Lee 1984; Thompson 1986).

Parents, particularly the mother, often play a prominent role in the acquisition of feeding skills, and premature separation of infants from their family group may have lasting detrimental effects. Even young that are no longer nursing may be dependent on their parents for acquiring food preferences and honing feeding skills critical to their future survival and well-being. Preferences for particular food items may be learned from adult conspecifics through observation and imitation (Edwards 1976; Leuthold 1977; Provenzo and Balph 1987) or through food sharing (Hoage 1982; Ruiz-Miranda et al. 1999). Learning plays a particularly important role in the development of adult feeding in carnivores. In felids, for example, kittens first observe their mother killing and consuming prey, then interact with prey captured by their mother, and finally progress to killing prey independently of their mother (Caro and Hauser 1992).

Premature separation of mother and infant may result in aberrant or incompetent feeding behaviors. Regurgitation and reingestion of food is widespread among captive gorillas, yet absent in the wild. Wild-caught and captive-born hand-reared gorillas show much higher rates of regurgitation and reingestion than captive-born mother-reared individuals, suggesting that this abnormal behavior may result in part from deficits in early social development (Gould and Bres 1986). In predatory species, lack of experience with prey items in early development leads to a lack of ability or inclination to hunt live prey in adulthood (Adamson 1960, 1969; Leyhausen 1965; Ewer 1973).

If captive-born young must be hand reared, prompt reintroduction to adult conspecifics may allow the development of normal feeding strategies. Providing a captive environment that allows the normal development of feeding skills is especially important when reintroduction to the wild is a goal, since animals deprived of early experience may never become fully competent at foraging in a natural setting.

PLAY

Play is one of the most conspicuous behaviors exhibited by young mammals and has been described in almost all mammalian orders (Fagen 1981). It appears to be especially frequent and elaborate in the primates, carnivores, ungulates, and rodents, and it is in these taxonomic groups that play has been most thoroughly studied. Theorists have had great difficulty formulating a comprehensive definition of play behavior, because it is so diverse and so closely resembles other types of behavior, such as aggressive combat, prey catching, and predator avoidance (ibid.; Martin and Caro 1985). Martin and Caro (ibid.), after reviewing various definitions of play, concluded that play is best characterized by the *absence* of the endpoints in which "serious" versions of the behavior patterns culminate. For example, play fighting does not result in injury or differential access to a disputed resource; likewise, predatory play does not involve killing and consuming prey. There has also been much speculation about the precise benefits young animals receive from play; but research in this area has been sparse, and the function of play still remains somewhat obscure. Growing evidence suggests that play causes permanent changes in the developing nervous system, thus allowing animals to react appropriately to unpredictable events that are physically and emotionally challenging (Byers and Walker 1995; Spinka, Newberry, and Bekoff 2001).

Characteristics of juvenile play. Play is commonly subdivided into 3 basic categories: object, locomotor, and social (Fagen 1981). These categories are not entirely mutually exclusive, however, since object and locomotor play frequently occur in social contexts, and elements of all 3 types of play frequently occur within single play bouts. Object play involves repetitive manipulation of objects in the infant's environment, and often incorporates behaviors used in foraging or in the handling and capture of live prey, although many of the more inventive manipulations have no obvious parallel in the adult behavioral repertoire. Locomotor play is composed of vigorous body movements such as running, jumping, head tossing, and body twists and typically bears a strong resemblance to the behaviors seen in predator evasion (Wilson and Kleiman 1974) (fig. 29.2). Social play involves the interactions of 2 or more individuals, each of whose movements are oriented toward the other and whose responses are influenced

Fig. 29.2. Locomotor play in Asian elephant calves. (Photograph courtesy of Ringling Brothers and Barnum & Bailey Center for Elephant Conservation. Reprinted by permission.)

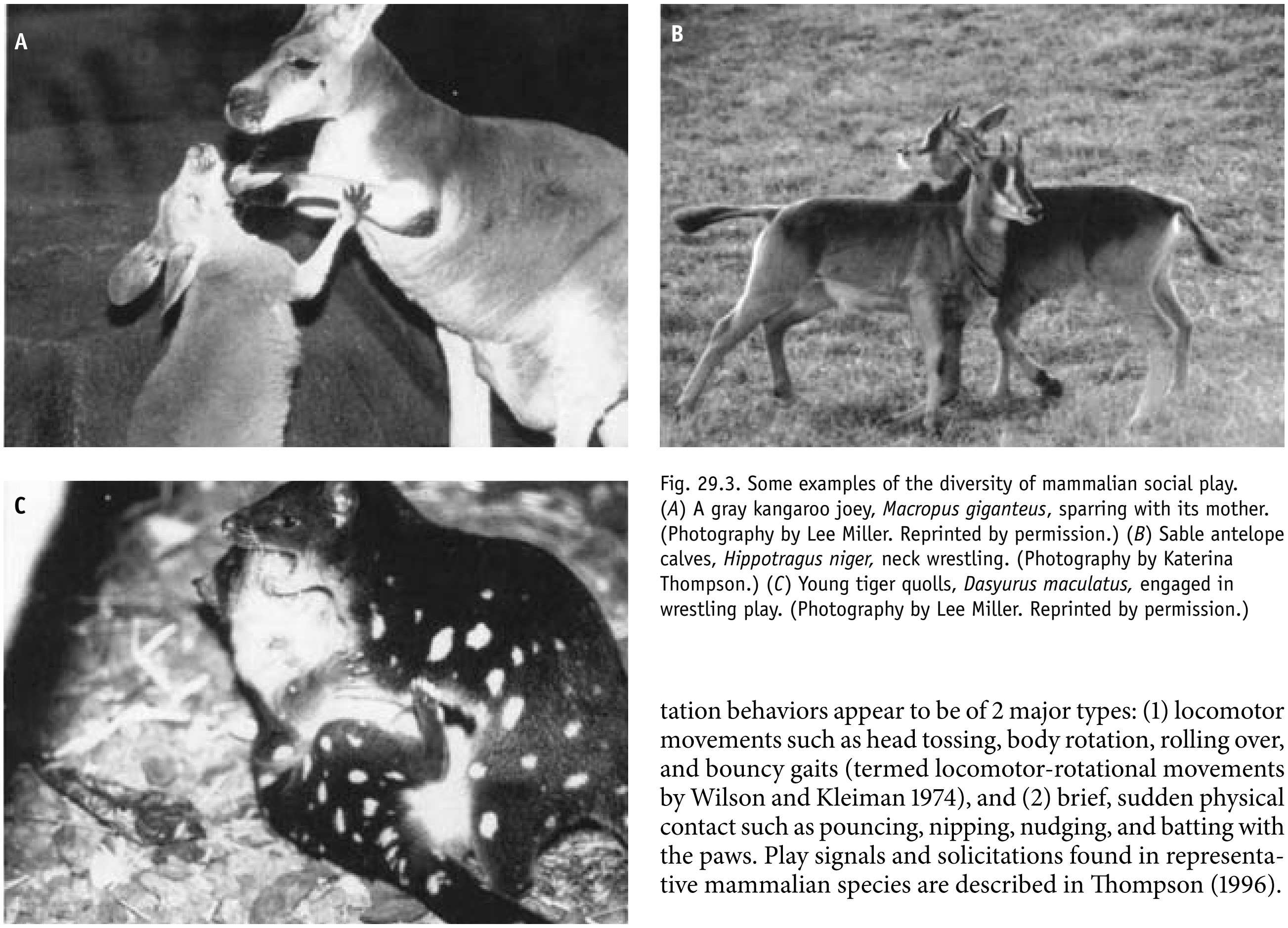

Fig. 29.3. Some examples of the diversity of mammalian social play. (*A*) A gray kangaroo joey, *Macropus giganteus*, sparring with its mother. (Photography by Lee Miller. Reprinted by permission.) (*B*) Sable antelope calves, *Hippotragus niger,* neck wrestling. (Photography by Katerina Thompson.) (*C*) Young tiger quolls, *Dasyurus maculatus,* engaged in wrestling play. (Photography by Lee Miller. Reprinted by permission.)

by the other's actions (fig. 29.3). Common forms of social play include play fighting, which mimics serious fighting, and approach-withdrawal play, in which individuals take turns chasing and being chased.

In general, solitary forms of play (object and locomotor play) precede social forms in ontogeny. There is also a general trend toward increasing play complexity and more interactive play as the infant matures. While play frequency, complexity, and duration peak during infancy and the juvenile period, play sometimes persists at low levels into adulthood, especially in captive animals. Most social play in adults is directed toward offspring and younger siblings (reviewed by Thompson 1996).

Play is frequently accompanied by the presence of play signals, communicatory behaviors that occur virtually exclusively in the context of play. These signals, typically vocalizations or facial expressions, may be displayed almost continuously throughout play bouts and, because of their specificity, are useful indicators of the playful nature of social interactions. The play face (fig. 29.4), characterized by a relaxed, open-mouthed expression with the lips usually covering the teeth, appears to be an almost universal mammalian play signal. In addition to play signals, certain specific behaviors, known as play solicitation behaviors, tend to be associated with the initiation of social play bouts. Play solicitation behaviors appear to be of 2 major types: (1) locomotor movements such as head tossing, body rotation, rolling over, and bouncy gaits (termed locomotor-rotational movements by Wilson and Kleiman 1974), and (2) brief, sudden physical contact such as pouncing, nipping, nudging, and batting with the paws. Play signals and solicitations found in representative mammalian species are described in Thompson (1996).

Sex differences in play. Male juveniles engage in social play more frequently and more vigorously than their female peers, particularly in species with polygynous mating systems where adult males must aggressively compete for mates (Meaney, Stewart, and Beatty 1985). In species in which frequencies of adult aggression are similar between the sexes, no sex differences are seen in juvenile play (meerkats, *Suricata suri-*

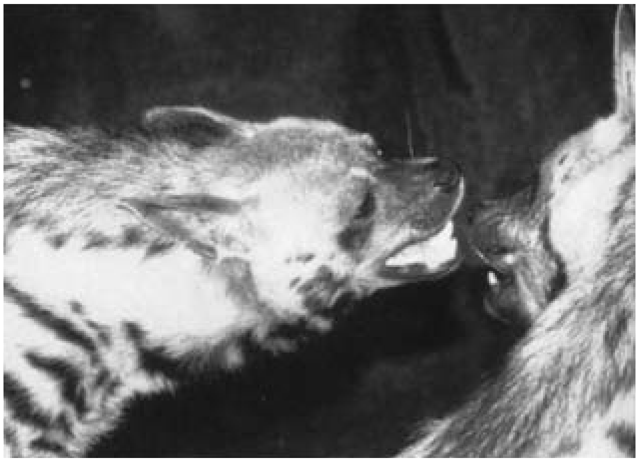

Fig. 29.4. Two striped hyenas, *Hyaena hyaena,* exhibiting play faces during a play bout. (Photography by Lee Miller. Reprinted by permission.)

catta: Sharpe 2005; monogamous canids: Bekoff 1974; Hill and Bekoff 1977; monogamous primates: Stevenson and Poole 1982; solitary mustelids: Biben 1982a; solitary felids: Lindemann 1955; Barrett and Bateson 1978). Sex differences in locomotor play are apparently uncommon. Most studies have found little difference between the sexes in locomotor play (e.g. gorillas: Brown 1988; bighorn sheep: Berger 1979b), but occasionally female juveniles exhibit more of this type of play (domestic horses: Crowell-Davis, Houpt, and Kane 1987; domestic sheep: Sachs and Harris 1978).

Social and environmental factors influencing play. The particular individuals with which a juvenile initiates social play are determined by a multitude of factors. In general, play is more likely among relatives and among individuals that are close in age. In species where sex differences in play are pronounced, individuals may show positive assortment by sex or may favor partners of one sex over the other. Thus, play is usually facilitated in large social groups, since they are more likely to contain cohorts of similarly aged immature animals.

Play frequency is severely affected by food scarcity (Baldwin and Baldwin 1976; Müller-Schwarze, Stagge, and Müller-Schwarze 1982), but this effect is only temporary. In fact, when the quality and quantity of food resources are restored to favorable levels, play rebounds, often reaching frequencies higher than exhibited before periods of food scarcity (vervet monkeys: Lee 1984; rhesus macaques: Oakley and Reynolds 1976). This finding suggests that juveniles may be able to compensate for brief periods of play deprivation by increasing subsequent play frequencies, in effect "making up for" lost play time. Play may also be inhibited by extremes of temperature (Rasa 1971; Oakley and Reynolds 1976; Crowell-Davis, Houpt, and Kane 1987).

Play is often facilitated in habitats with certain specific features. Play in several species of ungulates is concentrated on grassy slopes, sandbowls, and snowfields (Darling 1937; Altmann 1956; Berger 1980). Collared peccaries, *Pecari tajacu*, play preferentially on well-worn, scent-marked "playgrounds" near bedding sites (Byers 1985), and play bouts occurring there involve more individuals and last longer than play bouts in other locations. Sandboxes, where a great deal of scent marking occurs, are the preferred sites for locomotor play in captive salt desert cavies, *Dolichotis salinicola* (see Wilson and Kleiman 1974). The physical attributes that make these locations popular sites for play have yet to be identified, but perhaps they are places that are relatively safe from predation and where the risk of injury is low.

Not surprisingly, sick animals play less than healthy ones (Fagen 1981), and lack of play may be one of the first symptoms of illness. Gaughan (1983) reported the case of a captive snow leopard female that, in contrast with others studied, rarely played with her cubs. Her lack of play was noted by observers well before the appearance of more obvious signs of illness, such as lethargy and loss of appetite. Medical examination revealed the animal to be seriously ill. Heavy parasite infestation may similarly inhibit play (bighorn sheep: Bennett and Fewell 1987; elk, *Cervus canadensis nelsoni*: Altmann 1952).

Promoting play in captivity. Captivity, which produces profound changes in an animal's immediate physical and social environment, often has significant effects on play. In general, play is more frequent in captive animals than in their free-ranging counterparts. For example, Stevenson and Poole (1982) observed common marmosets, *Callithrix jacchus*, in a free-ranging Brazilian population and in a laboratory colony, and noted that social play was much more frequent in captivity. The higher rates of play seen among captive animals are commonly attributed to unlimited food resources and the absence of predators (Shoemaker 1978).

Adult animals, in particular, seem to show more play in captivity (Fagen 1981). Fagen (ibid.) suggested that this might represent a reversion to a more infantile state, since in captivity virtually all of an animal's needs are provided for.

Since play is sensitive to so many social and environmental factors, its presence or absence in captive individuals can be used as an index of the adequacy of the captive environment. Observations of "too little play" have indeed been the impetus for reevaluation of the appropriateness of exhibit substrates, the quantity of shade, and herd parasite load in at least one zoo (Bennett and Fewell 1987).

It is desirable to provide captive animals with ample opportunities for play. Playing animals are highly visible to zoo visitors and are likely to hold a visitor's attention for a longer period of time. Also, several studies have shown that exhibit modifications that increase the amount of time captive animals spend playing often result in substantial decreases in abnormal behaviors (e.g. chimpanzees: Paquette and Prescott 1988). Play experience has further been shown to lessen the damaging effects of early social deprivation in rats (Einon, Morgan, and Kibbler 1978; Potegal and Einon 1989).

Some objects and exhibit modifications that promote play in captive animals are listed in table 29.3. The most important features of play objects are novelty and the ability to stimulate multiple senses (Kieber 1990; Paquette and Prescott 1988; Hutt 1967). Rotating play objects among different enclosures is a highly effective way of preserving their appeal (Kieber 1990; Paquette and Prescott 1988). If preserving the natural appearance of the exhibit is a primary objective, conspicuously man-made play objects can be restricted to off-exhibit areas (Kieber 1990).

The enigmatic nature of the function of play makes it extremely difficult to assess whether immature animals in captive environments are obtaining adequate amounts and types of play experience. Perhaps the most conservative approach to ensuring optimal juvenile development is to attempt to mimic natural social groupings and features of the native habitat such that opportunities for locomotor, object, and social play are as similar as possible to those of free-ranging animals. All captive immature animals should be provided with enough space to engage in vigorous locomotor play, a variety of objects to manipulate, and conspecifics, preferably of similar ages, with which to engage in social play. Allowing access to a wide range of play experiences may be the best way to ensure that captive animals avoid physiological and behavioral deficits.

TABLE 29.3. Methods of promoting play behavior in captive mammals

Taxonomic group	Exhibit modification or addition	Type of play promoted	References
Ungulates	Open space	Locomotor	
	Hills, sloped surfaces, rock piles	Locomotor and social	
Carnivores	Wooden balls, leather balls, sticks, stones, logs, tires, cardboard boxes, large paper bags, hanging rope, plastic jugs (with lids removed), rawhide bones, beef bones	Object	Kieber 1990; Biben 1982b; Hediger 1968
	PVC tubing	Locomotor	Biben 1982a
Rhinoceroses and elephants	Planks, stumps, blocks of wood	Object	Hediger 1968
Aquatic mammals	Pieces of floating wood, blocks of ice with embedded fish	Object	Sanders 1987; Hediger 1968
Monkeys	Networks of branches with flexible attachment points, hanging milk crates, rope swings	Locomotor	Clark 1990; Hutchins, Hancocks, and Crockett 1978
	Nylon balls	Object	Renquist and Judge 1985
Great Apes	Tire swings	Locomotor	Paquette and Prescott 1988
	Loose tires, burlap feedbags, heavy rubber feed tubs, heavy plastic drums (cut in half), straw or hay, branches, rubber balls	Object	Cole 1987; Goerke, Fleming, and Creel 1987; Cole and Ervine 1983; Sammarco 1981; Brent and Stone 1996

DEVELOPMENTAL EFFECTS ON PARENTAL CARE

EARLY POSTNATAL EXPERIENCE

Mother rearing versus hand rearing. It is accepted as near doctrine that mother-reared animals are more likely to exhibit competent parental behavior themselves than are individuals reared by human foster parents (e.g. Kleiman 1980). Negative effects of hand rearing on adult maternal behavior have been documented for several primate and laboratory species (rhesus macaques: Harlow, Harlow, and Suomi 1971; Ruppenthal et al. 1976; gorillas: Ryan et al. 2002; domestic rats: Thoman and Arnold 1968). On the other hand, Martin (1975) reported that hand-reared tree shrews, *Tupaia belangeri*, and lesser mouse lemurs, *Microcebus murinus*, were as successful as mother-reared individuals, and indicated that under certain circumstances hand-reared individuals could be more successful because they are less reactive to human disturbance.

For most species, however, data are distressingly lacking. While there are literally hundreds of reports of hand rearing in the literature, information on the subsequent parental behavior of the hand-reared individuals is rarely published. In general, single institutions do not have sufficient sample sizes for valid comparisons of mother-reared versus hand-reared individuals, but the information is often obtainable through multi-institutional surveys or studbooks. We suspect that the paucity of reports is partially due to the fact that hand-reared individuals of some species are less likely to reproduce at all, reducing opportunities to assess impact of hand rearing on parental behavior. Studbook keepers could contribute to our understanding of this issue by analyzing their databases for any differences in reproductive and rearing success between hand-reared and mother-reared individuals, and including these results in their studbooks (e.g. Rettberg-Beck and Ballou 1988 for golden lion tamarins).

Although hand rearing is sometimes suggested to produce more tractable adults (e.g. duikers: Barnes et al. 2002) or because of the lower infant mortality rates for certain species or individuals, the following section is written with the assumption that in most cases mother rearing is preferable.

Alternatives to hand rearing. Some degree of human intervention is often unavoidable for infants whose mother has died or who have had to be removed from their mother because of maternal abuse, neglect, or illness. A number of methods have been developed to avoid birth-to-weaning rearing by a human caretaker (Watts and Meder 1996).

In some cases, after a short period of hand rearing, infants can be returned to biological mothers that were initially unresponsive or incompetent (e.g. orangutan: Cole et al. 1979; Keiter, Reichard, and Simmons 1983; aardvark: Wilson 1993). Tranquilization of the mother to facilitate acceptance has been reported occasionally (giraffe, *Giraffa camelopardalis*, and camel, *Camelus dromedarius*: Gandal 1961; orangutan: Cole et al. 1979; margay, *Leopardus wiedii*: Paintiff and Anderson 1980), as has confinement of the mother in a small space with her litter (lemurs: Katz 1980; red-ruffed lemur, *Varecia rubra*: Knobbe 1991; cheetah: Laurenson 1993; golden lion tamarin: A. J. Baker, personal observation), although the latter technique may provoke abuse or cannibalism. Zhang et al. (2000) reported the reintroduction of an infant giant panda to its mother after the mother was given a stuffed panda toy covered in her infant's urine. After several weeks of exposure to the toy, during which the female began to respond maternally to it, the infant was successfully reintroduced. In any reintroduction of an infant, the risk of injury to the infant and the ability of zoo staff to intervene if necessary must be assessed in advance.

Alternatively, infants can be fostered to conspecific females (see Baker, Baker, and Thompson 1996 for review). This technique is most likely to work in species that bear altricial young and in which mothers lack strong infant identification mechanisms. Among species that bear precocial young and have strong and early bonding mechanisms (e.g. ungulates), fostering can potentially be accomplished if the foster mother has had little or no contact with her own infant and the infant to be fostered is presented shortly after parturition (domestic sheep: Smith, Van-Toller, and Boyes 1966; domestic cattle: Hudson 1977; domestic goats: Klopfer and Klopfer 1968), or if feces or birth fluids from the biological offspring are rubbed on the neonate to be fostered (Hart 1985). Tranquilizers have been used to facilitate acceptance of foster neonates in domestic sheep (Neathery 1971), and might be considered in attempts to foster an exotic neonate to a female of a domestic species.

It is sometimes possible to provide supplementary feeding to infants that remain with their mother, e.g. in cases in which primate mothers will otherwise care for their infants but will not nurse them, or in which females cannot provide sufficient milk because of physiological problems or large litter size. Mothers can be trained to tolerate this feeding while the infant is being carried (e.g. orangutan: Fontaine 1979), or the infant can be removed for feeding. Infants themselves have also been trained to approach a caretaker for feeding, which allows them to be reintroduced to a social group before weaning is complete (ungulates: Read 1982; Mayor 1984; stump-tailed macaque, *Macaca arctoides*: Chamove and Anderson 1982; Celebes macaque, *Macaca nigra*: Hawes et al. 1991).

Managing hand-reared infants. The most extensive information on the maternal competence of hand-reared females comes from work on rhesus macaques (Ruppenthal et al. 1976; Suomi and Ripp 1983), which shows that early integration of hand-reared infants into a peer group and maintaining stability of social groups throughout adulthood and parturition greatly reduce the rate of neglect and abuse by "motherless mothers." This result is probably broadly applicable for mammals and suggests the following conservative guidelines for mammalian hand rearing. Infants should be reared with a peer (preferably a conspecific or, alternatively, an individual of a closely related species) whenever possible, even if transfer of individuals between institutions is necessary. With some species, it may be necessary to isolate infants initially to prevent injurious sucking (mouse lemurs: Glatston 1981; cats: Richardson 1991; red pandas, *Ailurus fulgens*: Glatston 1992; gazelles: Lindsay and Wood 1992). For solitary species, conspecific contact should be continued until the age at which the individual might disperse from its littermates and/or mother. For social species, the ultimate goal should be integration into a stable social unit, ideally one mirroring a "natural" group.

LATER POSTNATAL EXPERIENCE

Postweaning socialization can be very important in the development of appropriate maternal behavior, especially for individuals that experience social deficits before weaning. Rogers and Davenport (1970) found that common chimpanzees that had remained with their mother for more than 18 months were more successful in rearing their own infants than were individuals separated from their mother before this age. Wild Japanese macaques, *Macaca fuscata*, orphaned before 4 years of age were more likely to mishandle and less likely to rear their first infants than were nonorphaned females, although they were as successful as nonorphans with subsequent infants (Hasegawa and Hiraiwa 1980). In general, it is advisable to provide juvenile and subadult animals the same opportunities to interact with infants, peers, parents, and other elders that they would have in a typical natural social group.

In the wild, females of many group-living species are exposed to infants before their own first parturition, which gives them the opportunity to become accustomed to (or perhaps lose fear of) the visual, olfactory, and auditory stimuli presented by neonates. Among cooperatively breeding species, mostly primates and carnivores (callitrichids: Epple 1975; Box 1977; Hoage 1977; dwarf mongoose: Rood 1980; African wild dog: Malcolm and Marten 1982), pre-reproductive subadults and adults are not only exposed to neonates but also participate in all facets of infant care except nursing. Studies on captive primates (reviewed by Hannah and Brotman 1990; Baker, Baker, and Thompson 1996; Kuhar et al. 2003; Leong, Terrell, and Savage 2004) suggest that individuals with pre-reproductive infant-handling experience have greater rearing success with their own. Cornell et al. (1987) suggest that nulliparous bottle-nosed dolphins, *Tursiops truncatus*, also benefit by being housed with females that are rearing calves.

Adjustment to human presence during infancy can reduce the stress that a captive individual experiences as a reproductive adult. The caretaker-animal relationship developed during this time probably affects the individual's perception of the threat represented by humans in general. Mellen (1988) advocates daily handling of mother-reared small cats as a technique for reducing adult fearfulness, and Petter (1975) suggests a similar procedure for mouse lemurs.

EXPERIENCE AS A MOTHER

Rearing failure with first infants or litters is common in zoos and is not necessarily predictive of failure with subsequent young, since a female's maternal skills typically improve with experience. In making decisions regarding removal of infants from primiparous females or previously unsuccessful multiparous females, several points should be considered.

Baker, Baker, and Thomson (1996) found relatively low rearing success among primiparas for a number of species, with a particularly high representation of primates and carnivores. This pattern held for both captive and wild populations. In many species, captive individuals may give birth at an earlier age than do their wild counterparts (e.g. gorillas: Harcourt 1987); psychosocial immaturity (i.e. age effects independent of parity effects) may therefore be an additional factor in the high rate of failure among primiparous females in captivity. Analyses of available records (e.g. by studbook keepers) to separate age and parity effects, clarify any systematic taxonomic variation in such effects, and elucidate potential interactions between parity, age, and hand rearing versus mother rearing would be useful for shaping managers' expectations and guiding their actions.

Second, variation in maternal behavior is to be expected, and apparently aberrant behaviors that are not directly threatening to infants often should be tolerated (e.g. Maple and Warren-Leubecker 1983), especially with primiparous females.

Finally, experience with one offspring, whether ultimately successful or not, can increase the probability of appropriate behavior toward subsequent offspring. "Motherless mother" rhesus macaques allowed to keep an infant for at least 2 days, even if they were abusive, were more likely to rear their next infants than were females who had less than 2 days of infant contact (Ruppenthal et al. 1976).

CONCLUSIONS

Understanding parental behavior and the natural course of development in each mammalian species is critical for ensuring that the captive population remains viable and self-sustaining. We now know that deficits in early development (most notably social development) have far-reaching and often permanent consequences (see also McPhee and Carlstead, chap. 25, this volume). The best way to ensure that captive-born infants become competent adults is to allow infants to be mother reared in a diverse and spacious physical environment and in a social environment that closely approximates that in the wild. When mother rearing is not possible, other alternatives, in order of their desirability, are (1) using another lactating female as a foster mother, (2) hand rearing the infant without removing it from the social group, and (3) hand rearing the infant with conspecific peers. Before removing infants for hand rearing, zoo staff must weigh the value of the experience that the new mother might gain along with the perceived risk to the infant, the likelihood of successful hand rearing, and the likelihood of subsequent behavioral competency in the hand-reared individual. These factors, in turn, will depend on such variables as the history of the female, the age of the female, the sex of the infant(s), the species-specific value of maternal experience, and the species-specific effects of hand rearing on behavior. Long-term gain in maternal competence often may outweigh the short-term loss of a single infant or litter, but for many species, we are still lacking the data necessary to make informed decisions.

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30

Data Collection in the Zoo Setting, Emphasizing Behavior

Carolyn M. Crockett and Renee R. Ha

INTRODUCTION

Systematic observations and record keeping are essential for consistent advances in the management of zoos and related facilities. Casual observations of the outcomes of innovative exhibit modifications are of much greater value when supplemented by data collected using appropriate quantitative methods. Quantification is important because qualitative observations may provide inaccurate estimates of what is really occurring. A great deal of "success" in zoo exhibitry may be serendipity—the right combination of individual animals that happen to be of a species able to thrive in marginal conditions. Only systematic data collection can lead to the conclusion that particular management decisions had anything to do with success.

This updated chapter benefits from the expertise of a second author (RRH), who has taught a zoo behavior course incorporating new data collection technologies, and whose background includes teaching statistics. We provide an overview of techniques sufficient to allow an inexperienced researcher to design and conduct a quantified study of zoo animals. Observational research on behavior is emphasized, but we suggest ways these methods can be applied to the systematic collection of other data pertinent to zoo management. For further details on methodology, serious researchers should consult Bakeman and Gottman (1997), Martin and Bateson (1993), Altmann (1974, 1984), Lehner (1996), and Sackett (1978b).

As this chapter covers a variety of topics, we recommend that the reader skim the section headers in advance for a preview of content and organization.

PLANNING A ZOO RESEARCH PROJECT

Most research in zoos is nonexperimental. The researcher usually is unable to manipulate environmental conditions or group membership in a well-controlled manner. Collection of physical information (e.g. measurements, urine specimens) may be too invasive to perform on a regular basis. Thus, many studies are primarily descriptive and based on observational data. Information is collected, and after some period of time, an effort is made to determine what it means. Such studies frequently remain unpublished because of their unfocused and possibly ungeneralizable conclusions. This fate can be avoided by clearly identifying research questions before beginning data collection.

FORMULATION OF A RESEARCH QUESTION

Data collection methods are designed with respect to the question being asked, and therefore, an appropriately formulated question is the first step in research design (Altmann 1974). Research questions may develop out of interest in a particular aspect of the animal's biology or behavior. Alternatively, a management issue may have arisen that requires research to address. Identifying a research question usually requires preliminary "reconnaissance" observations (Lehner 1996). In a zoo setting, possible research questions might include the following:

1. Is visitor interest higher when animals are more active? For example, Margulis, Hoyos, and Anderson (2003) evaluated the effect of felid activity on visitor interest.
2. What steps can zoos take to reduce aggression between surplus males? For example, can endogenous levels of testosterone be suppressed using Gonadotropin-releasing hormone (GnRH) and result in reduced aggression between males, e.g. several species of ungulates (Penfold et al. 2002)?
3. What behavioral indicators of pregnancy can be identified, and are they correlated with physical characteristics, e.g. lowland gorillas, *Gorilla gorilla gorilla* (Meder 1986) (fig. 30.1)?

Fig. 30.1. Zoo research might focus on the behavioral indicators of pregnancy. Lowland gorilla Nina supports one-hour-old infant Zuri, still attached by the umbilical cord. (Photography by Carol Beach, Woodland Park Zoo. Reprinted by permission.)

4. Does pacing decrease in felids when food is presented more frequently during the day (Shepherdson et al. 1993)?

RESEARCH DESIGN CONSIDERATIONS

Independent and dependent variables. After identifying the research question, the next step is to identify the relevant dependent and independent variables. A variable is any property that may take on different values at different times and may change with various conditions. The values can be one of 4 types:

1. Nominal data are on a categorical, and often qualitative, scale rather than one that is quantitative.
2. Ordinal data are on a categorical scale, in which categories can be ranked in relative order.
3. Interval data are collected in a manner that measures actual magnitude and which has equal intervals between possible scores, but does not have a meaningful absolute zero point.
4. Ratio data are collected in a manner that measures magnitude, has equal intervals between possible scores, and contains an absolute zero point (table 30.1).

TABLE 30.1. Summary of the properties of measurement scales

Scale	Order	Magnitude	Equal intervals	Absolute zero
Nominal	No	No	No	No
Ordinal	Yes	Some	No	No
Interval	Yes	Yes	Yes	No
Ratio	Yes	Yes	Yes	Yes

The property that the researcher either manipulates experimentally or records as a naturally changing condition is described as the *independent variable*. A clear distinction between the *independent variable* and the *dependent variable* is that the independent variable is the predictor variable. The dependent variable is the response variable, or what the observer actually measures. The dependent variable is often referred to as the outcome variable (Ha and Ha, forthcoming).

Some independent variables are interval variables, such as ambient temperature or time of day. Others are nominal variables, such as sex (male or female), enclosure type (naturalistic or bare concrete), or physical condition (pregnant or not pregnant). It is important to consider that interval variables can be grouped into nominal categories (e.g. morning and afternoon; hot, warm, cool, cold [could also be ordinal rank of declining temperature]). Independent variables can also include age/sex composition of groups, the rearing conditions of individuals whose behavior serves as dependent variables, food delivery schedule, size of enclosure, and many others (fig. 30.2). Thus, the importance of having accurate and systematic records available to draw on becomes obvious. Furthermore, when independent variables of particular interest are identified in advance, they can be specified and filled in on each data collection sheet.

Dependent variables can include behavioral measures such as rates of aggression, sexual behavior, or play (fig. 30.2). They can also be physical measurements such as food intake or weight. Occurrence of injuries, interbirth interval length, and infant survival rate are some dependent variables that can be derived from daily reports.

Alternative hypotheses, confounding, and bias. Much research in zoos is descriptive in nature (we don't know what is going on and want to find out). However, research data are most amenable to statistical analysis and interpretation when null and alternative hypotheses are specified beforehand. The null hypothesis suggests that any effect or relationship between 2 variables is due to chance factors, whereas the alternative hypothesis proposes that there is an effect or relationship between the variables of interest.

Whether or not a specific hypothesis is formulated, the methodology must be appropriate for ruling out alternative hypotheses. For example, the researcher may hypothesize that males use the top branches in an enclosure more than females do. Suppose that data are collected on males in the morning and on females in the afternoon. Further suppose that these data suggest that males do use the top branches a greater percentage of the time. Under these circumstances, one cannot rule out the alternative hypothesis that animals, regardless of sex, spend more time in the top branches in the morning. In other words, time of day and sex are confounded in this study, and we cannot determine which effect (time of day or sex) is driving the result. (In this example, the independent variables are sex *and* time of day, while the dependent variable is the percentage of time spent in the top branches.)

A common goal of zoo research is to identify changes in behavior occurring as a result of a change in the zoo envi-

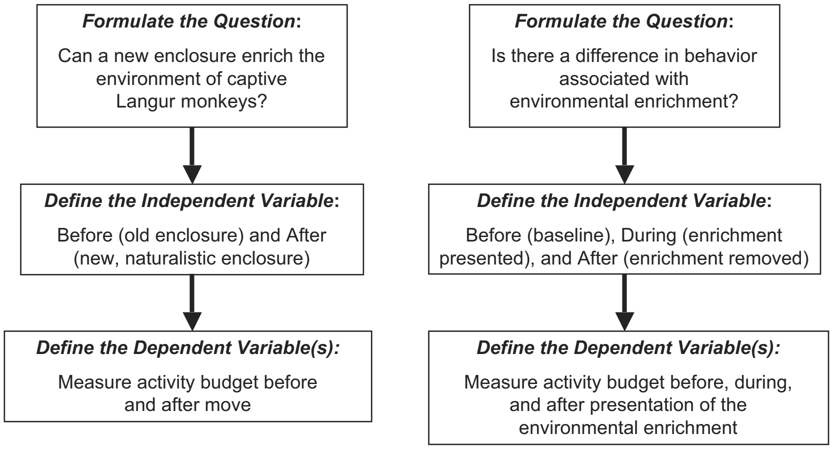


Fig. 30.2. Independent and dependent variables and 2 research designs. (Little and Sommer 2002; Young 2003.)

ronment, such as the addition of "furniture" or the introduction or loss of a group member. To assess unambiguously the effects of such a change, all other factors must be held constant. Since such control is often difficult or impossible in a zoo setting, the interpretation of results must take into account the possible effects of any extraneous, uncontrolled events. For example, if a new branch were introduced into a cage and a few days later a new infant were born, one might not be able to conclude unequivocally that changes in activity or enclosure utilization (dependent variables) were a result of one and only one of these factors (independent variables)—that is, they are "confounded." To resolve this confounding, the branch would have to be removed and reintroduced, replicating the experimental manipulation. Seasonal and weather changes may also influence the behavior of one's subjects in a manner that can confound interpretation of a project's results. These factors must be recorded systematically if their effects are to be assessed. Thus, the researcher not only needs to take into account changes that were intentionally brought about, but also must characterize factors that may represent environmental changes from the animals' point of view.

Ideally, the influence of a change, such as addition of a new form of environmental enrichment, would follow an ABA design, where A is the baseline, B is the enriched condition, and A is postbaseline, after the removal of the enrichment (Young 2003) (fig. 30.2). This type of design usually is not possible when evaluating responses to a new enclosure (Little and Sommer 2002) (fig. 30.2).

It is usually impractical and expensive to collect data 24 hours a day, every day. For this reason, sampling methods have been devised to ensure unbiased estimates of behavior based on a subset of total time. *Unbiased* means that the observations are representative of what is going on when observations are not being made, and that, when data are being collected, researchers do not inadvertently record data supporting their hypotheses at the expense of data refuting it. Observer bias will be discussed further in the section on sampling methods (see table 30.2). Lehner (1996) describes various potential sources of error in observational research, in addition to observer bias, including observer error (making recording or computational mistakes of various sorts), observer effect (affecting the behavior of the subjects by being present), and errors of apprehending (when the physical location or attributes of the subject make it more or less visible than other potential subjects).

When and how often to collect data. Another preliminary consideration in research design is when to observe. If the re-

TABLE 30.2. Summary of sampling methods

Sampling method	Scoring basis	Mutually exclusive	Exhaustive	Comments and uses
Ad libitum	Behavior change	No	No	Longhand field notes. Preliminary observations; ethogram development; reconnaissance observations.
Continuous	Behavior change	Yes	No	For frequencies (onsets) of selected behaviors, especially infrequent behaviors of short duration.
		Yes	Yes	When relative frequencies are to be calculated from onsets (table 30.3).
		Yes	Yes	For transition times (to calculate durations if start and stop times are recorded during data collection). Time budgets can be calculated from mutually exclusive behaviors with start and stop times.
Scan/instantaneous	Time-point	Yes[1]	Yes	Especially useful for time budgets, activity patterns, group behavioral synchrony; usually produces high interobserver reliability. More appropriate for states than events (table 30.3).
One/zero	Time-interval	Yes[2]	Yes	Not recommended except for special circumstances (see text).

[1] Simultaneous behaviors can be scored and later combined into mutually exclusive categories.

[2] More than one mutually exclusive category can be scored per interval.

search question focuses on diurnal variation in behavior, then all time periods of interest must be sampled (Brannian and Cloak 1985; Heymann and Smith 1999; Vickery and Mason 2004). It may be practical to eliminate the hours of darkness from the sample if preliminary observations indicate that the animals are mostly inactive then. Around-the-clock observations are essential for studies of parturition and other events whose exact timing may be impossible to predict (Robeck et al. 2005).

To study day-to-day changes in behavior, such as correlates of estrous cycles or infant development, daily or almost daily records are necessary. If the amount of time available for data collection is limited, making observations at the same time each day will eliminate the confounding factor of time of day. However, this will also sacrifice the ability to generalize to other time periods unless diurnal variation in behavior has been ruled out first. If specific behaviors are of interest, preliminary observations will determine the best times to record them. For example, preliminary observations of ibex revealed that 95% of play (the behavior of interest) occurred between 0500 and 0700 and between 1900 and 2115, so observations were done at those times (Byers 1977).

Longitudinal studies (e.g. developmental) raise the question of how often observations must be made in order to provide valid estimates and yet be practical from a time and resource point of view. Kraemer et al. (1977) suggested a method for evaluating the spacing and timing of observations to minimize sample error and cost of data collection. For physical data (e.g. weight) that cannot be taken daily, records at approximately equal intervals are desirable (e.g. once a week). Weights should be taken at approximately the same interval since last feeding (Kawata and Elsen 1984).

TABLE 30.3. Terms pertinent to behavioral data collection

Term	Definition
Event	The onset or the single defining instant of any behavior; instantaneous behavior; momentary behavior (Sackett 1978a).
State	Behavior with appreciable duration (durational behavior), or any behavior at a given instant in time.
Duration	Time spent in a state.
Transition time	Time of onset or termination of behavior; changing from one state to another.
Frequency	Number of occurrences; can refer to events or states (see "bout"). Try not to be confused by the fact that in genetics gene "frequency" refers to the proportion of an allele in the population, and that in other contexts "frequency" is a "rate" (occurrence per unit time; see below), such as radio frequency.
Bout	One occurrence of a durational behavior or a behavior sequence (e.g. a play bout).
Rate	Frequency (number of occurrences) per unit time; requires knowledge of sample duration. Rates are most usefully interpretable when translated to a common time base, e.g. frequency per hour (see table 30.4).
Exhaustive	Behavior taxonomy is all-encompassing; subject is always recorded as doing something, even if "not visible" or "other."
Mutually exclusive	Recording categories do not overlap; within a given set of categories, the subject is never recorded as doing more than one thing simultaneously.

Note: Several definitions are paraphrased from Altmann (1974).

Determining what information is important. Determining what types of information are needed to answer a research question requires a reading of the relevant literature on the topic or species in question and preliminary observations. Knowing what has been done before may suggest useful techniques and avoid unnecessary duplication. Decide what behaviors are of interest and what parameters are of biological importance (Altmann 1984). For example, is it more relevant to know how often the behaviors occur (e.g. hourly rate), how much of the time is spent in particular activities (percentage of observation time), or how long the animals tend to engage in a behavior once it begins (bout duration) (see tables 30.3 and 30.4)? Determine whether sequences of behavior are important, as in courtship interactions. Their recording and analysis greatly complicate a research design (Lehner 1996; Bakeman and Gottman 1997).

Decide whether identification of individual animals is essential, e.g. to record actors and recipients of social interactions. In some cases, subjects can be lumped into age and sex classes without loss of essential information. If identification is necessary, marking of individuals may be required (see Kalk and Rice, appendix 2, this volume). If enclosure use is a subject of study, obtain accurate maps or blueprints of the exhibit.

Preliminary analyses. As a final preliminary consideration, data collection methods should be planned with some thought to subsequent data analysis. A good rule is to try some preliminary analyses after some initial data collection. Determine whether all the research questions posed are indeed answerable with the method chosen. *Preliminary analyses are important.*

GATHERING DATA FOR THE RESEARCH PROJECT

DEFINING WHAT DATA TO RECORD

To record research data systematically, appropriate definitions of behaviors or other types of data must be developed. Precise definitions for each element to be recorded must be written out, to ensure that observers do not "drift" from the original definition and to enable other researchers to use the same recording system. Part of this task follows from prior identification of independent and dependent variables, as all must be defined in some way. In general, defining recording categories for nonbehavioral data is more straightforward than developing them for behavioral data. Catalogs of an animal's behavioral repertoire, also known as a behavioral inventory or taxonomy, are called ethograms. For behavioral and nonbehavioral categories, a thorough literature search will reveal whether adequate categories have already been defined. When preexisting categories are used, not only does the researcher avoid "reinventing the wheel," but the previous literature can also be cited, thus shortening a manuscript prepared

TABLE 30.4. Useful calculations for analyzing behavioral data

Calculation	Definition
Raw scores	Unadjusted totals per observation (or focal sample) period (e.g., total occurrences per behavior, recorded with any sampling method); can be used in statistical tests if all observation periods are of equal duration.
Adjusted or corrected scores	Raw scores weighted so that all scores are equivalent (e.g., to adjust when observation periods are unequal across subjects or days.
Proportion	A fraction expressed in decimals, e.g., 5/8 = .63.
Probability	Expressed by a proportion; for example, if a study's results show that during the full moon an average of 5 of 8 females in a group are in estrus, one may conclude that the probability of any female being in estrus during the full moon is .63.
Percentage	Same calculation as proportion but multiplied by 100 so that unity = 100% (unity for proportions and probabilities = 1.0)
Range	Highest and lowest score (e.g., of frequencies, durations, rates, percentages).
Mean	The sum of the scores / sample size or number of scores (*N*).
Median	The midpoint of the scores (half are greater and half are smaller).
Variability	Measures of variation in scores about the mean; see any general statistics book for calculating standard deviations and other variability (error) measures.
Rate (e.g., of occurrence of solitary behavior or social interaction)	Frequency / observation time.
Hourly rate (frequency per hour)	Frequency / hours of observation, in decimals.
Relative frequency	Frequency of one behavior / total behavior changes (total number of behaviors); indicates probability of a particular behavior being observed at a randomly selected behavior change (Sackett, Ruppenthal, and Gluck 1978).
Mean duration per bout	Total duration of a behavior / its frequency.
Mean duration per hour (mean minutes per hour in a state)	Total duration in minutes / hours of observation, in decimals.
Mean rate (or duration or percentage) per individual (e.g., averaged across the entire group or within age/sex classes)	Sum of mean rates (or durations or percentages) for all individuals / total number of individuals in group (or subgroup).
Percentage of time (continuous sampling)[a]	(Total duration of behavior / total duration of observation) × 100.
Percentage of time (scan sampling)[a]	(Number of point samples when behavior was scored / total number of point samples) × 100.

[a] When these percentages are expressed as proportions, they indicate the probability that a given behavior will be seen during any randomly selected moment.

for publication. This practice also facilitates direct comparisons with the results of prior research.

Ethograms. In the early days of ethology (the study of how natural selection shapes adaptive behavior), an ethogram was always the first step and was sometimes itself the objective of many years' study (Tinbergen 1951; Lorenz 1958). Defining behaviors is still an essential step, but the extensiveness and detail with which this needs to be done depend on the specific question at hand. One of the first tasks of a project is to formulate a list of well-named, carefully defined behaviors relevant to the research objectives. Select the behaviors essential to a study to avoid being swamped during data collection (Hinde 1973).

Behavior descriptions are of 2 basic types, empirical and functional (Lehner 1996): Empirical, objective descriptions include body parts, movements, and postures, whereas functional descriptions include interpretations as to the purpose of the behavior. In general, when formulating an ethogram, first try to use objective names and operational definitions and avoid subjective inference regarding function. For example, in describing a facial expression common to many monkeys, "open-mouth stare" is more objective than "open-mouth threat" (fig. 30.3). The function of some behaviors, such as nest building, may be readily agreed on, but still need to be described for different species (Lehner 1996).

Researchers may find, after some experience, that it is appropriate to lump behaviors into a larger functional category such as "threat" or "aggression." This may occur during, or as a result of, data analysis. A behavioral taxonomy might be restricted to discrete categories of behavior. On the other hand, researchers not especially concerned with sequences of behavior might record fairly predictable sequences, such as "copulation" and "rough and tumble play," as single units of behavior (G. P. Sackett, personal communication). If several types of behavior are included within one scored category, each type should be described in the ethogram. For some classes of behavior, observer judgment is very important. For example, in discriminating between rough play and aggression in monkeys, the ability to make reliable judgments may require many hours of observation to develop.

Some examples of ethograms for studies conducted in zoos and similar facilities are published (Byers 1977, pp. 201–2; Freeman 1983, p. 7; Kleiman 1983; Stanley and Aspey 1984, pp. 91, 94–95, 103; Traylor-Holzer and Fritz 1985, p. 119; Nash and Chilton 1986, p. 40; Tasse 1986, p. 119; Macedo-

Fig. 30.3. In formulating an ethogram, use objective names and operational definitions. The function of this open-mouth expression given by an adult male lion-tailed macaque should be verified from quantitative observations. (Photography by Joy Spurr, Woodland Park Zoo. Reprinted by permission.)

nia 1987, p. 58; Merritt and King 1987; Margulis, Whitham, and Ogorzalek 2005, p. 630, including definitions for recording spatial locations in evaluating enclosure use; White et al. 2003, p. 274). The Behavioral Advisory Group of the American Zoo and Aquarium Association, facilitated by Lincoln Park Zoo, Chicago, maintains a Web site of ethograms of zoo animals: www.ethograms.org (Behavioral Advisory Group 2002).

Exhaustive and mutually exclusive recording categories. For purposes of data recording and analysis, it is often advantageous (and for some sampling methods, necessary) to define categories that are both exhaustive and mutually exclusive. *Exhaustive* means that the subject (S) is always recorded as doing something, even if "inactive," "other," or "not visible." *Mutually exclusive* means that the subject is never recorded as doing more than one thing simultaneously; that is, S can be "sitting" or "grooming," but not both. The recording system should include rules for establishing priorities or precedence, such as recording the "action" rather than the "posture" (Sackett 1978a). For example, a tiger, *Panthera tigris*, might be lying down but licking its paw, and this would be recorded as grooming, not lying down. Within a particular scoring system (e.g. a check sheet), more than one set of mutually exclusive and exhaustive categories can be included: e.g. the subject could be scored, simultaneously, for one behavior, one location, and one proximity relationship (e.g. nearest neighbor identity and distance).

Codes. Codes are useful for recording behavior in a variety of sampling schemes. Depending on the number of behaviors to be scored, one may simply code each behavior with one to 3 letters or numbers. When there are many behaviors to record and codes to memorize, reliability is improved by use of mnemonic abbreviations, such as GR = groom and AP = approach, or a dimensionalized coding scheme in which the first letter or number designates a general category and the second, the specific behavior, such as LW = locomotion-walk, LC = locomotion-climb, HG = handle-groom, HH = handle-hit (Bobbitt, Jensen, and Gordon 1964; Sackett, Stephenson, and Ruppenthal 1973; Astley et al. 1991; Lehner 1996, pp. 240–41).

Codes also can be used to identify individuals, actors and recipients, and locations. When developing codes that eventually will be analyzed by computer, keep in mind what the available computer system or existing programs can handle. If a coding system is incompatible with an analysis package, it is relatively easy to modify codes with the Find and Replace features of Microsoft Excel.

CHOOSING SAMPLING METHODS

Sampling methods are used to make estimates about an entire population (e.g. all lions in captivity) based on a subset, or sample, of that population (e.g. the lions in one zoo observed for 200 hours). Certain methods of sampling have been devised to ensure that the estimate obtained is unbiased (Altmann 1974). Even though a research project usually has predefined categories of all the possible things to record, some behaviors, individuals, or locations might be momentarily more interesting than others. If who, what, or when to observe were entirely up to the observer's whims, his or her data recording might focus on certain events to the exclusion of others that also had been predetermined to be important. This is the essence of observer bias.

Table 30.2 summarizes the major sampling methods, table 30.3 gives some pertinent definitions, and table 30.4 presents some useful calculations.

"Focus" of observations. The most common focus is on a single individual ("focal animal"), and all behaviors of interest initiated by that animal are recorded. In some sampling systems, all interactions in which the subject (S) is the recipient are also recorded. Although recording S as both actor and recipient allows one to collect more complete information about interactions, this protocol requires special consideration during data analysis. If one chooses to focus on one animal at a time, then total observation time may have to be increased if each focal subject is to occur often enough in the sample to be characterized adequately. The focus can be an individual, subgroup, group, or behavior, depending on the research question and the appropriate sampling method:

1. Focal animal: selected from the total group or a subset of it. Note that what Altmann (1974) called "focal-

animal sampling," we call "continuous sampling" (see "Continuous Sampling," below, and Altmann [1984]).

2. Focal subgroup: for example, "mother-infant pair" or "all females."
3. Group or subgroup, one individual at a time (see "Instantaneous and Scan Sampling" below) (Martin and Bateson 1993).
4. All occurrences of certain behaviors (Altmann 1974) or behavior sampling (Maestripieri 1996): focusing on the total group while restricting attention to certain behaviors, such as aggression, sexual behavior, or a particular facial expression.
5. Sequences of behavior (Altmann 1974, sequence sampling): Sequence sampling was effectively used by Byers (1977).

Random sampling and balanced observations. To avoid observer bias, the order in which focal subjects are sampled during each observation period should be randomized (fig. 30.4). Random sampling can be accomplished by using the table of random numbers found at the end of most statistics textbooks, or with the RAND() function in Microsoft Excel. An easy way is to write each subject's name on a small card. Shuffle the cards, put them in an envelope, and select one. Repeat until all the cards have been drawn and their order recorded. This is random sampling without replacement, which ensures that each subject is observed only once during an observation period. Random sampling should be repeated for each observation period. Remember that if subject A's card is drawn and A is not visible, data must still be recorded on this individual under the "not visible" category. Subject A may appear sometime during the sample period.

A methodology in which observation times were selected at random rather than being prescheduled would reduce other sources of bias. However, interobservation variability might swamp any meaningful results unless a large number of observations were made at each time of day to eliminate the potential error introduced by diurnal variation in behavior. Given the nature of the zoo setting and the schedules of observers, many of whom are zoo staff or students, observation times are unlikely to be randomized. Under such circumstances it is more important for them to be "balanced," that is, to schedule the same number of observation periods during each of several selected time blocks. If several time blocks are being sampled and observations occur only once a day, some effort should be made to avoid scheduling consecutive days' observations during the same time block; this will reduce bias imposed by abnormal streaks of weather or other factors (i.e. confounding of weather and time-of-day effects). Such potential bias is eliminated if all subjects are observed daily during all time blocks sampled. If daily observations are not possible, evenly spaced observations, such as every third day, provide "balance" as long as there are no behavioral cycles coinciding with the same interval. If at all possible, a pilot study should be conducted to determine the optimal observation schedule (Kraemer et al. 1977; Thiemann and Kraemer 1984). Scheduling observation periods well in advance will allow the project to run more smoothly, especially if arrangements for after-hours admission must be made. Times of day routinely allocated for daily husbandry activities should be avoided unless related to project goals.

Bases for recording data. Essentially, there are 2 kinds of events that activate the observer to record data: a change in behavior or the passage of time (Sackett 1978a). A *behavior change* scoring system, as the name implies, usually involves recording the onset of a new behavior, but it may also include recording the termination of the current behavior or the transition time between 2 behaviors. Behavior-change scoring usually is associated with continuous sampling sys-

Fig. 30.4. To avoid observer bias, observe focal subjects such as these patas monkeys, *Erythrocebus patas*, in random order. (Photography by Mark Frey, Woodland Park Zoo. Reprinted by permission.)

tems. For some behaviors the transition from one to another "bout" (see table 30.3) can be ambiguous. In such cases, the behavior taxonomy should include defining events that signal when a new behavior should be recorded: e.g. a certain number of seconds of inactivity that must elapse before a new behavior bout is recorded, or a certain critical distance that must be reached before "approach" is scored.

In a *time sampling* scoring system, the observer either scores the behavior occurring at the moment of a transition between intervals (scan, instantaneous, or point sampling), or scores the occurrence or nonoccurrence of each behavior of interest during the interval (one-zero sampling). A stopwatch or other device with a programmable alarm is used to signal the end of an interval. These methods and the factors contributing to choice of time interval length are discussed below.

Sample period. For ease of data analysis, it is useful to divide observation periods into equal-length sample periods. There are several types of sample periods, but generally the primary or focal sample period is considered to be the length of time during which a particular individual or behavior is the focus of observation. Individual subjects are the most common focus, so the more individual subjects there are to be observed during the observation period, the shorter the focal sample period will be, or the whole sampling period could be longer. However, increasing focal sample duration will reduce between-sample variability, which is desirable for some kinds of analysis.

A simple system is to define a basic observation period that includes a complete replication of data collection; i.e., each subject is observed once and only once in random order. Let's say that the basic observation period is one hour. If 5 subjects are to be observed, then the focal sample period ought to be 10 minutes, providing an additional 10 minutes during the basic observation period to shuffle papers and to deal with unexpected events or to record different kinds of data between focal samples. Within each focal sample period, smaller time intervals may be employed, as in all time-sampling scoring systems or to keep a time base in continuous sampling. When methodology dictates collecting more than one kind of data, define the basic observation period to allow for this. When there is only one subject, or when the whole group is observed at once, the basic observation period is synonymous with the focal sample period. The length of the basic observation period should be shorter than the "fatigue threshold," which is likely to be reached faster when a noisy public is present to distract the researcher. A focal sample period should not be less than 5 minutes, so if the group is large, it might have to be observed over more than one observation period.

Although projects by zoo staff and students may be constrained by other schedules, or by the nature of the project itself, for the sake of data analysis and statistical tests it is best for each observation day to be uniform in terms of total observation duration and the number of focal samples taken.

SAMPLING METHODS: USES AND LIMITATIONS

Ad-lib sampling. Ad-lib sampling (Altmann 1974) is equivalent to traditional field notes or reconnaissance observations and generally involves nonsystematic, informal observations preliminary to quantified study. This technique is useful for recording rare, unusual events and often takes the form of a comments section on the data sheet.

Continuous sampling. In continuous sampling (focal-animal sampling: [Altmann 1974]; continuous real-time measurement: [Sackett 1978a]), the start time (and, for durations, ending time) of specified behaviors and interactions are recorded. This behavior-change method usually records behavior initiated by (and in some protocols, directed toward) focal subject(s), but can be modified to record focal behaviors, sequences, or use of enclosure locations.

Continuous sampling always allows for the calculation of frequency, rates, and (if stop times recorded) durations of behavior (table 30.2). Continuous sampling of a focal animal potentially allows for the most complete record of behavior and is the only way to collect data on sequences without missing anything. Analyzing continuous data can be very time-consuming if many behaviors or subjects are involved, unless electronic recording devices are used. If sequences are not important, and a computer is not to be used, a check sheet can be designed to simplify data collation and analysis. If the behaviors of the most interest are momentary or relatively infrequent, continuous sampling is the method of choice. If the frequency of behaviors is the main interest, then only the onset of behavior need be recorded, simplifying the analysis.

Instantaneous and scan sampling. Instantaneous and scan sampling (Altmann 1974), also known as point sampling (Dunbar 1976), are time-sampling-based systems in which the observer records the behavioral state (table 30.3) at the instant ending a predefined interval—e.g. on the minute. To avoid bias, the observer must record only what the subject is doing at that instant, whether an ongoing behavior, the onset of a new behavior of some duration, or a brief behavior that happens to coincide with the sampling instant.

One potential problem with these methods is the difficulty of identifying a particular behavior or subject at a single glance. An effective solution is to observe the subject for, say, 5 seconds after the signal and then record the behavior observed at the last instant (e.g. on the count of five) (Sackett 1978a). This "count-to-five" method worked very well in a field study of red howler monkeys, *Alouatta seniculus*, scanned at 15-minute intervals (C. M. Crockett, personal observation). When the time intervals are short ($\leq$30 seconds), the observer is likely to anticipate the next time signal so that behavior determination can be made without the counting method. Some researchers record the first behavior that lasts for a defined duration, such as 5 seconds (Mahler 1984, "sustained" behavior), but this leads to underrepresentation of instantaneous behaviors and should be avoided (Clutton-Brock 1977). If the main interest is instantaneous "events" rather than "states" (tables 30.2 and 30.3), then continuous sampling is more appropriate.

Instantaneous sampling refers to time-activated recording methods in which the focus is a single individual (the reason to avoid using Altmann's [1974] term *focal-animal sampling* to refer to the continuous sampling method). Scan sampling involves scoring an entire (sub)group, hence the observer must visually "scan" to record the behavior of all individuals. Although it takes more than an "instant" to scan a group, the observer records only the behavioral state occurring when each individual is first seen. To avoid bias, scans should be performed in a systematic manner, such as always from the left to the right of the enclosure. In principle and in common usage, "instantaneous" and "scan" sampling are equivalent.

Scan sampling provides the easiest method for estimating the percentage of time spent in specific activities or percentage usage of different enclosure locations (table 30.4). Scan sampling is thus particularly well suited to studies of activity cycles (variation in behavior as a function of time of day). It is less suitable for collecting data on specific social interactions, since they often occur in sequences that cannot be recorded using a scan sample. Infrequent behaviors of short duration are generally missed unless the interval between scan samples is very short or the total duration of observation is long. Rates and bout durations cannot be calculated with this method. The great advantage of scan sampling is its relative simplicity: naive observers can quickly learn to score clearly defined behaviors if the number to choose from is relatively small. Thus, inter- and intraobserver reliability is usually high.

The interval length chosen for scan sampling depends on various factors, such as the subject's activity level (how often it changes behavior, and how long the behaviors scored typically last), group size (how many individuals are to be scanned per interval), whether a single or a mixed sampling strategy is to be used, and whether temporal autocorrelation is an issue in statistical analysis. In general, the shorter the interval, the closer data collection approximates what can be recorded with continuous sampling. Shorter intervals, however, mean more data to analyze, since data are scored for each interval. Longer scan intervals are more practical for relatively inactive animals, especially when combined with continuous sampling of selected behaviors of brief duration (i.e. a mixed sampling strategy). Some types of information, such as food intake or animals' locations plotted on a map of the enclosure, can be recorded only once a day and can still be treated as a scan sample. For statistical purposes, once-a-day records generally avoid the problem of temporal autocorrelation.

One-zero sampling. In one-zero (or 1-0) sampling (Altmann 1974), also known as modified frequency (Sackett, 1978a), time intervals are established just as in scan sampling. However, each behavior category occurring during the interval is given an arbitrary score of 1 regardless of its true frequency. For example, a behavior observed 5 times during an interval is still scored as 1, and a behavior of longer duration is given a score of 1 for every interval in which it occurs, regardless of onset. Thus, more than one behavior category can be scored per interval.

Because true durations, true frequencies, and true percentages of observation time spent in different activities cannot be calculated with this method, Altmann (1974) advised that it not be used. In response, a number of studies were published comparing how estimates of rates, durations, and percentages of time varied depending on the sampling method used to score the same series of events (Dunbar 1976; Chow and Rosenblum 1977; Leger 1977; Sackett 1978a; Kraemer 1979; Tyler 1979; Rhine and Ender 1983; Suen and Ary 1984). The results indicate that, although the 2 time-sampling-based methods provide results that are generally positively correlated with one another, the degree to which they reflect the true occurrence of behavior depends a lot on the sampling interval length relative to behavior rate and bout duration (Suen and Ary 1984). Of course, average rate and duration will vary from behavior to behavior. Where bouts or flurries of specific behaviors are of greater interest than specific rates or time budgets, the simplicity of one-zero sampling might make it an acceptable choice, but be aware of its drawbacks (Bernstein 1991).

One-zero sampling should be avoided when estimates are to be compared with those of other studies using other methods. However, because one-zero is easy to score and analyze and produces high interobserver reliability, it can be employed when many observers are to be used or direct comparison with other studies is not important. Nevertheless, proper training and data collection design usually can achieve equally high interobserver reliability in studies using scan sampling.

One-zero sampling can also be used to quantify past daily reports in which the information recorded is accurate only to that level. For example, occurrence or nonoccurrence (1-0) in the written record can be scored for sexual behavior, consumption of particular foods, use of a new cage furnishing, fresh injuries, and so on for each individual present that day. Some events tend to be biologically important at the one-zero level, e.g. whether a female mates at least once during estrus or whether an animal eats at least once during a day. Such one-zero scoring of keepers' records was used effectively to supplement systematic data on proceptive calling by female lion-tailed macaques, *Macaca silenus* (see Lindburg 1990).

DATA RECORDING SYSTEMS

There are many ways to record data, and they vary in their reliability, ease of use, cost, and time required for transcription and analysis. Audio- and video-recorded data, for example, require at least twice the time to transcribe as to record. However, video or audio recording an ongoing event that is unpredictable, such as the introduction of a new animal, may be the most successful way to preserve rapidly occurring interactions. Handycams are a good option, yielding digital files that can be coded by various methods. Transcription is easier if the observer narrates ongoing behavior using memorized codes. Laptop computers or personal digital assistants (PDAs) can be programmed to accept coded data (entered by keyboard, touch screen, voice recognition software, or a barcode reader) that can then be analyzed by the device itself or transferred to a desktop computer for analysis (Forney, Leete, and Lindburg 1991; Grasso and Grasso 1994; Paterson, Kubicek, and Tillekeratne 1994; White, King, and Duncan 2002). Commercially available products can turn a personal computer or a PDA (fig. 30.5) into a behavior coding and tabulating system. Among these are The Observer, www.noldus.com/ (Cronin et al. 2003, includes example of use; Noldus 1991, 2005), EVENT (Ha 1991; Ha and Ha 2003, includes example of use), and JWatcher, www.jwatcher.ucla.edu/ (Blumstein, Evans, and Daniel 2000). Computer tech-

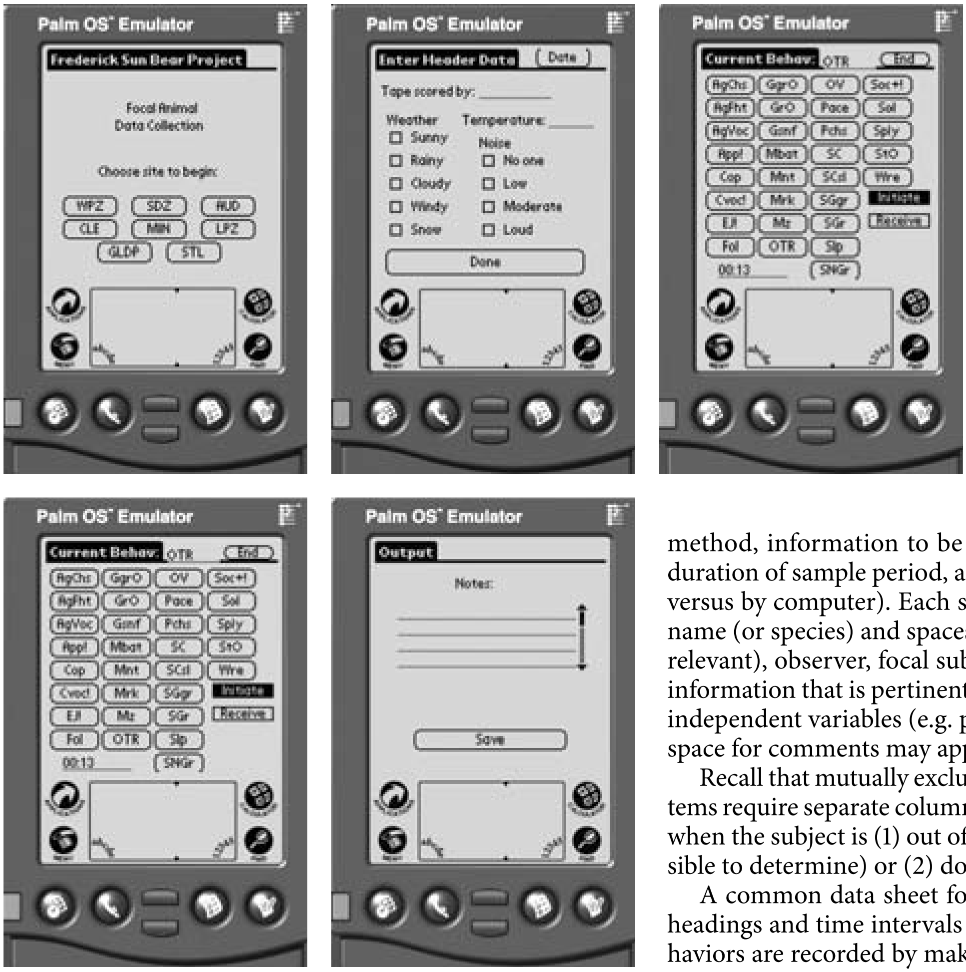


Fig. 30.5 (*A–E*). EVENT-Palm Software. Cheryl Frederick of the Woodland Park Zoo, Seattle, and University of Washington worked with James C. Ha (1991) to develop a custom PDA program to collect focal data on endangered sun bears at 6 zoos across the United States. Users touch the screen with a stylus to select coded behavior buttons, and the data are recorded into a database program for later analyses.

nology is the method of choice when large amounts of data are to be collected. The advantages of these techniques include simultaneous data entry with data collection, the potential of safeguards in the program to prevent "impossible" entries, and elimination of transcription error from data entry errors. However, for many projects, paper and pencil data sheets are perfectly adequate, are more cost effective, and are the recommended starting point for beginning observers.

PAPER AND PENCIL METHODS

For many zoo research projects, a photocopied *data sheet* is a suitable and inexpensive method of recording data. Experiment with preliminary versions before a final version is adopted. Professionally printed NCR (no carbon required) paper is a good choice if duplicate data records are important.

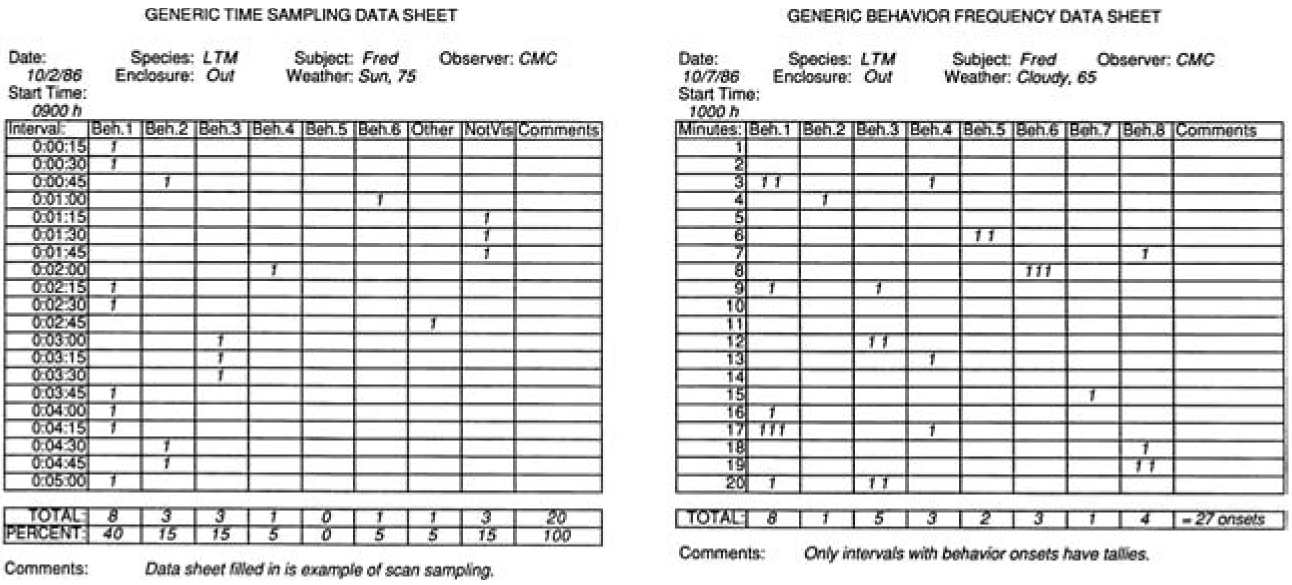
Hinde (1973) gives a number of useful suggestions regarding the format of data sheets. Published papers rarely include samples of the data sheet used, but examples can be found (see Kleiman 1974; Price and Stokes 1975; Crockett and Hutchins 1978; Lehner 1996; Paterson 2001). Figures 30.6 through 30.8 present "generic" data sheets suitable for different sampling methods and purposes. The data sheet format that a researcher selects will be a function of sampling method, information to be recorded, number of subjects, duration of sample period, and method of analysis (by hand versus by computer). Each sheet should include the project name (or species) and spaces to enter date, time, weather (if relevant), observer, focal subject, location in zoo, and other information that is pertinent to the project and may serve as independent variables (e.g. phase or conditions of study). A space for comments may appear on the data sheet.

Recall that mutually exclusive and exhaustive scoring systems require separate columns, categories, or codes to record when the subject is (1) out of sight (and where, if that is possible to determine) or (2) doing something undefined.

A common data sheet format lists behaviors as column headings and time intervals as row headings (fig. 30.6). Behaviors are recorded by making a check mark in the appropriate cell or by entering the code of the recipient of social behavior or the location of the focal animal. This format is suitable for time sampling (fig. 30.6, left) and for continuous sampling of behavior frequencies (fig. 30.6, right) when sequence is not important. When a format such as that shown in figure 30.6, left, is used to scan more than one individual per interval, each individual's ID code could be entered in the appropriate cell.

To record continuous sequences, codes for actors, behaviors, and recipients can be written in the order in which they occur, using the first column of each row to enter time of onset (fig. 30.7, top). Alternatively, time intervals can be prelabeled such that behavior is recorded in the row indicating the minute period (or other time interval length) in which it occurred (fig. 30.7, bottom). Durations can be estimated if a mutually exclusive and exhaustive set of behaviors is recorded, and it is predetermined which ones are "events" (e.g. ca. one second duration) and which are "states" (variable duration). The onset of the next behavior is assumed to terminate the previous one. Transcription of data recorded with this method is tedious and time-consuming unless a computer is used.

Maps can be used to record various kinds of data. On a scale map of the enclosure, one can code each animal's location, using a scan sampling technique. Later, interindividual distances and location preferences can be calculated from map plots, as done by Kirkevold and Crockett (1987). It may



GENERIC TIME SAMPLING DATA SHEET

Date: *10/2/86* Species: *LTM* Subject: *Fred* Observer: *CMC*
Enclosure: *Out* Weather: *Sun, 75*
Start Time: *0900 h*

Interval:	Beh.1	Beh.2	Beh.3	Beh.4	Beh.5	Beh.6	Other	NotVis	Comments
0:00:15	1								
0:00:30	1								
0:00:45		1							
0:01:00						1			
0:01:15								1	
0:01:30								1	
0:01:45								1	
0:02:00				1					
0:02:15	1								
0:02:30	1								
0:02:45							1		
0:03:00			1						
0:03:15			1						
0:03:30			1						
0:03:45	1								
0:04:00	1								
0:04:15	1								
0:04:30		1							
0:04:45		1							
0:05:00	1								

TOTAL:	8	3	3	1	0	1	1	3	20
PERCENT:	40	15	15	5	0	5	5	15	100

Comments: *Data sheet filled in is example of scan sampling.*

GENERIC BEHAVIOR FREQUENCY DATA SHEET

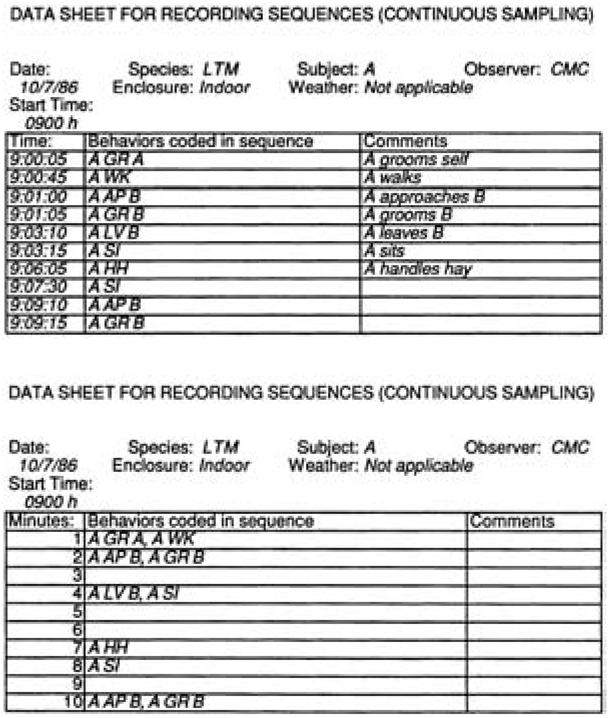
Date: *10/7/86* Species: *LTM* Subject: *Fred* Observer: *CMC*
Enclosure: *Out* Weather: *Cloudy, 65*
Start Time: *1000 h*

Minutes:	Beh.1	Beh.2	Beh.3	Beh.4	Beh.5	Beh.6	Beh.7	Beh.8	Comments
1									
2									
3	1 1			1					
4		1							
5									
6					1 1				
7								1	
8						111			
9	1		1						
10									
11									
12			1 1						
13				1					
14									
15							1		
16	1								
17	111			1					
18								1	
19								1 1	
20	1		1 1						

TOTAL:	8	1	5	3	2	3	1	4	= 27 onsets

Comments: *Only intervals with behavior onsets have tallies.*

Fig. 30.6. (*Left*) Time-sampling data sheet for 8 mutually exclusive and exhaustive behavior categories. For scan sampling, the behavior occurring at the instant of the interval marker is checked; there is only one tally per row (interval), as shown here. For one-zero sampling, all behaviors occurring during the interval would be checked once. (*Right*) Data sheet for recording behavior frequency during continuous sampling. Behavior onsets are recorded by checking the cell corresponding to the time interval of occurrence. Multiple tallies may occur in one cell, and some rows (intervals) may have no tallies because no new behavior onsets occurred.



DATA SHEET FOR RECORDING SEQUENCES (CONTINUOUS SAMPLING)

Date: *10/7/86* Species: *LTM* Subject: *A* Observer: *CMC*
Enclosure: *Indoor* Weather: *Not applicable*
Start Time: *0900 h*

Time:	Behaviors coded in sequence	Comments
9:00:05	A GR A	A grooms self
9:00:45	A WK	A walks
9:01:00	A AP B	A approaches B
9:01:05	A GR B	A grooms B
9:03:10	A LV B	A leaves B
9:03:15	A SI	A sits
9:06:05	A HH	A handles hay
9:07:30	A SI	
9:09:10	A AP B	
9:09:15	A GR B	

DATA SHEET FOR RECORDING SEQUENCES (CONTINUOUS SAMPLING)

Date: *10/7/86* Species: *LTM* Subject: *A* Observer: *CMC*
Enclosure: *Indoor* Weather: *Not applicable*
Start Time: *0900 h*

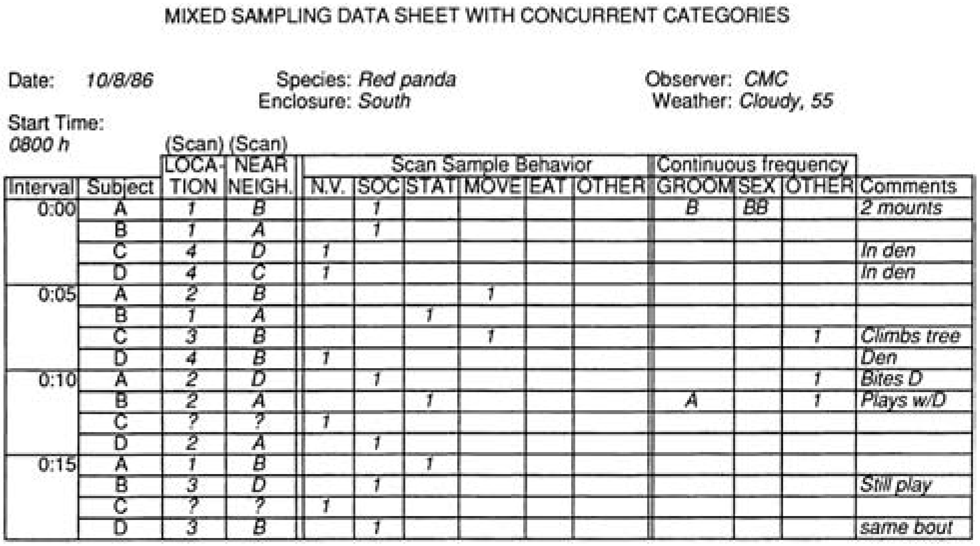
Minutes:	Behaviors coded in sequence	Comments
1	A GR A, A WK	
2	A AP B, A GR B	
3		
4	A LV B, A SI	
5		
6		
7	A HH	
8	A SI	
9		
10	A AP B, A GR B	

Fig. 30.7. Data sheets for recording sequences of behavior using continuous sampling. (*Top*) Data sheet for recording onset time (recording the onset of behaviors is necessary for later calculation of durations of behaviors). (*Bottom*) Data sheet for recording within time intervals.

also be possible to record simple behavior categories next to the individual's identification code. The map technique is a good method to use when it is not clear from the outset of the project which location divisions might be important for analysis.

Another format for recording data is a matrix table, e.g. with columns labeled with behavior names and rows labeled with locations. Each matrix could be for a single subject for an observation of specified duration, or one matrix could be used for all animals in the enclosure if their ID codes were recorded. A matrix tally sheet could be used for scan sample data, using one tally mark per scan, or for continuous recording of frequency data (behavior by location). For recording all occurrences of one interactive behavior, a matrix could list actors as row headings and recipients as column headings; using continuous sampling, a tally mark would be made in the proper cell whenever the specified interaction occurred, e.g. supplanting (Lehner 1996).

For many projects conducted in the zoo setting, more than one type of data must be recorded. As described above, location and behavior data can be recorded at the same time using either continuous or scan sampling. However, in many cases a "mixed" sampling strategy is most appropriate. In such cases, scan data can be recorded in columns on the left side of the page and continuous data on the right (fig. 30.8). Generally, "mixed" sampling strategies record location, nearest neighbor, and general behavior category on the scan, and frequency or interaction data using continuous sampling. For example, one scan sample category might be "social behavior," whereas specific behavior, actor, and recipient would be recorded continuously. Another possibility is to observe focal subjects in random order, recording data using continuous sampling;



MIXED SAMPLING DATA SHEET WITH CONCURRENT CATEGORIES

Date: *10/8/86*
Species: *Red panda*
Enclosure: *South*
Observer: *CMC*
Weather: *Cloudy, 55*
Start Time:
0800 h

		(Scan) LOCA-TION	(Scan) NEAR NEIGH.	Scan Sample Behavior						Continuous frequency			
Interval	Subject			N.V.	SOC	STAT	MOVE	EAT	OTHER	GROOM	SEX	OTHER	Comments
0:00	A	*1*	*B*		*1*					*B*	*BB*		*2 mounts*
	B	*1*	*A*		*1*								
	C	*4*	*D*	*1*									*In den*
	D	*4*	*C*	*1*									*In den*
0:05	A	*2*	*B*				*1*						
	B	*1*	*A*			*1*							
	C	*3*	*B*				*1*					*1*	*Climbs tree*
	D	*4*	*B*	*1*									*Den*
0:10	A	*2*	*D*		*1*							*1*	*Bites D*
	B	*2*	*A*			*1*				*A*		*1*	*Plays w/D*
	C	*?*	*?*	*1*									
	D	*2*	*A*		*1*								
0:15	A	*1*	*B*			*1*							
	B	*3*	*D*		*1*								*Still play*
	C	*?*	*?*	*1*									
	D	*3*	*B*		*1*								*same bout*

Fig. 30.8. Mixed sampling data sheet for scoring 3 concurrent scan categories as well as continuous data. Scan data are recorded at the beginning of each interval, and continuous data are recorded throughout the interval. Observation period duration for the sheet shown here is 20 minutes. NEAR NEIGH., nearest neighbor; N.V., not visible; SOC, social; STAT, stationary.

then, between focal samples, record scan data on all subjects (e.g. their locations and general activity). This method was used by Stanley and Aspey (1984).

In addition to its use in specific research projects, systematic data collection can be applied to the day-to-day management of animals. Systematic records are facilitated by using standard forms for recording information. Such forms may be a part of daily reports, or they may be designed for special events. For example, Lindburg and Robinson (1986) developed a form for systematically recording the conditions and outcome of animal introductions. Even if a PDA or laptop program is to be used, the researcher needs to think about the layout of data collection.

DATA SHEETS AND COMPUTER ANALYSIS

When data recorded by hand are to be analyzed by a software package such as SPSS or SAS (Tabachnick and Fidell 2001), it is most appropriate for the data sheet to resemble figure 30.7, top, rather than check-sheet column formats like figures 30.6 and 30.8. This is because the computer program can use routines such as cross-tabulation to count frequencies of, e.g., coded behaviors per coded actor. Microsoft Excel has a useful feature called Pivot Table that computes cross-tabulation. New programs with more features are being released regularly, and it is worth the effort to evaluate a program's capabilities for the price before purchase. Some powerful programs are available inexpensively through site licenses to universities, such as SYSTAT version 11.0 (Wilkinson 2004). A personal favorite for the Macintosh is Data Desk (Velleman 1997, recent version 6.2 [2003]), with entering and preparing the data file in Microsoft Excel completed beforehand. Some simple statistical analyses are even built into Microsoft Excel. To view these features, select Tools, then Add-Ins, and check the Analysis ToolPak and Analysis ToolPak VBA boxes. Upon returning to Tools, a new option, called Data Analysis, should appear; it includes the ability to conduct both descriptive statistics and inferential hypothesis tests.

REPLICATION AND INTER- AND INTRAOBSERVER RELIABILITY

The methods used in a research project should be defined clearly enough so that another researcher could use the same technique based on the written description provided in the final report or publication. Unequivocal behavior definitions are thus especially important.

An observer should be consistent in data collection from day to day (intraobserver reliability). Thus, if at all possible, preliminary data collection should be used as "practice" and either not be analyzed or be analyzed selectively (the least equivocal data being used). When more than one observer is to be used in a project, formal interobserver reliability testing is recommended. A common method involves having 2 or more persons collect data on the same subject simultaneously. The recorded data are then compared and the percentage of agreement calculated. A common calculation of agreement is

$$\%\ \text{Agreement} = [\text{Agreements}/(\text{Agreements} + \text{Disagreements})] \times 100.$$

Errors can be made regarding identifications of individuals, behaviors, sequence of interaction, and so on. Depending on the methodology, reliability should be 85%–95% before a new observer's data are used in analysis.

Percentage of agreement is the easiest way to calculate reliability, but it is considered the poorest index of reliability from a statistician's point of view: it does not account for the likelihood of observers agreeing purely due to chance factors, and thus inflates the actual agreement between observers (Watkins and Pacheco 2000). On the other hand, any measure of reliability is better than none at all: observers who knew that they were being assessed showed significantly higher observer agreement scores than did uninformed observers (Hollenbeck 1978). Large projects involving many observers could use videotaped "real" sequences as a "standard" by which to measure agreement. Ideally, observers should be assessed repeatedly over time. Generally, many zoo projects are conducted by a single observer who improves in reliability over time through practice. Someone collecting data for a self-conceived, self-designed project is likely to be inherently more reliable, although the danger of observer bias—recording "predicted" behavior in ambiguous situations—may be increased. Martin and Bateson (1993), Lehner (1996), and Caro et al. (1979) discuss various factors affecting reliability and techniques for evaluating reliability.

Currently, the Kappa statistic (Cohen 1960) is the preferred measurement of interobserver reliability (Bakeman and Gottman 1997). If there are only 2 observers, it is simple to hand-calculate Kappa on the nominal categories (or number of times they both chose the same behavioral code; example adapted from Watkins and Pacheco [2000]). The 2 observers recording behavioral codes are compared by cross-tabulating one observer's recorded observations into columns and the other observer's recorded observations into rows. Sometimes the observations will be in agreement and sometimes they will not be in agreement, but we can calculate how often they are in agreement and whether that value is above chance levels.

$$\text{Kappa} = \frac{P_o - P_c}{1 - P_c}$$

P_o = Observed proportion of agreement

$$= \frac{\textit{Agreements}}{\textit{Agreements} + \textit{Disagreements}}$$

P_c = Chance proportion of agreement

$$= \left(\frac{R_1 \times C_1}{N^2}\right) + \left(\frac{R_2 \times C_2}{N^2}\right) + \left(\frac{Rn \times C_n}{N^2}\right),$$

where
R_1 = Sum of the observations for row 1
R_2 = Sum of the observations for row 2
Rn = Sum of the observations for the last row
C_1 = Sum of the observations for column 1
C_2 = Sum of the observations for column 2
Cn = Sum of the observations for the last column

The Observer 5.0 (Noldus 2005) data coding system includes a reliability calculation, as does Systat (Wilkinson 2004) and SPSS. Online programs to calculate reliability are available; e.g. http://department.obg.cuhk/reseachsupport/Cohen_Kappa_data.asp

High observer reliability is needed only at the measurement level of analysis: if only rank orders are analyzed in statistical tests (true of most nonparametric tests, which are explained below), then observers' accuracy in recording behavior needs to be precise only at the level of rank order (Sackett, Ruppenthal, and Gluck 1978). For example, as long as the observer accurately records that male A is aggressive more often than male B, and B is aggressive more often than C, the outcome of a rank-order statistical test will not be changed if a few aggressive acts are missed.

DATA PRESENTATION AND ANALYSIS

The purpose of this section is to introduce the reader to some considerations and techniques that are useful in the analysis of data collected in the zoo setting. It is not intended to provide all the skills needed and should be used in conjunction with the more thorough references cited. Some aspects of data analysis should be considered before a data recording method is adopted. Again, preliminary analyses are important: they may suggest a revision to the data sheet, data collection schedule, or collation protocol.

DATA COLLATION

General considerations and techniques. During data collation (e.g. when the observer is totaling up a data sheet), 2 important considerations ought to be taken into account.

1. Data for each subject and/or observation session should be equivalent—based on the same amount of observation time. If observation times differ, equivalence can be achieved by converting raw scores to rates or percentages. Decide whether to use total observation time (or total number of scans) as a base, or the amount of time (or number of scans) during which the subject is visible as a base.
2. Data summaries should not be collapsed across all observation sessions until it is determined whether scores per focal sample period or some other time block will be used in statistical tests. In any event, when observation periods are not of equal length, it is often advisable for each session or day to contribute equally. Observation schedules in which each subject is observed for the same amount of time (per time block, if relevant) avoid many problems. When time "not visible" varies across subjects and observation days, this complicates analysis.

To facilitate the collating and transcribing of data from the original data sheets, some attention should be paid to the design of summary or tabulation sheets. Where possible, include summary rows on the data sheets themselves (e.g. fig. 30.6). Some tabulation sheets may be in the form of matrices. Tabulation can be facilitated by use of a spreadsheet program, such as Microsoft Excel.

Estimates based on continuous focal-animal sampling. When recording the interactive behaviors of a focal animal, one may decide to record all behaviors directed toward the subject, S, as well as those initiated by the subject. This method allows efficient use of observation time but requires special considerations in some data analyses. Thus, in samples in which *Si* is the focal animal and in samples in which *Sj* is the focal animal, all their interactions will be recorded. Each of the samples (*i* or *j*) or both (*i* + *j*) will give an estimate of their rate of interaction (Altmann 1974), as shown in table 30.5.

Consider the interaction data summarized in table 30.6. When the sum of observation time for subject I and subject J is used as a time base, each cell in the frequency matrix can be used to calculate a valid estimate of that dyad's hourly rate of

TABLE 30.5. Estimates of interaction rates

Subject	Sample duration	Number of interactions$_{i,j}$	Rate
i	20 min (1/3 hr)	5	15/hr
j	10 min (1/6 hr)	3	18/hr
i + j	30 min (1/2 hr)	8	16/hr

TABLE 30.6. Social grooming interactions for subjects I, J, and K

Sample duration	Focal subject	Interaction	Frequency
60 min	I	I grooms J	5
		J grooms I	3
60 min	J	J grooms I	6
		I grooms J	4
60 min	K	K grooms I	5
		I grooms K	1
180 min = 3 hr			24

Frequency matrix						Hourly rate					
		Groomee						Groomee			
		I	J	K	Total			I	J	K	Total
Groomer	I		9	1	10	Groomer	I		4.5	.5	5.0
	J	9		0	9		J	4.5		0	4.5
	K	5	0		5		K	2.5	0		2.5
	Total	14	9	1	24		Mean grooming rate per individual:				4.0

interaction. In this example, subject I was observed to groom J a total of 9 times while they were focal subjects, and I groomed K once while K was the focal subject, totaling 10 grooms by I. Although I, J, and K were each focal animals for one hour of observation, one cannot divide 10 grooms by 3 hours to yield a grooming rate of 3.3 for I, because focal sampling of J does not reveal interactions between I and K (e.g. during the hour that J was the focal subject, I could have groomed K 5 times). To calculate a mean rate per individual, rates per dyad must be calculated, then summed and divided by the number of individuals. See Michener (1980) and Shapiro and Altham (1978) for other considerations in estimating interaction rates.

The problem of visibility. When estimates of behavioral rates or percentages are based only on the duration of the sample when the subject is visible, such as done by Ralls, Kranz, and Lundrigan (1986), it is important to consider that the animal's behavior when visible may not be a random sample of total behavior. The animal may be performing the same behaviors at different rates or may be engaging in different behaviors when out of sight. Many zoo enclosures have indoor and outdoor sections. The observer should sample both sections before concluding that behavior inside is the same as (or different from) behavior outside. If behavior is the same inside and out, then rates can be calculated using time observable as the divisor. In other situations, a subject may be unobservable because it has entered a den or nest box, where perhaps only a few behaviors are likely to occur. In such cases, total sample time should probably be the divisor, and "in den" should be considered a behavior. Similarly, some animals in naturalistic enclosures may be scored as "not visible" primarily when they are lying down, concealed by tall vegetation; in this case using observation time while "visible" as the divisor would overestimate the actual percentage of "active" behavior. The results of such a study might therefore include a category for "percentage of time not visible," which would be combined with "percentage of time inactive" for some analyses. If a large percentage of observation time occurs when the subjects are out of sight, results should be interpreted with this consideration in mind.

STATISTICAL TESTS

All behavioral research projects will involve some descriptive statistics (e.g. table 30.4). Behavioral researchers should also use statistical tests in order to test hypotheses and draw conclusions (Lehner 1996). Otherwise, the conclusions may be unjustified. The purpose of statistical tests is to "determine how large the observed differences must be before we can have confidence that they represent real differences in the larger group from which only a few events were sampled" (Siegel 1956, 2). Statistical tests are posed in such a manner that, given a large enough difference, the null hypothesis can be rejected. For example, a null hypothesis might be that the means (averages) of 2 samples, such as mean aggression rates in 2 enclosures, do not differ. Rejection of the null hypothesis suggests that the 2 sample means are statistically significantly different.

If the results of a research project are to be applied to management decisions in a zoo or aquarium, it is doubly important that the conclusions of the study have some statistical basis. However, statistical significance alone should not dictate decisions, because the magnitude of the effect, the "effect size," is really more important (Martin and Bateson 1993). Even if expensive enclosure modifications resulted in statistically significantly reduced aggression, they might not be worth applying throughout the zoo if the behavior change was small and no reduction in injuries could be demonstrated. On the other hand, behavior might be altered dramatically in some individuals but not in others, resulting in marginal statistical significance but a large average-effect size.

"Significant" differences usually cannot be eyeballed from graphed data unless error (variability) measures are included. When graphing and comparing means, it is appropriate to use the standard deviation of the mean, which is commonly called the standard error (SE) or standard error of the mean (SEM). The notation for the standard error of the mean is σ_n, where σ is the standard deviation of the scores and n is the sample size.

$$\sigma_n = \frac{\sigma}{\sqrt{n}}$$

To show significant differences that can be seen from the graphed means, simply graph the means for each group ±2 SE (Streiner 1996). Descriptive statistics (mean or median) should always include range and/or standard error or standard deviation, and sample sizes.

Parametric versus nonparametric tests. Parametric statistics are based on assumptions about "parameters," such as the mean (average) and variability measures (variance or its square root, the standard deviation), that describe the "population" from which the sample data have been selected. These parameters define mathematical distributions such as "the normal distribution" on which statistical equations for particular tests are based. Nonparametric tests are "distribution free" and do not require many assumptions about the "population" from which the data were drawn (Lehner 1996).

The beginning statistician should learn which statistical tests are appropriate for which comparisons or kinds of data. Gradually expand the statistical repertoire with experience. Learning about statistics is much like becoming fluent in a foreign language—familiarity comes with use. Siegel (1956) and Conover (1999) describe most nonparametric tests in detail, and Lehner (1996) provides an adequate and usable summary of the most common ones. Furthermore, Lehner (1996) uses examples that are more relevant to zoo studies (also see Brown and Downhower [1988]). Some readers may be unfamiliar with some of the statistical terminology used in this chapter. The textbook by Ha and Ha (forthcoming) is a good general introduction to descriptive, parametric, and nonparametric statistics. Some advanced statistics books emphasize biological examples (Sokal and Rohlf 1995; Zar 1999). Tabachnick and Fidell (2001) describe multivariate statistics and computer programs that calculate them. Manuals to statistical software packages can be particularly helpful in improving understanding of statistics and data analysis (Velleman 1997; Wilkinson 2004).

Table 30.7 lists a variety of nonparametric tests. Most can be done rather easily by calculator or formulas entered into an Excel spreadsheet. To become familiar with these tests, it can be useful to look at published research and see which tests were used in which situations. Try to determine what the unit of analysis was, or exactly how the data might have been set up to do the test. Be warned, however, that inappropriately applied statistics sometimes do get published.

Parametric tests (table 30.8) can be used if certain assumptions, such as homogeneity of variance and a normal distri-

TABLE 30.7. Summary of common nonparametric tests

Type of data	Statistical test	Examples of use
Nominal—frequency	Chi-square (association and goodness-of-fit)	Byers 1977; Izard and Simons 1986; Margulis, Hoyos, and Anderson 2003; Ralls, Brugger, and Ballou 1979
	G-test (multiway contingency)	Crockett and Sekulic 1984
	Binomial	Izard and Simons 1986
Ordinal—rank order		
Two samples		
Independent	Mann-Whitney *U*	Byers 1977; Freeman 1983; Kleiman 1983; Macedonia 1987; Vickery and Mason 2004
Correlated (paired)	Wilcoxon signed ranks	Byers 1977; Freeman 1983; Kleiman 1980, 1983; Mallapur and Chellam 2002
	Sign test	Ralls, Brugger, and Ballou 1979
	Spearman's correlation	Freeman 1983; Macedonia 1987; Margulis, Hoyos, and Anderson 2003
Three or more samples		
Independent	Kruskal-Wallis one-way ANOVA	Margulis, Whitham, and Ogorzalek 2003; Vickery and Mason 2004
Correlated	Friedman two-way ANOVA	Nash and Chilton 1986

Note: Conover (1999), Siegel (1956), Lehner (1996), Zar (1999), and Sokal and Rohlf (1995) may be consulted for details and more tests.

TABLE 30.8. Choosing the appropriate parametric test

No. of groups OR conditions	Type of design*	Assumptions (see numbered text)	Type of test to use (Ha and Ha, forthcoming)
One sample	Single sample	1, 2, 4, and 5 are all met	Single sample *z*-test
One sample	Single sample	1, 2, and 4 are all met	Single sample *t*-test
2	Independent (between) groups	1, 2, and 3 are met	Independent *t*-test
2	Dependent (within) groups	1 and 2 are both met	Paired *t*-test (correlated *t*-test)
3 or more	Independent (between) groups	1, 2, and 3 are met	ANOVA

Note: Assumptions are as follows.

1. The data must be interval or ratio.

2. The data are normally distributed, meaning (a) the population raw scores are known to be normally distributed, or (b) the sample size is ≥30, or (c) the skewness and kurtosis values are approximately between −1.0 and +1.0.

3. The variances are equal between the groups, called homogeneity of variance (HOV). The variances can be up to 4 times different from each other, but no more than that, and still be considered "equal." To find HOV, divide the larger variance by the smaller variance.

4. Known population mean

5. Known population standard deviation

*A single sample test compares a sample to known population data. This might be useful if there are verified data on wild populations and you wish to compare that mean to your sample mean. A within-groups design is one in which the same subjects are measured more than once (e.g. before, during, and after for some dependent variable), and thus participate in the study as their own control. Alternatively, within-groups designs can also be pairs of associated individuals that are being compared. In other words, within-groups designs are appropriate when you cannot assume that the data are independent. In contrast, independent, or between-groups, designs are appropriate when comparing samples that are not associated by repeated measures or relatedness (Woodland Park Zoo elephant feeding behavior versus Point Defiance Zoo and Aquarium elephant feeding behavior).

bution, are met (Ha and Ha, forthcoming). It is important to recognize that both of these assumptions are robust for minor violations of the assumption (Kirk 1994; Ha and Ha, forthcoming). Parametric tests are preferable to nonparametric tests, because they have a much greater "power"; i.e. smaller differences are required to reject the null hypothesis. Power also increases as the sample size increases: for a given magnitude of difference (e.g. between 2 means), the difference is more likely to be statistically significant when the means are based on more individual data points. In some cases, a parametric test is necessary for multivariate analysis, or when unequal sample sizes make use of the Friedman ANOVA inappropriate (Lehner 1996, and table 30.7). Parametric tests can be conducted using one of the numerous statistical packages on the market (e.g. Microsoft Excel, Minitab, SPSS, STATA, Systat, Data Desk).

Whenever percentages or proportions are to be used in parametric statistics, it is recommended that the data first be arcsine-transformed to normalize the distribution (Lehner 1996, p. 378). This transformation was used by Stanley and Aspey (1984). Transformations are useful in correcting some violations of parametric assumptions, and advanced readers should consult Lehner (1996) or Zar (1999) for information on square root and logarithmic transformations.

While nonparametric tests are one alternative when the assumptions of parametric tests are not met, the reduction in power due to rank transformations is a significant disadvantage. Resampling, or randomization, tests are increasingly being used as a more powerful alternative to nonparametric tests (Adams and Anthony 1996). These tests generate probabilities based on empirical repeated sampling (resampling) of the raw data to create a randomization distribution (Hayes 2000). This technique is particularly useful when the assumption of a normal distribution is not met, but the assumption of approximately equal variances is met (ibid.). See the reviews by Adams and Anthony (1996) and Crowley (1992) for more information on the different techniques and software to derive randomization distributions. These techniques may be particularly useful when one's data are repeated samples of the same individual, a common occurrence in zoo research (e.g. Cantoni 1993).

The unit of analysis. To perform statistical tests, one has to decide on the unit of analysis. In experimental studies, this is usually obvious, e.g. the number of trials before a rat learns a task. In studies of observed behaviors in which the researcher defines the behaviors, the issue is more complicated. The unit of analysis might be the total number of occurrences (frequency) of a behavior, its hourly rate of occurrence, the percentage of time spent performing the behavior, the total duration of the behavior, or mean bout duration. Furthermore, the researcher must determine whether each animal's overall "score" (total frequency, mean rate, duration, or whatever) will be a data point, or whether each animal will contribute one score per observation period or designated time block (e.g. age) and thus the data points are not independent. Perhaps individuals cannot be distinguished, and each observation period contributes one score that is the average or total of all individuals. The appropriate unit of analysis will depend in part on the statistical test to be used.

Fig. 30.9. The Mann-Whitney *U* nonparametric statistic was used to test for behavioral differences between successfully and unsuccessfully breeding snow leopard pairs. Boris is the cub of a successful pair. (Photography by Cathy Shelton, Woodland Park Zoo. Reprinted by permission.)

For some statistical tests, minimum sample sizes are required in order to demonstrate significance (Siegel 1956). Freeman (1983) used the Mann-Whitney *U* to test differences between successfully and unsuccessfully breeding snow leopard, *Uncia uncia*, pairs, analyzing data for each sex separately (fig. 30.9). For the sample sizes in that study (3 successful and 5 unsuccessful pairs), in order to achieve a 2-tailed level of significance (at a probability of 0.05 or less), there could be no reversals. In other words, significant differences could be demonstrated only if all 3 successful pairs ranked above (or below) the 5 unsuccessful pairs.

Many studies of captive animals involve small groups, in some cases too few individuals to use one data point per subject for some kinds of statistical tests. In such cases, the sample size (and statistical power) can be increased by using one score per subject per observation period or time block. These data could be used in a repeated-measures design, or in multiple tests of the null hypothesis that an individual's behavior (as opposed to the group's behavior) did not vary from one condition to another (e.g. after moving to a new enclosure). This is also a situation where the new randomization techniques dis-

Fig. 30.10. *Galago senegalensis* in the Nocturnal House at Woodland Park Zoo, Seattle. (Photography by Karen Anderson. Reprinted by permission.)

cussed earlier apply. One cannot simply lump multiple scores from one individual with those of others without the possibility of committing a type I error—i.e. rejecting the null hypothesis when it is in fact true (Machlis, Dodd, and Fentress 1985, "the pooling fallacy"). Such an error can occur when within-individual variance (i.e. between observations of the same animal) is less than between-individual variance (Leger and Didrichsons 1994). Some ways to avoid this problem while maximizing statistical power include (1) using a more complex design (e.g. a repeated measures test), (2) examining the sources of variance in detail, using the results to determine the grouping into units of analysis (Kraemer et al. 1982; Thiemann and Kraemer 1984), (3) using the mean or sum across all individuals within a basic observation period so that each individual and observation period contribute equally, and (4) testing each subject's data separately, which might be done if each individual's response to a change was of interest.

Some examples from the literature illustrate different units of analysis. Byers (1977, figures 4 and 5) used a Wilcoxon matched pairs test to determine whether play events occurred at different rates on different substrates. For example, for each individual ibex, *Capra sibirica*, kid, the total number of "butt" play events that occurred on sloped surfaces was paired (matched) with the same kid's total number of "butt" play events on flat surfaces. Sloped and flat areas each made up about half the enclosure; otherwise the play events per S would have been multiplied by the proportion of the enclosure made up of the surface type on which they occurred to correct for differences in "available" area. To compare sex differences in behavior, Freeman (1983) matched male and female percentages of time spent in selected behaviors (calculated from scan samples) for members of 8 mated snow leopard pairs. Since pairs were studied for different numbers of years, "cat-mean" data (mean percentage per leopard across years of study) were used in statistical tests. In Kleiman's (1980) figure 50.4, the total amount of time that the sexually active male golden lion tamarin, *Leontopithecus rosalia*, spent grooming the female was matched with the total duration of grooming by the sexually inactive male for each observation period. Thus, each observation session contributed one score per male, and the data from each trio (2 males and one female housed together) were statistically tested separately. In Nash and Chilton's (1986) study, each galago, *Galago senegalensis* (fig. 30.10), was observed for the same amount of time for each of 3 "phases," except that infants' observation sessions were twice as long. The analyzed data for each behavior scored consisted of total frequency per individual per phase (i.e. "raw" scores), except for infants, whose frequencies were halved, i.e. "corrected" or "adjusted," to make them equivalent. Alternatively, raw frequencies could have been converted to hourly rates. In a longitudinal study of chimpanzee, *Pan troglodytes*, development, all observations—made 3 days a week—over a 3-month seasonal period for a single subject were combined into a single data point for analysis (Kraemer et al. 1982).

OTHER STATISTICAL CONSIDERATIONS

The problem of independence. Theoretically, for purposes of statistical analysis, data points (e.g. the units of analysis described above) should be independent. For example, one individual's rate of performing a given behavior should be unrelated to another individual's rate, or the occurrence of one behavior type should not influence the probability of occurrence of another. In reality, the independence assumption is often violated in the case of interactive social behaviors (most zoo studies), which usually influence the behavior of other group members and thus may be inherently correlated (G. P. Sackett, personal communication). Furthermore, when more than one of a mutually exclusive and exhaustive set of behaviors is tested, the outcome of one statistical test is not independent of the outcome of the other: if behaviors are categorized as either "social" or "nonsocial," rejecting the null hypothesis that social behaviors did not differ between conditions guarantees that the difference in nonsocial behaviors will also be statistically significant (Sackett, Ruppenthal, and Gluck 1978). For this reason, adjustments to probability levels are sometimes applied to make tests more conservative (Stanley and Aspey 1984). Fortunately, new techniques are quickly being developed to eliminate this problem. Advanced readers should explore the topics of Monte Carlo Simulations, Modeling, and Resampling Techniques for more information on how to deal with violations of the assumption of independence (Crowley 1992; Todman and Dugard 2000).

Temporal autocorrelation. Another aspect of independence is temporal autocorrelation, or the probability that the occurrence of a behavior at one point in time will affect its likelihood of being observed at the next point in time. Obviously, the shorter the time interval between successive "points," the more likely that temporal autocorrelation will occur. For scan or instantaneous samples that are converted to percentages, this poses no problem; shorter intervals generally produce more accurate estimates of true percentages of time spent performing the behavior in question. However, contingency analyses (chi-square, goodness-of-fit tests) require independent data points (Siegel 1956). If, for example, one wanted to compare the use of several different enclosure locations, one possibility would be to count the number of times that the subject was scored in each location. However, these counts could not be used in a chi-square test if the points in time were temporally autocorrelated—that is, if the animal's location on a particular branch was not independent of the fact that it was found there in the previous interval.

The interval at which independence can be assumed varies with behavior, species, and so forth, so no general rule can be stated; the appropriate interval must be determined from the data. For example, Janson (1984) found that nearest neighbors of wild brown capuchins, *Cebus apella*, usually were temporally autocorrelated at 5-minute intervals, rarely were at 10-minute intervals, and never were at 15-minute intervals. Thus, only records at 15-minute intervals were used for analyses requiring independence. A pilot study using continuous sampling could be used to choose the appropriate scan interval. In this manner, Slatkin (1975) computed the autocorrelation time for adult male geladas, *Theropithecus gelada*, and yellow baboons, *Papio cynocephalus*, and found the correlation time to be about one minute for the geladas and 4–5 minutes for the yellow baboons.

Ketchum (1985) studied enclosure utilization by snow leopards at Woodland Park Zoo, Seattle. Scan samples were taken every 20 seconds, an interval likely to be highly autocorrelated. The enclosure was divided into 4 location categories (based on visibility to the public and distance that the cats could visualize), and the percentage of scan samples spent in each area was calculated. To analyze these data with a chi-square goodness-of-fit test, which requires independence as well as frequency (i.e. not percentage) data, the percentages were multiplied by the number of focal sample periods. This calculation produces adjusted frequencies approximately equivalent to randomly sampling the location of the subject once per period. Since the sample periods were at least 2 hours apart, and often more than a day apart, these adjusted frequencies were accepted as independent. The expected frequencies were calculated by multiplying the number of sample periods by the percentage of the enclosure area that each location category constituted. (Expected frequencies in this test are the values that we would "expect" if the snow leopards were using the locations in proportion to their availability, i.e. showing no preference.)

Lehner (1996) describes a test for comparing 2 percentages; however, if this test is used on scan sample data, the scan intervals must not be temporally autocorrelated. If there is reason to believe that they are, a simple but statistically conservative solution is to use the number of observation periods as *n* in the equation.

The logic of the independence requirement is simple: Recall that the power of the statistical test improves with sample size. Obviously, the closer the scan samples, the more samples there will be in a given observation period. An inflated sample size will increase the likelihood of refuting the null hypothesis (and committing a type I error), and scan sample interval length will be inversely related to achieving statistical significance. Clearly, it is not valid to pick a sampling interval that would guarantee significance. On the other hand, using the technique of multiplying percentages by the number of observation periods makes the test unnecessarily conservative when the true interval of independence is less than the sample duration.

Whenever each focal sample period contributes a data point, the underlying assumption is that each session is an independent estimate of the animal's behavior. This further stresses the importance of scheduling balanced or randomized observation periods so as not to introduce systematic bias.

The violation of the independence assumption restricts the number of conventional statistical tests that can be applied to certain behavioral data. Dunbar and Dunbar (1975) describe some considerations and solutions with respect to the independence assumption. Also, see the section on randomization tests, mentioned previously.

CONCLUSION

Data collection in the zoo setting can provide answers to management questions as well as basic information about the biology of captive animals. Research is now being recognized as important and is expanding in many zoos (Finlay and Maple 1986; Leong, Terrell, and Savage 2004; Maple and Bashaw, chap. 24, this volume). For example, the benefits of environmental enrichment are being evaluated (Mellen and MacPhee 2001; Mellen and MacPhee, chap. 26, this volume; Young 2003). To be most useful, data should be quantified in a manner amenable to statistical analysis, whether it is statistical testing or straightforward description. Furthermore, proper sampling methods should be used so as to avoid observer bias and other sorts of sampling error. This chapter has summarized the major sampling methods and has provided some hints for data analysis.

Systematic data collection is not difficult and mostly requires systematic thinking ahead of time. A project is more likely to be successful if these guidelines are followed:

1. Formulate a specific research question.
2. Keep data collection simple.
3. Perform preliminary analyses on some sample data before finalizing the data collection design.
4. Collate and begin to analyze data while data collection is in progress.
5. Finally, if the results of the study seem to be of general interest, publish them.

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Part Seven

Reproduction

Introduction

Devra G. Kleiman

The management of reproduction is the key to the long-term maintenance of species in zoos and breeding centers. This section details the advances we have made in the past 10 years in our understanding of the physiology of reproduction and its application to species management.

Asa presents a thorough description of the physiological processes involved in mammalian reproduction, including the role played by the brain and other reproductive organs and the interactions of hormones, beginning with the changes occurring during puberty. For males and females separately, she reviews anatomy, endocrinology, and the interaction of hormones and behavior. She then discusses the factors affecting reproductive capacity, such as seasonality (photoperiod, rainfall, and temperature), nutrition, and social characteristics.

Studies of the reproductive physiology of male exotic mammals have been thriving since the earliest attempts to store sperm and conduct artificial insemination (AI) in the mid-1960s. Spindler and Wildt focus on the evaluation and control of male reproductive function. They provide an update on the limits of male fertility assessment and the diverse methods for evaluating a male's reproductive capabilities, beginning with anatomical assessments and the measurement of reproductive and pituitary hormones. Spindler and Wildt provide the most up-to-date techniques for collecting (e.g. electroejaculation, artificial vaginas, and manual stimulation) and evaluating sperm for use in AI or for long-term cryopreservation. With recent advances in storage and AI techniques, the development of genome banks to retain the genetic diversity of endangered species has become a potential mechanism for conserving biodiversity through the twenty-first century.

Infant giant anteater riding on its mother's back at the Smithsonian's National Zoological Park, Washington, DC. Photography by Mehgan Murphy, Smithsonian's National Zoological Park. Reprinted by permission.

Hodges, Brown, and Heistermann summarize the tremendous advances that have been made in the noninvasive measurement of hormones and thus of reproductive function and stress in exotic mammals. It is now possible to measure hormone levels in blood, urine, feces, and saliva and to do so without negatively affecting the welfare of zoo mammals. Noninvasive hormone measurement is a powerful tool for assessing welfare conditions for individual animals and thus for improving exhibit environments.

A major goal of any successful management program for a species maintained in zoos is the control of reproduction, especially since uncontrolled population growth is impossible in limited enclosure space. Ten years on, it is interesting that the zoo community has put much more effort and resources into measuring reproductive status, cryopreservation techniques, AI, and even cloning when compared with contraception. There are still limited options available for use with exotic mammals.

Asa and Porton review the contraceptive techniques in use for males and females, be they endocrine, mechanical, or immunocontraceptive. They separate reversible from nonreversible techniques and summarize the differences in target for males and females when developing a contraceptive strategy. Asa and Porton consider the modes of delivery of the different contraceptive methods, especially those that target the endocrine system, and provide guidance in choosing the best method in each individual case.

Despite the basic similarity in the physiological processes of all male and all female mammals, it is often difficult to extrapolate from one species to another, even when they are very closely related. All these chapters emphasize the importance of keeping species differences in mind. For example, the small but significant differences in species physiology and the structure of mammalian spermatozoa result in a need for species-specific recipes for the collection and cryopreservation of male gametes. In females, differences in physiology may result in some contraceptive techniques being reversible in one species and nonreversible in a second related species. Mammal managers need to take care when testing new techniques, to prevent the potential for the undesirable sterilization of females.

In all these chapters on reproduction, authors emphasize the need to understand and be sensitive to the effect of reproductive status and its manipulation on behavior, especially in social species. Changes in reproductive status and intervening in the reproduction of zoo mammals, however it is accomplished, have an impact on individual and group behavior that can have negative effects on animal welfare and the messages that a zoo wishes to portray in its exhibits. Thus, the behavioral implications of reproductive management need constant attention.

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Reproductive Physiology

Cheryl S. Asa

INTRODUCTION

An understanding of reproductive processes is the only solid foundation on which to build successful, long-term captive breeding programs. Even for species that now reproduce naturally in captivity, genetic management may require artificial insemination or other assisted reproduction technology, and their use in exotic species requires at least a basic knowledge of male reproduction, ovulatory cycle dynamics, and perhaps even control of ovulation. Likewise, control of reproduction through contraception is most effectively and safely applied during appropriate reproductive stages. This chapter will review the events and processes of reproductive physiology, primarily from the broader base of literature on laboratory and domestic animals, supplemented with examples from exotic species when possible.

PUBERTY

An animal's reproductive life begins at the time of puberty, a complex, not yet fully understood process that culminates in fertility. For males, puberty is marked by the first production of sperm. In nonprimate and some primate females, puberty is denoted by first ovulation and, in menstruating primates, by first menstruation, or menarche. Reviews of pubertal processes can be found in Plant (1998), and Foster and Ebling (1998). During puberty in both males and females, the secretion of GnRH (gonadotropin-releasing hormone) from the hypothalamus increases markedly, which in turn stimulates production of the anterior pituitary gonadotropins LH (luteinizing hormone) and FSH (follicle-stimulating hormone). Although LH and FSH were first named for their activity in females, the same hormones are produced in males, but they go on to stimulate testicular and not ovarian target cells. As a possible mechanism for controlling onset of puberty in both males and females, the "gonadostat hypothesis" proposes that decreasing sensitivity of the hypothalamus to negative feedback from gonadal steroid hormones allows GnRH secretion to increase. Some species differences have been described, and as yet no mechanism has been identified to explain the shift in sensitivity. Interestingly, the onset of reproduction each year in seasonally breeding species very closely resembles the onset of puberty (Goodman et al. 1982).

Important changes occur in hormone profiles which result in activation and growth of gonads, germ cells, and often species-specific, secondary sex characteristics. In the male, increases in LH, FSH, and prolactin (PRL) from the anterior pituitary, and androgens from testicular Leydig cells are correlated with increases in testis and accessory sex organ weight, e.g. seminal vesicles and prostate. These changes are necessary for the stimulation of testicular Sertoli cells, which are involved in initiation and maintenance of normal sperm production. An external sign of first sperm production in the male rat, *Rattus rattus* (Korenbrot, Huhtaniemi, and Weiner 1977), which also may occur in other species, is separation or opening of the prepuce of the penile sheath. Many of the processes are similar in the female, where levels of pituitary LH, FSH, and PRL, and ovarian progesterone and estradiol accompany the increase in ovarian weight.

Adrenal cortical hormones may play a role in puberty onset in some species, a process called adrenarche, in which increases in the adrenal androgen dehydroepiandrosterone (DHA or DHEA) or androstenedione accompany puberty. A minimal level of adrenal corticosterone may be required for normal puberty onset, but excess adrenal-corticotropic hormone (ACTH) (Hagino, Watanabe, and Goldzieher 1969) or glucocorticoids (Ramaley 1976), associated with what are interpreted as stressful situations such as crowding, can cause a delay in puberty (see Moltz 1975).

A factor involved in the timing of puberty is attainment of a critical body weight. However, nutritional plane rather than an absolute body weight may be more important. A higher level of nutrition or its resultant increased growth rate advances puberty in many species, whereas food restriction can prevent reproductive development. Leptin, a hormone correlated with nutritional plane and adipose tissue stores, is permissive to onset of puberty (Clarke and Henry 1999; Zieba, Amstalden, and Williams 2005).

Particularly among primates, initial ovarian cycles following puberty are often infertile, a condition termed adolescent sterility (Spear 2000). Conception rate also is low during the postpubertal period in cattle (Byerley et al. 1987). A related phenomenon, follicular development and atresia without ovulation, commonly precedes the first real ovulation of puberty in rats (Dawson and McCabe 1951), cattle (Schams et al. 1981), and sheep, and may well be common in other species.

MALE REPRODUCTION

In general, the male reproductive system has been studied less than that of the female, and most information that does exist comes from studies of laboratory and domestic species. The dearth of basic knowledge of male reproductive processes in exotic species is particularly notable. Spindler and Wildt (chap. 32, this volume) focus on the assessment and management of male fertility and its role in assisted reproduction.

ANATOMY

Testes function to produce spermatozoa and to synthesize and secrete androgens, especially testosterone. Spermatogenesis occurs within the densely packed seminiferous tubules, supported and sustained by Sertoli cells. Leydig cells, responsible for androgen production, lie in the interstitial spaces between the seminiferous tubules. Spermatozoa are transported from the testis via the rete testis into the efferent ducts (ductuli efferentes), then the epididymal duct. The efferent duct and head (caput) of the epididymis resorb fluid, the body (corpus) is secretory, and the tail (cauda) is relatively inactive. Spermatozoa pass from the epididymis through the vas deferens, or ductus deferens, where the accessory fluids are added, and then out via the penis (see Setchell 1978; Austin and Short 1982).

Only in mammals do testes descend from the abdominal cavity into a scrotum. However, the degree of descent varies among orders and families, ranging from virtually no migration (Monotremata; elephant shrews, Macroscelididae; seacows, Sirenia; sloths and anteaters, Edentata; elephants, Proboscidea; and hyraxes, Hyracoidea), migration to caudal abdominal cavity (armadillos, Dasypodidae; whales and dolphins, Cetacea), migration just through the abdominal wall (hedgehogs, Erinaceidae; moles, Talipidae; and some seals, Otariidae), and subanal swellings (pigs, Suidae; Rodentia; Carnivora), to a pronounced swelling (Primates; ruminants; most Marsupalia) (Carrick and Setchell 1977). The function and significance of these differences are not understood (see Bedford 1978 for discussion). In species with external (i.e. scrotal) testes, failure of descent (cryptorchidism) results in reduction or absence of spermatogenesis (see Setchell 1978). However, testosterone production may be unaffected or only moderately depressed by cryptorchidism or temperature increase (Moore 1944; Glover 1955).

For most species, testicular descent is permanent, but in some, descent occurs only during the breeding season, e.g. bats, Chiroptera (Eckstein and Zuckerman 1956); some rodents, *Rattus*, *Sciurus*, and *Tamias* spp.; and some primates, *Loris* and *Perodicticus* spp. (Prasad 1974 in Van Tienhoven 1983).

Major accessory sex glands include seminal vesicles and prostate and bulbourethral (Cowper's) glands, all of which secrete components of the seminal fluid. Only prostate glands have been universally found in mammals. Van Tienhoven (1983) provides a synthesis of the occurrence of the various accessory organs in a wide range of mammals.

Two species-specific morphological features of male mammals are the penile baculum (os penis) and penile spines. The baculum, a bony core, occurs in members of 5 mammalian orders: Insectivora, Chiroptera, Primates, Rodentia, and Carnivora (Long and Frank 1968; Patterson and Thaeler 1982; Dixson 1987; Ferguson and Lariviere 2004), and may facilitate intromission and prevent collapse of the urethra during copulation.

Penile spines of the rat (Beach and Levinson 1950); cat, *Felis catus* (see Aronson and Cooper 1967); ferret, *Mustela putorius*; mink, *M. vison*; marten, *Martes americana*; raccoon, *Procyon lotor* (see Zarrow and Clark 1968); spotted hyena, *Crocuta crocuta*; striped hyena, *Hyaena hyaena*; aardwolf, *Proteles cristatus* (see Wells 1968); and African shrew, *Myosorex varius* (see Bedford et al. 1998), may provide additional stimulation during copulation, perhaps most importantly in species with induced ovulation.

ENDOCRINOLOGY OF THE TESTIS

Gonadotropin-releasing hormone (GnRH, also sometimes called luteinizing hormone–releasing hormone, or LHRH) stimulates anterior pituitary secretion of both FSH and LH. FSH is necessary for spermatogenesis via its action on Sertoli cells, whereas LH stimulates androgen production by the Leydig cells. Circulating androgens exert negative feedback on both hypothalamic GnRH and pituitary LH production and release, helping maintain relatively stable androgen levels. Testosterone is the primary androgen secreted by the adult testis, and androstenedione, although present in smaller amounts, is relatively more prominent in prepubertal and aging males. Other androgens include dehydroepiandrosterone (DHA or DHEA), dihydrotestosterone (DHT), androstenediol, and androstanediol (Setchell 1978). Androgens are necessary for the maintenance of spermatogenesis, the accessory sex organs, secondary sex characteristics (e.g. antlers), sebaceous glands, and libido.

The source of most circulating DHEA is the adrenal cortex, not the testis (Gandy and Peterson 1968). Most DHT is formed by reduction of testosterone in accessory reproductive and neural tissue (Setchell 1978; Milewich and Whisenant 1982; Martini 1982). Estrogens are produced by aromatization from testosterone in both the testis and the peripheral tissues (Callard, Petro, and Ryan 1978).

Although the seminiferous tubules can convert progesterone to androgens, the interstitial Leydig cells are by far the more important source (Christensen and Mason 1965; Hall, Irby, and deKretser 1969). The pituitary gonadotropin LH stimulates testicular androgen production (El Safoury and Bartke 1974). Each pulsatile release of LH results, in 15 to 30 minutes, in a pulse of testosterone (cattle: Katongole, Naftolin, and Short 1971; sheep: Schanbacher and Ford 1976; dog: De Palatis, Moore, and Falvo 1978). In measuring circulating LH or testosterone, account must be taken of this pulsatile secretion in addition to diurnal rhythms or possible seasonal rhythms. Because these changes in testosterone are correlated with changes in testicular size, testis measures may be adequate for assessing reproductive status or changes when blood sampling is not practical (Willett and Ohms 1957; Möller 1989; de Jong et al. 2005; Penfold et al. 2005).

In hibernating male bats (primarily Vespertilionidae and Rhinolophidae), reactivation of several reproductive functions may be temporally separated. Spermatogenesis may precede the rise in testosterone by several months. Testosterone peaks to maximally stimulate accessory organs, epididymal sperm storage, libido, and mating late in the spermatogenic phase (Crichton 2000).

Other factors can affect testosterone secretion. Circulating levels are generally lower in aging males (Chan, Leathem, and Esashi 1977) and can be reduced by anesthetics, with the decrease sometimes continuing for days after administration (Setchell, Waites, and Lindner 1965; Cicero et al. 1977). Undernutrition also adversely affects androgen production (sheep: Setchell, Waites, and Lindner 1965; hyrax, *Procavia capensis*: Millar and Fairall 1976; horse: Johnson et al. 1997).

SPERMATOGENESIS

A complete review of spermatogenic processes is beyond the scope of this chapter (see excellent sources such as Setchell 1978; Phillips 1974; Austin and Short 1982; and Hess 1998). Spermatogenesis is initiated by FSH and testosterone but can be maintained by testosterone alone. Sperm pass into the epididymis, where maturation is completed, and are stored until ejaculation. Sperm that are not ejaculated may be phagocytized or leaked into the bladder (Bedford 1979). Longevity of epididymal sperm varies greatly by species (domestic cattle: 60 days, White 1974; mole, *Talpa europaea*: up to 3 months, Racey 1978; bats, Chiroptera: up to 10 months, Racey 1979). Sexual activity can enhance spermatogenesis, whereas elevated ambient temperature can depress it.

Both whole-body and localized X-irradiation also profoundly disrupt sperm production by damaging germinal cells (Ellis 1970). Greater doses damage spermatocytes that are still capable of fertilization but induce genetic abnormalities, which prevent complete embryonic development (Chang, Hunt, and Romanoff 1957). High-frequency sound waves (ultrasound) can cause testicular damage and sterility (Dumontier et al. 1977).

Nutrient deficiencies can depress spermatogenic function either directly or by reducing LH concentrations. The results of dietary restriction can range from no observable effect to complete cessation of spermatogenesis, depending on the species and degree of restriction (Leathem 1975; Blank and Desjardins 1984). Swanson et al. (2003) found a relationship between poor nutrition and sperm morphology in some wild felids. Androgen production in these cases is relatively less affected. Overfeeding that results in overly fat males can result in increased incidence of secondary sperm abnormalities, probably due to increased testis temperature from the insulating scrotal fat (Skinner 1981).

Deficiencies of amino acids, essential fatty acids, zinc, and vitamins A, B, C, and E all negatively affect spermatogenesis although at different points in the process (see Setchell 1978 for discussion). In addition, an extensive array of substances have been shown to cause chemical damage to testicular tissue (see ibid.; Zaneveld 1996).

HORMONES AND BEHAVIOR

Androgens are generally responsible for species-specific arrays of reproductive behavior, ranging from aggression-related mate or territory defense to scent marking, courtship, and copulation. Not only do androgens stimulate reproductive behavior, but social factors can cause an increase in hormone levels. Rams living with ewes have higher circulating testosterone concentrations and show more sexual and aggressive behavior than those not with ewes (Illius, Haynes, and Lamming 1976). Likewise, territorial male impala, *Aepyceros melampus*, had higher testosterone levels (Illius et al. 1983). Acute increases in testosterone (and in LH and prolactin when measured) are stimulated by mating activity (rabbit: Saginor and Horton 1968; rat: Kamel and Frankel 1978; giant panda, *Ailuropoda melanoleuca*: Bonney, Wood, and Kleiman 1981; rhesus macaque, *Macaca mulatta*: Katangole, Naftolin, and Short 1971).

Sexual activity resulted in testosterone elevation in zebu males previously rated as having low libido, but not in those with high libido (Bindon, Hewetson, and Post 1976). Replacing the resident female mouse with a new female also can cause a testosterone increase in male partners (Macrides, Bartke, and Dalterio 1975). In the male tammar wallaby, *Macropus eugenii*, seasonal LH and testosterone increases occurred only in the presence of females (Catling and Sutherland 1980).

FEMALE REPRODUCTION

In the following overview, I describe the basic reproductive phenomena of mammalian females and attempt to convey an appreciation for the wide array of strategies which various species have evolved to accomplish the same end, i.e. production of young. Details of endocrine and cellular events of ovarian cycles are available in Rowlands and Weir (1977), Hansel and Convey (1983), Adams (1999), and Robker et al. (2000). Summaries of species-specific reproductive data can be found in the compendium by Hayssen, van Tienhoven, and van Tienhoven (1993).

ANATOMY

The major structural components of the female reproductive system are ovaries, oviduct, uterus, cervix, vagina, and/or urogenital sinus. Notable interspecies variability occurs in uterine and vaginal morphology. The prototheria (Monotremata) have paired uteri, which open not into a vagina, but the urogenital sinus that terminates at the cloaca (Hughes and Carrick 1978). Metatherians (Marsupialia) have 2 uteri, 2 cervices, and 2 vaginae, with several variations, such as the midline vagina of the kangaroo, *Macropus* spp. (Sharman 1976).

Among Eutheria (placental mammals), 4 anatomical types have been described: (1) duplex uterus with 2 separate uterine horns connected to the vagina by 2 cervices (e.g. rabbit); (2) bicornuate uterus with its 2 horns joined just anterior to the single cervix and vagina (e.g. pig); (3) bipartite uterus in which the 2 horns open into a prominent uterine body anterior to the single cervix and vagina (e.g. cattle, sheep, and horses); and (4) the simplex uterus with a single uterine body, cervix, and vagina (e.g. most primate species). Some variations on these 4 patterns are seen in the sloth, *Bradypus* spp., which has a simplex uterus and one cervix but a double vagina, and the armadillo, *Dasypus* spp., with a simplex uterus but one cervix, which opens into a urogenital sinus rather than a vagina (Hafez 1970; van Tienhoven 1983).

Of external features, a ventral pouch is characteristic of monotremes and marsupials. An os clitorides, homologous to the male baculum, is present in females of various rodent and carnivore species (see Long and Frank 1968; Ewer 1973). Most unusual are the genitals of the female spotted hyena, *Crocuta crocuta*. The hypertrophied clitoris is virtually indistinguishable from the male penis, and fibrous swellings resemble a scrotum (Neaves, Griffin, and Wilson 1980).

OVARIAN CYCLES

Of the variety of terms that have been applied to female reproductive cycles, most are restrictive. For instance, only primates are considered to have menstrual cycles; induced ovulators can have cycles of follicular growth that are not ovulatory at all, making the term *ovulatory cycle* inappropriate; and the estrous cycle better describes behavioral than physiological events. The term *ovarian cycle* best encompasses the wide range of patterns described to date, by focusing on follicular growth and development. These follicles may ovulate or may undergo regression or atresia. Figure 31.1 is a model incorporating various ovarian cycle events and options of mammalian females.

The following is a description of the phases which may constitute an ovarian cycle, although components may vary by species. Figures 31.2 to 31.5 illustrate the major events of the rat; horse; gorilla, *Gorilla gorilla*; and island fox, *Urocyon littoralis*, ovarian cycles.

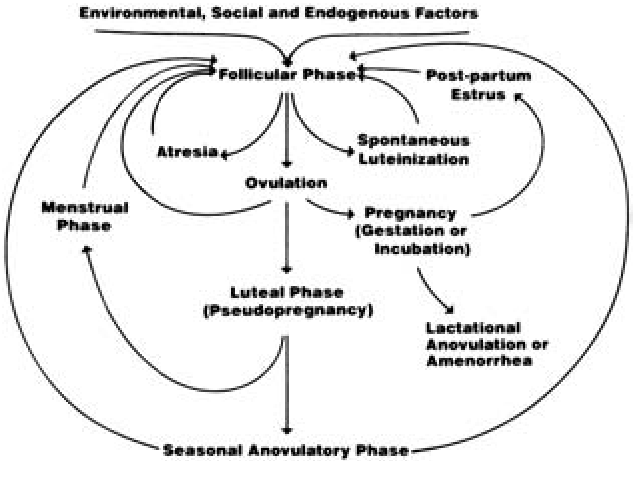

Fig. 31.1. Model incorporating various ovarian cycle events and options of mammalian females.

Follicular phase. Sometimes also called the proliferative phase, which relates to uterine development, the follicular phase is characterized by the growth and development of a follicle or follicles for subsequent rupture and release of an ovum (ova). Oocyte and follicular growth culminate in the mature, tertiary, or Graafian follicle with its fluid-filled antrum. Mature follicle size is generally correlated with the animal's body size, with

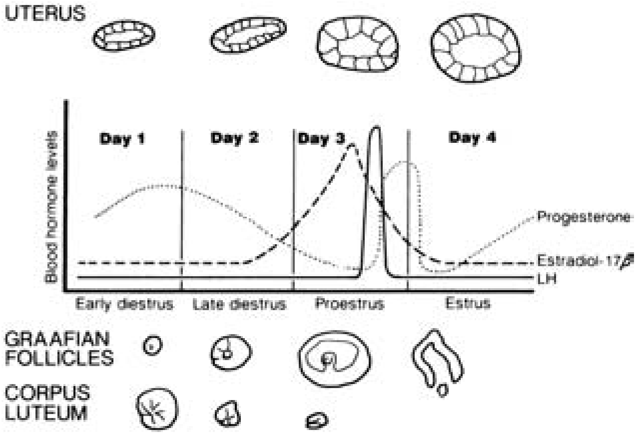

Fig. 31.2. Estrous cycle of the laboratory rat: blood hormone levels and representational changes in the uterus, Graafian follicles, and corpus luteum. (From Bentley, P. J. 1976. *Comparative vertebrate endocrinology*. Cambridge: Cambridge University Press. Reprinted by permission.)

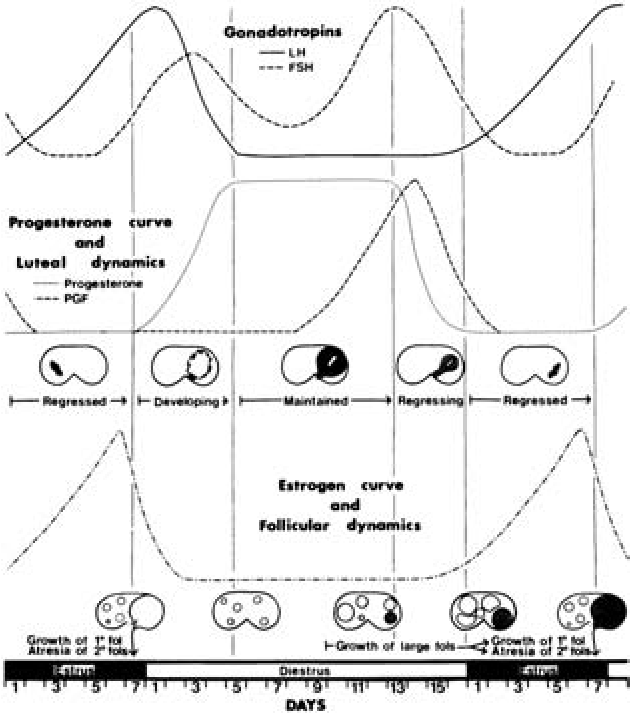

Fig. 31.3. Estrous cycle of the horse: blood hormones, primary and secondary follicles, and corpus luteum. (From Ginther 1979; reprinted by permission of the author.)

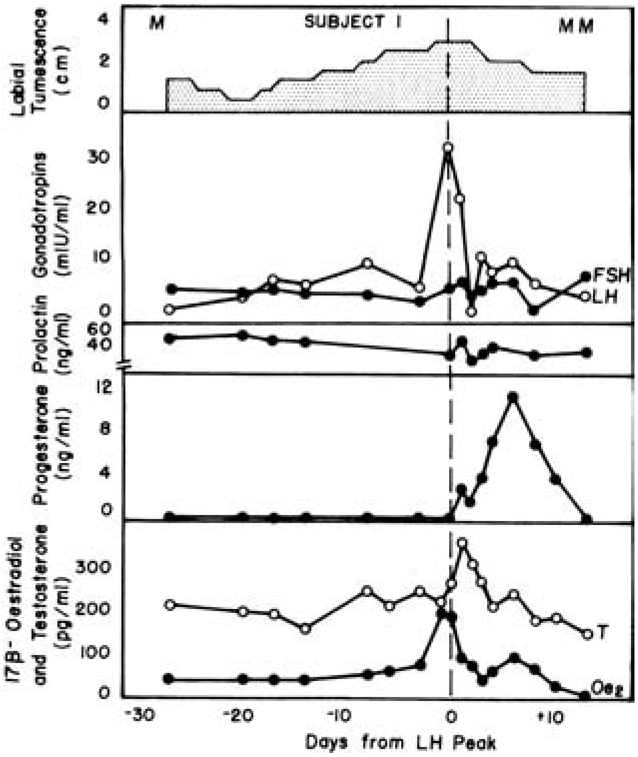

Fig. 31.4. Menstrual cycle of the lowland gorilla: blood hormones, changes in labial tumescence, and occurrence of menses (solid bars). (From Nadler, R. D. 1980. Reproductive physiology and behaviour of gorillas. *J. Reprod. Fertil. Suppl.* 28: 79–89. © Society for Reproduction and Fertility. Reproduced by permission.)

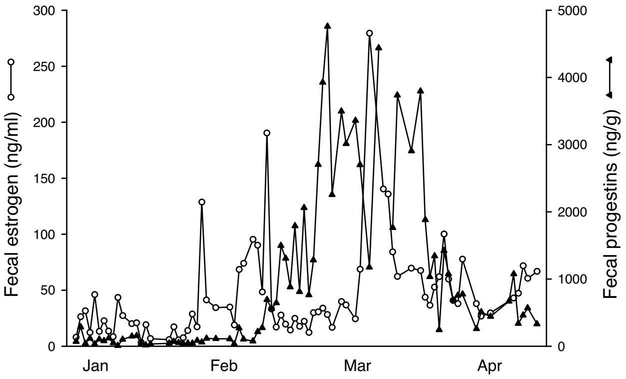

Fig. 31.5. Ovulatory cycle, including endocrinological pseudopregnancy, in the island fox (*Urocyon littoralis*).

TABLE 31.1. External signs of the follicular phase

Species	Reference
Activity increase	
Cattle, *Bos taurus*	Kiddy 1977
Buffalo, *Syncerus caffer*	Williams et al. 1986
Camel, *Camelus dromedarius*	Ismail 1987
Labial or perineal swelling	
Flying squirrel, *Glaucomys volans*	Sollberger 1943
Horse, *Equus caballus*	Ginther 1979
Camel, *Camelus dromedarius*	Ismail 1987
Raccoon, *Procyon lotor*	Whitney and Underwood 1952
Martin, *Martes americana*	Enders and Leekley 1941
Stoat, *Mustela erminea*	Gulamhusein and Thawley 1972
Ferret, *M. putorius*	Hammond and Marshall 1930
Red fox, *Vulpes vulpes*	Mondain-Monval et al. 1977
Fennec fox, *V. zerda*	Valdespino et al. 2002
Bush dog, *Speothos venaticus*	DeMatteo et al. 2006
Bushbaby, *Otolemur crassicaudatus*	Hendrickx and Newman 1978
Red ruffed lemur, *Varecia variegata*	Karesh et al. 1985
Ruffed lemur, *Varecia variegata*	Boskoff 1977
Tarsier, *Tarsius bancanus*	Wright, Izard, and Simons 1986
Talapoin, *Miopithecus talapoin*	Rowell 1977
Gelada baboon, *Theropithecus gelada*	Dunbar and Dunbar 1974
Chacma baboon, *Papio ursinus*	Saayman 1972
Hamadryas baboon, *P. hamadryas*	Hendrickx 1967
Olive baboon, *P. anubis*	Hendrickx and Kraemer 1969
Yellow baboon, *P. cynocephalus*	Hendrickx and Kraemer 1969
Rhesus macaque, *Macaca mulatta*	Czaja et al. 1977
Crab-eating macaque, *M. fascicularis*	Nawar and Hafez 1972
Pig-tailed macaque, *M. nemestrina*	Bullock, Paris, and Goy 1972
Chimpanzee, *Pan troglodytes*	Nadler et al. 1985
Gorilla, *Gorilla gorilla*	Nadler 1980
Uterine bleeding, nonmenstrual	
Dog, *Canis familiaris*	Evans and Cole 1931
Gray wolf, *C. lupus*	Seal et al. 1979
Raccoon, *Procyon lotor*	Whitney and Underwood 1952
Vaginal discharge, nonsanguinous	
Elephant shrew, *Elephantulus rufescens*	Lumpkin, Koontz, and Howard 1982
Camel, *Camelus dromedarius*	Ismail 1987

the notable exceptions of the vespertilionid bats and plains viscacha, *Lagostomus maximus* (see Rowlands and Weir 1984), which have unusually large follicles.

Not all developing follicles are destined to ovulate; most undergo atresia or regression (Adams 1999). As its name suggests, the pituitary hormone FSH (follicle-stimulating hormone) stimulates follicular growth, as well as the production and release of steroid hormones, primarily estrogens. LH (luteinizing hormone), the other pituitary gonadotroph, also plays a role in follicular steroid production. According to the 2-cell theory of ovarian steroid synthesis, theca interna cells in preovulatory follicles under the influence of LH convert cholesterol to androgen, which is transferred to granulosa cells where FSH enhances the aromatization of androgen to estrogen (Fortune 1981). In addition to estrogens, the ovaries secrete androgens, primarily testosterone and androstenedione, in particular, during the periovulatory phase.

Estrogens secreted by follicular granulosa cells have many effects. Unlike in the male, estrogens can exert both positive and negative feedback. They inhibit the secretion of FSH, but just before ovulation enhance release of LH. Estrogens also stimulate species-specific features of estrus, such as labial tumescence, perineal swelling and reddening, and proestrous sanguinous uterine discharge (see table 31.1). In addition, estrogens are responsible for a constellation of behaviors that promote courtship and copulation.

Although the follicular phase is primarily characteristic of nonpregnant female ovarian cycles, follicular growth can also occur both early (horse: Squires et al. 1974; cat: Schmidt, Chakraborty, and Wildt 1983; chinchilla, *Chinchilla laniger*: Weir 1973; Asian elephant, *Elephas maximus*: Perry 1953) and late in pregnancy (European hare, *Lepus europaeus*: Martinet 1980 and Flux 1967; and black mastiff bat, *Molossus rufus*: Rasweiler 1988). Ovulation early in the period of delayed implantation is typical for the mink, *Mustela vison*, and results in 80 to 90% of the embryos carried to term (Hansson 1947; Enders and Enders 1963).

Ovulation. The processes that culminate in ovulation are still not fully understood. Various mechanisms to explain follicular rupture include increases in intrafollicular pressure or changes in enzymes, vascularity, muscular activity, or biochemical milieu. The number of follicles ovulated is characteristic for each species. Larger mammals are more likely to be monovular, i.e. to ovulate one ovum at each estrus, whereas medium and smaller species tend to be polyovular. Among polyovular species, the number of ova is usually equivalent to the litter size. Exceptions include elephant shrews (Macroscelidae) (Tripp 1971) and the plains viscacha (Weir 1971a), which ovulate approximately 120 and 800 ova, respectively, although each gives birth to only 2 offspring per litter. Another anomaly is demonstrated by the tenrec, *Tenrec ecaudatus*, in which each follicle may contain more than one ovum (Nicoll and Racey 1985).

Monotremes are unique among mammals in that a shell is added to the ovulated, fertilized egg during its passage through the oviducts and uterus. Then eggs are incubated in an external pouch (Hill 1933; Hill 1941). Unusual features of marsupial reproductive cycles as they relate to gestational events are presented in Thomas, Asa, and Hutchins (chap. 28, this volume).

Mammalian females are often categorized as either induced or spontaneous ovulators, terms that indicate whether the stimulation of coitus is required for ovulation to occur. However, some species considered induced ovulators may at times ovulate without mating (e.g. mink: Sundqvist, Amador, and Vartke 1989; lion, *Panthera leo*: Schmidt et al. 1979). Table 31.2 lists species classed as induced ovulators.

In species that typically ovulate spontaneously, mating or artificial stimulation of the vagina and cervix can induce uterine contractions (rat: Toner and Adler 1986) or hasten ovulation (pig: Signoret, du Mesnil du Buisson, and Mauleon 1972). In the domestic cow, the ovulatory LH surge is closely related in time to the bull's ejaculation, implicating coital stimulation (Umezu et al. 1981). In the bactrian camel, *Camelus bactrianus*, ovulation is reported to be influenced by a factor in the male's semen (Chen, Yuen, and Pan 1985).

Jöchle (1973, 1975) contends that many species classed as spontaneous ovulators are sensitive to copulatory as well as other external stimuli such as cohabitation, and should be termed facultative induced ovulators. However, because one or the other of these mechanisms predominates in any given species, the distinction remains useful (see Milligan 1982 for review).

TABLE 31.2. Induced ovulators

Species	Reference
Soricomorpha	
Short-tailed shrew, *Blarina brevicauda*	Pearson 1944
Water shrew, *Neomys fodiens*	Price 1953
White-toothed shrew, *Crocidura russula*	Hellwing 1973
Asian musk shrew, *Suncus murinus*	Dryden 1969
European shrew, *Sorex araneus*	Brambell 1935
American mole, *Scalopus aquaticus*	Conaway 1959
Rodentia	
Thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*	Foster 1934
Palm squirrel, *Funambulus pennantii*	Seth and Prasad 1969
Bank vole, *Myodes glareolus*	Westlin and Nyholm 1982
Red tree vole, *Arborimus longicaudus*	Hamilton 1962
Short-tailed vole, *Microtus agrestis*	Breed and Clarke 1970
California vole, *M. californicus*	Greenwald 1956
Montane vole, *M. montanus*	Cross 1972
Prairie vole, *M. ochrogaster*	Richmond and Conaway 1969
Meadow vole, *M. pennsylvanicus*	Clulow and Mallory 1970
Pine vole, *M. pinetorum*	Kirkpatrick and Valentine 1970
Townsend's vole, *M. townsendii*	MacFarlane and Taylor 1982
Collared lemming, *Dicrostonyx groenlandicus*	Hasler and Banks 1973
Laboratory rat, *Rattus rattus*	Aron, Asch, and Roos 1966
Lagomorpha	
Rabbit, *Oryctolagus cuniculus*	Walton and Hammond 1929
European hare, *Lepus europaeus*	Hediger 1950
Snowshoe hare, *L. americanus*	Rowlands and Weir 1984
Jack rabbit, *L. californicus*	Rowlands and Weir 1984
Eastern cottontail, *Sylvilagus floridanus*	Rowlands and Weir 1984
Carnivora	
Domestic cat, *Felis catus*	Dawson and Friedgood 1940
Ferret, *Mustela putorius*	Marshall 1904
Mink, *M. vison*	Hansson 1947
Weasel, *M. nivalis*	Deanesly 1944
Raccoon, *Procyon lotor*	Whitney and Underwood 1952
Artiodactyla	
Bactrian camel, *Camelus bactrianus*	Chen, Yuen, and Pan 1985
Dromedary camel, *C. dromedarius*	Marie and Anouassi 1986
Llama, *Lama glama*	England et al. 1969
Alpaca, *L. pacos*	Fernandez-Baca, Madden, and Novoa 1970

The proximate hormonal stimulus for ovulation is a surge of LH, the result of either estrogen positive feedback in spontaneous ovulators or coitus in induced ovulators. In at least the rat, progesterone from the adrenal cortex participates in LH induction (Mann, Korowitz, and Barraclough 1975). Ovarian progesterone secretion begins to increase just before ovulation in the dog (Concannon, Hansel, and Visek 1975) and some rodents, e.g. the guinea pig, *Cavia porcellus* (Joshi, Watson, and Labhsetwar 1973). Small amounts of preovulatory progesterone and one of its metabolites, 20α-hydroxyprogesterone, are reportedly secreted from ovarian interstitial, and not follicular, cells in the female rhesus monkey (Resko et al. 1975). For most species, however, the progestins are characteristic of the postovulatory luteal phase, being secreted by luteal tissue.

Mating and insemination. Female estrous or sexual behavior is stimulated by the steroid hormones present at or before ovulation. The presence and sequence of each hormone may vary by species, e.g. estrogen alone stimulates sexual behavior in most species, but progesterone synergizes with estrogen to facilitate estrous behavior in some others. In some rodents (rat: Powers 1970; hamster, *Mesocricetus auratus*: Ciaccio and Lisk 1971; guinea pig: Frank and Fraps 1945) and the dog (Concannon, Hansel, and Visek 1977), estrogen followed by progesterone induces sexual receptivity. Although estrogen alone produces the full complement of sexual behavior in the horse and cow, the addition of progesterone further intensifies the response (Asa et al. 1984; Melampy et al. 1957). In much the same way, GnRH synergizes with estrogen to further stimulate estrous behavior in the lab rat (Moss and McCann 1973). Testosterone and other androgens that increase during the periovulatory period may also stimulate sexual behavior in the female (rat and cat: Whalen and Hardy 1970; rabbit: Beyer, Vidal, and Mijares 1971; cattle: Katz, Oltenacu, and Foote 1980).

In fall-breeding ungulates such as the sheep (Robinson, Moore, and Binet 1956); fallow deer, *Dama dama* (see Asher 1985); white-tailed deer (Harder and Moorhead 1980); moose, *Alces alces* (see Simkin 1965); elk; red deer (Morrison 1960); and Père David's deer, *Elaphurus davidianus* (see Curlewis, Loudon, and Coleman 1988), it appears that progesterone must precede estrogen for stimulation of estrous behavior, but not during the same cycle. Thus, there is no overt sexual behavior with the first ovulation or wave of follicular growth of the season, but a period of progesterone production follows that primes the female's system to respond to the estrogen of the next cycle.

Progesterone alone inhibits sexual behavior in all species investigated to date, resulting in suppression of sexual behavior during the luteal phase. However, progestin-based contraceptives are sometimes accompanied by estrous behavior, because the minimum effective contraceptive dose may still allow some follicular growth that stimulates sexual behavior (Croxatto et al. 1982). Similarly, in some species during early pregnancy (e.g. horse: Asa, Goldfoot, and Ginther 1983), follicular growth may stimulate signs of estrus.

Following copulation, a copulatory plug consisting of gelatinous seminal fluid is left in the vaginal canal of females of a wide variety of species: opossum, *Didelphis virginiana* (see Hartmann 1924); some insectivores (Eadie 1948); muroid rodents (Baumgardner et al. 1982); sciurids (see Koprowski 1992); Heteromyidae (Daly, Wilson, and Behrends 1984); many primates (reviewed in Dixson and Anderson 2002); and one carnivore, the masked palm civet, *Paguma larvata* (see Jia et al. 2002). In rhinolophid and vestpertilionid bats (see Oh, Mori, and Uchida 1983; Van Heerdt and Sluiter 1965), the plug may consist of secretions of the male urethral gland, but the outer layer, at least in some species, is composed of sloughed vaginal epithelium (Oh et al. 1983). This plug, the copulatory physical lock of canids, and the behavioral "lock" of stump-tailed macaques, *Macaca arctoides*, may serve as a form of mate guarding, prevent sperm leakage, or stimulate sperm transport (Voss 1979, Adler 1978). Oxytocin (Gwatkin 1977) and/or epinephrine (Fuchs 1972) released in response to copulation also may stimulate uterine contractions, which may aid sperm transport. Another possible function for plugs is gradual release of sperm from the plug reservoir (Voss 1979). Copulatory plugs gradually dissolve and copulatory locks end in what seem to be species-specific intervals, or they may be removed by the female (Koprowski 1992).

Mating typically coincides with ovulation. Sperm have been reported to survive for up to 72 hours in the female rhesus monkey (Dukelow and Bruggeman 1979); 120 hours in *Lama* and *Camelus* spp. (Stekleniov 1968, cited in Thibault 1973); 5 days in the horse (Bain 1957); 12 days in the dog (Doak, Hall, and Dale 1967); and 2 weeks in the Australian native cat, *Dasyurus viverrinus* (see Hill and O'Donoghue 1913), and brown marsupial mouse, *Antechinus stuartii* (see Selwood and McCallum 1987). Sperm storage in the female reproductive tract is common among vespertilionid bats (Crichton 2000) and ranges from 16 days in *Pipistrellus ceylonicus* (see Gopalakrishna and Madhavan 1971) to 198 days in *Nyctalus noctula* (see Racey 1973).

Luteal phase. This period following ovulation, characterized by luteal tissue growth and secretory activity, is also referred to as the secretory phase in primates, referring to uterine phenomena, and as the diestrous phase in domestic ungulates, indicating its occurrence between estrous periods. The term *luteal phase* will be used in this chapter, acknowledging the dominance of the corpus luteum among associated features.

Following rupture and expulsion of the oocyte, the follicle is converted to the corpus luteum (CL), or yellow body, named for its characteristic color in many species. Corpora lutea are the primary producers of the progesterone necessary for preparation of the uterus and mammary glands for pregnancy. Although progesterone is the primary circulating hormone of the luteal phase, a luteal rise in estrogen also has been reported for some species (cattle and sheep: Hansel, Concannon, and Lukaszewska 1973; langur, *Semnopithecus entellus*: Lohiya et al. 1988; chimpanzee, *Pan troglodytes*: Graham et al. 1972; gorilla, *Gorilla gorilla*: Nadler 1980). The ovulatory cycles of the owl monkey, *Aotus trivirgatus* (see Bonney, Dixson, and Fleming 1979), and common marmoset, *Callithrix jacchus* (see Preslock, Hampton, and Hampton 1973), are unusual in that curves of estrogen and progesterone concentrations are almost superimposed, making follicular and luteal phases indistinguishable by steroid measurement.

Corpus luteum formation spontaneously follows ovulation in most species. However, in several rodent species, CL formation requires copulatory stimulation in the same way that ovulation must be induced in other species. Thus, in the rat (deGreef, Dullaart, and Zeilmaker 1977), mouse (Rowlands and Weir 1984), and hamster (Anderson 1973), ovulation is spontaneous, but in infertile cycles no luteal phase separates it from the subsequent follicular phase unless copulation occurs. Fertile mating, of course, results in pregnancy, and sterile mating is followed by a luteal phase, sometimes called pseudopregnancy. Sustained CL function or pseudopregnancy approximately the length of gestation occurs spontaneously in most canids and following sterile mating in induced ovulators (see Thomas, Asa, and Hutchins, chap. 28, this volume).

Depending on the species, LH, prolactin, or estrogen may be luteotrophic, i.e. supportive of CL function. If pregnancy does not ensue, there is CL regression. In at least some species, demise is not passive but is caused by prostaglandin $F_{2\alpha}$ secreted by the uterus (cattle: Beal, Milvae, and Hansel 1980; sheep: Flint and Hillier 1975; horse: Douglas and Ginther 1976; guinea pig: Illingworth and Perry 1973; rat: Pharriss and Wyngarden 1969).

Menstrual phase. Characteristic of many primates, this period of bloody uterine discharge is associated with relatively low hormone levels (table 31.3). In fact, menstrual blood flow results from the withdrawal of luteal-phase estrogen and progesterone (see Shaw and Roche 1980 for review). Although menstruation traditionally was thought to be restricted to Old World monkeys and apes, slight hemorrhage may occur during the cycle of *Cebus*, *Ateles*, and *Alouatta* spp. (Ioannou 1983), but not the squirrel monkey, *Saimiri sciureus* (see Clewe 1969); common marmoset; or cotton-top tamarin, *Saguinus oedipus* (see Hodges and Eastman 1984). There are reports of sanguinous discharge in 2 prosimians, the slender loris, *Loris tardigradus* (see Rao 1927), and tarsier, *Tarsius* spp. (Catchpole and Fulton 1943). However, Izard and Rasmussen (1985) detected no blood during the slender loris ovulatory cycle.

TABLE 31.3. External signs of the menstrual phase

Species	Reference
Chiroptera	
Vampire bat, *Desmodus rotundus*	Quintero and Rasweiler 1974
Long-tongued bat, *Glossophaga soricina*	Rasweiler 1972, 1979
Short-tailed fruit bats, *Carollia* spp.	Rasweiler and de Bonilla 1992
Macroscelidea	
Elephant shrew, *Elephantulus* sp.	van der Horst and Gillman 1942
Scandentia	
Tree shrews, *Tupaia* sp. (possible)	Conaway and Sorenson 1966
Primates	
Capuchin, *Cebus apella*	Wright and Bush 1977
Rhesus macaque, *Macaca mulatta*	Nadler, Collins, and Blank 1984
Pig-tailed macaque, *M. nemestrina*	Krohn and Zuckerman 1937
Japanese macaque, *M. fuscata*	Nigi 1975
Celebes black ape, *M. nigra*	Mahoney 1970
Chacma baboon, *Papio ursinus*	Gillman and Gilbert 1946
Yellow baboon, *P. cynocephalus*	Hendrickx and Kraemer 1969
Olive baboon, *P. anubis*	Zuckerman 1937
Hamadryas baboon, *P. hamadryas*	Zuckerman and Parkes 1932
Gelada baboon, *Theropithecus gelada*	Matthews 1953–1956
Woolly monkey, *Lagothrix* spp.	Hafez 1971
Orangutan, *Pongo pygmaeus*	Nadler, Collins, and Blank 1984
Chimpanzee, *Pan troglodytes*	Nadler et al. 1985
Gorilla, *Gorilla gorilla*	Nadler et al. 1979

Even among Old World monkeys and apes, menstrual flow may be undetectable in some individuals (gorilla: Nadler 1980; stump-tailed macaque: Stenger 1972; vervet monkey, *Chlorocebus pygerythrus*: Else et al. 1986; Sykes' monkey, *C. mitis*: Rowell 1970) or detectable only by swabs (*C. pygerythrus*: Hess, Hendrickx, and Stabenfeldt 1979; *C. mitis*: Else et al. 1985).

Menstruation in molossid and phyllostomid bats appears similar to that seen in Old World primates, with endometrial breakdown and sloughing accompanied by blood flow (Rasweiler and Badwaik 2000). However, the sanguinous discharge of canids is not physiologically comparable to menstruation, because uterine blood flow occurs during proestrus, sometimes continuing into estrus, and is in response to estrogen stimulation, not estrogen or progesterone withdrawal (Asa, unpublished observations).

Anovulatory period and lactational anovulation. The anovulatory or anestrous phase is similar to the menstrual phase in that there are relatively low or absent levels of ovarian steroids. It is, simply, a time of no overt reproductive activity. Sexual behavior does not occur regularly during the anovulatory period or following ovariectomy except in the musk shrew, *Suncus murinus* (see Dryden and Anderson 1977); horse (Asa et al. 1980); and stump-tailed macaque (Slob et al. 1978).

Many species have an anovulatory season (see "Environmental Effects" later in this chapter). In others, anovulation results from nursing newborn young. This latter phenomenon is termed lactational amenorrhea when applied to primates and lactational anovulation or anestrus for nonprimate species. Lactational anovulation is not widespread among nonprimate species, many of which experience ovulation soon after parturition, often called postpartum estrus.

Lactation suppresses follicular development in many species (e.g. lab rat: Taya and Greenwald 1982; hamster: Greenwald 1965; cattle: Short et al. 1972; pig: Peters, First, and Cassida 1969; sheep: Kann and Martinet 1975; rhesus monkey: Weiss et al. 1976). Lactational anovulation is likely mediated by the ability of the high levels of prolactin which accompany lactation to suppress GnRH and/or LH (Friesen 1977).

Reproductive senescence. Most species exhibit a gradual decline in reproductive function with age, but complete cessation of reproduction has been documented only in some Old World monkeys and apes, cetaceans, and domestic species. The absence of complete senescence in free-ranging animals suggests that for many species this may be an artifact of captivity, perhaps attributable to life spans extended beyond that which would occur in the wild (Hirshfield and Flaws 1998). However, data from sperm whales, *Physeter catodon*, and short-finned pilot whales, *Globicephala macrorhynchus* (Marsh and Kasuya 1984), spotted porpoise, *Stenella attenuata* (see Perrin, Coe, and Zweiffel 1976), and the estuarine dolphin, *Sotalia fluviatilis* (see Rosas and Monteiro-Filho 2002), indicate cessation of ovulation late in life, perhaps related to the length of time needed for the last offspring to reach puberty. A similar possibility exists for elephants, but without clear documentation as yet.

METHODS FOR MONITORING OVARIAN CYCLES

A wide variety of physical and physiological changes accompany ovarian changes, e.g. labial swelling, perineal reddening, and sanguinous discharge. Table 31.1 lists these changes, most observable noninvasively, along with increases in activity level and nonsanguinous vaginal discharge characteristic of the periovulatory phase. Visual observation of changes in the vaginal membrane can be used for most rodent species as well as a few other taxa (see table 31.4 for references). The membrane occludes the vagina except at times of breeding—for some during the entire breeding season, in others only during estrus.

Changes in vaginal cytology, which reflect ovarian cycle stage, are detectable by smears or lavage, techniques verified for a very wide range of species (table 31.4). A decrease in basal body temperature accompanies ovulation in at least some primates. Although taking daily temperatures by traditional means is impractical in most cases, basal body temperature transmitters can be implanted and read telemetrically (see Asa 1991). Another technique increasing in popularity for monitoring follicular growth and ovulation is ultrasound (table 31.4). Improvements in hormone assay of feces and urine permit noninvasive assessment of levels of estrogen and progesterone metabolites in a wide variety of species (see Hodges, Brown, and Heistermann, chap. 33, this volume).

FACTORS AFFECTING REPRODUCTIVE CAPACITY

ENVIRONMENTAL FACTORS

Many species inhabiting the temperate zones have seasonal breeding strategies to cope with the changing environmental conditions (see Bronson 1989). Negus and Berger (1972) divide these species along a facultative-obligate continuum. Facultative seasonal breeders live in unpredictable environments and respond to favorable conditions as they occur, e.g. plant growth due to irregular rainfall in deserts. Obligate seasonal breeders live in predictable environments in which conditions favorable to survival of young occur at times invariant from year to year.

Photoperiod. The most common proximate cue used by obligate seasonal breeders is change in photoperiod. Photoperiod-sensitive species are typically separated into long-day or short-day breeders, meaning that they come into breeding condition either in the spring, when daylight hours are increasing, or during fall, when daylight is decreasing. Most seasonally breeding mammals are long-day breeders, with ungulates being the major exception. What they all have in common is young being born in spring or summer, when conditions are most favorable. Thus, timing of the mating period is a function of gestation length.

Photic information is processed by the pineal gland via the superior-cervical ganglion. Photoperiod effects are mediated production of melatonin in response to changes in relative hours of sunlight to dark (see Goldman and Nelson 1993). However, the impala (Murray 1982) and wildebeest, *Connochaetus taurinus* (see Sinclair 1977), appear to respond to phases

TABLE 31.4. Methods for monitoring ovarian cycles

Species	Reference
Vaginal membrane opens during breeding season	
Myomorph and Sciuromorph rodents	Rowlands and Weir 1984
European mole, *Talpa europaea*	Matthews 1935
Vaginal membrane opens during preovulatory period	
Hystricomorph rodents (except coypu, *Myocastor coypus*)	Weir 1974
Galago, *Galago senegalensis*	Darney and Franklin 1982
Greater galago, *Otolemur crassicaudatus*	Hendrickx and Newman 1978
Mouse lemur, *Microcebus murinus*	Perret 1986
Ruffed lemur, *Varecia variegata*	Boskoff 1977
Vaginal cytology	
Common wombat, *Vombatus ursinus*	Peters and Rose 1979
Potoroo, *Potorous tridactylus*	Hughes 1962
Short-nosed rat kangaroo, *Bettongia lesueur*	Tyndale-Biscoe 1968
Hedgehog, *Hemiechinus auritus*	Munshi and Pandey 1987
Shrew, *Sorex araneus*	Brambell 1935
Musk shrew, *Suncus murinus*	Sharma and Mathur 1976 (disputed by Dryden 1969)
Rat, *Rattus rattus*	Long and Evans 1922
Golden hamster, *Mesocricetus auratus*	Orsini 1961
Guinea pig, *Cavia porcellus*	Stockard and Papanicolau 1917
Slender loris, *Loris tardigradus*	Ramaswami and Kumar 1962
Bushbaby, *Otolemur crassicaudatus*	Eaton, Slob, and Resko 1973
Tarsier, *Tarsius* spp	Catchpole and Fulton 1943
Ring-tailed lemur, *Lemur catta*	Evans and Goy 1968
Ruffed lemur, *Varecia variegata*	Boskoff 1977
Squirrel monkey, *Saimiri sciureus*	Gould, Cline, and Williams 1973
Capuchin, *Cebus apella*	Wright and Bush 1977
Langur, *Semnopithecus entellus*	Lohiya et al. 1988
Bonnet macaque, *Macaca radiata*	Kanagawa et al. 1973
Rhesus macaque, *M. mulatta*	Parakkal and Gregoire 1972
Cynomolgous monkey, *M. fascicularis*	Mehta et al. 1986
Olive baboon, *Papio anubis*	Hendrickx 1967
Hamadryas baboon, *P. hamadryas*	Zuckerman and Parkes 1932
Long-tongued bat, *Glossophaga soricina*	Rasweiler 1972
Domestic cat, *Felis catus*	Shille, Lundstrom, and Stabenfeldt 1979
Cheetah, *Acinonyx jubatus*	Asa et al. 1992
Domestic dog, *Canis familiaris*	Gier 1960
Gray wolf, *Canis lupus*	Seal et al. 1979
Fox, *Vulpes vulpes*	Bassett and Leekley 1942
Fennec fox, *V. zerda*	Valdespino, Asa, and Bauman 2002
Bush dog, *Speothos venaticus*	DeMatteo et al. 2006
Brown hyena, *Hyaena brunnea*	Ensley et al. 1982
Basal body temperature	
Wombat, *Vombatus ursinus*	Peters and Rose 1979
Langur, *Semnopithecus entellus*	Lohiya et al. 1988
Rhesus, *Macaca mulatta*	Balin and Wan 1968
Chimpanzee, *Pan troglodytes*	Graham et al. 1977
Orangutan, *Pongo pygmaeus*	Asa et al. 1994

of the moon, with estrus and ovulation occurring between full moons. Factors considered to mediate the effect include changes in light intensity or even in gravitational forces.

Temperature. Extremes in temperature, either hot or cold, can suppress reproduction (see Piacsek and Nazian 1981; Thatcher and Collier 1980; Newsome 1973). The effect of both stimulus extremes may be mediated by alterations in pineal functions (Urry et al. 1976).

Rainfall. The breeding seasons of many species coincide with periods of rainfall, particularly in tropical areas, where photoperiod varies little. These include both facultative (desert jerboa, *Jaculus jaculus*: Ghobrial and Hodieb 1973) and obligate (rhesus monkey: Eckstein and Kelly 1966) seasonal breeding. However, the true stimulus is likely the nutritional content of the resultant vegetation, not the rainfall itself.

Nutrition. Nutritional status, at least in herbivores, may be linked to changes in rainfall, photoperiod, or temperature, conditions that promote plant growth; for carnivores, the effect is secondary (see Bronson 1989). Most studies of the impact of nutrition on reproductive parameters have focused primarily on caloric or protein levels of diet, or on assessment of body condition. As with the study of other aspects of reproduction, domestic species have received the most attention. In general, the nutritional requirements for courtship and mating are not different from those for healthy maintenance.

Fasting or chronic undernourishment can suppress LH concentrations and interfere with reproductive processes in both males and females. In fact, LH levels change along with those of glucose or other indicators of metabolic state (e.g. volatile fatty acids in ruminants) in many species (Williams 1998). Leptin, from adipocytes, may serve as the link between metabolic state and the reproductive system (Zieba, Amstalden, and Williams 2005). Reproductive potential can sometimes be enhanced by increased consumption of fats or overall nutritive intake (Williams 1998), which is especially effective after a period of undernutrition in ruminants, mimicking the condition many seasonally breeding species face in nature (Pope 1972; Ransom 1967). Specific requirements for protein and other nutrients such as minerals, vitamins, and essential fatty acids vary by species.

Compounds present in sprouting vegetation have been found to stimulate reproduction in *Microtus montanus* (see Berger, Negus, and Rowsemitt 1987) and rabbits (Gooding and Long 1957). In contrast, coumestrol, a plant compound with estrogenic effects and present in clover and other leguminous plants, can inhibit reproduction by blocking gonadotropin release (Leavitt and Wright 1965). Compounds with estrogenic activity, and presumably the potential to interrupt ovarian events if present in large quantities, also have been identified in barley grain, *Hordeum vulgare*; oat grain, *Avena sativa*; apples, *Pyrus malus*; cherries, *Prunus avium*; potatoes, *Solanum tuberosum*; and Bengal gram, *Cicer arietinum* (Hafez and Jainudeen 1974). Water restriction can also deleteriously affect reproduction (Nelson and Desjardins 1987; Lidicker 1973). Soy-based foods can interfere with reproduction in females of some species (Axelson et al. 1984; Setchell et al. 1987) and have been associated with increased aggression and decreased affiliative behavior in male rhesus macaques (Simon et al. 2004).

SOCIAL FACTORS

Social interactions can either stimulate or suppress reproductive function, often through chemicals of olfactory communication, more popularly called pheromones. Reproductive suppression resulting from dominance interactions or from changes in population density has been related to changes in the adrenal cortex, although the proximate sensory modality is still not known in most cases.

Priming pheromones. Mammalian chemical communication may produce either behavioral or physiological responses. The latter, called priming pheromones, regulate reproductive processes in various ways (Vandenbergh 1988). Stimuli from other females or from family members can suppress female reproductive activity, as documented predominantly in rodents and primates (French 1997; Vandenbergh 1988). Induction of ovarian synchrony or changes in cycle length by stimulation of either the same or the opposite sex occurs in various rodent species. In contrast, the onset of ovarian cycles at puberty or beginning of the breeding season can be advanced by stimuli from adult males in various rodent, ungulate, and primate species (Vandenbergh 1988). Termination of pregnancy in response to exposure to strange males or their urine occurs in pine voles, *Microtus pinetorum* (see Schadler 1981), and mice (Parkes and Bruce 1962). An increased incidence of ovulation has also been demonstrated in nonseasonally breeding goats exposed to males (Chemineau 1983). In the female gray opossum, *Monodelphis domestica* (see Fadem 1987); cuis, *Galea musteloides* (see Weir 1971b); cape porcupine, *Hystrix africaeaustralis* (see Van Aarde 1985); and possibly the island fox, *Urocyon littoralis* (see Asa et al. 2007), the presence of a male induces (not merely enhances) estrous behavior and ovarian activity, although the mechanism may not be exclusively pheromonal.

Social effects. Social subordination can result in delay of puberty or suppression of ovulation in adults of a number of species (see Bronson 1989). In some cases the suppression has been linked to higher cortisol levels. However, relatively higher adrenal cortical activity has been correlated with dominance in some species and with subordinate status in others (e.g. Creel et al. 1997; Abbott et al. 2003). The lower fecundity of subordinate females also may result from lower access to resources.

High population density has been shown to result in decreased fertility, primarily in experiments with rodents (*Mus musculus*: Christian 1980; *Peromyscus maniculatus*: Terman 1973). The mechanism that translates density into a physiological response may be increased levels of aggression and adrenal cortical response proportional to the degree of crowding. An unusual example of adrenal stress response and reproduction are male dasyurid marsupials, *Antechinus* spp., in which adrenal weight and corticosteroid levels increase just after mating and appear to lead to death.

Housing solitary species in social groups can result in high cortisol levels and poor reproductive success, even in the absence of crowding (e.g. mouse lemur, *Microcebus murinus*: Perret and Predine 1984). Female cheetahs housed with other females may remain anestrous (Wielebnowski et al. 2002). In contrast, social isolation of the normally gregarious house mouse can depress reproductive potential (Rastogi, Milone, and Chieffi 1981). Similarly, in both olive, *Papio anubis*, and chacma, *P. ursinus*, baboons, social isolation results in longer follicular phases and thus longer cycles than those females in social contact with other female baboons. However, the period of perineal tumescence was longer in the chacma (Howard-Tripp and Bielert 1978), but shorter in the olive baboon (Rowell 1970) females that were isolated than in those socially housed.

Stress. Regardless of the cause or the definition of stress, factors that stimulate the hypothalamo-pituitary adrenocortical axis can interfere with reproduction (Rivier and Rivest 1991). However, response to acute stress can differ from chronic stress, in that acute stressors may actually stimulate reproductive hormones, particularly in males of some species (Welsh, Kemper-Green, and Livingston 1998). The discrepancy may be related to the differential mediation of acute and chronic stress by epinephrine and glucocorticoids, respectively. However, adrenal mediated stressors generally have a negative impact on reproductive function.

CONCLUSIONS

We are only just beginning to understand the reproductive processes of a very small percentage of species. The successes to date in manipulating reproductive function in domestic and laboratory species are built on decades of research. The further from known species our studies venture, the more variability on the theme of reproduction we find. Thus, for effective captive management of reproduction for exotic species, we must recognize this variability and commit time and resources toward building a foundation of biological knowledge on which to base such management programs.

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32

Male Reproduction: Assessment, Management, Assisted Breeding, and Fertility Control

Rebecca E. Spindler and David E. Wildt

INTRODUCTION

Understanding male reproductive physiology is critical to optimizing reproduction of wildlife species. Well-studied species have benefited from the study of male reproductive physiology, with the "normal" male of these species being well documented. However, the etiology of infertility generally remains obscure. In domestic livestock and laboratory animals, eliminating suspect males is usually more economical than therapeutically improving reproductive performance. Consequently, human investigations provide much of the information for addressing poor male reproduction.

There is limited scientific literature detailing approaches for manipulating male reproductive activity in zoo mammals. Most studies have evaluated the semen of a few animals of selected species or established baseline concentrations of circulating hormones, predominantly testosterone and luteinizing hormone (LH). There is a need to expand such studies for 2 major reasons. First, understanding the reproductive characteristics of the "normal" male is a prerequisite for identifying and treating subfertile or suspect individuals. Second, assisted reproductive technologies, especially artificial insemination and gamete cryopreservation, have potential for propagating and genetically managing wildlife populations (Pukazhenthi and Wildt 2004). The success of these approaches rests on a thorough understanding of male physiology.

This chapter provides information on factors known to influence male reproduction and describes strategies for assessing and manipulating male reproductive activity. For more detail, we encourage readers to examine the review articles in the latest edition of *Campbell's Urology* (Goldstein 2002; Schlegel and Hardy 2002; Sigman and Jarow 2002) and *Physiology of Reproduction* (Kerr et al. 2006; Malpaux 2006; O'Donnell et al. 2006; Stocco and McPhaul 2006) as well as an earlier valuable work by Sherins and Howards (1985), all of which we have relied on for this chapter. Since mammals (even those closely related taxonomically) exhibit species-specific and even population-specific reproductive and endocrine norms, a successful approach to studying or manipulating male reproduction in one species may well need to be modified (or it may fail completely) in another species. However, within reason, these evaluative and therapeutic concepts should have valid, generalized application to many zoo-maintained animals.

THE CONTROL OF MALE REPRODUCTIVE FUNCTION

The testes produce spermatozoa and secrete hormones, each function being segregated anatomically (Amann 1986; Kerr et al. 2006;). The interstitial or Leydig cells are influenced by the pituitary hormone LH and produce testosterone and estradiol. Most of the testis (90%) is composed of seminiferous tubules, the site of spermatogenesis. Diffuse Sertoli cells extend from the tubular base to the lumen. Adjacent to the Sertoli cells, spermatogonia divide to form spermatocytes, which eventually form spermatids. Sertoli cells bind another pituitary hormone, follicle-stimulating hormone (FSH), necessary for germ cell development. Spermatogenesis is controlled by FSH and testosterone acting directly on the seminiferous tubular epithelium.

Testicular function is controlled through a complex feedback system involving the hypothalamus (which secretes gonadotropin-releasing hormone, GnRH), pituitary (which releases FSH and LH, collectively known as gonadotropins), and testes (see O'Donnell et al. 2006; Stocco and McPhaul 2006 for review). GnRH is released from the hypothalamus in discrete pulses that induce the pituitary to secrete FSH and LH. LH production is immediate and pulsatile, whereas FSH release is more attenuated and static. Circulating gonadal steroids (primarily testosterone but also estradiol) regulate FSH and LH by influencing GnRH secretion and pituitary sensitivity to GnRH. If testicular activity wanes, the resulting low levels of steroids alleviate negative feedback on the hypothalamus and pituitary, increasing GnRH, FSH, and LH secretion and steroid production. Pituitary FSH release also is attenuated by inhibin, a complex family of proteins (McLachlan et al. 1987; Plant et al. 1993) that are similar enough to activin (which induces FSH secretion) to bind the receptor but not elicit FSH secretion (Moore, Krummen, and Mather 1994). Inhibin may also act to prevent FSH production by decreasing the amount of FSH-β mRNA (Clarke et al. 1993; Attardi and Winters 1993; Burger et al. 2001).

Since this feedback system is affected by olfactory, auditory, and visual stimuli along with nutrition, stress, and seasonality, an andrological evaluation must include a consideration of the range of potential perturbing factors, from seasonality to captivity-induced stress.

THE LIMITATIONS OF MALE FERTILITY ASSESSMENT

The most accurate and consistent male fertility assessment requires evaluating seminal traits as well as reproductive history and physical health. Laboratory tests may also be necessary, including blood, urine, or fecal concentrations of hormones and the functional capacity of sperm in vitro. Probably the most effective measure of reproductive health is comparison of the suspect male to fertile conspecifics of about the same age that are maintained in a comparable environment. *A single evaluation of an individual animal with no definitive reproductive history is of limited value* unless compared with data from a large "normal" population. A proven breeder that produces an ejaculate containing high numbers of motile sperm with few abnormal cells generally can be categorized as physiologically normal. But *a single azoospermic (no living sperm) ejaculate from a proven or unproven male does not warrant a diagnosis of infertility*. A minimum of 3 assessments over time, including at least one during the breeding season, is necessary to suspect a male of being physiologically impaired.

EVALUATION OF THE MALE

HISTORY AND PHYSICAL EXAMINATION

Collecting data on (1) age, (2) reproductive seasonality, (3) disease, illness, injury, (4) the captive environment, (5) nutrition, (6) pregnancies and offspring produced, (7) libido, (8) reproduction of close relatives, and (9) records of toxic agent exposure (e.g. pesticides and heavy metals) is an important first step in male reproductive assessment. This information must be considered in the context of the spermatogenic cycle, as sperm present in the epididymis on any given day began development many days earlier.

During a physical examination to identify a cause of infertility, any abnormality of body conformation or genitalia needs examination. For example, strong hind legs and quarters are essential to supporting the male's weight and thrusting during copulation. However, testicular integrity, size, and tonicity are the most important elements in a reproductive examination. Displacing or manipulating each testis within the scrotal sac can reveal adhesions. Length and width measures (cm) of each testis (using laboratory calipers) can be converted to testicular volume with this formula: $\text{volume} \times 0.524 \times \text{width(cm)}^2 \times \text{length(cm)}$ (Howard et al. 1983). Alternatively, in species with a pendulous scrotum, scrotal circumference (SC) can be determined with flexible tape (Ott 1986). Testicular volume/size measures as part of the medical records for a given male allow comparison over time within and across individuals, including between proven breeders and males experiencing infertility. This is important, because testicular volume is highly heritable and correlates well with sperm production and fertility in humans and domestic bulls (Sherins and Howards 1985; Larson 1986; Ott 1986; Sigman and Jarow 2002).

Testicular size fluctuates markedly in most seasonal breeders—e.g. seasonal testicular recrudescence in the black-footed ferret, *Mustela nigripes*, is one of the primary indices of breeding season onset (Wolf et al. 2000a; Wolf et al. 2000b). Testicular volume in rhesus macaques, *Macaca mulatta*, is double during the breeding season compared to the inactive season (Wickings et al. 1986). In circannual studies of red deer, *Cervus elaphus*, Eld's deer, *Rucervus eldii*, and merino and corriedale rams, *Ovis aries*, males with the greatest SC value also had the best quality ejaculates when compared to herdmates (Haigh et al. 1984b; Monfort et al. 1993a; Perez et al. 1997; Zamiri and Khodaei 2005). However, changes in testicular volume may be subtle or results ambiguous. In fact, in some taxa, there is little relation between testes volume and seminal quality (Wildt, Brown, and Swanson 1998). From a diagnostic perspective, when males have small (hypoplastic) or flaccid testes during the "breeding season," gonadal function is likely compromised. Leydig cell activity is often retained, so libido and virilization traits are rarely affected (Sherins and Howards 1985).

Unilateral cryptorchidism (a single testis retained in the abdominal cavity) has been reported in zoo-maintained maned wolves, *Chrysocyon brachyurus* (M. Rodden, personal communication), jaguars, *Panthera onca* (R. E. Spindler and R. Morato, personal observation), free-living Florida panthers, *Puma concolor coryi* (see Roelke, Martenson, and O'Brien 1993), cheetahs, *Acinonyx jubatus* (see Crosier et al. 2007), Florida black bears, *Ursus americanus* (see Dunbar et al. 1996), black-footed ferrets (S. Wisely and J. G. Howard, personal communication), and giant pandas, *Ailuropoda melanoleuca*, in the *ex situ* population (Howard et al. 2006). These males often mature normally physically and behaviorally. In most species, one scrotal testis is adequate for fertility. Bilateral cryptorchidism, which causes sterility, is less common than the unilateral condition. Because of the hereditary nature of the condition (Palmer 1991), *no cryptorchid male should be used in breeding programs*.

Testicular integrity, homogeneity, and blood flow can be assessed noninvasively using ultrasonography (Foresta et al. 1998; Souza et al. 2005; Hildebrandt et al. 2006). Cystic lesions, scar tissue formation, and parenchymal degeneration of the testis are identifiable by their unique echogenic qualities (Hildebrandt et al. 2006), but no correlation has yet been made between these abnormalities and overall fertility. Conversely, intratesticular blood flow is predictive of sperm recovery upon aspiration or biopsy. Areas of high blood flow may indicate optimal sites of sperm recovery for assisted reproduction (Foresta et al. 1998; Souza et al. 2005).

In some species, all regions of the epididymis can be palpated. Hyperplasia of the epididymis caused by inflammation, fibrosis, tumors, abscesses, or sperm granulomas occludes sperm flow from the testes. Obstructive azoospermia is detectable using ultrasonography, which we recommend before selecting males for breeding programs (Hildebrandt et al. 1998).

The anatomy of most species allows direct observation or palpation of the penis and external genitalia. Abnormal development of the penis and preputial sheath can result in a persistent frenulum (or adhesion), a genetic defect preventing vaginal penetration (noted in the Florida panther and cheetah). Penile papillofibromatas or hematomas likewise can interfere with copulation. Phimosis is an abnormal constriction of the sheath inhibiting penile extrusion, as seen in ocelots, *Leopardus pardalis*, and jaguars (Swanson et al. 2003; Spindler, personal observation). These anomalies sometimes are the result of physical trauma, and can often be treated through surgical or nonsurgical methods (Wohlfarth 1990; Dominguez et al. 1996; Zampieri et al. 2005). However, because this condition has a genetic origin, such individuals should not be used for breeding. In larger species, accessory glands and surrounding aspects of the male reproductive tract can be rectally palpated. Abnormalities of the ductus deferens ampullae, vesicular glands, and prostate may result from inflammations and can result in infertility.

ENDOCRINE DIAGNOSTICS

Endocrinology is important, because hormones are essential regulators of reproductive success. Although gonadal steroids are primary targets, adrenal glucocorticoids also have attracted interest as an index of adrenal activity and its influence on reproduction. Noninvasive evaluations of hormonal metabolites in urine or feces rather than blood allows for longitudinal, noninvasive assessment of endocrine status of wild animals otherwise available only as a snapshot during a physical examination. There are now excellent reviews of the applicability of this technology to both captive and wild individuals/populations (see Monfort 2003; Pickard 2003; Hodges, Brown, and Heistermann, chap. 33, this volume).

Male-oriented investigations to determine basic reproductive characteristics such as onset of puberty (Ginther et al. 2002), seasonality (Morai et al. 2002; Morato et al. 2004b; Pereira, Duarte, and Negrao 2005), social status interrelationships (Bales et al. 2006), and responsiveness to stressful stimuli (Wasser et al. 2001; Morato et al. 2004a) are rapidly increasing. Probably the most important need in hormone analysis is for longitudinal sampling, due to the dynamism of normal secretory (or excretory) patterns. For males, hormonal values are most valuable when combined with ejaculate characteristics or when used to establish species baseline physiological norms. Simultaneous collection of blood provides the opportunity to evaluate protein hormones not normally measurable in urine or feces.

TESTOSTERONE

Measuring testosterone in body fluids or waste is useful for identifying male sexual maturity, pituitary gonadotropin deficiency, impaired Leydig cell activity, the presence of an interstitial cell tumor, and causes of impaired libido. Circulating testosterone (1) is higher in the free-ranging impala, *Aepyceros melampus*, white rhinoceros, *Ceratotherium simum simum*, and koala, *Phascolarctos cinereus*, defending territory or mates when compared to lone, nonterritorial males (Illius et al. 1983; Cleva, Stone, and Dickens 1994; Kretzschmar, Ganslosser, and Dehnhard 2004); (2) is elevated in the male Asian elephant, *Elephas maximus*, exhibiting musth (Jainudeen, Katongole, and Short 1972; Niemuller and Liptrap 1991); (3) correlates with testicular size in wild blesbok, *Damaliscus pygargus phillipsi* (see Illius et al. 1983), but not the koala (Cleva, Stone, and Dickens 1994); (4) is similar between free-ranging and zoo-maintained cheetahs (Wildt et al. 1987a); (5) correlates with puberty in the tiger, *Panthera tigris*, and Arabian oryx, *Oryx leucoryx* (see Wildt et al. 1987b; Mialot et al. 1988; Ancrenaz et al. 1998); (6) is similar in the male and female free-ranging spotted hyena, *Crocuta crocuta* (see Racey and Skinner 1979; Frank, Smith, and Davidson 1985; Lindeque, Skinner, and Millar 1986), but is attenuated in adult males in social transition (Holekamp and Sisk 2003); (7) varies markedly among taxonomically related felids (Wildt et al. 1988); and (8) changes with season in many species (Stokkan, Hove, and Carr 1980; Bubenik et al. 1982; Schams and Barth 1982; Sempere and Lacroix 1982; Haigh et al. 1984a; Brown et al. 1991a, 1991c; Monfort et al. 1993a, 1993b).

Although circulating testosterone has correlated positively with seminal quality in many species, males with higher testosterone do not necessarily produce better-quality ejaculates (Abdel Malak and Thibier 1982; Resko 1982; Gould 1983; Wildt et al. 1984; Noci et al. 1985; Brown et al. 1991b). There is a possible inverse relationship between testosterone and proportions of pleiomorphic (structurally abnormal) spermatozoa, common among felids, as Pukazhenthi, Wildt, and Howard (2001) found that certain cats classified as teratospermic (producing >60% abnormal sperm) have lower circulating testosterone than normospermic counterparts. The impact on fertility is unknown, although sperm from teratospermic ejaculates are unable to penetrate oocytes.

The ability of the testes to respond to a hormonal stimulus is most efficiently evaluated by challenging the male with synthetic GnRH. After induction of anesthesia, blood samples are collected before and then at 15- to 30-minute intervals (for 2 to 3 hours) after an injection of 25 to 100 μg GnRH. In normal males, GnRH stimulates pituitary LH release, causing detectable increases in serum testosterone within 15 to 90 minutes. A lack of testosterone rise indicates a pituitary or Leydig cell abnormality. GnRH has induced acute elevations in serum testosterone in the male cheetah, lion, leopard, *Panthera pardus*, tiger, clouded leopard, *Neofelis nebulosa*, spotted hyena, African elephant, impala, Cape buffalo, *Syncerus caffer*, woodchuck, *Marmota monax*, tammar wallaby, *Macropus eugenii*, and nonhuman primates (Wildt et al. 1984, 1986b, 1987b; Lindeque, Skinner, and Millar 1986; Blank 1986; Wickings, Marshall, and Nieschlag 1986; Brown et al. 1988, 1989, 1991a, 1991b, 1991c; Concannon et al. 1998; Dloniak et al. 2004; Herbert et al. 2004).

FSH AND LH

In primates and some laboratory animals, elevated serum FSH has helped identify individuals with germ cell depletion or germinal aplasia (Gould and Kling 1982; Freischem et al. 1984; Stanwell-Smith et al. 1985) and is associated with low sperm count (Bruno et al. 1986). Similar studies are rare in other species, because (1) historically there has been a disinterest in FSH, (2) it is technically difficult to assay, and (3) profiles appear "noisy" due to the extreme dynamism of its secretion. FSH heterologous assays were developed to provide species-normative data from serum of the leopard (Brown et al. 1988, 1989), lion (Brown et al. 1991b), leopard cat, *Felis bengalensis* (see Howard and Wildt 1990), Cape buffalo (Brown et al. 1991a), impala (Brown et al. 1991c), and Eld's deer, *Rucervus eldii* (see Monfort et al. 1993b).

In comparison, there is recent evidence that LH is clearly detectable in the urine of selected species, including the sun bear, *Helarctos malayanus*, white rhinoceros, Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (T. Robeck, personal observation), bottlenose dolphin, *Tursiops truncatus*, and killer whale, *Orcinus orca* (Kretzschmar, Ganslosser, and Dehnhard 2004; Schwarzenberger et al. 2004; Robeck et al. 2005; Robeck and Monfort 2006). Research so far has focused on ovulation detection in the female. While the relationship between circulating LH and male infertility is ambiguous, circulating LH in cheetahs with azoospermia is double that of normal males (Wildt et al. 1984).

Assessment of LH is confounded by the pulsatile secretory pattern of the hormone, which varies markedly across species (Lincoln and Kay 1979; Wickings, Marshall, and Nieschlag 1986; Brown et al. 1989, 1991a, 1991b). Thus, sampling frequency must be sufficient to reflect profiles accurately (Wildt et al. 1986b, 1988; Brown et al. 1988, 1989, 1991a, 1991b, 1991c). Realistically, understanding pulsatile gonadotropin activity will be difficult, since species must be behaviorally conditioned to stand completely conscious while catheters are placed or serial blood samples drawn, which has been accomplished in the Eld's deer (Monfort et al. 1993a, 1993b).

A more viable approach for male reproductive assessments is assaying circulating FSH and LH after injection of GnRH, using a similar protocol to that used to measure testosterone responsiveness (see above). GnRH stimulates a sharp rise in serum LH in males from a diversity of species, including felids, African elephant, lion, Cape buffalo, impala, Eld's deer, woodchuck, tammar wallaby, and nonhuman primates (Wildt et al. 1984, 1986b, 1987b; Wickings, Marshall, and Nieschlag 1986; Brown et al. 1988, 1989, 1991a, 1991b, 1991c; Monfort et al. 1993b; Concannon et al. 1998; Herbert et al. 2004). If serum LH fails to rise within 60 minutes of a 25- to 100-µg intramuscular or intravenous GnRH injection, then there may be a pituitary anomaly.

ESTROGENS

Monitoring blood or urinary/fecal estrogen concentrations in males may be of value in diagnosing Sertoli cell tumors or seminomas. For example, dogs with this neoplasm produce circulating estradiol-17ß levels that are 2 to 5 times higher than normal (Nachreiner 1986). However, not all Sertoli cell tumors are estrogenic, and others secrete estrogens other than estradiol-17ß. Thus, in this case it might be advantageous to evaluate excreted hormonal metabolites assessed with broad spectrum antibodies.

GLUCOCORTICOID HORMONES

Measuring adrenal glucocorticoid or "stress" hormones could be a particularly valuable approach for assessing environmental effects on male reproductive ability. In well-studied species, chronically elevated glucocorticoid concentrations suppress GnRH-LH pulsatility (see Smith et al. 2003 for review). Adrenal hormone patterns appear to be remarkably different among species, even those within the same family (Wildt et al. 1984, 1987b, 1988; Brown et al. 1991b). Acute elevations of corticoid release as a result of perturbation rapidly return to normal baseline (Wildt et al. 1984) and with no apparent adverse influence on male reproductive function. Normal pituitary function can be tested using ACTH, the synthetic adrenocorticotropic hormone that acts to provoke adrenal gland release of glucocorticoids. In the wildebeest, *Connochaetes taurinus*, greater kudu, *Tragelaphus strepsiceros*, and lion, anesthesia plus electroejaculation fail to elicit an adrenal response of the same magnitude of that after an exogenous ACTH challenge (Schiewe et al. 1991). The long-term effects of chronic stress on male fertility are poorly understood in wildlife species.

THYROID HORMONES

The relationship of thyroid activity and male reproductive function is controversial, but thyroid hormones alter gonadotropin (Chandrasekhar et al. 1985) and steroid hormone metabolism, spermatogenesis, and fertility in men (Krassas and Pontikides 2004).

INFERTILITY AS RELATED TO MALE REPRODUCTIVE BEHAVIOR

Behavioral abnormalities may compromise reproductive performance by preventing the male from copulating with the female. Such defects may have a hormonal origin or may be stress related. Some captive male giant pandas that were considered "nonbreeders" in adulthood eventually learned to mate later in life (Snyder et al. 2006), suggesting that some mating behaviors are learned rather than innate (Zhang, Swaisgood, and Zhang 2004).

TECHNIQUES OF SEMEN COLLECTION

Sexual activity affects seminal quality; thus, males scheduled for a fertility evaluation should be isolated from females for 3 to 7 days before semen collection. Assessments should also be avoided after stresses, vaccination, or parasite treatment. Methods for wildlife species include electroejaculation, manual stimulation, an artificial vagina, or postmortem recovery. Electroejaculation is the most commonly used approach, because the technique requires little training and can be used while the animal is under anesthesia. Viable spermatozoa also may be obtained up to 72 hours after death, by recovery from the epididymides and ductus deferentia.

ELECTROEJACULATION

Electroejaculation has been used for seminal collections from more than 90 species, ranging from the mouse to the elephant. Howard (1993) and Citino (2003) contain reference values for some representative species; table 32.1 lists additional examples. Electrical stimulators manufactured for do-

TABLE 32.1. Species with published records of electroejaculation

Common name	Scientific name	Reference
Banteng	*Bos javanicus*	McHugh and Rutledge 1998
Black-footed ferret	*Mustela nigripes*	Curry et al. 1989; Wolf et al. 2000b
Black rhinoceros	*Diceros bicornis*	Schaffer et al. 1998
Blesbok	*Damaliscus pygargus phillipsi*	Howard et al. 1981
Bongo	*Tragelaphus eurycerus*	Wirtu et al. 2005
Bottle-nosed dolphin	*Tursiops truncatus*	Schroeder and Keller 1989
Brushtail possum	*Trichosurus vulpecula*	Rodger, Cousins, and Mate 1991
Cape buffalo	*Syncerus caffer*	Brown et al. 1991a
Dorcas gazelle	*Gazella dorcas*	Howard et al. 1981; Howard et al. 1984
Cheetah	*Acinonyx jubatus*	Wildt et al. 1987a, Wildt et al. 1983
Clouded leopard	*Neofelis nebulosa*	Wildt et al. 1986a
Eland	*Taurotragus oryx*	Merilan et al. 1978
Eld's deer	*Rucervus eldii thamin*	Monfort et al. 1993a
Elephant (Asian)	*Elephas maximus*	Portas et al. 2007
Elephant (African)	*Loxodonta africana*	Howard and Wildt 1990
Giant panda	*Ailuropoda melanoleuca*	Spindler et al. 2004; Howard et al. 2006
Greater kudu	*Tragelaphus strepsiceros*	Schiewe et al. 1991
Impala	*Aepyceros melampus*	Brown et al. 1991c
Indian rhinoceros	*Rhinoceros unicornis*	Schaffer et al. 1998
Koala	*Phascolarctos cinereus*	Johnston et al. 1998
Leopard	*Panthera leo*	Wildt et al. 1988
Leopard cat	*Felis bengalensis*	Howard et al. 1983
Lion	*Panthera leo*	Brown et al. 1991b; Wildt et al. 1987c
Lion-tailed macaque	*Macaca silenus*	Wildt 1985
Mongolian wild ass	*Equus hemionus onager*	Howard et al. 1981
Przewalski's horse	*Equus przewalskii*	Durrant 1990
Rhesus monkeys	*Macaca mulatta*	Harrison 1980
Scimitar horned oryx	*Oryx dammah*	Morrow et al. 2000
Speke's gazelle	*Gazella spekei*	Merilan, Read, and Boever 1982
Springbok	*Antidorcas marsupialis*	Merilan, Read, and Boever 1982
Tammar wallaby	*Macropus eugenii*	Paris et al. 2005a
Tiger	*Pant hera tigris*	Wildt et al. 1987b
White rhinoceros	*Ceratotherium simum*	Schaffer et al. 1998
White-tailed gnu	*Connochaetes gnou*	Schiewe et al. 1991

mestic animal semen collection generally are adaptable for use in zoo species. Unfortunately, comparative evaluations of stimulation requirements are difficult, because the different laboratories do not standardize the stimulation current, frequency, voltage, and waveform. The electrostimulator used should have gauges that accurately monitor voltage and amperage. The use of anesthesia with electroejaculation requires that food be withheld for 12 to 24 hours in monogastric species and up to 72 hours in ruminants. Certain sedatives, including xylazine (Rompun), diazepam (Valium), metatomidine (Domitor), and phenothiazine derivatives such as acetylpromazine (acepromazine), relax the urethral musculature and may cause urine contamination of the ejaculate.

Direct electrical stimulation of the penis of restrained, unanesthetized males can induce an ejaculatory response. Although effective in monkeys and some canids, this approach is neither humane nor practical for use by zoos. Reproductive biologists prefer to have animals in a surgical plane of anesthesia and to employ a rectal probe that has copper or stainless steel electrodes mounted on the surface in either a ring or longitudinal configuration. The use of longitudinal electrodes is preferable, because only moderate somatic stimulation results. The optimal diameter of a rectal probe generally is about the size of normal stool, which permits adequate contact between the electrodes and the adjacent rectal tissue.

Howard, Bush, and Wildt (1986) and Howard (1993) describe in detail the general procedures for electroejaculation. Inexplicably, ease of collection and semen quality vary among even closely related species. For example, high-quality semen is more easily obtained from certain equids, such as the Mongolian wild ass and Przewalski's horse, than from others such as the zebra, *Equus burchellii*, and domestic horse (Howard, Bush, and Wildt 1986; Durrant 1990). Similarly, although electroejaculates have been obtained from the timber wolf, *Canis lupus*, various foxes (Graham et al. 1978), the African wild dog, *Lycaon pictus* (Hermes et al. 2001), and maned wolf (N. Songsasen, personal observation), digital collection of semen from the domestic dog generally is easier than electroejaculation and provides ejaculates superior in volume, although not quality (Ohl et al. 1994). Other species challenging to electroejaculate include the giraffe, *Giraffa camelopardalis*, and certain marsupials (red kangaroo—*Macropus rufus*, potoroo—*Potorous tridactylus apicalis*, bandicoot—*Isoodon macrourus*, and dasyurids) (Howard et al. 1986; Rodger and Pollitt 1981). Undoubtedly the unique anatomy of the male reproductive tract in different species contributes to some of the difficulties in successfully using conventional equipment originally designed for farm livestock. Therefore, a worthwhile area for research is designing new electrodes and stimulation techniques, as well as altering anesthetic protocols that may inhibit ejaculation. For example, a new technical approach has overcome challenges that prevented consistent successful electroejaculation in the rhinoceros (Hermes et al. 2005).

Rectal probe electroejaculation is safe when used correctly. Thousands of semen samples have been recovered from wild mammals without causing injury or death. We know little about the impact of electroejaculation on the libido or breeding of animals, but there are no effects on circulating testosterone levels (Wickings, Marshall, and Nieschlag 1986), and males have been known to copulate readily with females within days of the procedure (Wildt et al. 1993). Fertility is normal, as electroejaculated males subsequently produce offspring—e.g. a free-living Florida panther and a captive cheetah were observed copulating with females just days after electroejaculation, and these females subsequently gave birth to healthy cubs (ibid.).

ARTIFICIAL VAGINA AND MANUAL STIMULATION

An artificial vagina (AV) is commonly used for farm livestock; the male mounts a teaser female or a fabricated dummy and directs the penis into a collection device. The male requires training, and there always is the danger of injury to the animal handler. Nevertheless, semen has been collected successfully with an AV from the camel, *Camelus bactrianus*, reindeer, *Rangifer tarandus*, red deer, alpaca, *Lama pacos*, chimpanzee, *Pan troglodytes*, gorilla, *Gorilla gorilla*, Eld's deer, Père David's deer, *Elaphurus davidianus*, and cheetah (see Watson 1978; Durrant, Schuerman, and Millard 1985; Gould, Martin, and Warner 1985; Durrant, Yamada, and Millard 1989; Marson et al. 1989). Manual stimulation of the penis to produce ejaculation also has been successful in certain canids, including the maned wolf, arctic fox, *Vulpes lagopus*, and silver fox, *Vulpes vulpes*, as well as the timber wolf and various marine mammals (Keller 1986; Farstad, Fougner, and Tones 1992; Robeck and O'Brien 2004; D. E. Wildt and D. Schmidt, personal communication). AV collection is mainly possible in situations where (1) repeated semen samples are required from a male or (2) novel techniques or training can be used to avoid personal injury. Ejaculates collected using an AV usually are smaller in volume but contain more sperm per unit volume than electroejaculates.

SPERM RECOVERY POSTMORTEM AND FOLLOWING CASTRATION

Spermatozoa can be collected postmortem by flushing the ductus deferentia and caudae epididymides with warmed medium. Experts recommend maintaining tissue at 50°C before flushing, and flushing as soon as possible after death. Tissues should not be exposed directly to an ice surface or frozen during transport. Initial motility of epididymal spermatozoa often is poor, but can be improved by dilution with an appropriate medium or semen extender and incubation at 21° to 37°C. This technique permits preservation of sperm from males that die unexpectedly (Wildt et al. 1986c; Herrick, Bartels, and Krisher 2004). Examples of the successful cryopreservation of epididymal sperm include Iberian red deer, *Cervus elaphus hispanicus*, Sika deer, *Cervus nippon*, blesbok, African buffalo, springbok, and white-tailed gnu (Comizzoli et al. 2001; Herrick, Bartels,and Krisher 2004). Living offspring of the domestic dog and Spanish ibex have resulted from the use of cryopreserved epididymal sperm (Klinc et al. 2005; Santiago-Moreno et al. 2006).

SEMEN ANALYSIS

Before diagnosing subfertility in an individual male, it is necessary to know the minimal ejaculate criteria for the given species that result in normal fertility. This information is unknown or, at best, estimated for most mammals, including humans. However, the range in ejaculate factors for proven breeders is being determined gradually for many species, including zoo animals. If the population size is large, then comparing an individual with conspecifics provides information on his reproductive status, including potential for being fertile.

A thorough seminal analysis requires examining multiple factors and always in a consistent fashion, with ejaculate volume and pH evaluated immediately after sample collection. An ejaculate aliquot (usually about 10 μl) is assessed microscopically at 37°C for sperm motility (percentage) and progressive sperm status (a subjective evaluation of forward progression based on a scale of 0–5: 0, no motility or movement; 1: slight side-to-side movement with no forward progression; 2: moderate side-to-side movement with occasional slow forward progression; 3: side-to-side movement with slow forward progression; 4: steady forward progression; 5: rapid, steady forward progression). Practitioners examine a minimum of 4 microscopic fields (400×).

A variety of environmental insults, including heat, cold, and chemical contamination of the collection vessel, can compromise sperm motility. When sperm concentration is excessive, it is essential to dilute the semen with a suitable medium before assessing cell motility. Swirling masses of motile sperm will be evident in samples of this density, but because individual cells cannot be identified, it is impossible to determine accurately cellular motility or velocity. Certain taxa, especially the marsupials, produce semen containing densely packed globular cells (prostatic bodies), which make motility estimates difficult and require dilution with medium (Rodger and Hughes 1973; Rodger and White 1975, 1978; Wildt et al.

1991; Johnston et al. 1997). The semen of most primates, rodents, and marsupials coagulates immediately after ejaculation, posing difficulties in handling and evaluation. The coagulum from some of these species has been digested by incubating the ejaculate in normal saline at 37°C or by adding a 1 to 2% solution of the enzyme trypsin or pronase (Howard, Bush, and Wildt 1986; Wildt 1986).

Multiple estimates of sperm viability over time (e.g. in 30- to 60-minute intervals for several hours) can detect rapid motility loss associated with infertility (Soderberg 1986; Pusch 1987). Some sperm motility decline in vitro is attributable to urine contamination, which is detectable by observing seminal color and pH using commercially available pH test strips. Urine contamination increases (alkanalizes) ungulate seminal pH above normal, but decreases carnivore semen pH.

Undiluted sperm in felid semen maintains motility in vitro for 5 hours or less. It is possible to improve the motility of fresh sperm significantly from these and other species by (1) diluting the semen with a tissue culture medium, (2) removing seminal fluid by low-speed centrifugation (300 × *g* for 10 minutes) (Howard et al. 1983), or (3) allowing centrifuged spermatozoa to "swim up" into a culture medium layered onto the sperm pellet (Makler et al. 1984; Howard and Wildt 1990; Howard et al. 1990). Passing semen samples through Percoll gradients can also trap immotile and structurally abnormal sperm (Ericsson, Langevin, and Nishino 1973; Tang and Chan 1983; O'Brien and Roth 2000), improving motility and morphology but depressing sperm concentrations in the recovered fraction (Brandeis and Manuel 1993).

Recently, computer-assisted semen analysis (CASA) has shown potential for providing objective indices of sperm motility percentage, swimming curvature/speed, linear progression, and morphology (Lenzi 1997; Verstegen, Iguer-Ouada, and Onclin 2002). However, CASA is no different from visual evaluation of motility in predicting fertilizing capacity of spermatozoa (Krause and Viethen 1999), and the dilution steps associated with preparing the semen for computer analysis can alter sperm motility characteristics (Smith and England 2001). Furthermore, the computer settings cannot be standardized across species and, therefore, may be limited in ability to detect specific types of sperm (Holt, Holt, and Moore 1996; Smith and England 2001). Therefore, in most zoo settings, it is overly expensive and complex to replace simple direct microscopic assessments with high-tech CASA.

Manual determination of sperm concentration is possible using a commercially available erythrocyte assay kit (1:200 dilution ratio) and hemocytometer, or using automated counting systems such as the Coulter Counter and spectrophotometry. However, these methods can be imprecise, particularly when sperm numbers are less than 10 million/ml or when the ejaculate contains extraneous cells and other debris. Sperm morphology is an accurate fertility predictor in some species (Bostofte, Serup, and Rebbe 1982; Freischem et al. 1984). Sperm morphology is evaluated by fixing ejaculate aliquots in 0.3% glutaraldehyde and then examining at least 100 spermatozoa. Sperm morphology classification categorizes cells affected with various structural defects (pleiomorphisms). The spermatozoon's sole function is to deliver its DNA load into an oocyte, and any structural abnormalities, such as deformities in head size or mitochondrial sheath, flagellar derangement, or acrosomal abnormalities that interfere with this objective, is of concern. The acrosome (the sperm's cap) is integral to the fertilization process and normally is closely adhered to the nucleus. Defects in the acrosomal region usually are expressed as vesiculations or irregularities in the cell border or a loosening of the membrane itself (fig. 32.1). Any of these abnormalities can render the spermatozoon incapable of oocyte penetration and fertilization.

For a given species, there may often be a wide range in ejaculate values reported. Some of this variation is due to differences among laboratories in technique and subjective criteria. However, ejaculate volume, sperm concentration, and sperm motility percentage can vary profoundly within a species or even between ejaculates from a single individual. Therefore, when assessing male fertility, it is important to accumulate seminal data on each male over time. Electroejaculations of males suspected of reproductive dysfunction should be done on at least 3 occasions at 3- to 4-week intervals before making a final judgment of fertility status.

Practitioners should not use any single seminal trait exclusively to assess ejaculate status. We believe that traditionally, insufficient emphasis has been given to progressive sperm status and sperm morphology. A preponderance of abnormal cells may indicate sexual immaturity, endocrine dysfunction, or degenerative changes in the testicular seminiferous epithelium, and strongly correlates with infertility (Rogers et al. 1983; Pukazhenthi, Wildt, and Howard 2001). With teratospermia there is a high proportion of pleiomorphisms, but also more total sperm ejaculated, apparently due to (1) an increased rate of production and (2) reduced germ cell loss (apoptosis) during spermatogenesis (Neubauer et al. 2004). O'Brien and others link this characteristic in felids to loss of

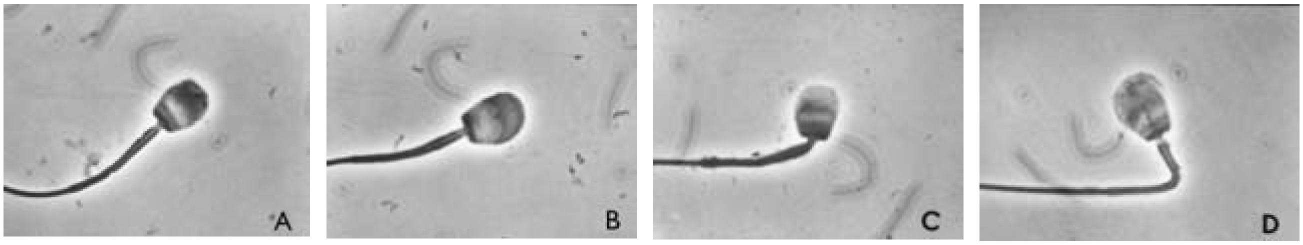

Fig. 32.1. Acrosomal integrity of black-footed ferret sperm: (*A*) intact; (*B*) damaged; (*C*) missing; and (*D*) loose acrosomal membrane. (From Santymire et al. 2006. Reprinted by permission.)

genetic variability (inbreeding) (Wyrobek 1979; O'Brien et al. 1983, 1985; Wildt et al. 1983, 1987c, 1988). While we know that these structurally deformed cells are severely compromised in vitro, the impact of teratospermia on whole animal fertility is less clear. Some female cheetahs can mate only once with a male producing 70% abnormal sperm and routinely become pregnant. In contrast, the Asian lions of India, *Panthera leo persica*, are also known to produce about 65% pleiomorphic sperm and experience low conception rates and a high incidence of stillborn cubs (Wildt et al. 1987c). Likewise, at least one Florida panther male producing an extraordinary number of pleiomorphic sperm (>90% per ejaculate) is known to have repeatedly copulated with estrous females that failed to conceive (Miller et al. 1990). Thus, although it is certain that deformed sperm do not participate in fertilization, some species tolerate a comparatively high number of sperm defects without impaired fertility. From a physiological perspective, the cheetah may be unusually efficient reproductively, with its ability to conceive from a single mating despite producing a severely teratospermic ejaculate.

TESTICULAR BIOPSY

Spermatogenic function can be assessed through testicular biopsy. Microscopic analysis of cellular elements may identify aspermatogenic testes versus those producing sperm. It is possible in oligozoospermic males to identify the cause of acquired infertility and its severity, and to formulate a prognosis. However, even seminiferous tubules of normal testes can contain significant numbers of degenerating sperm cells, so quantifying spermatogenesis in biopsy material involves counting the spherical nuclei of spermatids in tubular cross-sections per unit volume of testis (Amann 1986).

A tissue sample is obtained after inducing anesthesia and surgically preparing the scrotal area. Cohen et al. (1984) reported the use of needle biopsies, although there may be too little tissue recovered for a successful evaluation. A more direct approach involves using an ultrafine surgical blade to make an incision through the scrotum, tunica vaginalis, tunica albuginea, and 2 to 3 mm into the testicular parenchyma. The neck of the scrotal wall is moderately constricted, which everts tissue on the testis surface through the incision site. The sample is "shaved" from the testis with a surgical blade and immersed in glutaraldehyde or Karnovky's, Bouin's, or Zenker's fixative (Amann 1986). Practitioners do not use formalin as a testicular tissue fixative, because it distorts tubular walls and cell chromatin patterns. After suturing all layers of the biopsy site, we recommend administering prophylactic antibiotics. We have used this approach to successfully recover testicular biopsies in the lion, Cape buffalo, and impala.

Biopsy and histology can be used to assess the severity of testicular degeneration in animals with acquired infertility. For example, examination of gorilla testicular tissue has revealed marked testicular atrophy, degeneration, and fibrosis of seminiferous tubules (Dixson, Moore, and Holt 1980; Foster and Rowley 1982). There are many factors that can perturb cellular structure within the testis, including hypogonadotropism, neoplasms, inflammatory or vascular diseases, cryptorchidism, drugs, and genetic disorders.

Generally, biopsy of the male gonad is considered safe if the procedure is performed carefully, minimal tissue is recovered, and the epididymal region is not traumatized. However, temporary decreases in sperm concentration and motility have been reported in human males and dogs after bilateral biopsy. While this may be the result of sperm antibody formation, studies have detected no circulating sperm-immobilizing or sperm-agglutinating antibodies in biopsied men or dogs (Burke 1986). Any reduced fertility likely is transient (Cosentino et al. 1986).

BIOCHEMICAL CHARACTERISTICS OF SEMEN

The biochemical components of semen reflect the relative contributions of the epididymides and accessory glands. Because variations in ejaculatory abstinence, level of sexual excitement, and sperm concentration can alter the semen composition, this fluid has limited value in assessing male fertility.

CLASSIFICATION AND ETIOLOGY OF MALE INFERTILITY DISORDERS

Comprehensive descriptions of male infertility etiology are available in historical and recent reviews (Morrow, Baker, and Burger 1986; Goldstein 2002; Schlegel and Hardy 2002; Sigman and Jarow 2002).

HEAT

Warming the testes to internal body temperature damages primary spermatocytes and subsequently decreases sperm concentration and motility. Even acute heat insults (as short as 30 minutes) can cause oligozoospermia for as long as 5 weeks. High fever, scrotal dermatitis, or testicular/epididymal inflammation all can increase intratesticular temperature. The anatomy of some species (e.g. the small scrotal sac and hair of the gorilla) and sitting on heated floors have been suggested sources of temperature-induced testicular damage (Gould 1983). This type of damage usually is reversible when the testes are exposed to lower temperatures.

NUTRITIONAL DEFICITS

Malnutrition (insufficient calorie intake) alters LH and testosterone secretory patterns in the rhesus monkey (Lado-Abeal, Veldhuis, and Norman 2002) and delays puberty and reduces fecundity in the marmoset, *Callithrix jacchus* (see Tardif and Jaquish 1994), and water buffalo, *Bubalus bubalis* (see Oswin-Perera 1999). Total energy supply to the fetus and neonate also appears important to maintaining reproductive function in later life (Borwick et al. 1997). However, zoo animals rarely suffer from an insufficient amount of total energy—more common is a lack of specific nutrients. Few published data demonstrate that nutritional deficiencies influence the reproductive performance of zoo animals, particularly males. However, there is evidence that felids fed strictly muscle meat (which is low in minerals and vitamins) produce poor-quality ejaculates (Swanson et al. 1995). In most cases, semen quality improves markedly when the diet includes bones, whole carcasses, and vitamin/mineral supplements. Isolating a single nutrient responsible for infertility may be difficult, as the relationship between nutrition and reproduction is varied and multifaceted.

In cattle, rats, and humans fed a zinc-deficient diet, there is a decrease in circulating testosterone and number of spermatids, and seminiferous tubules atrophy (Prasad et al. 1996; Hamdi, Nassif, and Ardawi 1997). Males exposed to zinc deficits in utero generally experience low birth weights and abnormal adult behaviors including inept breeding behavior (Gordon et al. 1982; Black 2001). Hypocalcaemia can contribute to erectile dysfunction, reduced spermatogenesis, and poor fertilization (Andonov and Chaldakov 1991; Stricker 1999; Mills, Chitaley, and Lewis 2001). Manganese deficiency can cause testis degeneration, low libido, and sterility in the rat and rabbit, *Oryctolagus cuniculus* (see Kuhlman and Rompala 1998). Low selenium levels can result in aspermia or spermatozoa that are immotile and morphologically abnormal (Wu et al. 1979; Olson et al. 2004). Magnesium is essential for sperm production (Kiss and Kiss 1995), and vitamin D deficiency can delay onset of male puberty and fertility (Halloran and DeLuca 1979).

Arachidonic acid is essential for normal spermatogenesis (MacDonald et al. 1984), and must be supplied to felids due to their lack of desaturating enzymes that facilitate arachidonic acid production from shorter chains (Rivers, Sinclair, and Crawford 1975). Sperm-egg interactions rely closely on the lipid composition of the sperm membranes; therefore, polyunsaturated fatty acids play a significant role in reproduction. However, excess serum levels of polyunsaturated fatty acids are known to interfere with ovarian function (Grummer 1995), but the impact of excessive polyunsaturated fatty acids on male reproduction is unknown.

ENDOCRINE DISORDERS

The main hormonal cause of human male infertility is gonadal deficiency that results in hypogonadotropic hypogonadism (or suboptimal endogenous gonadotropin concentrations that, in turn, can cause poor testes function) (Sherins and Howards 1985). This disorder has been identified in the mink, *Mustela vison* (see Tung et al. 1984), and probably exists in other mammalian species. Prepubertal males fail to achieve sexual maturity, whereas adults have low libido, fewer male sexual characteristics, and aspermatogenesis.

FEED CONTAMINATION AND ENVIRONMENTAL TOXINS

There is the possibility of exposing zoo animals to environmental toxins, through food contaminants or via cleaning or pest removal practices. Pre- and postnatal exposure to mercury and polychlorinated biphenyls can cause feminization of the male fetus, including perhaps in the Florida panther (Facemire, Gross, and Guillette 1995). Ackerman et al. (1999) report that copper contamination is associated with increasing proportions of sperm abnormalities in the impala. The fungicide/pesticide dibromochloropropane is associated with testicular atrophy, azoospermia, and oligozoospermia in men (Whorton and Foliart 1983). Sperm quality also is believed to be harmed by a wide range of organic compounds, including acetone, tetrachloroethylene, ethylene glycol ethers, and aromatic hydrocarbons as well as high lead and cadmium concentrations (Baillie, Pacey, and Moore 2003). Fetal exposure to environmental estrogens may alter development of the male reproductive tract (McLachlan and Dixon 1977).

KARYOTYPE ABNORMALITIES

Karyotype abnormalities have been associated with a variety of testicular disorders in humans. In men, the presence of an additional X chromosome (Klinefelter's syndrome, XXY) usually causes azoospermia, an elevated FSH and LH, and low testosterone concentrations (Resko 1982). An additional Y chromosome (XYY syndrome) causes azoospermia or oligospermia.

There is little information on the relationship between chromosomal anomalies and reproductive performance in zoo-maintained mammals. Populations of Kirk's dik-dik, *Madoqua kirkii*, have 2 distinctive karyotypes, cytotype *a* or *b*. Pedigree surveys indicate that animals representing the 2 cytotypes originated from different geographic regions of Kenya. Cytotype *a* dik-diks have a diploid number of 46 chromosomes, whereas males and females of cytotype *b* have 47 and 46 chromosomes, respectively. The 2 genotypes will hybridize to produce F1 offspring, which have reduced fertility. Cytotype *a* and *b* males produce high-quality and comparable spermic semen samples, whereas the ejaculates of the cytohybrids (*ab* males) contain only immature spermatozoa. Histological analyses indicate the presence of meiotic activity, but no spermiogenesis (sperm maturation) and no mature sperm within the seminiferous tubules or the epididymis (Howard et al. 1989). These observations illustrate the importance of understanding the fundamental genetics of wild species populations before the onset of propagation programs.

INBREEDING

Small populations, including zoos, offer a limited pool of unrelated mates that may decrease with each generation (see Taylor 2003 for review). Without the importation of new founder genes, the genetic complement of all possible mating pairs eventually will have shared alleles, which increases the chance for the expression of recessive deleterious alleles.

Male reproductive characteristics, especially sperm form and function, appear especially sensitive to inbreeding, as previously documented for the African and Indian lion (Wildt et al. 1987c) and the Florida panther (Barone et al. 1994). Interestingly, outbreeding one generation of Florida panthers with another subspecies of puma from Texas resulted in improved sperm traits (J. G. Howard, personal communication). In Cuvier's gazelle, *Gazella cuvieri*, there is a positive correlation between homozygosity and proportions of abnormal spermatozoa (Gomendio, Cassinello, and Roldan 2000). Strict adherence to genetic management plans and the mating of only unrelated individuals are two of the most effective means of ensuring normal male reproductive function.

STRUCTURAL ABNORMALITIES

Anatomical disorders that prevent sperm production, maturation, and outflow include varicocele, ductal occlusion, ejaculatory dysfunction, ischemia, orchitis, and epididymitis. In some cases surgery, antibiotics, anti-inflamatory or sympathomimetic drugs, and certain antihistamines may reverse damage if applied in time (Sherins and Howards 1985). Males with orchitis as a result of an infection (e.g. *Brucella*) should not be used for breeding.

DRUGS AND RADIATION

Most drugs commonly used in wildlife medical management do not harm male reproductive function, although prolonged steroid administration and nitrofurantoin antibiotics can arrest spermatogenesis. Anesthetics may temporarily depress hypothalamic-pituitary-gonadal activity. Chemotherapeutic agents used for treating malignancies can affect germ cell production. Because of rapid cell division within the germinal epithelium, the testes are highly radiosensitive, making appropriate shielding of the genital region essential during therapy.

HORMONAL TREATMENT OF MALE INFERTILITY

Hormonal therapies have been used to address 2 types of male infertility: (1) hypogonadotropic hypogonadism (i.e. suboptimal endogenous gonadotropin levels causing poor gonadal function) and (2) idiopathic infertility (i.e. reproductive failure of unknown origin) (see Sherins and Howards 1985 and Wickings, Marshall, and Nieschlag 1986 for greater detail).

VALUE OF ASSISTED REPRODUCTION TECHNIQUES

Treating idiopathic male infertility is unreliable. Thus, assisted reproductive techniques (ART) have become increasingly popular in humans, and in the livestock industry for increasing offspring production, especially from genetically valuable individuals (Loskutoff 2003; Thibier 2000; Skakkebaek et al. 2000). A lack of basic knowledge about wild mammal reproduction hampers the application of ART to zoo species (Wildt et al. 2003). However, semen cryopreservation, artificial insemination (AI), in vitro embryo production (IVP), and embryo transfer have been successful in some zoo species, especially those with a closely related domestic animal "model" (Wildt et al. 1986c; Loskutoff and Betteridge 1992).

Due to its comparative simplicity, AI has been the most effective of the assisted breeding technologies, finding its niche especially in genetic management programs where sexual incompatibility between desirable pairs is common, e.g. the cheetah (Howard et al. 1997), black-footed ferret (Howard, Marinari, and Wildt 2003), and giant panda (Howard et al. 2006). Artificial insemination also is useful for transporting germplasm between facilities in situations where it is extremely difficult to move individuals between breeding venues, e.g. elephants (Hildebrandt et al. 1998) and killer whales (Robeck et al. 2004). To our knowledge, AI has not been used to produce offspring with wild males with diagnosed infertility (i.e. oligospermia), although progress has recently been made in the sexing of sperm to increase the numbers of females produced, specifically in nonhuman primates and marine mammals (O'Brien et al. 2005; J. K. O'Brien and T. R. Robeck, personal communication). Although AI technically involves only the collection, processing, and deposition of sperm, there are many species-specific issues that require attention before offspring can be produced routinely. For example, the type of medium and holding temperature required for fresh sperm varies across species, even those within the same family. Perhaps the most challenging aspect is timing the AI, which requires clear knowledge of the precise time of female estrus and ovulation, as well as the sometimes tortuous process of sperm deposition deep within the cervix or preferably within the uterus.

The IVP technique would be suitable for attempting to produce young from oligozoospermic males, or after rescuing sperm from a male postmortem, as it can succeed with far fewer sperm than required for a natural mating or AI. In vitro embryo production has been successful in a wide array of wild species, e.g. baboon, *Papio hamadryas*, rhesus macaque, marmoset, gorilla, African wild cat, *Felis silvestris*, Siberian tiger, ocelot, caracal, *Caracal caracal*, Armenian red sheep, *Ovis ammon gmelini*, water buffalo, gaur, *Bos gaurus*, red deer, and llama, *Lama glama* (Donoghue et al. 1990; Loskutoff 1998; Pope et al. 1997; Pope and Loskutoff 1999; Pope 2000; Swanson and Brown 2004). Even fewer sperm are required for sperm injection into the perivitelline space (the area between the zona pellucida [the protective coating of the ovum] and the inner cytoplasmic membrane) or directly into the cytoplasm. However, unlike AI, none of these embryo-related technologies have ever been used for genetically managing zoo populations (Pukazhenthi and Wildt 2004), mainly due to the lack of basic knowledge about embryogenesis in wildlife species.

Considerable progress has been made in the field of sperm cryobiology for wildlife (see Holt et al. 2003). In general, if viable sperm can be recovered, then there will be fair-to-good post-thaw viability. Exceptions include black-footed ferrets (Howard, Marinari, and Wildt 2003; Santymire et al. 2006) and red wolves (Goodrowe et al. 1998). Sperm cryopreservation and AI can resolve problems of geographic isolation and behavioral compatibility. Additionally, growing concerns about animal welfare and stress may result in greater use of AI with frozen sperm as an alternative to shipping animals.

SEASONAL INFLUENCES ON MALE REPRODUCTION

In most wild mammals, the season regulates essential activities of the life cycle (feeding, migration, and reproduction) (Malpaux 2006), thereby ensuring that young are born at times maximizing their chances of survival. Often photoperiod acts as the proximate factor modulating onset and cessation of reproductive activity. Free-ranging males in natural habitats may exhibit more profound variations in the hypothalamic-pituitary-testicular axis than their counterparts in captivity, where artificial photoperiods and diets are typical.

Malpaux (2006) offers a classical summary of the seasonal aspects of testicular function in both domestic and wildlife species, while Lincoln, Andersson, and Hazlerigg (2003) provide an excellent overview of mechanisms of action. In the natural habitat, males usually achieve full sexual competence some weeks before females are receptive, and male fertility extends over the full period when successful mating may occur (Lincoln 1981).

There have been numerous studies of diverse species showing functional changes in the testes attributable to season, e.g. the vole, *Microtus agrestis* (see Grocock and Clarke 1975), mole, *Talpa europaea* (see Racey 1978), mongoose, *Herpestes javanicus auropunctatus* (see Gorman 1976), brown hare, *Lepus europaeus* (see Lincoln 1974), rock hyrax, *Procavia capensis* (see Millar and Glover 1970), clouded leopard (Wildt et al. 1986b), tiger (Byers et al. 1990), jaguar (Morato et al. 2004b), ocelot, margay, *Leopardus wiedii*, oncilla, *Leopardus tigrinus* (see Morai et al. 2002), blesbok, kudu, springbok, and impala (Brown et al. 1991c; Skinner 1971), hartebeest, *Alcelaphus buselaphus* (see Skinner, van Zyl, and van Heerden 1973), Cape buffalo (Brown et al. 1991c), tammar wallaby (Paris et al. 2005b), rhesus macaque (Zamboni, Conaway, and Van Pelt 1974), and killer whale (Robeck and Monfort 2006). Seasonal elevations in testosterone correlate with increases in sexual activity, aggressiveness, and testicular size, these factors being maximally coincident with the onset of female cyclicity.

Although bears, felids, and ungulates are usually seasonal breeders in nature, electroejaculation from zoo-maintained males in North America results in viable-appearing sperm throughout the year (Howard, Bush, and Wildt 1986). In contrast, sperm of acceptable quality can only be recovered during the breeding seasons of rodents (Concannon et al. 1996), mustelids (Sundqvist, Lukola, and Valtonen 1984), or large canids (Koehler et al. 1998). The captive environment may affect the synchrony of male and female peak reproductive performance. Female captive clouded leopards exhibit estrous activity from late December through February (Wildt et al. 1986a; 1986b), but males produce the greatest number of motile sperm in June or July. The data suggest that a physiological asymmetry may exist in peak reproductive performance between the male and female clouded leopard, perhaps as a result of differing adaptations to the captive environment.

INHIBITION OF MALE REPRODUCTION AND AGGRESSION

Most reproductive research focuses on improving rather than inhibiting male fertility. However, zoo management programs require reproductive control methods to maintain genetic diversity and optimal demography. As breeding techniques improve and animal space becomes more limited, dealing with "surplus" animals, especially males, will be a continuous challenge (see Carter and Kagan, chap. 21, this volume).

The management of male aggression is often necessary to avoid injury, because males tend to be more aggressive than females, particularly when housed in close proximity. Limiting hormone production offers a viable approach to managing male aggression in captivity. Asa and Porton (2004) (see also Asa and Porton, chap. 34, this volume) address methods for inhibiting male reproduction. In brief, there are 2 basic approaches to male contraception: (1) blocking testicular function and (2) preventing gamete transport. Many methods of contraception that reduce testosterone production or action also are effective in reducing aggression in the male.

THE FUTURE

Substantial progress has been made in the last decade in understanding the physiology of male (as well as female) mammals, a prerequisite for successfully reproducing wildlife species in zoos. This has been partly due to increased comfort with collecting physiological data through invasive methods and rapid advancements in urinary and fecal hormone monitoring (see Hodges, Brown, and Heistermann, chap. 33, this volume). Combined, these invasive and noninvasive methods have resulted in improved management of health and reproduction, including improvements gained by assisted breeding. Much of this success also has been due to increased cross-disciplinary collaboration. Zoos need to allow continued access to animals in their collections, because without data from "normative" specimens, there is little hope for identifying or rectifying infertility cases. Therefore, we recommend the continued emphasis on collecting and publishing as much data as possible about male reproduction in every mammal species.

Given its growing popularity and noninvasive nature, we need to to direct more efforts at endocrine monitoring in males via urine or feces, especially for examining the relationship between adrenal stress and gonadal hormone patterns. A major question remains to be answered: is the captive environment compromising reproduction in male mammals? If so, can this be measured hormonally in urine or feces, correlated to behavioral indices, and be reversed by modifying the environments?

We lack information on the actual incidence of male infertility in zoo animals. Thus, there is a need to characterize and document every case and to examine potential perturbing factors to male reproductive success, such as nutrition, genetics, and the causes of behavioral incompatibility. Future zoo research should emphasize the sexing of sperm to increase the number of female young produced, and investigations into the sex ratio of offspring produced in captivity. A related area of concern for research is suppressing aggression to allow males to be maintained in bachelor herds. Finally, we recommend more studies of males living in nature, since it is now possible to collect vast amounts of reproductive data from free-living males, including those that are captured for short periods as "data and specimen donors." In at least one species, the cheetah, sperm collected from free-living individuals in Africa were cryopreserved, transported intercontinentally, and used to produce offspring by AI in North American zoos (Wildt et al. 1997), a success based on the collection of basic data from both wild and captive cheetahs. Thus, we believe that a high priority for research is to extend the cheetah model to other mammals, to demonstrate how reproductive studies can contribute to sustaining wildlife *ex situ* and *in situ* through metapopulation management.

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Endocrine Monitoring of Reproduction and Stress

Keith Hodges, Janine Brown, and Michael Heistermann

INTRODUCTION

Most wild mammals kept in captivity are managed intensively. Under such conditions, the ability to monitor reproductive status can greatly facilitate attempts to enhance breeding success for many species. More specifically, objective and reliable methods for monitoring key reproductive events, such as ovulation and pregnancy, not only find widespread application in the management of natural breeding, but also provide the basis for efforts designed to accelerate reproduction by assisted/artificial means.

Animal welfare is also a key management issue when maintaining wild mammals in a captive situation (see Kagan and Veasey, chap. 2, this volume). Avoidance of stress (and of situations and procedures likely to cause it) is therefore a very important aspect of the overall zoo management paradigm, but until recently, physiological measures by which stress in zoo animals can be assessed were difficult to obtain.

This chapter provides an overview of the available endocrine-based methodologies for monitoring reproduction and stress in captive wild mammals. Although coverage includes measurement of hormones in blood, we emphasize methods based on noninvasive sample collection. Thus, we provide a bibliography of selected studies describing the use of urinary and fecal hormone analysis for determination of reproductive status and stress in males and females across the main mammalian taxa. The database for this derives predominantly from studies carried out since the original edition of this volume was published in 1996.

ENDOCRINE METHODOLOGIES FOR ASSESSING PHYSIOLOGICAL STATUS

GENERAL CONSIDERATIONS

Hormone analysis is the most precise of the indirect methods for monitoring the functional status of the reproductive and stress axes. However, since correct interpretation of hormonal data requires at least some knowledge of the physiology of the species in question, monitoring methods based on hormonal analysis first need to provide the basic physiological information (hormone metabolism, patterns of secretion and excretion) on which their subsequent application depends. Although certain basic commonalities exist among mammal species concerning the endocrinology of reproductive and adrenal function, marked differences in the nature, patterns, and levels of hormones secreted and/or excreted make extrapolation of results from one species to another difficult and potentially misleading.

Hormones are present and can be measured in various biological matrices, including blood, saliva, urine, and feces. The choice of which to use for analysis depends on a range of factors, including the type of information required, the assay techniques involved, species differences in steroid metabolism and route of excretion, and the practicality of sample collection, particularly when repeated sampling over extended periods is necessary. In general, the advantages of sample collection without the need for animal contact mean that noninvasive approaches based on urine and (more recently) fecal analysis are the preferred option in most situations.

HORMONE ASSAYS

Measurements of hormones and their metabolites are usually carried out by immunological procedures using hormone- or hormone-group-specific antibodies. Two main types of immunoassays are available: radioimmunoassays (RIA), which use radioactively labeled hormone as the competitive tracer in the quantification process, and enzymeimmunoassays (EIA), in which either enzyme- or biotin-labeled preparations are employed. Being nonisotopic, EIAs avoid the problems associated with use and disposal of radioactivity and are also less costly. Furthermore, the end point is a color change that is simple to quantify and relies on less expensive instrumentation. As such, EIAs are potentially more suitable for zoos and other institutions where sophisticated laboratory facilities are not available.

Since all immunoassays are highly sensitive, assay performance has to be carefully assessed both during the initial setup phase and during routine use. There are 4 main criteria of validation: *sensitivity* (minimum amount of hormone that can be detected), *precision* (within- and between-assay repeatability), *accuracy* (ability to detect the correct amount of hormone in the sample), and *specificity*. The latter has 2 components: the degree of specificity of the antibody itself and the possible influence of interfering substances (matrix effects), which need to be controlled for and, if present, removed by incorporating additional sample purification steps or preparation of standards in hormone-stripped sample. Concerning antibody specificity, highly specific assays may be useful when the identity of the major metabolite is known and when species comparisons are of interest. Since, however, excreted samples (especially feces) can contain a large number of metabolites, specific measurement is often difficult to achieve and might be less useful in cases where the antibody detects only metabolites of low abundance. Group-specific assays utilize antibodies that cross-react with several metabolites of related structure. Since knowledge of the relative abundance of individual metabolites is not necessary, these assays have advantages in that they can usually be applied to a wider range of species (see Heistermann and Hodges 1995; Heistermann, Palme, and Ganswindt 2006; Schwarzenberger et al. 1996a; Wasser et al. 2000), thus helping to overcome the problems of species specificity in hormone metabolism. Care needs to be taken, however, in order to avoid problems arising from the comeasurement of structurally related but physiologically distinct substances, which can generate misleading results (e.g. comeasurement of androgens of adrenal and testicular origin in fecal assays).

One frequently asked question is whether commercial immunoassay kits developed for humans can be used in exotic species. The answer is not straightforward, because validity depends on species, hormone, and sample matrix. For example, kits effectively measure steroids in serum of many species, but usually not urine or feces. Kits for chorionic gonadotropin (hCG) and luteinizing hormone (hLH) work well with urine and/or serum in most great apes, but generally not other species. No commercial kit should be used without proper validation.

SAMPLE COLLECTION AND STORAGE

Blood. For measurement of most hormones, blood serum or plasma can be used. Steroids usually need to be extracted from the matrix before evaluation; however, many assay kits now are available that do not require sample preparation before assay. Care should be taken to avoid repeated freeze-thaw cycles, which can damage protein hormones.

Saliva. Many animals can be trained to provide saliva samples on demand using positive reinforcement and food rewards. With larger animals, it is possible to collect several milliliters directly into a container (e.g. Gomez et al. 2004), whereas in smaller animals, it may be necessary to obtain samples using cotton swabs or other absorbent materials. Offering chew items to an animal is another way to collect saliva samples. Samples should be frozen after collection, and most assays require fairly extensive extraction procedures. Some commercial companies have developed assays specific for saliva to avoid problems associated with matrix effects.

Urine. Samples can be collected midstream (uncommon), from a container placed underneath a drain or channel in the floor of the enclosure, or by aspiration from the ground using a pipette or syringe. If possible, samples should be centrifuged to remove cellular or other debris. Volumes as small as 0.2 mL are sufficient for most assays, and it is generally not necessary to collect more than 1 mL. Samples should be stored frozen, preferably in 2 aliquots to avoid excessive freeze-thaw cycles and as a precaution against leakage.

Feces. Fecal samples are collected directly from the floor; a thumbnail-size amount generally is enough for analytical purposes. A larger aliquot may be needed for samples with a high proportion of fibrous material (e.g. rhinoceroses, *Ceratotherium*, *Diceros*, *Rhinoceros*, and *Dicerorhinus*; elephants, *Loxodonta* and *Elephas*; giant panda, *Ailuropoda melanoleuca*). Because steroids in feces can be unevenly distributed, samples should be homogenized using a gloved hand or improvised spatula before transfer to storage container (Brown et al. 1994b; Wasser et al. 1996; Millspaugh and Washburn 2003). Fecal processing and storage methods can differentially affect steroid metabolite concentrations, with responses being species specific (e.g. Terio et al. 2002; Hunt and Wasser 2003; Galama, Graham, and Savage 2004; Millspaugh and Washburn 2003). In this respect, storing fecal samples by simply freezing at −20°C is the most effective way of preserving steroid hormones for long periods of time and should therefore be preferred over storage of samples in alcoholic solvents. In fact, significant alterations in fecal steroid concentrations can occur during long-term storage in ethanol, even when samples are frozen (Khan et al. 2002; Hunt and Wasser 2003). Feces imported into some countries may require special treatment in order to kill pathogens (e.g. autoclave, formalin, acetic acid, ethanol, sodium hydroxide), and this could potentially influence steroid levels (Millspaugh et al. 2003).

For both urine and feces, it is essential to collect only samples of known origin and to avoid cross-contamination (feces with urine and vice versa) as well as contamination with water and any form of detergent. However, as long as urine samples are not overly dilute, indexing by creatinine should account for fluid differences. For example, steroids in feral horses were measured using urine-soaked snow (Kirkpatrick, Shideler, and Turner 1990).

Since diurnal patterns of secretion are particularly pronounced for some hormones (e.g. testosterone and glucocorticoids), time of sample collection is a variable that needs to be controlled. Although the magnitude of diurnal changes is most evident in blood and urine, they can still also be noticeable in the feces of certain small-bodied species (e.g. callitrichids: Sousa and Ziegler 1998; rodents: Cavigelli et al. 2005) in which fecal passage rate is relatively high. Thus, wherever possible, samples should be collected at roughly the same time each day.

Hodges and Heistermann (2003) deal with other practical aspects concerning the use of urinary and fecal assays to generate hormonal data for monitoring physiological function (e.g. sampling frequency, sample preparation, interpretation of results, etc.).

MEASUREMENT OF HORMONES IN DIFFERENT BIOLOGICAL MATRICES

BLOOD

Measurement of hormones in blood is still probably the most informative and widely used approach to monitoring physiological function in laboratory and domestic animals. The advantages include fewer problems associated with sample preparation (e.g. less need for complicated extractions and hydrolysis), no need for indexing concentrations, real-time reflection of hormonal status (little or no time lag), and the possibility of monitoring short-term endocrine changes. In most zoo animals, however, difficulties associated with capture or restraint necessary for the collection of blood samples makes this procedure impractical for routine (i.e. repeated and/or regular) application. There are, nevertheless, situations in which blood sampling is justifiable, because either suitable alternatives are lacking or husbandry practices and/or degree of animal training are of sufficient level that venipuncture represents little additional risk or stress. For example, in North America the reproductive status of Asian and African elephants is routinely monitored by blood progestin analyses (Brown 2000), and numerous studies have characterized circulating pituitary, adrenal, and ovarian hormone profiles in these species (Kapustin et al. 1996; Carden et al. 1998; Brown 2000; Brown, Wemmer, and Lehnhardt 1995; Brown et al. 1999; Brown, Walker, and Moeller 2004). Longitudinal blood sampling also has been used to monitor steroid and protein hormones during the estrous cycle and pregnancy in a number of wildlife species, including rhinoceroses (Berkeley et al. 1997; Roth et al. 2001, 2004), Baird's tapir, *Tapirus bairdii* (see Brown et al. 1994a), beluga whales, *Delphinapterus leucas* (see Robeck et al. 2005a), mithuns, *Bos frontalis* (see Mondal, Rajkhowa, and Prakash 2005), yaks, *Bos grunniens* (see Sarkar and Prakash 2006), buffalo, *Bubalus bubalis* (see Mondal and Prakash 2004), camelids (see Bravo et al. 1991, 1996), and felids (see Brown 2006 for a review). Moreover, blood sampling is often conducted as part of the validation procedure for noninvasive monitoring techniques in order to demonstrate good correspondence between circulating and excreted hormone profiles (e.g. Brown et al. 1995; Berkeley et al. 1997; Heistermann, Trohorsch, and Hodges 1997; Goymann et al. 1999; Walker, Waddell, and Goodrowe 2002).

SALIVA

Minute quantities of steroids are also present in saliva and can be measured using highly sensitive immunoassay procedures. Hormones enter saliva by passive diffusion, so concentrations are not affected by salivary flow rate (e.g. Riad-Fahmy et al. 1982). Salivary steroid concentrations usually are significantly lower than circulating levels, because only the unbound fraction is present. While the collection of saliva can, under certain circumstances, be called a noninvasive procedure, and as such has proved useful for monitoring physiological status in women, domestic livestock, and dogs (e.g. Negrão et al. 2004; Queyras and Carosi 2004), there have only been a few studies in which salivary hormone analyses have been used in exotic species. Most of these have involved analysis of salivary cortisol to assess adrenal activity in relation to stress (e.g. Ohl, Kirschbaum, and Fuchs 1999; Lutz et al. 2000; Cross and Rogers 2004), although monitoring reproductive steroids has been reported in the rhinoceros (Czekala and Callison 1996; Gomez et al. 2004). Other studies, however, have reported limited usefulness of salivary analyses for assessing reproductive function, with poor correlations observed between circulating and secreted concentrations (Atkinson et al. 1999; Fenske 1996). In a study on the Indian rhinoceros, *Rhinoceros unicornis*, several estrogen and progestin RIAs and EIAs gave poor results, whereas commercial assay kits designed specifically for human saliva were effective (Gomez et al. 2004). Thus, the inability to detect biologically relevant immunoactivity in saliva may be due to assay matrix effects. One recent study reported the successful use of liquid chromatography–mass spectrometry to measure salivary testosterone in the bottlenose dolphin, *Tursiops truncatus* (Hogg, Vickers, and Rogers 2005).

URINE

The primary motivation for the development of urinary hormone assay methodology was the growing awareness (and demand) in the early 1980s for more scientific input into zoo animal management, and the establishment of efficient, coordinated breeding programs for targeted species. Urinary hormone analysis was seen as the most likely alternative to preexisting invasive procedures required for blood sampling. As a result of a large number of studies carried out in the early to mid-1980s (see Hodges 1985; Lasley 1985; Heistermann, Möstl, and Hodges 1995 for references), there were major advances in urine hormone analysis methodology, in terms of ease of performance, sensitivity, and reliability. The ensuing methods and their subsequent application have generated an enormous comparative database on reproductive and, more recently, stress physiology in wild mammals and other vertebrate taxa.

Because most urine samples are either single voidings or incomplete 24-hour collections, creatinine determination is used to compensate for differences in urine concentration and volume. Despite certain limitations involved in the use of creatinine measurements, there is a good correlation between the hormone/creatinine index and 24-hour excretion rates (e.g. Hodges and Eastman 1984), and the method has successfully generated hormone profiles in diverse species.

Most steroids in urine are present in the conjugated form, either as sulphate or glucuronide residues. Early analyses of steroids in urine involved the laborious process of hydrolysis and solvent extraction before assay; however, the subsequent introduction of nonextraction assays allowing direct measurement of steroid conjugates has greatly simplified procedures for most species (e.g. Shideler et al. 1983; Lasley et al. 1985; Hodges and Green 1989; Heistermann and Hodges 1995). By avoiding the need for hydrolysis, a process that itself can be inefficient, direct assays for steroid conjugates have the additional advantage of often generating a more informative hormone profile than previously possible with extraction methods (e.g. Shideler et al. 1983; Lasley and Kirkpatrick 1991).

Depending on clearance rate (which can vary according to both hormone and species) and frequency of sampling, there is a certain time lag between any given secretory event (and resulting change in circulating hormone level) and its detection in urine. The lag time from steroid production/secretion to appearance in excreted urine can be as short as 2 hours (e.g. Bahr et al. 2000), but is generally within the range 6 to 14 hours (Czekala et al. 1992; Brown, Wemmer, and Lehnhardt 1995; Monfort et al. 1995, 1997; Busso et al. 2005). Thus, in practical terms, changes in the pattern of urinary hormone excretion usually reflect physiological events that happened several hours earlier, and this has to be taken into account when interpreting urinary hormone profiles.

Although most urinary-based assays are directed toward the measurement of steroid hormones, gonadotrophic hormones (pituitary LH, FSH, and, in some species, chorionic gonadotrophins) are also excreted into the urine. Since the structure of all such peptide hormones (beta subunit) is species specific, care needs to be taken when selecting antibodies for heterologous assays, as is usually the case in studies of exotic species. One particularly versatile monoclonal antibody against bovine LH has been shown to demonstrate good cross-reactivity with LH from diverse mammalian species as well as with hCG and eCG (Matteri et al. 1987), and has been used to characterize urinary LH profiles during the ovarian cycle in a number of wildlife species, including primates (Ziegler, Matteri, and Wegner 1993; Shimizu et al. 2003a), marine mammals (Robeck et al. 2004, 2005b), and rhinoceroses (Stoops, Pairan, and Roth 2004). Urinary prolactin (Ziegler et al. 2000a; Soltis, Wegner, and Newman 2005), chorionic gonaotrophin (Munro et al. 1997; Shimizu et al. 2003a; Tardif et al. 2005), and FSH (Shimizu et al. 2003a; Shimizu 2005) also have been measured in several nondomestic mammalian species. One important caveat is that identification of protein hormones in circulation does not mean that they will necessarily be measurable in urine; they may be structurally altered before excretion or not excreted in significant amounts.

FECES

In addition to urinary excretion, large amounts of steroids are excreted into feces. In fact, in several mammalian species (e.g. many of the Felidae—Shille et al. 1990; Brown et al. 1994a; Graham and Brown 1996), fecal excretion predominates. Radiometabolism studies in particular have yielded important data on the relative importance of the urinary and fecal pathways of steroid excretion. From these studies, it is clear that major differences exist, not only between species, but also between hormones within the same species. Thus, among primates for example, the squirrel monkey, *Saimiri sciureus*, excretes both estrogen and progesterone metabolites mainly (~70%) via the fecal route (Moorman et al. 2002), whereas the cotton-top tamarin, *Saguinus oedipus*, also a New World monkey species, eliminates estrogens almost exclusively (~92%) via the urinary pathway (Ziegler et al. 1989) but progestagens (~95%) into feces (ibid.). Similarly, both the Sumatran rhinoceros, *Dicerorhinus sumatrensis* (see Heistermann et al. 1998), and African elephant, *Loxodonta africana* (see Wasser et al. 1996), excrete estrogens primarily into urine and progestagens predominantly into feces.

One of the main advantages of fecal analysis is the relative ease of collection of fecal samples from animals living in group situations or under natural conditions. Generally, it is not necessary to separate animals; thus, caretakers can avoid physical disruption of the group and maintain social context. In most situations, fecal sampling also provides the only feasible option for longitudinal studies in the wild (although there are examples where urine collection has been successful), thus explaining the increasing interest in fecal assay methodologies over the last 5 to 10 years.

Unlike urinary analysis, where direct (nonextraction) assays are the norm, measurement of steroids in feces requires an extraction step before assay. There are numerous described extraction procedures, the choice being partially dependent on the hormone being measured, the method of sample storage used, or personal preference (Heistermann, Tari, and Hodges 1993; Shideler et al. 1994; Schwarzenberger et al. 1996b; Palme and Möstl 1997; Whitten et al. 1998; Moreira et al. 2001). In general, extraction with organic solvents (ethanol, methanol) containing 5 to 20% water results in good steroid recoveries. In most species, steroids are excreted in the free (unconjugated) form into the feces. Species of some taxa, however, such as felids (Brown et al. 1994b, 1995) or some callitrichids (Ziegler et al. 1996), do excrete hormones into feces predominantly as conjugates, which often can be measured using antibodies that directly quantify conjugates or cross-react with them. However, there are situations where hydrolysis following fecal extraction can improve results (ibid.).

Fecal samples vary considerably in consistency and water content, and this needs to be controlled, generally by expressing hormone levels per unit weight (gram) using either the wet weight of the portion of fresh material to be extracted or the weight of the dry powder after lyophylization (e.g. Hodges and Heistermann 2003). Gut passage time adds to clearance rate, which markedly increases the lag time (delay between hormone secretion and excretion) when comparing fecal and urinary measurements. Time lags associated with fecal analysis are longer and more variable (e.g. 6 to >48 hours), both between and within species. Additionally, a variety of factors, including diet, health status, and stress level, can affect gut passage times. Radiometabolism studies indicate that in most large-bodied mammals for which data are available, steroids are excreted in feces 24 to 48 hours after their appearance in circulation (see Schwarzenberger at al. 1996a for review), although shorter times of <20 hours have been described for sheep (Palme et al. 1996), the domestic cat (Brown et al. 1994a), and the small-bodied common marmoset, *Callithrix jacchus* (4 to 8 hours: Bahr et al. 2000; Möhle et al. 2002). Knowledge of the time lag for the hormone and species in question is therefore important in order to interpret correctly the changes in fecal hormone levels in relation to physiological events.

An additional biological validation step is generally advisable in order to demonstrate that excreted hormonal measures (particularly those in feces) accurately reflect physiological events. For assessing ovarian activity, it is useful to demonstrate a predicted rise and fall in metabolite concentrations coincident with behavioral measures of estrus, time of ovulation, or onset of pregnancy. Alternatively, a cause-and-effect relationship between physiological changes (and resultant secretory events) and excretion of hormone metabolites can be demonstrated by administration of pharmacological agents known to stimulate hormonal production (e.g. gonadotrophin-releasing hormone [GnRH] or adrenocorticotrophic hormone [ACTH]).

NONINVASIVE REPRODUCTIVE ASSESSMENT IN FEMALES

For many years, particularly in the 1980s and early 1990s, urinary hormone analysis was the predominant method for monitoring reproductive function in exotic mammals. The method was applied extensively across all major mammalian taxonomic groups and, apart from its immediate practical value in the zoo-management context, yielded a tremendous amount of basic information on comparative aspects of female reproductive cycles (see table 33.1 for examples).

Although urinary hormone monitoring is quick and inexpensive, urine samples can be difficult to collect. Due to the relative ease of collection of fecal material, zoo professionals now prefer analyses of estrogen and progestagen metabolites excreted in feces to assess female reproductive function in most mammalian taxa (table 33.2), even though there are certain disadvantages in terms of increased labor and cost of processing samples.

Tables 33.1 and 33.2 mainly summarize studies carried out in the captive environment (with the exception of pri-

TABLE 33.1. Selected studies in which urinary hormone analysis has yielded information on endocrine profiles in exotic mammals helpful in monitoring ovarian function and pregnancy

Species	Ovarian cycle/ovulation	Pregnancy
Primates		
Lemuridae		
Red-bellied lemur, *Eulemur rubriventer*		Gerber, Moisson, and Heistermann 2004
Blue-eyed black lemur, *Eulemur flavifrons*		Gerber, Moisson, and Heistermann 2004
Northern bamboo lemur, *Hapalemur occidentalis*		Gerber, Moisson, and Heistermann 2004
Callitrichidae		
Common marmoset, *Callithrix jacchus*	Nivergelt and Pryce 1996	Nivergelt and Pryce 1996
Wied's black-tufted-ear marmoset, *Callithrix kuhlii*	French et al. 1996	French et al. 1996
Pygmy marmoset, *Cebuella pygmaea*	Carlson, Ziegler, and Snowdon 1997	
Saddle-back tamarin, *Saguinus fuscicollis*	Heistermann and Hodges 1995	Heistermann and Hodges 1995
Geoffroy's tamarin, *Saguinus geoffroyi*	Kuhar et al. 2003	Kuhar et al. 2003
Golden lion tamarin, *Leontopithecus rosalia*	Monfort, Bush, and Wildt 1996	
Golden-headed lion tamarin, *Leontopithecus chrysomelas*	De Vleeschouwer, Heistermann, and Van Elsacker 2000; French et al. 2002	
Goeldi's monkey, *Callimico goeldii*	Pryce, Schwarzenberger, and Doebeli 1994	Jurke et al. 1994
Cebidae		
Capuchin monkey, *Cebus apella*	Carosi, Heistermann, and Visalberghi 1999	
Pitheciidae		
White-faced saki, *Pithecia pithecia*	Shideler et al. 1994; Savage et al. 1995	Shideler et al. 1994; Savage et al. 1995
Titi monkey, *Callicebus moloch*	Valleggia et al. 1999	Valleggia et al. 1999
Atelidae		
Muriqui, *Brachyteles arachnoides*	Ziegler et al. 1997	
Red howler monkey, *Alouatta seniculus*	Herrick et al. 2000	Herrick et al. 2000
Black-handed spider monkey, *Ateles geoffroyi*	Campbell et al. 2001	Campbell et al. 2001
Cercopithecinae		
Tonkean macaque, *Macaca tonkeana*	Thierry et al. 1996; Aujard et al. 1998	Thierry et al. 1996
Japanese macaque, *Macaca fuscata*	Fujita et al. 2001	
Rhesus monkey, *Macaca mulatta*	Gilardi et al. 1997	
Long-tailed macaque, *Macaca fascicularis*	Shideler et al. 1993a; Shimizu et al. 2003a, b	Shideler et al. 1993a
Baboon, *Papio ssp.*		French et al. 2004
Owl-faced guenon, *Cercopithecus hamlyni*	Ialeggio et al. 1997	
Colobinae		
Hanuman langur, *Semnopithecus entellus*	Heistermann, Finke, and Hodges 1995	
Yunnan snub-nosed monkey, *Rhinopithecus bieti*	He et al. 2001	He et al. 2001
Black and white colobus, *Colobus guereza*	Harris and Monfort 2003	
Hylobatidae		
White-handed gibbon, *Hylobates lar*	Nadler, Dahl, and Collins 1993	

(*continued*)

TABLE 33.1. continued

Species	Ovarian cycle/ovulation	Pregnancy
Hominidae		
Common chimpanzee, *Pan troglodytes*	Deschner et al. 2003; Shimizu et al. 2003a	Shimizu et al. 2003a
Bonobo, *Pan paniscus*	Heistermann, Palme, and Ganswindt 1996; Jurke et al. 2000	Heistermann, Palme, and Ganswindt 1996
Lowland gorilla, *Gorilla gorilla*	Bellem, Monfort, and Goodrowe 1995	Bellem, Monfort, and Goodrowe 1995
Pongidae		
Orang utan, *Pongo pygmaeus*	Asa et al. 1994; Shimizu et al. 2003b	
Perissodactyla		
Rhinocerotidae		
White rhinoceros, *Ceratotherium simum*	Hindle, Möstl, and Hodges 1992	
Black rhinoceros, *Diceros bicornis*	Hindle, Möstl, and Hodges 1992	
Indian rhinoceros, *Rhinoceros unicornis*	Stoops, Pairan, and Roth 2004	
Sumatran rhinoceros, *Dicerorhinus sumatrensis*	Heistermann et al. 1998	
Equidae		
Grevy's zebra, *Equus grevyi*	Asa et al. 2001	Ramsay et al. 1994
Grant's zebra, *Equus burchelli*		Ramsay et al. 1994
Hartman's mountain zebra, *Equus zebra*		Ramsay et al. 1994
Przewalski's horse, *Equus przewalskii*		Ramsay et al. 1994
Tapiridae		
Tapir, *Tapirus spp.*		Ramsay et al. 1994
Proboscidea		
African elephant, *Loxodonta africana*	Heistermann, Trohorsch, and Hodges 1997; Fiess, Heistermann, and Hodges 1999	Fiess, Heistermann, and Hodges 1999
Asian elephant, *Elephas maximus*	Niemüller, Shaw, and Hodges 1993; Czekala et al. 2003b	Niemüller, Shaw, and Hodges 1993; Brown and Lehnhardt 1995
Artiodactyla		
Bovidae		
Bison, *Bison bison*	Kirkpatrick, Bancroft, and Kincy 1992	Kirkpatrick, Bancroft, and Kincy 1992
Dall's sheep, *Ovis dalli*	Goodrowe et al. 1996	Goodrowe et al. 1996
Dik-dik, *Madoqua guentheri*	Robeck et al. 1997	Robeck et al. 1997
Camelidae		
Llama, *Lama glama*	Bravo et al. 1993	Bravo et al. 1996
Alpaca, *Lama pacos*	Bravo et al. 1993	Bravo et al. 1996
Cervidae		
Eld's deer, *Rucervus eldii*	Monfort, Arthur, and Wildt 1990; Hosack et al. 1997	Monfort, Arthur, and Wildt 1990
Moose, *Alces alces*	Monfort, Brown, and Wildt 1993	Monfort, Brown, and Wildt 1993
Père David's deer, *Elaphurus davidianus*	Monfort, Martinet, and Wildt 1991	Monfort, Martinet, and Wildt 1991
Giraffidae		
Okapi, *Okapia johnstoni*	Schwarzenberger et al. 1999	Schwarzenberger et al. 1999
Edentata		
Myrmecophagidae		
Tamandua, *Tamandua tetradactyla*	Hay et al. 2000	
Carnivora		
Canidae		
African wild dog, *Lycaon pictus*	Monfort et al. 1997	Monfort et al. 1997
Herpestidae		
Mongoose, *Helogale parvula*	Creel et al. 1992, 1995	Creel et al. 1992, 1995
Ursidae		
Giant panda, *Ailuropoda melanoleuca*	Monfort et al. 1989; Czekala et al. 2003a; Steinman et al. 2006	Monfort et al. 1989; Steinman et al. 2006
Cetacea		
Delphinidae		
Bottle-nose dolphin, *Tursiops truncatus*	Robeck et al. 2005b	
Killer whale, *Orcinus orca*	Robeck et al. 2004	
Rodentia		
Mouse, *Mus musculus*	deCatanzaro et al. 2003, 2004; Muir et al. 2001	deCatanzaro et al. 2003, 2004

TABLE 33.2. Selected studies in which fecal hormone analysis has yielded information on endocrine profiles in exotic mammals helpful in monitoring ovarian function and pregnancy

Species	Ovarian cycle/ovulation	Pregnancy
Primates		
Lemuridae		
Mongoose lemur, *Eulemur mongoz*	Curtis et al. 2000	Curtis et al. 2000
Red-fronted lemur, *Eulemur rufus*	Ostner and Heistermann 2003	Ostner and Heistermann 2003
Indriidae		
Verreaux's sifaka, *Propithecus verreauxi*	Brockman et al. 1995; Brockman and Whitten 1996	Brockman et al. 1995; Brockman and Whitten 1996
Lorisidae		
Pygmy loris, *Nycticebus pygmaeus*	Jurke, Czekala, and Fitch-Snyder 1997	Jurke, Czekala, and Fitch-Snyder 1997
Callithrichidae		
Common marmoset, *Callithrix jacchus*	Ziegler et al. 1996	
Cotton-top tamarin, *Saguinus oedipus*	Ziegler et al. 1996	
Goeldi's monkey, *Callimico goeldii*	Pryce, Schwarzenberger, and Doebeli 1994	
Golden lion tamarin, *Leontopithecus rosalia*	French et al. 2003	French et al. 2003
Cebidae		
Capuchin monkey, *Cebus apella*	Carosi, Heistermann, and Visalberghi 1999	
Squirrel monkey, *Saimiri sciureus*	Moorman et al. 2002	Moorman et al. 2002
Pitheciidae		
White-faced saki, *Pithecia pithecia*	Shideler et al. 1994	Shideler et al. 1994
Atelidae		
Black-handed spider monkey, *Ateles geoffroyi*	Campbell et al. 2001; Campbell 2004	Campbell et al. 2001
Muriqui, *Brachyteles arachnoides*	Ziegler et al. 1997; Strier and Ziegler 1997	Strier and Ziegler 1997
Cercopithecinae		
Long-tailed macaque, *Macaca fascicularis*	Shideler et al. 1993b; Engelhardt et al. 2004	Shideler et al. 1993b
Japanese macaque, *Macaca fuscata*	Fujita et al. 2001	
Lion-tailed macaque, *Macaca silenus*	Heistermann et al. 2001	
Sooty mangabey, *Cercocebus atys atys*	Whitten and Russell 1996	
Yellow baboon, *Papio cynocephalus*		Wasser 1996
Colobinae		
Hanuman langur, *Semnopithecus entellus*	Heistermann, Finke, and Hodges 1995; Ziegler et al. 2000b	Ziegler et al. 2000b
Douc langur, *Pygathrix nemaeus*	Heistermann, Ademmer, and Kaumanns 2004	
Hylobatidae		
White-handed gibbon, *Hylobates lar*	Barelli et al., 2007	
Hominidae		
Common chimpanzee, *Pan troglodytes*	Emery and Whitten 2003	
Bonobo, *Pan paniscus*	Heistermann et al. 1996; Jurke et al. 2000	Heistermann et al. 1996
Lowland gorilla, *Gorilla gorilla*	Miyamoto et al. 2001; Atsalis et al. 2004	
Perissodactyla		
Rhinocerotidae		
White rhinoceros, *Ceratotherium simum*	Schwarzenberger et al. 1998b; Brown et al. 2001	Patton et al. 1999
Black rhinoceros, *Diceros bicornis*	Berkeley et al. 1997; Brown et al. 2001	Schwarzenberger et al. 1996b; Brown et al. 2001
Indian rhinoceros, *Rhinoceros unicornis*	Schwarzenberger et al. 2000	Schwarzenberger et al. 2000
Sumatran rhinoceros, *Dicerorhinus sumatrensis*	Heistermann et al. 1998; Roth et al. 2001	Roth et al. 2001
Equidae		
Grevy's zebra, *Equus grevyi*	Asa et al. 2001	Asa et al. 2001
Chapman's zebra, *Equus burchelli antiquorum*		Skolimowska et al. 2004b
Przewalski mare, *Equus przewalskii*	Scheibe et al. 1999	
Domestic horse, *Equus caballus*	Barkhuff et al. 1993	Palme et al. 2001; Skolimowska, Janowski, and Golonka 2004a
Proboscidea		
African elephant, *Loxodonta africana*	Wasser et al. 1996; Fiess et al. 1999	Fiess, Heistermann, and Hodges 1999
Artiodactyla		
Bovidae		
Bison, *Bison bison*	Kirkpatrick, Bancroft, and Kincy 1992; Matsuda et al. 1996	Kirkpatrick, Bancroft, and Kincy 1992
Bighorn sheep, *Ovis canadensis*		Borjesson et al. 1996; Schoenecker, Lyda, and Kirkpatrick 2004

(*continued*)

TABLE 33.2. continued

Species	Ovarian cycle/ovulation	Pregnancy
Mhorr gazelle, *Nanger dama mhorr*	Pickard et al. 2001	Pickard et al. 2001
Sable antelope, *Hippotragus niger*	Thompson, Mashburn, and Monfort 1998; Thompson and Monfort 1999	
Scimitar-horned oryx, *Oryx dammah*	Morrow and Monfort 1998; Morrow et al. 1999; Shaw et al. 1995	
Camelidae		
Vicuña, *Vicugna vicugna*	Schwarzenberger, Speckbacher, and Bamberg 1995	
Cervidae		
Moose, *Alces alces*	Schwartz et al. 1995	Schwartz et al. 1995
Père David's deer, *Elaphurus davidianus*	Li et al. 2001	Li et al. 2001
Pudu, *Pudu puda*	Blanvillain et al. 1997	
Sika deer, *Cervus nippon*	Hamasaki et al. 2001	Hamasaki et al. 2001
Giraffidae		
Giraffe, *Giraffa camelopardalis*	del Castillo et al. 2005	del Castillo et al. 2005; Dumonceaux, Bauman, and Camilo 2006
Okapi, *Okapia johnstoni*	Schwarzenberger et al. 1993, 1999	Schwarzenberger et al. 1993, 1999
Hippopotamidae		
Hippopotamus, *Hippopotamus amphibius*	Graham et al. 2002	Graham et al. 2002
Edentata		
Myrmecophagidae		
Giant anteater, *Myrmecophaga tridactyla*	Patzl et al. 1998	Patzl et al. 1998
Carnivora		
Canidae		
Blue fox, *Vulpes lagopus*	Sanson, Brown, and Farstad 2005	Sanson, Brown, and Farstad 2005
Fennec fox, *Vulpes zerda*	Valdespino, Asa, and Bauman 2002	Valdespino, Asa, and Bauman 2002
Maned wolf, *Chrysocyon brachyurus*	Velloso et al. 1998	Velloso et al. 1998
Red wolf, *Canis rufus*	Walker, Waddell, and Goodrowe 2002	Walker, Waddell, and Goodrowe 2002
African wild dog, *Lycaon pictus*	Monfort et al. 1997	Monfort et al. 1997
Felidae		
Cheetah, *Acinonyx jubatus*	Czekala et al. 1994; Brown et al. 1996b	Czekala et al. 1994; Brown et al. 1996b
Clouded leopard, *Neofelis nebulosa*	Brown et al. 1995b	Brown et al. 1995b
Ocelot, *Leopardus pardalis*	Moreira et al. 2001	
Pallas' cat, *Felis manul*	Brown et al. 2002	Brown et al. 2002
Tiger, *Panthera tigris*	Graham et al. 1995	Graham et al. 1995
Mustelidae		
Black-footed ferret, *Mustela nigripes*	Brown 1997; Young, Brown, and Goodrowe 2001	Brown 1997; Young, Brown, and Goodrowe 2001
Otter, *Enhydra lutris*	Larson, Casson, and Wasser 2003; Da Silva and Larson 2005	Larson, Casson, and Wasser 2003; Da Silva and Larson 2005
Herpestidae		
Meerkat, *Suricata suricatta*	Moss, Clutton-Brock, and Monfort 2001	Moss, Clutton-Brock, and Monfort 2001
Ursidae		
Sun bear, *Helarctos malayanus*	Schwarzenberger et al. 2004	Schwarzenberger et al. 2004
Hokkaido brown bear, *Ursus arctos lasiotus*	Ishikawa et al. 2002	
Giant panda, *Ailuropoda melanoleuca*	Steinman et al. 2006	Steinman et al. 2006
Ailuridae		
Red panda, *Ailurus fulgens*	MacDonald, Northrop, and Czekala 2005	Spanner, Stone, and Schultz 1997; MacDonald, Northrop, and Czekala 2005
Rodentia		
Erethizontidae		
Porcupine, *Erethizon dorsata*	Bodgan and Monfort 2001	Bodgan and Monfort 2001
Muridae		
Mouse, *Mus musculus*	deCatanzaro et al. 2004; Muir et al. 2001	
Cetacea		
Right whale, *Eubalaena glacialis*		Rolland et al. 2005

mates), but both urine (under certain circumstances) and feces can generate much useful data on hormonal status of animals in the wild; e.g. urinary hormone analysis was useful for monitoring female reproductive status in free-ranging vervet monkeys, *Chlorocebus pygerythrus* (see Andelman et al. 1985), and chimpanzees, *Pan troglodytes* (see Deschner et al. 2003). Fecal hormone changes during the estrous cycle and pregnancy have been measured in free-ranging African wild dogs, *Lycaon pictus* (see Creel et al. 1997), meerkat, *Suricata suricatta* (see Moss et al. 2001), bison, *Bison bison* (Kirkpatrick et al. 2001), and black rhinoceros, *Diceros bicornis* (see Garnier et al. 1998). Fecal steroid measures have provided single-sample pregnancy diagnosis in a variety of ungulates, such as bighorn sheep, *Ovis canadensis* (see Schoenecker, Lyda, and Kirkpatrick 2004), elk, *Cervus elephas* (see Stoops et al. 1999; Garrott et al. 1998), and moose, *Alces alces* (see Berger et al. 1999). Monfort (2003) provides a review of urinary and fecal studies on free-ranging wildlife.

NONINVASIVE REPRODUCTIVE ASSESSMENT IN MALES

Determining testicular endocrine activity in male mammals is an important step in the assessment of male reproductive function and fertility (see Spindler and Wildt, chap. 32, this volume). The secretion of testosterone (the major androgen secreted by the testis) is highly pulsatile; thus, circulating testosterone concentrations can vary markedly within hours or even minutes, making interpretation of endocrine condition based on single (or infrequent) samples difficult. The noninvasive approach, based on the analysis of the breakdown products of testosterone excreted in urine and feces, is therefore useful, not only in providing a more integrated picture (measures represent cumulative secretion over a number of hours), but also when longitudinal information on male testicular endocrine activity is desirable. To date, however, there is limited information on the metabolism of testosterone, its route of excretion, and the nature of the metabolites excreted (e.g. cats: Brown, Terio, and Graham 1996; primates: Möhle et al. 2002; Hagey and Czekala 2003; African elephant: Ganswindt et al. 2002, 2003). These studies have shown that testosterone metabolism is highly complex and often species specific, resulting in excretion of a number of metabolites, with native testosterone usually being quantitatively of minor importance (and virtually absent in feces of several species). There can even be considerable variation in excreted androgen steroid metabolite forms among closely related species (e.g. Hagey and Czekala 2003); thus, validation of any urinary and fecal androgen measurement as an index of testicular activity is essential before being used to assess male reproductive condition. In this respect, comeasurement of metabolites derived from androgens of extratesticular (e.g. adrenal) origin, such as dehydroepiandrosterone (DHEA), is a potential problem when using fecal measurements for assessing male gonadal status in primates (Möhle et al. 2002).

Although still relatively limited (in comparison to studies in females), the use of noninvasive endocrine methodologies for assessing male gonadal function has shown a marked increase over the last few years (table 33.3), largely due to improvements in the reliability of the laboratory methods. Many of the studies of primate species listed in table 33.3 were carried out in the wild, while most nonprimate studies were of captive animals. The vast majority of nonprimate studies used fecal material to measure androgens. It is not clear why there is such a paucity of urinary data in nonprimate species, but for felids it is known that nearly all androgen metabolites are excreted in feces (Brown, Terio, and Graham 1996).

NONINVASIVE ASSESSMENT OF STRESS

Since most (although not all) types of stressors induce an increased release of the stress hormones cortisol or corticosterone from the adrenal gland, glucocorticoid output is commonly used as a physiological (endocrine) measure of stress. Although blood glucocorticoid concentrations are an accepted indicator, the invasive nature of blood sampling (itself capable of eliciting a stress response) limits the application of this approach in wild animals.

Comparative information on the metabolism and route of excretion of glucocorticoids is limited (see Palme et al. 2005 for review). Nevertheless, the measurement of native cortisol excreted into urine has been used to monitor stress physiology in a variety of captive mammals (see table 33.4). Measurement of glucocorticoid metabolites in feces, however, is less straightforward. Although the use of this approach has increased recently (table 33.4), there are a number of confounding factors relating to both methodology and interpretation of data that continue to limit its utility. For example, since native glucocorticoids seem to be virtually absent from feces in most species, the use of standard cortisol or corticosterone assays is generally not appropriate for measuring fecal glucocorticoid output (although they have been successfully used in some species; see Wasser et al. 2000; Heistermann et al. 2006). Group-specific assays, capable of measuring a range of fecal glucocorticoid metabolites, are generally more suitable, in that they are more likely to detect at least some of the more abundant metabolites present and also have greater potential for cross-species application (e.g. Palme et al. 2005; Heistermann et al. 2006). However, when using these assays, it is difficult to know for any given species which and how many metabolites are being recognized and what their relative abundance is. Also, it has been shown that the group-specific assays have the potential to cross-react with structurally related testosterone metabolites (domestic dog: Schatz and Palme 2001; African elephant: Ganswindt et al. 2003; chimpanzee: Heistermann, Palme, and Ganswindt 2006), which can confound the actual glucocorticoid measurement and generate misleading results (e.g. measurement of glucocorticoid output during musth in African elephants: Ganswindt et al. 2003). Furthermore, a host of biological factors, such as seasonal changes in glucocorticoid excretion, reproductive and body condition, sex, age, social status, and diet, can all influence glucocorticoid levels, requiring the exercise of additional caution when interpreting fecal glucocorticoid measurements for the purposes of assessing stress (von der Ohe and Servheen 2002; Touma and Palme 2005; Millspaugh and Washburn 2003).

Additionally, not every type of stressor is mediated via increased activity of the hypothalamo-pituitary-adrenal (HPA) axis, which would result in elevations in glucocorticoid output. Negative findings with respect to glucocorticoid assess-

TABLE 33.3. Selected studies in which urinary and fecal hormone analysis has yielded endocrine information in exotic mammals helpful in the assessment of male reproductive activity

Species	Urinary analysis	Fecal analysis
Primates		
Indriidae		
Verreaux´s sifaka, *Propithecus verreauxi*		Brockman et al. 1998; Kraus, Heistermann, and Kappeler 1999
Lemuridae		
Red-fronted lemur, *Eulemur rufus*		Ostner, Kappeler, and Heistermann 2002
Ring-tailed lemur, *Lemur catta*		Cavigelli and Pereira 2000; Von Engelhardt, Kappeler, and Heistermann 2000; Gould and Ziegler 2007
Callithrichidae		
Common marmoset, *Callithrix jacchus*	Möhle et al. 2002	Möhle et al. 2002; Castro and Sousa 2005
Wied's black-tufted-ear marmoset, *Callithrix kuhlii*	Nunes et al. 2002; Ross, French, and Patera 2004	
Golden lion tamarin, *Leontopithecus rosalia*		Bales et al. 2006
Cotton-top tamarin, *Saguinus oedipus*	Ziegler et al. 2000c	
Cebidae		
Capuchin monkey, *Cebus nigritus*		Lynch, Ziegler, and Strier 2002
Atelidae		
Black howler monkey, *Alouatta caraya*		Morland et al. 2001
Mantled howler monkey, *Alouatta palliata*		Cristóbal-Azkarate et al. 2006
Cercopithecinae		
Japanese macaque, *Macaca fuscata*		Barrett et al. 2002
Long-tailed macaque, *Macaca fascicularis*	Möhle et al. 2002	Möhle et al. 2002
Chacma baboon, *Papio ursinus*		Beehner et al. 2006; Bergman et al. 2006
Pongidae		
Orangutan, *Pongo pygmaeus*	Maggioncalda, Sapolsky, and Czekala 1999	
Hominidae		
Common chimpanzee, *Pan troglodytes*	Möhle et al. 2002; Muller and Wrangham 2004	Möhle et al. 2002
Bonobo, *Pan paniscus*	Sannen et al. 2003; Dittami et al. 2007	
Lowland gorilla, *Gorilla gorilla*	Stoinski et al. 2002	
Mountain gorilla, *Gorilla beringei*	Robbins and Czekala 1997	
Perissodactyla		
Rhinocerotidae		
White rhinoceros, *Ceratotherium simum*		Brown et al. 2001; Kretzschmar, Ganslosser, and Dehnhard 2004
Equidae		
Grevy's zebra, *Equus grevyi*	Chaudhuri and Ginsberg 1990	
Plains zebra, *Equus burchelli*	Chaudhuri and Ginsberg 1990	
Proboscidea		
African elephant, *Loxodonta africana*	Ganswindt et al. 2002	Ganswindt et al. 2002; Ganswindt, Heistermann, and Hodges 2005
Artiodactyla		
Bovidae		
Bighorn sheep, *Ovis canadensis*		Pelletier, Bauman, and Festa-Bianchet 2003
Bison, *Bison bison*		Mooring et al. 2004
Cervidae		
Eld's deer, *Rucervus eldii*	Monfort et al. 1995	
Fringe-eared oryx, *Oryx beisa callotis*		Patton et al. 2001
Pampas deer, *Ozotoceros bezoarticus*		Pereira, Duarte, and Negrão 2005
Père David's deer, *Elaphurus davidianus*		Li et al. 2001
Sika deer, *Cervus nippon*		Hamasaki et al. 2001
Carnivora		
Canidae		
Maned wolf, *Chrysocyon brachyurus*		Velloso et al. 1998
Red wolf, *Canis rufus*		Walker, Waddell, and Goodrowe 2002
African wild dog, *Lycaon pictus*		Monfort et al. 1997

(*continued*)

TABLE 33.3. continued

Species	Urinary analysis	Fecal analysis
Felidae		
Jaguar, *Panthera onca*		Morato et al. 2004a, 2004b
Ocelot, *Leopardus pardalis*		Morais et al. 2002
Pallas' cat, *Felis manul*		Brown, Terio, and Graham 1996a, 2002
Eurasian lynx, *Lynx lynx*		Jewgenow et al. 2006
Iberian lynx, *Lynx pardinus*		Jewgenow et al. 2006
Hyenidae		
Spotted hyena, *Crocuta crocuta*		Dloniak et al. 2004
Mustelidae		
Black-footed ferret, *Mustela nigripes*		
Herpestidae		
Meerkat, *Suricata suricatta*		Moss, Clutton-Brock, and Monfort 2001
Ursidae		
Hokkaido brown bear, *Ursus arctos lasiotus*		Ishikawa et al. 2002
Malayan sun bear, *Helarctos malayanus*		Hesterman, Wasser, and Cochrem 2005
Ailuridae		
Red panda, *Ailurus fulgens*		Spanner et al. 1997
Rodentia		
Chinchillidae		
Chinchilla, *Chinchilla lanigera*	Busso et al. 2005	Busso et al. 2005
Muridae		
Blind mole rat, *Spalax ehrenbergi*	Gotterich et al. 2000	
Mouse, *Mus musculus*	Muir et al. 2001	Muir et al. 2001
Mongolian gerbil, *Meriones unguiculatus*		Yamaguchi et al. 2005

TABLE 33.4. Selected studies in which urinary and fecal hormone analysis has yielded endocrine information in exotic mammals helpful in the assessment of adrenal activity

Species	Urinary analysis	Fecal analysis
Primates		
Lemuridae		
Ring-tailed lemur, *Lemur catta*		Cavigelli 1999
Red-fronted lemur, *Eulemur rufus*		Ostner, Kappeler, and Heistermann 2007
Indriidae		
Verreaux's sifaka, *Propithecus verreauxi*		Fichtel et al. 2007
Callitrichidae		
Common marmoset, *Callithrix jacchus*	Torii et al. 1998; Bahr et al. 2000	Heistermann, Palme, and Ganswindt 2006
Wied's black-tufted-ear marmoset, *Callithrix kuhlii*	Smith and French 1997	
Bearded emperor tamarin, *Saguinus imperator subgrisescens*	McCallister, Smith, and Elwood 2004	
Golden lion tamarin, *Leontopithecus rosalia*		Bales et al. 2006
Cotton-top tamarin, *Saguinus oedipus*	Ziegler, Scheffler, and Snowdon 1995	
Goeldi's monkey, *Callimico goeldii*	Jurke et al. 1995; Dettling et al. 1998	
Cebidae		
Squirrel monkey, *Saimiri sciureus*	Soltis, Wegner, and Newman 2003	
Capuchin monkey, *Cebus apella*		Boinski et al. 1999; Lynch, Ziegler, and Strier 2002
Atelidae		
Spider monkey, *Ateles fusciceps rufiventris*	Davis, Schaffner, and Smith 2005	
Cercopithecinae		
Long-tailed macaque, *Macaca fascicularis*	Crockett et al. 1993	Wasser et al. 2000; Heistermann, Palme, and Ganswindt 2006
Pig-tailed macaque, *Macaca nemestrina*	Crockett, Shimoji, and Bowden 2000	
Lion-tailed macaque, *Macaca silenus*	Clarke, Czekala, and Lindburg 1995	
Barbary macaque, *Macaca sylvanus*		Heistermann et al. 2006
Baboon, *Papio* spp.	French et al. 2004	Wasser et al. 2000; Beehner and Whitten 2004
Douc langur, *Pygathrix nemaeus*		Heistermann, Ademmer, and Kaumanns 2004

(*continued*)

TABLE 33.4. continued

Species	Urinary analysis	Fecal analysis
Pongidae		
Orang utan, *Pongo pygmaeus*	Maggioncalda, Sapolsky, and Czekala 1999	
Hominidae		
Common chimpanzee, *Pan troglodytes*	Bahr et al. 2000; Muller and Wrangham 2004	Whitten et al. 1998; Heistermann, Palme, and Ganswindt 2006; Reimers, Schwarzenberger, and Preuschoft 2007
Lowland gorilla, *Gorilla gorilla*	Bahr et al. 1998; Stoinski et al. 2002	Heistermann, Palme, and Ganswindt 2006
Mountain gorilla, *Gorilla beringei*	Robbins and Czekala 1997	
Perissodactyla		
Rhinocerotidae		
White rhinoceros, *Ceratotherium simum*		Wasser et al. 2000; Turner, Tolson, and Hamad 2002
Black rhinoceros, *Diceros bicornis*		Brown et al. 2001; Turner, Tolson, and Hamad 2002
Equidae		
Domestic horse, *Equus caballus*		Möstl et al. 1999; Merl et al. 2000
Proboscidea		
African elephant, *Loxodonta africana*	Brown, Wemmer, and Lehnhardt 1995a; Ganswindt et al. 2003	Ganswindt et al. 2003; Ganswindt, Heistermann, and Hodges 2005
Asian elephant, *Elephas maximus*	Brown, Wemmer, and Lehnhardt 1995a	
Artiodactyla		
Bovidae		
Gerenuk, *Litocranius walleri*		Wasser et al. 2000
Scimitar-horned oryx, *Oryx dammah*		Wasser et al. 2000
Cervidae		
Eld's deer, *Rucervus eldii*	Monfort, Brown, and Wildt 1993	
Elk, *Cervus elaphus*		Millspaugh et al. 2001; Creel et al. 2002
Mule deer, *Odocoileus hemionus*	Saltz and White 1991	
Red deer, *Cervus elaphus*		Huber, Palme, and Arnold 2003
Roe deer, *Capreolus capreolus*		Dehnhard et al. 2001
Giraffidae		
Okapi, *Okapia johnstoni*		Schwarzenberger et al. 1998a
Carnivora		
Canidae		
Wild dog, *Lycaon pictus*		Monfort et al. 1998
Wolf, *Canis lupus*		Creel et al. 2002; Sands and Creel 2004
Felidae		
Cheetah, *Acinonyx jubatus*		Terio, Citino, and Brown 1999; Jurke et al. 1997
Clouded leopard, *Neofelis nebulosa*		Wielebnowski et al. 2002; Young et al. 2004
Jaguar, *Panthera onca*		Morato et al. 2004a
Leopard cat, *Felis bengalensis*	Carlstead et al. 1992; Carlstead, Brown, and Seidensticker 1993	
Herpestidae		
Mongoose, *Helogale parvula*	Creel et al. 1992; Creel, Creel, and Monfort 1996	
Hyenidae		
Spotted hyena, *Crocuta crocuta*		Goymann et al. 1999
Mustelidae		
Black-footed ferret, *Mustela nigripes*		Young, Brown, and Goodrowe 2001; Young et al. 2004
Domestic ferret, *Mustela putorius*	Schoemaker et al. 2004	
Ursidae		
Giant panda, *Ailuropoda melanoleuca*	Owen et al. 2004; 2005	
Grizzly bear, *Ursus arctos horribilis*		Hunt and Wasser 2003
Lagomorpha		
Leporidae		
European rabbit, *Oryctolagus cuniculus*		Cabezas et al. 2007
European hare, *Lepus europaeus*	Teskey-Gerstl et al. 2000	Teskey-Gerstl et al. 2000
Rodentia		
Chinchillidae		
Chinchilla, *Chinchilla lanigera*	Ponzio et al. 2004	Ponzio et al. 2004
Muridae		
Mouse, *Mus musculus*	Touma et al. 2003	Touma et al. 2003
Rat, *Rattus norvegicus*	Eriksson et al. 2004; Brennan et al. 2000	Eriksson et al. 2004; Cavigelli et al. 2005
Red-backed voles, *Myodes gapperi*		Harper and Austad 2000

ment (i.e. no elevation in glucocorticoid levels in response to stressful conditions) thus do not necessarily indicate that an animal is not under stress or not negatively affected by the situation under study. Thus, measurement of the pituitary hormone prolactin (measurable in urine but not feces) may provide useful complementary information on stress status in mammals. Although primarily involved in the initiation and maintenance of lactation in mammals, prolactin often increases in response to stress (e.g. Eberhart, Keverne, and Meller 1983; Maggioncalda et al. 2002).

Catecholamines are also released in response to environmental and psychosocial stress and are measurable in plasma and urine (Dantzer and Mormede 1983; Dimsdale and Ziegler 1991; Hjemdahl 1993; Hay et al. 2000). When samples are properly collected, analyzed, and interpreted, catecholamine data can provide valuable information on sympathoadrenal activity; however, analytical problems are common. Other methods of studying HPA function involve assessing changes in pituitary-adrenocortical reactivity by using adrenocorticotrophic hormone (ACTH) and corticotrophin releasing hormone (CRH) challenges and dexamethasone suppression tests (Hay et al. 2000). We do not know whether any of these techniques have been validated for wildlife species. However, given the growing concerns over maintaining animals in captivity, zoo professionals need more comprehensive protocols, involving a combination of behavioral as well as physiological measures, to evaluate stress objectively.

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34

Contraception as a Management Tool for Controlling Surplus Animals

Cheryl S. Asa and Ingrid J. Porton

INTRODUCTION

The idea of zoos serving as a collective ark to save endangered species has evolved over the past 10 years into a more holistic vision. The World Association of Zoos and Aquariums (WAZA) and regional zoo associations are moving toward a vision of zoos as institutions with the greatest capacity to integrate *in situ* and *ex situ* conservation and to become the public's most trusted and reliable voice for conservation. Maintaining captive populations as genetic reservoirs remains an objective for select taxa. However, the role of zoos in communicating conservation issues and ethics, leading or participating in conservation research, and raising funds for field conservation are equal, if not more important, objectives. Regardless of the long-term goal for maintaining a species in captivity, cooperative breeding programs are required for genetically, demographically, and behaviorally healthy populations to be sustained into the future.

Regionally managed breeding programs such as the Association of Zoos and Aquariums' Species Survival Plan (AZA SSP) and the European Association of Zoos and Aquaria's European Endangered Species Programme (EAZA EEP) originated in the early 1980s and proliferated in the 1990s (see Allard et al., chap. 20, this volume). The concept of AZA Taxon Advisory Groups (TAGs) grew out of the realization that further coordination of individual programs at a higher taxonomic level was required to balance thoughtfully the conservation objectives and the zoos' collective but limited resources. Years of experience with the intrinsic limitations of managing small populations have forced zoo professionals to confront the reality of finite enclosure space. Today, the most significant factor limiting the number of viable breeding programs that zoos can manage is the lack of sufficient appropriate housing. As such, each space becomes extremely valuable; unrestricted breeding of genetically overrepresented individuals or increasing the population of one species beyond that required for self-sustainability deprives underrepresented individuals and other species of captive habitat. Captive species are freed from most factors that regulate population growth in their wild counterparts; this inescapable reality places the burden and responsibility of population control directly onto the shoulders of animal managers and zoo administrators. How to control population growth is a matter that raises practical, philosophical, and ethical issues. The main options available to zoo managers are separation of the sexes, reversible contraception, permanent sterilization, euthanasia, or the transfer of surplus animals to facilities outside the managed breeding program. For reversible contraception to be a viable and realistic option, it is essential that information on contraceptive efficacy and safety is available to the zoo community.

SURVEY OF CONTRACEPTIVE METHODS CURRENTLY IN USE

Most contraceptive research and development have been for human or pet application or for wildlife or feral population management. In contrast, reproduction in captive animals has traditionally been viewed by zoo biologists as the ultimate indication of the health and well-being of the parents (Hediger 1964; Curtis 1982). Preventing reproduction was viewed as the antithesis of a breeding program. Indeed, the need to prevent reproduction was not viewed as a management tool but as a problem, the solution to which was more space (Perry, Bridgwater, and Horseman 1975) and less prohibitive legislation (Curtis 1982). The importance of reversible contraception was recognized and advocated by U. S. Seal in the mid-1970s as one method to aid in the establishment of genetically viable captive populations within the constraints of limited captive habitat (Seal et al. 1976). While the value of birth control gradually became more widely agreed on by zoo managers, information concerning contraceptive options for the diversity of mammals found in zoos was lacking (Knowles 1986). In response, the AZA formed the Contraceptive Task Force to compile and disseminate information on the efficacy and safety of contraceptive techniques and to coordinate and recommend research in alternative techniques (Wemmer 1989). The first contraception surveys, for primates and carnivores, were sent to just over 100 institutions. Because the work remained important, AZA elected to designate the task force as a standing committee, the Contraception Advisory Group (CAG), which in 1999 was folded into the AZA Wildlife Contraception Center. Today, a single survey that encompasses all mammal species is sent annually to over 500 institutions worldwide; results are entered into the Contraception Database, which in 2005 contained more than 20,000 contraceptive records for over 250 species.

The Contraception Database coupled with published research and results from ongoing contraceptive trials is used to formulate taxon-specific recommendations, which are reviewed and updated annually. Over the years, the recommendations have grown into a substantial document that is distributed to an ever-wider audience through the Internet. For the most up-to-date recommendations, readers should refer to the AZA Wildlife Contraception Center's Web site at www.stlzoo.org/contraception. For more thorough coverage of the issues surrounding contraceptive use, and how to choose and apply the available methods, see Asa and Porton (2005).

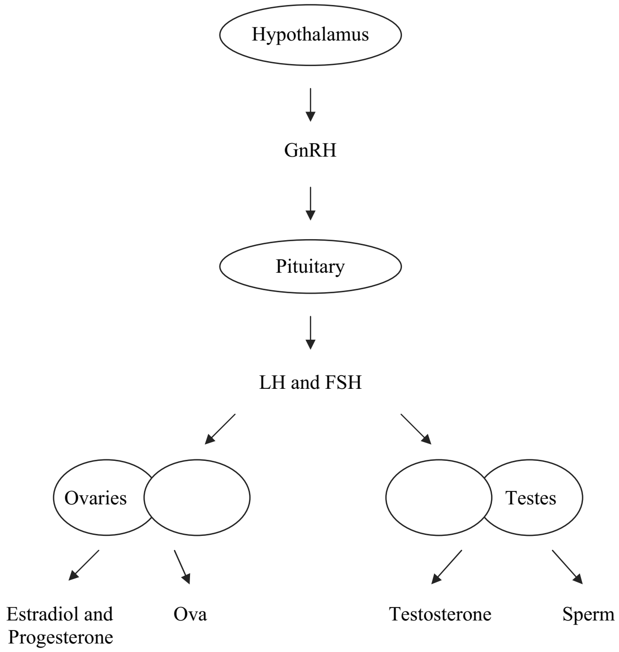

Fig. 34.1. Overview of the sources and targets of reproductive hormones.

METHODS FOR CONTROLLING REPRODUCTION

POTENTIAL TARGETS FOR CONTRACEPTIVE INTERVENTION IN FEMALES

The cascade of reproductive events begins, for both males and females, in the hypothalamus, with the production of gonadotropin releasing hormone (GnRH, also called luteinizing hormone–releasing hormone, LHRH). Release of GnRH stimulates release of both of the gonadotropins, follicle-stimulating hormone (FSH) and luteinizing hormone (LH), from the anterior pituitary. Although named for effects on the ovary, FSH and LH also support testosterone production and spermatogenesis in males (see fig. 34.1).

In the ovary, FSH stimulates follicles to secrete estradiol. Estradiol stimulates vulvar swelling, and changes in vaginal cytology and secretions and in the consistency of cervical mucus, as well as inducing estrous behavior. When estradiol reaches a critical threshold, it prompts a surge in LH, which is followed by ovulation. Following ovulation, follicular cells begin to secrete progesterone, which among other things readies the uterus for pregnancy. The ratio of estradiol to progesterone also influences embryo implantation and pregnancy maintenance.

These endocrine processes are controlled primarily by negative feedback from the gonadal hormones (testosterone, estradiol, and progesterone). Thus, suppression of GnRH or the gonadotropins can interfere with gonadal hormone production as well as with follicle growth, ovulation, and spermatogenesis. In the female, progesterone and estrogen dynamics are critical for sperm and egg transport, implantation of the embryo, and maintenance of pregnancy.

Following ovulation, the ova travel down the oviduct to its junction with the uterus. If copulation occurs, sperm must first penetrate the cervical canal, then travel through the uterus to this same junction and attempt penetration of the outer protective coating of the egg, the zona pellucida (ZP). If penetration is successful, fertilization occurs, followed after a species-specific period of time by egg transport into the uterus and implantation into the uterine endometrium.

Most of the currently available contraceptive methods interfere at some point in the sequence of hormone synthesis and release to control one or more reproductive events or processes (e.g. ovulation, spermatogenesis, sperm or egg transport, and implantation), while one, the ZP vaccine, directly impedes fertilization.

REVERSIBLE CONTRACEPTION FOR FEMALES

Steroid hormones: Progestins. Considerably more options are available for females than for males. Most are synthetic progestins (see table 34.1) in doses sufficient to prevent ovulation by negative feedback on LH, but they may also thicken cervical mucus so that sperm passage is impeded, interrupt sperm and ovum transport, and interfere with implantation (Brache, Faundes, and Johannson 1985; Diczfalusy 1968). Because higher doses are needed to block ovulation than to affect the other end points (Croxatto et al. 1982), ovulation may occur in adequately contracepted individuals (Brache et al. 1990). Progestins do not completely suppress follicle development, and the resulting estradiol can stimulate physical and behavioral signs of estrus, so those indications cannot be used to judge efficacy.

The contraceptive method most commonly used by zoos has been and remains the melengestrol acetate (MGA) implant introduced by U. S. Seal in the mid-1970s (Seal et al. 1976). Synthetic progestins such as MGA have proved effective in almost all mammalian species. MGA is also available incorporated in a commercial hoofstock diet (Mazuri, Purina Mills, LLC) and as a liquid to be added to food (Wildlife Phar-

TABLE 34.1. Currently available synthetic progestins used as contraceptives

Synthetic progestin	Product name	Manufacturer or supplier
Melengestrol acetate	MGA implants	Wildlife Pharmaceuticals
	MGA in feed (Mazuri)	Purina Mills LLC
	MGA 200 or 500 Pre-mix	Pfizer
	MGA liquid	Wildlife Pharmaceuticals
Megestrol acetate	Ovaban tablets	Schering-Plough
	Ovarid tablets (Europe)	Schering-Plough
Altrenogest	Regu-mate oral solution	Hoechst-Roussel
Medroxyprogesterone acetate	Depo-Provera injections	Pfizer
Proligestone	Delvosteron injections (Europe)	Intervet
Levonorgestrel	Norplant implants	Wyeth-Ayerst
	Jadelle implants (Europe)	
Etonogestrel	Implanon implants	Organon

maceuticals). A disadvantage of this approach is ensuring that the animal consumes the dose needed each day.

The second most commonly used contraceptive used by zoos, Depo-Provera (medroxyprogesterone acetate), is often preferred for seasonally breeding species (e.g. prosimians, bears, pinnipeds), for species in which anesthesia for implant insertion is problematic (e.g. giraffes, hippopotamuses), and as an immediately available interim contraceptive. Levonorgestrel (Norplant) is sometimes preferred, because the implants are considerably smaller than those containing MGA.

Yet another synthetic progestin, megestrol acetate (Ovaban, Ovarid, or Megace) in pill form, is sometimes used for bears or other carnivores. Equids are the exception to the species successfully treated with MGA. However, altrenogest (Regu-mate: Hoechst-Roussel), the only synthetic progestin effective in domestic horses for synchronizing estrus (Jöchle and Trigg 1994), should also be effective as a contraceptive, but at a higher dose.

Differences among various synthetic progestins in the degree of binding to glucocorticoid and androgen receptors (Duncan et al. 1964; Fekete and Szeberenyi 1965; Kloosterboer, Vonk-Noordegraff, and Turpijn 1988) can result in side effects (e.g. Sloan and Oliver 1975; Selman et al. 1997). MGA was chosen over medroxyprogesterone acetate (MPA, the synthetic progestin in Depo-Provera), because MPA altered cortisol levels (Seal et al. 1976). A further problem with MPA is androgenic activity, equated in some tests with dihydrotestosterone (Labrie et al. 1987), a natural androgen with potent morphological effects, especially during development. Among currently available progestins, levonorgestrel (the progestin in Norplant) has the highest binding affinity to androgen receptors, and is considered a potential health risk due to its effect on lipids and the cardiovascular system (Sitruk-Ware 2000).

In some species, progestin supplementation (e.g. Diskin and Niswender 1989) may help maintain pregnancy, whereas in others, especially early in gestation, they have been associated with embryonic resorption (Shirley, Bundren, and McKinney 1995; Ballou 1996). Progestins can interfere with parturition, since they are known to suppress contractility of uterine smooth muscle, as documented in white-tailed deer, *Odocoileus virginianus* (see Plotka and Seal 1989), but primates treated with progestins have given birth without incident (see Porton 1995). The discrepancy may be due to dosage or to species differences (Zimbelman et al. 1970; Jarosz and Dukelow 1975; Plotka and Seal 1989; Shirley, Bundren, and McKinney 1995). In general, all species except primates experience a decline in progesterone before onset of parturition, which may be necessary to reverse suppression of myometrial contractility. However, progestins appear to be generally safe for lactating females and nursing young. They do not interfere with milk production, and no negative effects on the growth or development of nursing infants have been found (WHO 1994a, 1994b).

Steroid hormones: Estrogens. Estrogens can effectively suppress follicle growth so that ovulation is prevented, but at contraceptive doses they have been associated in many species with side effects, most seriously cancer (Gass, Coats, and Graham 1964; Santen 1998). The estrogens diethylstilbestrol (DES), mestranol, estradiol benzoate, and estradiol cypionate have been used to block implantation following mismating in dogs. However, their tendency to stimulate uterine disease, bone marrow suppression, aplastic anemia, and ovarian tumors makes them inappropriate contraceptive compounds (Bowen, Olson, and Behrendt 1985).

Steroid hormones: Estrogen-progestin combinations. Some of the side effects associated with estrogen treatment, e.g. overstimulation of the uterine lining in primates, can be mitigated by adding a progestin. However, in carnivores the effect of progestin with estrogen is synergistic, not inhibitory, making the combination even more likely to result in uterine and mammary disease (e.g. Brodney and Fidler 1966; reviewed in Asa and Porton 1991). Because this synergy occurs in canids when progestin-only methods are initiated during proestrus, a time that natural estrogens are elevated, treatment should be initiated well in advance of the breeding season. When treatment is begun during deep anestrus, the side effects of synthetic progestins are minimized (Bryan 1973), even when continued for several years—a regimen that has proved safe during several decades of use in Europe (W. Jöchle, personal communication).

There are currently more than 50 orally active contraceptive products containing various combinations of an estrogen and a progestin at various doses that are approved for human use in the United States (*PDR* 2005). Ethinyl estradiol is the most common form of estrogen, although a few use mestranol. Norethindrone is the most common progestin ingredient; others include levonorgestrel, desogestrel, noregestrel, norgestimate, and ethynodiol diacetate. Oral contraceptive regimens designed for humans are intended to simulate the 28-day menstrual cycle, with 21 days of treatment followed by 7 days when either a placebo or no pill is taken, resulting in withdrawal bleeding that resembles menstruation. Continual delivery of ethinyl estradiol and MGA from silastic implants in spider monkeys, *Ateles geoffroyi*, resulted in endometrial hyperplasia that prompted cessation of the study (Porton, Dean, Asa, Plotka, and Rayne, unpublished observations). However, recent data from women indicate that continuous use of combination pills for up to 6 months (length of the study) results in an inactive endometrium (Kwiecien et al. 2003).

Steroid hormones: Androgens. Both testosterone and the synthetic androgen mibolerone (Cheque Drops: Pharmacia and Upjohn) are effective contraceptives (domestic dog: Simmons and Hamner 1973; Sokolowski and Geng 1977; domestic cat: Burke, Reynolds, and Sokolowski 1977; gray wolf, *Canis lupus*; leopard, *Panthera pardus*; jaguar, *P. onca*; and lion, *P. leo*: Gardner, Hueston, and Donovan 1985), but masculinizing effects include clitoral hypertrophy, vulval discharge, mane growth (female lion), mounting, and increased aggression. Mibolerone is approved for administration to dogs but not cats, and it is contraindicated for females that have impaired liver function, are lactating, or are pregnant, because female fetuses can be virilized. Mibolerone use in wildlife is inadvisable, primarily because of the potential for increased aggression.

GnRH analogs. Synthetic analogs of GnRH (gonadotropin-releasing hormone from the hypothalamus) can be *antagonists*, which block the action of the natural hormone, or *agonists*, which have the same effects (in this case, stimulatory) on target tissue as the natural hormone. Although antagonists would be the more logical selection for contraception, they are considerably more expensive, shorter acting, and less safe than the agonists, which limits their application (Vickery et al. 1989). In contrast to antagonists, GnRH agonist administration is followed first by an acute phase lasting for several days, when both LH and FSH are stimulated, which can result in estrus and ovulation (Bergfield, D'Occhio, and Kinder 1996; Maclellan et al. 1997). Continued treatment with long-acting preparations, such as implants or microspheres, is associated with the chronic phase, when FSH and pulsatile LH secretion are blocked due to down-regulation of GnRH receptors in the cells that produce LH and FSH (Huckle and Conn 1988). GnRH agonists also can interfere directly with follicle development (Parborell et al. 2002). The observed effects in the animal are similar to those following ovariectomy, but are reversed after the hormone content of the implant or microspheres is depleted.

A method for preventing estrus and ovulation during the acute phase has been tested in domestic dogs. The synthetic oral progestin megestrol acetate (Ovaban or Ovarid, Schering-Plough) given just before and during the first week following implant insertion successfully prevented both proestrus and estrus (Wright et al. 2001).

Several GnRH agonists are available (table 34.2), although most are quite expensive, since their human applications include treatment of prostate cancer and precocious puberty. Leuprolide acetate, as Lupron Depot injection (TAP Pharmaceuticals), has been used in zoos and aquariums for a variety of species. Deslorelin implants (Suprelorin, Peptech Animal Health, Australia, available in the United States by arrangement with the AZA Wildlife Contraception Center) have been effective in a variety of species: female domestic dogs (Trigg et al. 2001), domestic cats (Munson et al. 2001), domestic cows (D'Occhio et al. 2000), and several exotic species (lion; leopard; cheetah, *Acinonyx jubatus*; fennec fox, *Vulpes zerda*; wild dog, *Lycaon pictus*: Bertschinger et al. 2001, 2002). Fertility was restored when implants were removed or their hormone content was depleted; no pathology has been reported.

TABLE 34.2. Currently available GnRH agonists and antagonists

Product name	Generic name	Manufacturer or supplier
Agonists:		
Suprelorin implant	Deslorelin	Peptech Animal Health
Lupron Depot injection	Leuprolide acetate	TAP Pharmaceuticals
Viadur Implant	Leuprolide acetate	Bayer
Zoladex implant	Goserelin	Astra Zeneca
Synarel nasal spray	Nafarelin	Searle
Profact Depot injection	Buserelin	Aventis
Decapeptyl Depot	Triptorelin acetate	Ferring
Antagonists:		
Cetrotide	Cetrorelix	Serono
Antagon	Ganirelix	Organon

Immunocontraception: Zona pellucida vaccines. Immunization with zona pellucida (ZP) proteins results in antibodies that reversibly interfere with binding of sperm to the ZP, the glycoprotein coating of the mammalian oocyte, or egg. Initial treatment requires at least 2 injections of ZP proteins with an adjuvant, about one month apart. Subsequent boosters are needed annually for seasonal breeders and perhaps more frequently for continuous breeders. Porcine ZP (PZP) has been effective in a wide variety of ungulates and some carnivores (see Kirkpatrick et al. 1996), is safe when administered during pregnancy or lactation, and is reversible after short-term use. However, long-term studies with white-tailed deer and feral horses, *Equus caballus*, reveal that treatment for 5 or more years is increasingly associated with ovarian failure (Kirkpatrick et al. 1997). The possibility for permanent ovarian damage makes this method unsuitable for genetically valuable individuals or other cases in which reversibility is important.

In the cases where ZP vaccination results in permanent sterilization, it appears to act not only on the zona pellucida but also on the oocytes or their surrounding granulosa cells (VandeVoort, Schwoebel, and Dunbar 1995). Such damage to ovarian tissue can occur with even short-term treatment in dogs, so PZP vaccines are not recommended for carnivores.

When vaccine effect is restricted to preventing sperm entry so that ovarian activity is not disrupted, ovulatory cycles with estrous behavior continue. In some species, e.g. white-tailed deer, the failure to conceive results in a longer than usual breeding season, with continued estrous cycles accompanied by rutting behavior (McShea et al. 1997). Continued breeding activity may be desirable in some situations where it is seen as more natural than suppression, but it can also result in aggression and social disruption, especially when pregnancy does not ensue.

A further problem with ZP vaccines is that they are most effective when administered with Freund's Complete Adjuvant, which can produce reactions at the injection site and induce nonspecific responses to intradermal tuberculin tests. In felids, even more serious effects such as systemic pathology may occur. Other adjuvants have been successfully used to address these undesirable effects, and additional ones are being developed and tested.

Immunocontraception: GnRH vaccines. Immunization against GnRH can interrupt reproductive processes in much the same way as GnRH analogs (Hodges and Hearn 1977; Miller, Rhyan, and Killian 2003). Efficacy rate is variable and reversibility depends, among other things, on age, since permanent impairment of function was observed in some prepubertally treated females (Brown et al. 1995). Contraceptive efficacy of Canine Gonadotropin Releasing Factor Immunotherapeutic (Pfizer Animal Health), a GnRH vaccine approved in the United States for treatment of benign prostatic hyperplasia in dogs, has not been tested. Two other GnRH vaccine products from Pfizer Animal Health, Improvac (for boars) and Equity (for mares), are available in Australia and some other countries, but not in the United States. Although 2 of these products are marketed specifically for males, they could be effective in females as well.

Mechanical devices: Intrauterine devices. IUDs prevent pregnancy primarily by local mechanical effects on the uterus that impede implantation. Most designs include an electrolytic copper coating, which increases efficacy, since the copper ions are spermicidal. Although IUDs have been associated with pelvic inflammatory disease in humans, the risk of infection is statistically increased only during the first 4 months after insertion (Lee et al. 1983). Monofilament tail strings do not increase that risk (Triman and Liskin 1988), but, rather, attention to aseptic technique during insertion, with or without prophylactic antibiotics, is critical to preventing infection. IUDs can be ideal for lactating females (Díaz et al. 1997).

The IUDs marketed for humans (see table 34.3) may be appropriate for species with a uterine size and shape comparable to that of humans, in particular the great apes (e.g. orangutan, *Pongo pygmaeus*: Florence, Taylor, and Busheikin 1977; chimpanzee, *Pan troglodytes*: Gould and Johnson-Ward 2000) or even other primates (e.g. rhesus, *Macaca mulatta*: Mastrioanni, Suzuki, and Watson 1967). Various IUDs tested in domestic cows (Turin et al. 1997), ewes (Ginther, Pope, and Casida 1966), and goats (Gadgil, Collins, and Buch 1968) have also been shown to be effective, although in some cases estrous cycles have been suppressed, calling into question their site of action. An IUD recently developed for domestic dogs (Biotumer Argentina SA) has been found safe and effective in limited trials (Nagle and Turin 1997; Volpe et al. 2001).

TABLE 34.3. Currently available intrauterine devices

Product name	Composition	Manufacturer
ParaGard T 380A	Polyethylene T wound with copper wire	Ortho-McNeil Pharmaceuticals
Mirena	Polyethylene T encased in silastic that releases levonorgestrel	Berlex

PERMANENT METHODS FOR FEMALES

Removal of the ovaries eliminates the source of not only ova (eggs) but also the sex steroid hormones estradiol and progesterone, which precludes both ovulation and estrous behavior. Although it involves major surgery, ovariectomy (or ovario-hysterectomy, which also removes the uterus) may be preferable when exposure to naturally occurring reproductive hormones or steroid contraceptives may be associated with serious side effects. For example, in carnivores even endogenous reproductive hormones have been related to uterine infection and tumors. No data are available on the potential for decreased bone density following removal of the ovaries in long-lived animals such as great apes. Although removal of the uterus as well as the ovaries is common is domestic dogs and cats, a comparative study of the 2 procedures in dogs found no differences in incidence of any of the anticipated side effects (Okkens, Kooistra, and Nickel 1997).

Tubal ligation or otherwise cutting or blocking the oviducts may be an option for species in which gonadal hormones are not associated with pathology. Placement of the ligature at the level of the oviduct and not the uterine horn is important in taxa such as canids. During estrous cycles, hormone stimulation of the uterine endometrium results in secretions that can accumulate in the horn above the stricture (Wildt and Lawler 1985).

EFFECTS ON BEHAVIOR

Despite the decades of contraceptive use in wildlife, few studies have focused on behavior. The most obvious effect of ovariectomy and GnRH agonists is the elimination of sexual activity. Progestins may also suppress estrus, but typically only at higher doses; progestin-estrogen combinations are more likely to inhibit the follicular growth associated with estrous behavior, which itself can have further implications for social interaction. IUDs, and in many cases PZP vaccines, do not affect estrous cycles.

Research has linked progestin use with mood changes (MPA: Sherwin and Gelfand 1989), depression (MPA: Civic et al. 2000), and lethargy (Evans and Sutton 1989). But studies of social groups of hamadryas baboons, *Papio hamadryas* (see Portugal and Asa 1995), Rodrigues fruit bats, *Pteropus rodricensis* (see Hayes, Feistner, and Halliwell 1996), golden lion tamarins, *Leontopithecus rosalia* (see Ballou 1996), golden-headed lion tamarins, *Leontopithecus chrysomelas* (see De-Vleeschouwer et al. 2000), and lions (Orford 1996) found no significant effects on behavior or interactions of group members despite treatment of some or all females with melengestrol acetate (MGA). However, feral domestic cats treated with megestrol acetate, another progestin similar to MGA, were described as more docile (Remfry 1978).

POTENTIAL TARGETS FOR CONTRACEPTIVE INTERVENTION IN MALES

Understanding some of the basic parameters of sperm production can help inform the choice of method and timing of application. In the testes, FSH is needed for the initiation of spermatogenesis, both at puberty and at the beginning of each breeding season in species that do not produce sperm continuously. LH primarily stimulates testosterone production, which in turn stimulates and maintains spermatogenesis. Testosterone has multiple target tissues, especially the species-specific secondary sex characteristics such as deer antlers, the lion's mane, and muscle development, as well as brain regions that mediate aggression, territoriality, courtship, and mating.

Spermatogenesis begins at puberty for all species. For some it continues until death; for others it ceases entirely or may merely wane outside the breeding season. The time from initiation of the spermatogenic process to first ejaculation of mature sperm is 6–8 weeks in most mammals. In addition, mature sperm can survive in the male reproductive tract for many weeks, which is why males undergoing vasectomy are still considered potentially fertile for another 6–8 weeks, until the sperm already produced are either eliminated from the tract or begin to degenerate and become infertile. Thus, sufficient time must elapse before allowing treated males access to females.

Blocking production of all sperm is a difficult task, and blocking all sperm all the time can be even more daunting, which is one reason more techniques focus on the female. However, it may be less difficult to prevent the seasonal reinitiation of spermatogenesis than to shut it down, which perhaps makes contraception of seasonally breeding males somewhat more practical. When planning contraception for a seasonally breeding male, beginning treatment at least 2 months before the breeding season should be more successful.

REVERSIBLE CONTRACEPTION FOR MALES

GnRH agonists. The action of GnRH agonists on LH and FSH in males is similar to its action on LH and FSH in females, with an initial increase in testosterone followed by chronic suppression. In domestic dogs, deslorelin can achieve azoospermia (absence of sperm), probably as a result of testosterone suppression (Trigg et al. 2001). Testosterone, testis size, and sperm production were suppressed in cheetahs and an African wild dog, *Lycaon pictus*, treated with deslorelin. Trials with other wild canid males have been less successful (gray wolf; red wolf, *Canis rufus*; bush dog, *Speothos venaticus*: Bertschinger et al. 2001, 2002), but should be repeated at higher doses and more in advance of the breeding season. Evidence from some male primates (lion-tailed macaque, *Macaca silenus*, and mandrill, *Mandrillus sphinx*, unpublished data) suggests that downregulation may take more than the several weeks seen in male dogs and in females.

GnRH agonists, even at extremely high doses, have not been effective in blocking either testosterone or spermatogenesis in domestic cattle (D'Occhio and Aspden 1996), horses (Brinsko et al. 1998), or the other artiodactyls in which it has been evaluated (red deer, *Cervus elaphus*: Lincoln, 1987; zebu, *Bos indicus*: D'Occhio and Aspden 1996; gerenuk, *Litocranius walleri*; scimitar-horned oryx, *Oryx dammah*; and dorcas gazelle, *Gazella dorcas*: Penfold et al. 2002; wallaby, *Macropus eugenii*: Herbert et al. 2004). In these species, GnRH agonists succeed in blocking the pulsatile but not the basal secretion of both LH and testosterone (D'Occhio and Aspden 1996), leaving sufficient testosterone to support both spermatogenesis and male behavior.

Lupron-Depot has been used successfully in a variety of species, but few data on efficacy are published. Most records are for male marine mammals (Calle 2005).

GnRH vaccines. GnRH vaccine products developed for one gender may well be effective in the other, because GnRH is a hormone active in both males and females. As presented in the section above for females, Canine Gonadotropin Releasing Factor Immunotherapeutic (Pfizer Animal Health) has been approved in the United States for treatment of benign prostatic hyperplasia in dogs, but its contraceptive efficacy has not been demonstrated in either gender. Two other GnRH vaccine products from Pfizer Animal Health, Improvac (for boars) and Equity (for mares), are available in Australia and some other countries, but not in the United States.

PERMANENT METHODS FOR MALES

Male castration is a simple procedure except in species with undescended or partially descended testes (e.g. pinnipeds, cetaceans, elephants). However, effects on secondary sex characteristics caused by the decline in testosterone may involve loss (e.g. lion's mane) or disruption of the seasonal cycle (e.g. deer antlers). Following castration, especially in sexually experienced males, libido may decline slowly if at all. Declining testosterone following castration may result in reduced aggression, but learned behavior patterns may persist.

Vasectomy is an option for males when maintenance of secondary sex characteristics and male-type behavior is desirable. Although vasectomies are potentially reversible, the technique requires highly skilled microsurgery, after which high pregnancy rates have been achieved (e.g. Silber 1989a, 1989b; DeMatteo et al. 2006). The success of vasectomy reversals can be improved if the vasectomy is done with reversal in mind. One of the primary reasons for permanent damage is related to the pressure increase in the epididymis and testis following vas obstruction. A technique that leaves the testis end of the vas open lessens the chance of pressure-related damage and can increase the likelihood of successful reversal (Silber 1979; Shapiro and Silber 1979).

Permanent obstruction of sperm passage also can be accomplished by injecting a sclerosing agent into the cauda epididymis or vas deferens (Freeman and Coffey 1973; Pineda et al. 1977; Pineda and Dooley 1984). Treatment of the epididymis may be more successful, since the lumen of the tubule can be crossed several times during injection, but must be considered irreversible. Treatment of a discrete area of the vas would be more amenable to reversal, by excision and reanastomosis, but might not be as effective at ensuring sperm blockage.

Vasectomy is contraindicated for species with induced ovulation and susceptibility to progestin-induced deleterious effects (e.g. carnivores), since copulation is followed in their female partners by pseudopregnancies with elevated progesterone that can contribute to eventual uterine or mammary gland pathology. Even in canids, the obligate pseudopregnancy with elevated progesterone following spontaneous ovulation may contribute to uterine pathology. Thus, any method that allows repeated, nonfertile cycles without intervening pregnancies should be avoided. This would include simple separation of males from females, as well as treatments that render the male sterile.

EFFECTS ON BEHAVIOR

To the extent that GnRH agonists or GnRH vaccines succeed in suppressing testosterone, the effects on behavior should be similar to those following castration. In fact, GnRH agonists have been used in males for both contraception and aggression control.

MODES OF DELIVERY

Delivery methods currently available include implants, injections, pills, and liquid suspensions. An advantage to implants is the relatively long period of hormone delivery per handling episode. Steroids are most amenable to this route of administration, because they diffuse readily from silastic. However, newer implant matrices control release of peptides such as GnRH. For example, the deslorelin implant consists of a matrix of low-melting-point lipids and a biological surfactant (Trigg et al. 2001).

Problems with implants include possible loss and migration or fragility, resulting in difficulty removing them when desired (e.g. deslorelin implants). Loss can be minimized by using sterile technique during insertion. MGA implants should be gas sterilized and thoroughly de-gassed before insertion, since infection or gas residues can cause implant loss. Deslorelin and other commercially available implants are presterilized. When practical for social species, after surgical implant insertion, the individual should be separated from the group to prevent grooming until the incision is healed. Smaller implants such as Norplant and deslorelin may be less prone to loss due to their size and because they are inserted by trocar (a large needle), which reduces chances of loss by grooming, since there is no incision site. Similar results may be expected from the newer leuprolide acetate (Wildlife Pharmaceuticals) that forms an implant after injection. Loss of subcutaneously placed silastic implants may be common in perissodactyls (e.g. Plotka et al. 1988) and requires further study.

Adding radio-opaque material or an identity transponder microchip to MGA implants facilitates confirming presence and monitoring position. MGA implants can also be sutured to the muscle to impede migration. However, these modifications are not recommended for implants made from silastic tubing (e.g. Norplant) and are not possible for solid implants (e.g. deslorelin), because hormone release rates may be altered.

Injectable depot preparations have been formulated to release either peptide or steroid hormones (Lupron-Depot; Depo-Provera). Length of efficacy varies by dose and by species. Vaccines also are administered by injection. Although remote delivery via dart is possible for injectables, delivery of the complete dose cannot always be ensured or confirmed.

A disadvantage of biodegradable implants such as deslorelin is that, unlike Norplant and MGA implants that can be removed rather easily, they are somewhat fragile and prone to breakage when handled. Coupled with the variable duration of efficacy by species and by individual that has been reported, the inability to remove the deslorelin implants is a considerable disadvantage. Neither can reversal time be controlled with depot injections and vaccines, primarily because the duration of efficacy differs markedly among individuals. Yet ease of application of injectable products and the safety of GnRH agonists may be more important than timed reversals in some circumstances.

Oral delivery can be relatively simple in mammals that have been trained for daily contact or handling, e.g. marine mammals used in shows. A disadvantage of oral preparations is that they typically must be administered daily. However, they usually can be incorporated into food. Confirmation of ingestion is critical and can be difficult, especially in great apes.

EFFICACY AND REVERSIBILITY

Assessing contraceptive efficacy and reversibility might seem straightforward: no babies should be conceived and born during contraceptive treatment, and babies should be conceived and born following cessation of treatment. However, because individuals vary, such assessments are actually complex, since many factors affect the likelihood of conception, pregnancy maintenance, and parturition, even if a female has never been treated with contraceptives.

For females, major factors affecting contraceptive efficacy include (1) whether she was pregnant before the contraceptive was started; (2) latency to effect, i.e. time from initiation of treatment to time it can prevent pregnancy; and (3) whether the contraceptive remains in place (implants, IUD), the injection was delivered, or the medicated feed or pill was consumed.

Duration of efficacy is related to time to reversal. In general, orally active progestins must be administered daily to be effective, and missing one or two days may well result in conception. This rapid restoration of fertility is probably due to the inability of progestins to completely suppress follicular growth (Broome, Clayton, and Fotherby 1995; Alvarez et al. 1996). In fact, such a response is the basis for estrus synchronization protocols in many domestic species (Adams, Matteri, and Ginther 1992). In contrast, the estrogen component of combination birth-control pills is more effective at suppressing follicles, so even the weeklong placebo or pill-free period is not sufficient for completion of the follicular growth and ovulation (Mall-Haefeli et al. 1988). The effective period of injectable depot preparations such as Depo-Provera and Lupron Depot and for implants such as MGA, Norplant, and Suprelorin is quite variable. The release dynamics seem to vary by individual, making an accurate prediction of efficacy duration impossible, resulting in reliance on estimated ranges. Although the mechanism of action of vaccines differs considerably from that of the depot preparations or implants, the duration of efficacy of vaccines varies due to individual differences in immune response.

Misunderstanding the period of efficacy of implants can lead to erroneous conclusions regarding their reversibility. Recommendations for timing implant replacement are always conservative and based on the minimum duration of efficacy observed in the particular species. However, implants may be effective well beyond that minimum interval. This assumption may lead to the mistaken conclusion that the method may not be reversible (e.g. De Vleeschouwer et al. 2000; DeMatteo, Porton, and Asa 2002; Cheui et al. 2007).

Time to reversal can be measured many ways, since there are different points in the reproductive process that can be used as markers. Even females that have never been contracepted may not become pregnant during years of cohabitation with a male. Thus, pregnancy rates postcontraception should be compared not only to precontraceptive reproductive history, but also to the pregnancy rates of noncontracepted females that are matched at least for age and previous number of young. Many factors other than contraceptives affect the likelihood of ovulation and conception, including reproductive history, age, health, body weight, season, social status, and, of course, fertility of the partner or genetic incompatibility of the pair.

Factors that relate directly to contraceptive reversibility include latency to clearance of the drug following cessation of treatment (e.g. pills) or removal of implants. Latency to clearance of depot formulations (e.g. Depo-Provera, Lupron Depot) can vary considerably by individual. For example, time to first ovulation following the last injection of Depo-Provera ranges from 6 weeks to 2 years in women (Schwallie and Assenzo 1974; Nash 1975; Ortiz et al. 1977). The situation is comparable with vaccines such as PZP, since individual immune responses vary considerably, and in fact it may not be reversible in some species or in those treated for more than several years.

Because clearance of a drug usually cannot be determined, resumption of ovarian cycles using gonadal hormone assay, ultrasound exams, or external signs of estrus can indirectly measure resumption of reproduction. Conception, determined by pregnancy diagnosis, can confirm the return of fertility even if live birth does not follow. Although pregnancy loss may be mistakenly attributed to prior contraception, for species in which early pregnancy diagnosis is possible (many laboratory and domestic species, as well as humans), the data suggest that even in females never contracepted, between 20 and 66% of embryos are lost spontaneously (Perry 1954; Smart et al. 1982; Wilmut, Sales, and Ashworth 1986; McRae 1992). Thus, the true latency to first conception following cessation or removal of contraceptive treatment may well be shorter than when the criterion for success is the birth of healthy young.

Despite the numerous factors that affect the likelihood of pregnancy and parturition, the most conservative measure of successful contraceptive reversal is the birth of live young. There have been only 2 studies of reversibility that have incorporated previous reproductive history and details of captive management, e.g. duration of access to a mate (golden lion tamarin: Wood, Ballou, and Houle 2001; tiger: Chuei et al. 2007). After MGA implant removal, 75% of the female golden lion tamarins reproduced within 2 years (Wood, Ballou, and Houle 2001), a rate that was indistinguishable from that of control females that had never been implanted with MGA. However, only 63% of tigers reproduced by 5 years post implant removal, a difference that may reflect different species management styles. For both species, reproductive rate was much lower in females with implants left in place beyond the recommended 2 years, demonstrating that the actual duration of MGA efficacy can be more than 2 years.

For males, appearance of sperm in the ejaculate can verify reversal for methods that suppress spermatogenesis. The latency to passage of sperm can be affected by such things as age, social status, and time of year for seasonal breeders. Also, following resumption of spermatogenesis, there is a species-specific time (6 to 8 weeks for most mammals) before mature sperm finally are released into the vas deferens. Thus, once the contraceptive is removed or no longer effective, sperm cannot be expected in the ejaculate immediately.

CHOOSING THE APPROPRIATE CONTRACEPTIVE METHOD

Selection of the most appropriate contraceptive method for a particular individual should take multiple factors into account, including efficacy, safety, reversibility, method of delivery, behavioral ramifications, the age, health, and reproductive status of the individual, and consequences of failure (see table 34.4 for females and table 34.5 for males). Different forms of contraception may be appropriate to different stages in an animal's life span and to different management situations and objectives.

Because zoos and aquariums manage such a variety of mammalian species, not all the available contraceptive meth-

TABLE 34.4. Choosing a contraceptive method for females

Contraceptive	Effect on estrous behavior	Use during lactation	Use during pregnancy	Use before puberty
Progestins	Irregular signs of estrus may occur	Yes	Possibly safe very early, but NOT late in pregnancy for most species	Shown to be safe in domestic cows
Combination estrogen + progestin	Estrus signs likely during placebo period	No	No	No information
GnRH agonists	Suppresses estrus after initial stimulation	May be safe after lactation established	No	Shown to be safe in domestic cats
PZP vaccine	No	Yes	Yes	Yes
IUD without progestin	No	No	No	No information

TABLE 34.5. Choosing a contraceptive method for males

Objective	Method	Reversible
Block spermatogenesis and testosterone production	Castration	No
	GnRH agonists	Yes
	GnRH vaccine	Yes
Block spermatogenesis but not testosterone	Vasectomy	Potentially

ods have been used in all species; therefore, the basic question of whether a specific contraceptive is effective in a particular species is quite relevant. For those contraceptives that have a longer history of use and have proved effective in multiple species (e.g. the MGA implant), there is a broader foundation from which to make recommendations, particularly if the species in question is taxonomically similar to those already treated. Contraceptive products that show promise in trials with a limited number of species may prove to be effective in a new target species, but managers should realize that the specific dose and duration of effect may differ. This information can be obtained through controlled and more expensive research trials or through analysis of the collective experience gathered in AZA's Contraception Database. The animal manager must therefore consider the ramifications of an "unplanned" pregnancy when considering contraceptive methods for which limited data are available.

Safety of a contraceptive method must be defined—is safety related to increased risk of a lethal disease, a treatable disease, infertility, or shortened life span? Definitive information is typically difficult and slow to accumulate, which necessitates that managers consider all potential outcomes of different contraceptive methods within the context of individual animal welfare, population viability, and institutional consequences.

The term *contraception* is specific to methods of birth control that are reversible; therefore, the question of reversibility is central. However, reversibility itself is nuanced; a contraceptive method may be reversible, but time to reversal may vary significantly and be unacceptable for some breeding programs. Reversibility may be duration dependent; e.g. after *x* years of use the probability of a reversal decreases appreciably, and this window may differ by taxon.

The way in which a contraceptive method is administered is a fundamental aspect of birth control and requires that managers make decisions based on the housing, staff, and individual animal challenges they confront. Daily consumption of a birth control pill should only be selected if the manager feels confident that the facility's design and/or behavior of the individual animal will assure success. Contraceptives delivered by injection are more likely to be successful if an animal can be hand captured, held in a chute/squeeze, or trained to facilitate injection. Contraceptive methods that require immobilization and surgery may carry more risks for some species (e.g. giraffes, marine mammals) than others. Contraceptive implants such as MGA may be both effective and safe in some species, but in other species or particular individuals, the likelihood of implant loss (and thus efficacy!) is unacceptably high. The effectiveness of an injectable contraceptive may be very high, but if there is question about the dependability of staff in ensuring the appropriate timing of injections, a different method may be the better option. Ultimately, a contraceptive method proved to be reliable can only be effective when actually in use; therefore, the manager must evaluate which method of delivery is best for a specific situation.

Managers should consider the age, health status, and genetic importance of an individual animal when selecting a contraceptive. Preventing reproduction in animals reaching puberty may be highly desirable for reasons of exhibit value, limited space, or social benefits derived from offspring remaining within their natal group. Unfortunately, few data concerning the use of contraception in prepubertal animals are available. Limited reports of prepubertal domestic cows (Schul et al. 1970), male muntjac, *Muntiacus reevesi* (see Stover, Warren, and Kalk 1987), and female dogs (Bigbee and Hennessy 1977) that were treated with progestins and reproduced later in life suggest that progestins may not affect reproductive processes when administered before puberty. When birth control is needed for an aged animal or an individual compromised with one or more medical conditions, the potential health consequences associated with a particular method may be the decisive factor driving the selection. For example, progestins are contraindicated in animals that have diabetes. In some species, negative physiological consequences occur in females even though the selected contraceptive method is male directed. For example, vasectomizing the only male in a group of baboons will cause the sexually mature females to experience monthly estrous cycles and concomitant sexual swelling. This unnatural situation, over time, results in such large and heavy sexual swelling that female baboons develop back injuries (personal observation). In some carnivores, pairing a female with a vasectomized male results in nonconceptive estrous cycles and thereby repeated exposure to the female's endogenous steroidal hormones, which has led to uterine pathology (Asa, Porton, and Calle 2005). Managers who need to prevent reproduction temporarily in genetically important individuals, regardless of age, may wish to eliminate all contraceptive options in which reversibility or duration to reversal is uncertain.

For the most part, managers do not intentionally contracept pregnant females. However, there are exceptions, such as callitrichid species in which the father plays an important role in parental care, females experience a postpartum estrus, and removal of the male is not an option. Callitrichids have, therefore, been implanted with MGA during pregnancy to ensure the incision site is healed before the infants' birth and to prevent the postpartum estrus. Unintentional contraception of pregnant females has occurred when breeding behavior was not seen by caretakers and the female was not recommended or expected to breed. Managers should therefore be mindful whether any potentially negative consequences have been associated with a contraceptive method for the species in question. For example, progestins can reduce or suppress contractility of uterine smooth muscles and, in some species, inhibit parturition. While there are no such reports for nonhuman primates, there have been reports of hooved animals experiencing difficulties with labor when treated with progestins (Plotka and Seal 1989; Patton, Jöchle, and Penfold 2005).

The behavioral implications of using contraception must be assessed in terms of both the individual animal and its social group. Because contraception has an impact on reproduction at one or more levels, the ramifications can be multifaceted and should be carefully considered. Preventing pregnancy can be accomplished by separating the sexes, selecting a contraceptive method that either does or does not suppress mating behavior, or even sterilizing one sex (typically the male) while maintaining the reproductive potential of the female. In species classified as solitary, separation may be viewed as an acceptable form of birth control; however, there are many examples of solitary species that are compatibly housed with conspecifics. Separation may not be an appropriate option if social companionship appears to enrich the animals' lives, or if social housing allows them access to a more complex and enriching habitat. Separating individuals from their social group for the duration of the breeding season or even just during estrus can be problematic at multiple levels. For example, removing a reproductive male ungulate from his group may be an acceptable option if he is housed in a stimulating environment and his removal does not cause social conflict among the females. Removal of a male primate from a single male- or multimale-multifemale group is unlikely to be a good birth control option due to the likelihood that social alliances among group members may change during the male's absence and change again upon his return. The same can occur if a female is removed during her estrus; depending on her social status and role in the group, even a short absence can lead to internal conflicts among the females or place the isolated female at risk of aggression when she returns. Within species that form strong pair bonds and in which the male plays a large parental role (such as callitrichids and bush dogs), separating the pair is almost always unwise. On the other hand, separating the sexes through the formation of unisex groups for the short or long term may be a good option when the species' or individuals' social needs can be met.

Managers should think through the pros and cons of selecting a contraceptive method that does or does not inhibit sexual behavior. Some methods (e.g. PZP vaccine, vasectomy, tubal ligation, or IUDs) prevent pregnancy, but do not interfere with reproductive hormones or the expression of sexual behavior. Some steroid contraceptives may be administered at doses that do not fully prevent manifestations of estrus such as receptivity or the sexual swellings that occur in some primate species. Because managers work toward providing opportunities that encourage captive animals to exhibit a full range of their behavioral repertoire, selecting a contraceptive method that does not suppress sexual behavior may be preferred, particularly for species in which learning plays a role in the acquisition of appropriate sexual behavior (e.g. copulatory behavior in adolescent male chimpanzees, King and Mellen 1994). On the other hand, a maturing, healthy wild mammalian female typically has only a few estrous periods before she conceives, and the first pregnancy is followed by nearly continuous cycles of pregnancy, lactation, and infant care. Viewed in this manner, not only is it abnormal for a female to be sexually receptive throughout the species' breeding season or year, but it can be disruptive and lead to unnecessary conflict within the social group. In addition, contraceptives that suppress sexual behavior often facilitate offspring remaining in their natal group, which can be of great practical value when appropriate housing is limited. Since juveniles typically reach puberty at a younger age in captivity than the wild, adolescents may derive behavioral benefits from gaining greater social maturity before being removed from their family.

To date there is limited information on what impact contraception has on individual and social behavior. The sheer number of confounding factors that play a role in the expression of behavior make it unlikely that sufficient research comparing contracepted to noncontracepted individuals can be undertaken in the near future to allow even broad generalizations. First, there are many different contraceptive alternatives; e.g. managers cannot safely extrapolate that an individual female's behavioral response will be the same when contracepted with Depo-Provera or MGA, even though both are synthetic progestins. Medroxyprogesterone acetate, the progestin in Depo-Provera, binds readily to androgen receptors, is antiestrogenic, and has been linked to increased aggression in some females (Labrie et al. 1987; Sherwin and Gelfand 1989; unpublished reports from Contraception Database). Very observant and well-trained caretakers are important for noticing subtle changes in behavior that may be attributed to contraception. Second, social groups comprise individuals; therefore, their unique developmental and social history, age, sex, reproductive status, and familial bonds are all variables that contribute to the group's social dynamics. Lastly, the space, configuration, and complexity of the captive environment along with the husbandry protocols used by the staff to manage the animals can further affect relationships and group behavior. It is therefore important that animal caretakers and managers, who are in the best position to understand the above variables, share their insights with colleagues through the Contraception Database, publish case reports, or initiate/participate in research.

CONTRACEPTION, ANIMAL WELFARE, AND PROFESSIONAL ETHICS

Today, accredited zoos and aquariums are confronted with the greatest challenge they have ever faced: they need to manage captive populations to be genetically diverse and demographically stable; meet the behavioral and social needs of individual animals by designing larger, more complex displays and holding facilities; house animals in species-appropriate social groups; educate visitors by modeling a caring and proactive role in wildlife conservation and animal welfare; and accomplish all of this while severely constrained by the limited number of acceptable facilities to which "surplus" animals can be transferred.

WAZA, AZA, EAZA, and other regional zoo associations have developed professional standards that guide members in animal care, acquisition, and disposition. A review of AZA's disposition practices show how standards have changed over time (AZA 2000; Xanten 2001), yet today there are still widely divergent opinions on the issue (Lindburg 1991; Lacy 1995; Wagner 1995; Glatston 1998; Green 1999; Margodt 2000; Carter and Kagan, chap. 21, this volume). Should animal surplus policies be more taxon specific? Who defines appropriate quality of care? Is euthanasia preferable to transferring an animal out of the cooperatively managed breeding programs? Some zoo biologists believe that preventing reproduction deprives captive animals of an important and enriching component of their life. The idea that animal welfare goals are better met by euthanizing offspring when they reach dispersal age rather than preventing the birth of surplus is held by more European than North American zoo professionals (Holst 1998; Wiesner and Maltzan 2000; McAlister 2001). Lacy's (1995) belief that contraception is the most responsible approach to reducing the number of surplus animals is more widely accepted within the AZA. With moral questions regarding how zoos should manage the surplus animal issue unresolved, unlimited reproduction is plainly indefensible. Contraception can never provide the entire solution but is, in many cases, the best option to reduce population growth. Therefore, continuing research on the efficacy, safety, and reversibility of contraceptives and the development of new methods are essential responsibilities zoos must assume to ensure that animal managers have a range of options to achieve population management and animal welfare goals.

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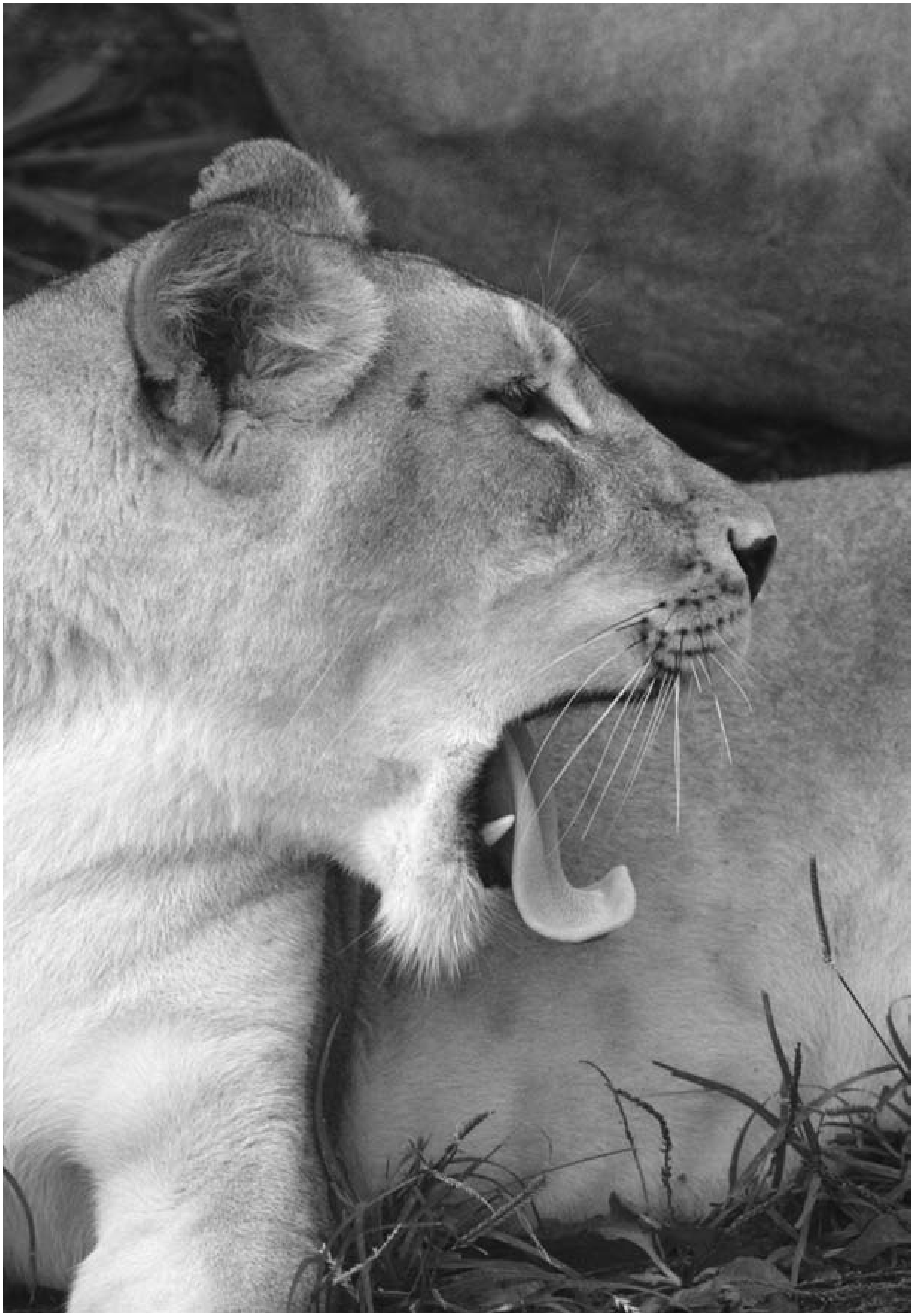

Appendixes

Introduction

Devra G. Kleiman

Record keeping in zoos has become essential to the effective management of zoo mammals. Tracking body size and weight changes is essential for monitoring animal well-being and reproductive condition, but also provides an important source of information about mammalian biology for researchers. Medical management, breeding records, interzoo loan agreements, and necropsy records all require accurate and consistent animal identification. Lundrigan presents the basic methods for measuring mammals, and Kalk and Rice present a variety of identification techniques ranging from recording simple natural marks and tattoos to more recent options, such as transponders (PIT tags), which are increasingly being used by zoos. The latter also discuss the suitability of the various techniques and their application to different mammal species. Bingaman Lackey summarizes the history and use of studbooks and the basic data needed for records systems, and provides a listing of the regional zoo associations. The past decade has seen an explosion of expanded record-keeping systems and greater coordinated management of mammal populations in zoos, all of which Bingaman Lackey documents. Finally, she provides a summary of the available services and software for ISIS (International Species Information System), including the new Zoological Information Management System software. In the final appendix, Kenyon provides an updated bibliography of useful materials for zoo professionals, organized by topics covered in this volume. The appendix lists books, journals, associations, and societies, and ranges from general issues to the more specific. Astonishingly, nearly 25% of this bibliography's content is Internet Web sites, demonstrating the major change in accessing information that has occurred since publication of the first edition of *Wild Mammals in Captivity.*

Lioness yawning at the Smithsonian's National Zoological Park, Washington, DC. Photography by Mehgan Murphy, Smithsonian's National Zoological Park. Reprinted by permission.

Appendix 1

Standard Methods for Measuring Mammals

Barbara Lundrigan

INTRODUCTION

Zoos and other captive animal facilities have an unparalleled opportunity to obtain valuable measurement data from animals—data that in many instances are impossible to obtain from their free-ranging wild conspecifics. Yet this important opportunity is often lost, because zoo management personnel are unwilling to collect such data, or because they do not use standardized techniques so that their data can be meaningfully compared with other data sets and made accessible to other researchers.

Field biologists typically collect a series of standard size measurements that are used in identification, in monitoring the effects of environmental or genetic change on body size and shape, and as baseline information for studies of the relationship between body size parameters and other aspects of biology (e.g. diet, reproductive rate, metabolic rate, home range size, and longevity).

With captive animals, the goals are much the same. Standard size measurements can be used to corroborate identifications, to monitor the effects of environmental or genetic changes (in this case, particularly changes associated with captive management, such as adjustments in diet, enclosure size, or breeding regime), and as baseline information for evolutionary and wildlife biologists. Although captivity may have a confounding effect on some body size parameters, the value of these data to evolutionary and wildlife biologists cannot be overemphasized. In many instances, measurements from wild conspecifics are simply not available. Moreover, captivity permits repeated measurements of the same individual over time, which is rarely possible in the field. Such longitudinal data can be used to assess changes in management practices, and are essential for establishing norms for growth and development.

This chapter describes the standard methods used by North American mammalogists for taking simple external measurements from small and large mammals; the same methods should be used when captive mammals are measured so that the data can be used for subsequent reference and comparison. I include only the relatively few measurements that mammalogists consider most important, and where possible provide references to more detailed information.

MEASURING MAMMALS

All measurements should be recorded in metric units. There are no rules regarding level of precision; however, Ansell (1965) includes suggested standards for mammals of various sizes. In general, weights of small mammals (i.e. less than 15 kg) are given to the nearest gram or tenth of a kilogram, and linear measurements to the nearest millimeter. Weights of large mammals (i.e. 15 kg or more) are given to the nearest kilogram, and linear measurements to the nearest millimeter or centimeter.

The following information should be recorded with the measurements: scientific name, sex, identifying number (i.e. zoo number and/or collector number), date of measurement, date of death (where applicable), reproductive condition (e.g. pregnant, lactating), general condition of the specimen (e.g. alive, recently killed, moderately decomposed), and any damage that might affect the accuracy of a measurement (e.g. a broken tail or torn ear). For captive animals, include the date of birth or date and locality of capture if possible.

MEASURING SMALL TERRESTRIAL MAMMALS

There are many excellent sources of information on measuring small mammals (i.e. less than 15 kg). These include works by Peterson (1965, bats only), Nagorsen and Peterson (1980), Hall (1981), Handley (1988, bats only), Skinner and Smithers (1990), and Martin, Pine, and DeBlase (2001). The basic equipment needed includes a metric ruler, calipers or dividers, and a metric weighing device.

The 5 standard external measurements for small mam-

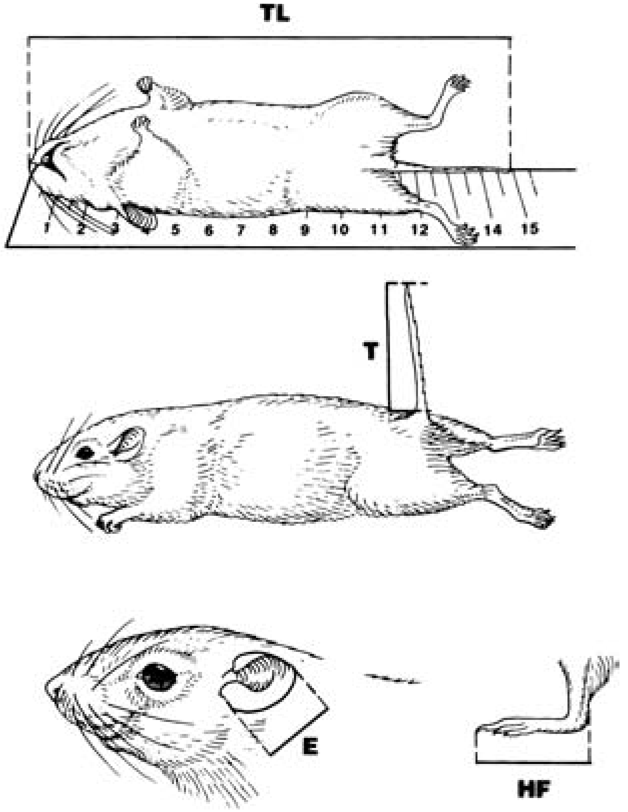

Fig. A1.1. Standard external measurements for small mammals: total length (TL), tail length (T), hind foot length cum unguis (HF), and ear length (E). (Adapted from Martin, Pine, and DeBlase 2001.)

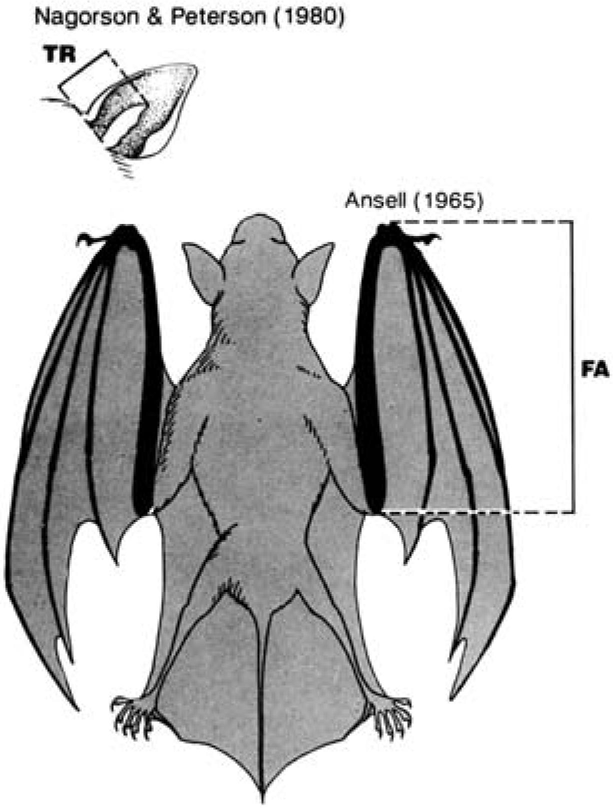

Fig. A1.2. Additional standard external measurements for bats: forearm length (FA) and tragus length (TR). (Adapted from Ansell 1965; Nagorsen and Peterson 1980.)

mals are total length (TL), tail length (T), hind foot length (HF), ear length (E), and weight (wt) (fig. A1.1). Two additional measurements, tragus length (TR) and forearm length (FA), are taken from bats (fig. A1.2). (Outside North America, mammalogists sometimes measure head plus body length [HB] instead of total length.) To record measurement data, most collectors use abbreviations, with dashes separating one measure from the next (e.g. TL 102—T 45—HF 11 (c.u.)—E 35—TR14—FA 44). The weight measurement follows the linear measurements (e.g. wt = 15 g).

Total length. Lay the animal on its back against the flat side of a ruler. The nose should extend forward and the body and tail should lie flat against the ruler but should not be stretched. Measure from the tip of the nose to the tip of the tail, excluding tail hair that extends beyond the tip. Alternatively, place the body on a soft board, insert pins to mark the tip of the nose and the tip of the tail, remove the body, and measure the distance between pins. If the animal is conscious, or for other reasons cannot be placed in a relaxed position, measure mid-dorsally, following the curves of the body from the tip of the nose to the tip of the tail; label "Along Curves."

Tail length. Lay the animal on its belly and hold the tail up at a 90° angle from the body. Using a ruler, measure along the dorsal (upper) surface of the tail from its junction with the body (root) to its tip, excluding hair that extends beyond the tip. In species for which it is difficult to locate the root of the tail (e.g. northern river otter, *Lontra canadensis*), measure from the middle of the anus and label "T M/A."

Hind foot length. Press the sole of the hind foot gently against the flat side of a ruler so that the toes are straightened. Measure from the calcaneum (heel) to the end of the claw on the longest toe. Mammalogists do not always include the claw in this measurement. Therefore, it is essential to indicate the method used: cum unguis (c.u.) for with claw, or sine unguis (s.u.) for without claw.

Ear length. Using calipers, dividers, or a ruler, measure from the base of the notch below the ear opening to the most distal point on the margin of the pinna (external ear), excluding ear hair that extends beyond this point.

Tragus length. The tragus is a leaflike structure projecting from the base of the ear in most bats. Using calipers, dividers, or a ruler, measure from the base of the tragus (where it joins the ear) to its tip, excluding hair that extends beyond the tip.

Forearm length. Fold the wing and, using calipers, dividers, or a ruler, measure on the dorsal surface of the wing from the tip of the ulna (elbow) to the most distant point on the carpus (wrist).

Weight. Most field collectors use spring-loaded scales (e.g. Pesola brand) to weigh small mammals, because these scales are light, inexpensive, and easy to handle. A digital balance is more cumbersome, but can provide greater accuracy. The abbreviation *ca.* (circa) is used to designate an approximate weight.

MEASURING LARGE TERRESTRIAL MAMMALS

Information on measuring large terrestrial mammals (i.e. 15 kg or more) can be found in works by Ansell (1965), Sachs (1967, ungulates only), and Nagorsen and Peterson (1980). The basic equipment needed includes 2 straight, stiff rods, a flexible metal tape measure, a ball of heavy string (for distances greater than the length of the tape measure), large calipers or dividers, and a metric weighing device.

The same standard external measurements recorded for small mammals (total length, tail length, hind foot length, ear length, and weight) are recorded for large mammals (fig. A1.3). Two additional measurements, shoulder height (SH) and axillary girth, are usually taken for ungulates and sometimes for other large mammals (fig. A1.3).

Total length. Lay the animal on its back or side with the nose pointed forward, the backbone in a natural, relaxed position, and the tail extended in line with the backbone. Place a rod perpendicular to the long axis of the body, touching the tip of the nose, and a second rod perpendicular to the long axis of the body, touching the tip of the tail (excluding tail hair that extends beyond the tip). Measure in a straight line by running a tape measure from rod to rod just above the body. If the animal is conscious or for other reasons cannot be placed in a relaxed position, measure mid-dorsally, following the curves of the body from the tip of the nose, across the back of the head and along the backbone, to the tip of the tail. Always indicate the method of measurement: "point to point" or "along curves."

Tail length. Hold the tail at a 90° angle above the dorsal surface of the body (or 30–45° for ungulates: Ansell 1965) and, using a tape measure, measure from the root of the tail to the tip of the tail, excluding hair that extends beyond the tip. In species for which it is difficult to locate the root of the tail (e.g. aardvark, *Orycteropus afer*), measure from the middle of the anus and label "T M/A."

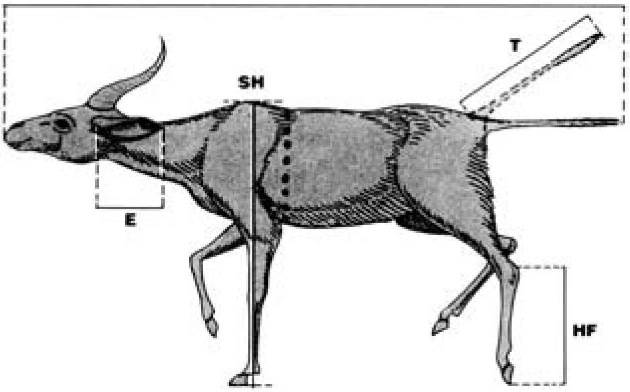

Fig. A1.3. Standard external measurements for large mammals: total length point to point (TL), tail length (T), hind foot length cum unguis (HF), ear length (E), shoulder height (SH), and axillary girth (dotted line). (Adapted from Ansell 1965.)

Hind foot. Hold the hind foot so that the toes are straightened and, using large calipers or dividers, measure from the calcaneum (heel or hock) to the end of the claw on the longest toe (or tip of the hoof). Mammalogists do not always include the claw (or hoof) in this measurement. Therefore, it is essential to indicate the method used: cum unguis (c.u.) for with claw (or hoof), or sine unguis (s.u.) for without claw (or hoof).

Ear. The ear should be measured as in small mammals.

Shoulder height. In a standing animal, shoulder height is the distance from the highest point on the shoulder (or withers) to the sole of the foreleg foot (or hoof). If the animal is lying on its side, hold the limb in its natural position, place one rod perpendicular to the long axis of the body, touching the highest point on the shoulder (or withers), and place a second rod perpendicular to the long axis of the body, touching the sole of the forefoot (or hoof). Measure in a straight line by running a tape measure from rod to rod just above the body.

Axillary girth. Axillary girth measurements should be taken only from live animals and fresh carcasses, as the body may become distended shortly after death. Using a flexible tape measure, measure the circumference of the body immediately behind the forelegs. If the tape cannot be passed around the body, measure from dorsal to pectoral midline and label "Half Axillary Girth."

Weight. Weights of large mammals are particularly valuable, because they are recorded so infrequently. Some captive mammals (e.g. many primates and some carnivores) can be enticed or trained to stand on a floor scale. Special equipment may be needed for weighing extremely large mammals (e.g. the Smithsonian's National Zoological Park, Washington, DC, borrows truck scales to weigh elephants). Large carcasses can be weighed in pieces, but an allowance should be made for fluid loss. For a discussion of techniques for weighing large mammals, see Schemnitz and Giles (1980).

MEASURING MARINE MAMMALS

Marine mammals (pinnipeds, cetaceans, and sirenians) differ in basic body structure from terrestrial mammals and therefore demand a somewhat different set of external measurements. The equipment needed is the same as for large terrestrial mammals.

Measuring pinnipeds. The best source of information on measuring pinnipeds (seals, sea lions, and walruses) is the recommendations of the American Society of Mammalogists Committee on Marine Mammals (1967). There are 5 standard external measurements for pinnipeds (fig. A1.4).

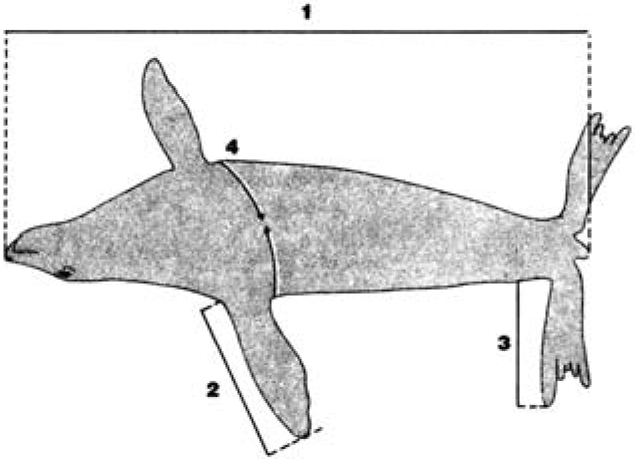

Fig. A1.4. Standard external measurements for pinnipeds recommended by the American Society of Mammalogists Committee on Marine Mammals: standard length (1), anterior length of front flipper (2), anterior length of hind flipper (3), and axillary girth (4). (Adapted from Committee on Marine Mammals 1967.)

Standard length. Standard length in pinnipeds is equivalent to total length in large terrestrial mammals and is measured in the same manner. If the animal is conscious or for other reasons cannot be placed in a relaxed, belly-up position, measure the shortest surface distance from the tip of the nose to the tip of the tail by following the curves of the body along the back, side, or belly, and label "Curvilinear Length."

Anterior length of front flipper. Hold the flipper at right angles to the body and, using a tape measure, large calipers, or dividers, measure in a straight line from the anterior insertion of the flipper to the tip of the first claw or fleshy extension.

Anterior length of hind flipper. Hold the flipper at right angles to the body and, using a tape measure, large calipers, or dividers, measure in a straight line from the anterior insertion of the flipper to the tip of the first claw or fleshy extension.

Axillary girth. Axillary girth in pinnipeds is equivalent to axillary girth in large terrestrial mammals and is measured in the same manner.

Weight. Many captive pinnipeds can be trained to stand on a floor scale. Large carcasses can be weighed in pieces; the Committee on Marine Mammals (1967) suggests a 10% allowance for loss of body fluids.

Measuring cetaceans. The best source of information on measuring cetaceans (whales, dolphins, and porpoises) is the recommendations of the American Society of Mammalogists Committee on Marine Mammals (1961). That committee provides a long list of external measurements recommended for the smaller cetaceans; 13 of the most important of those measurements are described below (fig. A1.5).

The first 7 measurements should be taken in a straight line parallel to the long axis of the body and labeled "Axial." For each measurement, place a rod perpendicular to the long axis of the body at each of the 2 reference points. Adjust the rods laterally so that the line between them is parallel to the body axis, and measure the straight-line distance between the 2 rods.

The primary reference point for the first 7 measurements is the anterior-most point on the head, excluding the lower jaw. This is almost always the anterior tip of the upper jaw; thus, "tip of the upper jaw" is used below. In species in which the two are not equivalent (e.g. dwarf sperm whale, *Kogia sima*), use the anterior-most point on the head, excluding the lower jaw, as the primary reference point.

1. (Total length): Tip of the upper jaw to notch between tail flukes (or midpoint of the fluke margin if no notch is present)
2. Tip of the upper jaw to corner of the mouth
3. Tip of the upper jaw to center of the eye
4. Tip of the upper jaw to center of the blowhole (or midpoint between the 2 blowholes if 2 are present)
5. Tip of the upper jaw to anterior insertion of the flipper
6. Tip of the upper jaw to tip of the dorsal fin
7. Tip of the upper jaw to center of the anus

The remaining measurements (except girth and weight) are straight-line distances measured from point to point (using a tape measure, calipers, or dividers).

8. Length of flipper: from the anterior insertion of the flipper to its tip

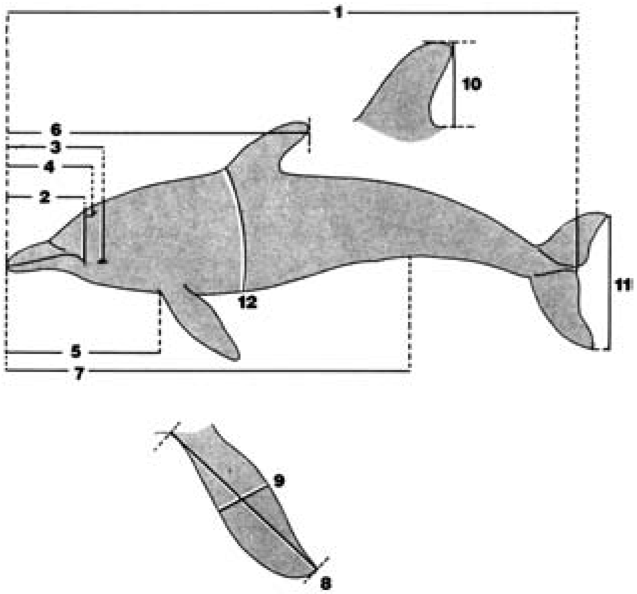

Fig. A1.5. Standard external measurements for cetaceans recommended by the American Society of Mammalogists Committee on Marine Mammals. (Adapted from Committee on Marine Mammals 1961.)

9. Width of flipper: the maximum width of the flipper, perpendicular to its long axis
10. Height of dorsal fin: from the base of the dorsal fin to its tip
11. Width of flukes: the width across the flukes, from tip to tip
12. Maximum girth: the circumference of the body at its widest point. Indicate the (axial) distance from that point to the tip of the upper jaw. If the tape measure cannot be passed under the body, measure from dorsal to ventral midline and label "Half Maximum Girth."
13. Weight: measured as for pinnipeds

Measuring sirenians. There is very little information on measuring sirenians (dugongs and manatees). Domning (1977) provides a long list of the external measurements he used to describe a dugong, *Dugong dugon*, and Murie (1874, 1885) provides a similar list for the West Indian manatee, *Trichechus manatus*. Many of the standard external measurements taken from cetaceans are also appropriate for sirenians. Measurements of sirenians should (minimally) include total length, length and width of flipper, maximum girth, width of tail, and body weight.

MEASURING TEETH

Although tooth row measurements are not considered standard external measurements, they are useful indicators of size. The most commonly taken tooth row measurements are of the upper (maxillary) tooth row.

ALVEOLAR LENGTH OF MAXILLARY TOOTH ROW

Using calipers or dividers, measure on one side of the upper tooth row from the anterior surface of the canine near its junction with the jawbone to the posterior surface of the last molar near its junction with the jawbone.

ALVEOLAR LENGTH OF MOLAR TOOTH ROW

This measurement is the same as alveolar length of maxillary tooth row, except that the canine tooth is not included in the measurement; the first reference point is the first premolar (or first molar if there are no premolars).

DISCUSSION

DATA AVAILABILITY

Measurement data are useful only if they are accessible for analysis. Data should be stored in an easily retrievable form, and large amounts of data on the same species should be published or otherwise made available. Standard measurements of mammals have been compiled in several sources, including *Walker's Mammals of the World* (Nowak 1999), *The New Encyclopedia of Mammals* (Macdonald 2001), *Grzimek's Animal Life Encyclopedia* (Hutchins et al. 2003), the American Society of Mammalogists *Mammalian Species* accounts (ASM 1969–present, www.science.smith.edu/departments/Biology/VHAYSSEN/msi/msiaccounts.html), and on the Animal Diversity Web (Myers 2001, animaldiversity.ummz.umich.edu/site/accounts/information/Mammalia.html).

Animals collected by field biologists are usually given to a museum, where they are accessioned, and the data associated with them maintained for future study. In contrast, zoological parks and other captive facilities often have no formal ties with museums. Animals that die in captivity are usually incinerated, and the associated data are placed in files that are not available to most researchers. Three primary goals of research-oriented captive facilities should be to collect standard measurement data, to maintain data files that are easily accessible to researchers both within and outside the facility, and to initiate transfer of valuable specimens to museum collections.

USING MEASUREMENT DATA

Morphological measurements taken from captive animals may differ considerably from those of wild-caught conspecifics. These differences may reflect increased inbreeding in captivity, nutritional differences between captive and wild populations, or the effects of differences in the physical environment. Whatever their causes, the source of a specimen should be considered in any application of the data. For management purposes, the differences themselves are of interest, as they can be used in assessing the effects of the captive environment. However, for those using data from captive mammals as estimates for wild conspecifics, these differences represent a potential source of error. A better understanding of phenotypic plasticity and the influence of captivity on body size would be useful in this context.

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Appendix 2

Identification and Marking Techniques

Penny Kalk and Clifford G. Rice

INTRODUCTION

While the exhibition of animals has increased in importance, especially when coupled with interpretive and educational programs, zoos also have become an essential element in efforts to conserve the earth's dwindling wildlife heritage (Conway 1967, 1969; Campbell 1978; Bendiner 1981). Consequently, mammal collection emphasis has shifted from maintaining a few specimens of a large number of species to increasing the numbers of individuals of fewer species. The decline of natural populations, combined with restrictive regulations concerning the import and export of wild animals, has made the acquisition of new specimens more difficult than it has been in the past, thereby further increasing the importance of propagating animals held in captivity.

This emphasis has resulted in a marked increase in the intensity with which zoo collections are managed. The techniques and concepts involved in this intensive management are the subjects of many other chapters in this volume. Nearly all these activities—maintaining accurate records, providing adequate medical care, applying genetic principles in breeding plans, and analyzing captive population dynamics—depend on accurately and consistently recognizing individual animals. Our objective in this chapter is to survey the techniques available to accomplish this. We have not attempted to provide a comprehensive review of these techniques, as this has been done previously by Jarvis (1968), Twigg (1975), and Ashton (1978). Rather, we have concentrated on giving the reader a description of the available techniques and an assessment of their advantages and disadvantages in the context of zoo operations. It is our hope that managers of zoological collections will be able to use this chapter to select and effectively apply the identification techniques best suited to their particular needs.

NATURAL MARKS

Individuals of many species can be recognized by natural marks alone. Such marks may be genetically controlled variations in pelage color or pattern (spots, blotches, stripes, facial markings), ridges, wrinkles, pigmentation, flaps of skin, whiskers, or other physical traits. Some examples of suitable characters are the facial markings of tigers, *Panthera tigris* (see Schaller 1967), vibrissae (whisker) spots of lions, *Panthera leo* (see Pennycuick and Rudnai 1970), skin flaps on Indian rhinoceroses, *Rhinoceros unicornis* (see Laurie 1978), flank stripes on Grevy's zebras, *Equus grevyi* (personal observation), and various features of primates (reviewed by Ingram 1978). Other characters may be acquired in the course of the animal's life, such as large scars or chipped, bent, or broken horns. Features that are temporary (antler size and configuration, small wounds and scars) are generally unacceptable for identification but may serve to distinguish individuals for short periods.

The suitability of these characters for distinguishing individuals varies greatly with the nature of the marks and the number of individuals that must be recognized. Members of a small collection may be recognized by a "Gestalt" impression, which takes into account the behavior of the animals as well as physical attributes (e.g. sex, age, body form, markings), the same means by which we recognize other humans. The greatest advantage of this method is the ease and speed with which it can be applied once it is learned. A problem with this method is that it is specific to the observer and therefore not easily transferable. It depends on memory, and is therefore unreliable. The learning process also becomes more difficult and time-consuming with increased numbers of animals.

It therefore may be necessary to employ specific characters in conjunction with, if not in place of, Gestalt recognition. Also, information on these characters needs to be permanently recorded in a manner decipherable to others. Optimally, someone entirely unfamiliar with the animals should be able to take this record and correctly identify all the individuals. Three methods are commonly used for making such a record: written descriptions, photographs, and drawings. A written description, simply stating the condition of a particular trait, is most suitable when only one or two characters can be used to distinguish an individual. Photographs are well suited to large and complex body markings such as those found on zebras, *Equus* spp., or giraffes, *Giraffa camelopardalis*. When drawings are used, it is often helpful to start with a standardized form incorporating a line drawing of the animal (or a part of it), onto which a pictorial representation of a given character can be sketched. A short written description in addition to the drawing may also be helpful.

There are 2 basic systems for choosing and processing the traits to be used in distinguishing individuals. The first is to examine each animal for one or perhaps 2 particular traits that distinguish it from all other individuals under consideration. In essence, all individuals must be examined for that particular trait to ensure that it is genuinely unique to that individual. However, once the uniqueness of the trait is established, only the unique trait needs to be recorded for each animal. Particular behavioral traits also sometimes can be used to distinguish individual animals.

The second system is to score all individuals as to the condition of a number of traits, with the object of establishing a unique combination of character conditions for each animal. This has been most frequently done with animals in natural populations. On the basis of the observed frequencies of the character conditions, it is possible to calculate the probability of a given combination of characters occurring more than once in a population of a given size. If this probability is unacceptably high, more characters must be included. Further details on the application of this system can be found in papers by Pennycuick and Rudnai (1970), Pennycuick (1978), and Hailey and Davies (1985). The strength of this system lies in its application to large, essentially unlimited populations. It may prove useful in captive breeding programs in which large numbers of animals are maintained under seminatural conditions. In the past, processing the information was too cumbersome for daily application in most zoological collections, but with the advent of digital images, notebook computers, and personal data assistants, these data-intensive operations can be performed quickly and on site.

MARKING TECHNIQUES

Many species do not have natural marks suitable for individual identification. Marking is therefore required to distinguish individuals. An ideal marking method for use in a zoological collection would have these 6 characteristics:

1. Permanent, to last the life of the animal
2. Legible at a distance (decipherable at a minimum of the flight distance of the animal), to make it unnecessary to handle an animal to establish its identity
3. Inexpensive, so as not to be a burden on the resources of the institution
4. Humane, for ethical and public relations reasons
5. Inconspicuous, to avoid detracting from the appearance of the animal
6. Fast and easy to use, to minimize stress to the animal

Unfortunately, no single marking method that meets all these criteria has yet been developed. One must therefore choose from a variety of methods that meet one or more of these criteria. Very often 2 methods are used in combination, each method chosen to compensate for the deficiencies of the other. Common marking methods currently used in zoos are described below. Some sources of marking materials and tools in the United States are given in tables A2.1 and A2.2. Readers interested in similar sources in the United Kingdom can refer to Twigg (1975) and Ashton (1978).

TABLE A2.1. Sources of equipment for marking mammals

Company	Transponders	Ear tags	Tattoos	Ear notching	Freeze marks	Temporary
American Veterinary Identification Devices	X					
Biomark, Inc.	X					
Bio Medic Data System	X					
Biosonics	X					
C. H. Dana		X	X		X	X
Digital Angel Corporation	X					
Edwards Agri-Sales, Inc.		X	X	X	X	X
Electronic ID, Inc.	X					
Handheld Computer Applications, Inc.	X					
Home Again	X					
InfoPet Identification Systems, Inc.	X					
Kyro Kinetics Associates, Inc.					X	
Nasco		X	X	X	X	X
Nasco-Modesto		X	X	X	X	X
National Band & Tag Co.	X	X	X	X	X	X
Omaha Vaccine			X	X	X	X
Stone Manufacturing and Supply			X	X	X	

TABLE A2.2. Addresses for sources of equipment for marking mammals

AVID American Veterinary Identification Devices
3185 Hamner St
Norco, CA 92860
800-336-2843
www.avid.com

Biomark, Inc.
703 S. Americana Blvd.
Boise, ID 83702
208-275-0011
www.biomark.com

Bio Medic Data Systems, Inc.
1 Silias Road
Seaford, DE 19973
800-526-2637 or 302-628-4100
302-628-4110 fax
www.bmds.com

Biosonics
3670 Stone Way North
Seattle, WA 98103
206-634-0123
206-634-0511

C. H. Dana Company, Inc
Hyde Park, VT 05655
800-451-5197

Digital Angel Corporation
490 Villaume Avenue
South St. Paul, MN 55075
800-328-0118; 651-552-6301
www.digitalangel.com

Edwards Agri-Sales, Inc.
721 Ballentine Road
Menominee, WI 54751
800-235-2038

Electronic ID, Inc.
3573 S. Nolan River Road
Cleburne, TX 76033
800-842-8725 or 817-517-7190
817-641-7991
www.Electronicidinc.com
eidl@aol.com

Handheld Computer Applications, Inc.
4220 Dayton Boulevard, Suite A
Chattanooga, TN 37415
423-870-5918
423-875-6301 fax
www.Chattanooga.net/HHCA/rf.html
brucew@chattanooga.net

HomeAgain
PO Box 2014
East Syracuse, NY 13057
866-738-4324
www.homeagainid.com

InfoPet Identification Systems, Inc.
517 W. Travelers Trail
Burnsville, MN 55337
612-890-2080
612-890-2054
info@infopet.biz
www.infopet.biz

Kyro Kinetics Associates, Inc.
PO Box 12490
Tucson, AZ 85732
520-293-5448

Nasco
901 Janesville Avenue
PO Box 901
Fort Atkinson, WI 53538
800-558-9595
920-568-5600
www.eNASCO.com
custserv@eNASCO.com

Nasco-Modesto
4825 Stoddard Road
Modesto, CA 95352
800-558-9595
209-545-1600
www.eNASCO.com
modestocs@enasco.com

National Band and Tag Co.
721 York Street
PO Box 72430
Newport, KY 41072
800-261-2035
800-261-8247
www.nationalband.com
tags@nationalband.com

Omaha Vaccine
11143 Mockingbird Dr.
Omaha, NE 68137
800-367-4444
800-242-9447
www.omahavaccine.com

Stone Manufacturing and Supply
1212 Kansas Avenue
Kansas City, MO 64127
816-231-4020
816-241-3336
www.stonemfg.net
cust.serv@stonemfg.net

Newborn animals should be marked as soon as possible, but there are some constraints as to when this can be done. For instance, in ungulates, one should ensure adequate time for the mother-infant bond to be established. At the Bronx Zoo, New York City, we have found that 24 to 48 hours is a sufficient delay, at which time the infant still can be easily hand caught (we also give a neonatal medical exam concurrently). For primates, we recommend waiting until an infant is spending some time moving about independently before marking it. When any marking technique that breaks the skin is used, the site should be cleaned well with alcohol and, in hairy species, excess hair clipped before marking to reduce the possibility of infection. Marking tools and tags should also be disinfected before each application.

ESTABLISHED MARKING METHODS

In this section we describe marking methods that are standardized and have been employed in zoos for some time.

TRANSPONDERS (PIT TAGS)

By far the biggest development in accepted marking techniques within zoos in the last decade has been the evolution in the use of transponders. Also referred to as passive integrated transponders (PIT tags), radio frequency identification devices (RFID), or simply microchips, the use of transponders has evolved from a secondary, developing marking method used by some zoos to the primary marking method used by most zoos. At the Bronx Zoo, transponders are the primary and often only method we use for marking our bats, small mammals, rodents, and many primate species. Likewise, federal and state regulatory agencies have come to recognize transponders as a primary means of permanently identifying mammals.

Transponders are tiny microchips with coiled antennae encased in rod-shaped glass capsules. The transponder has no internal power source. When scanned by a reader wand that emits low-frequency radio waves, the transponder resonates a particular frequency that is received by the reader and displayed in alphanumeric code. Each preprogrammed (during manufacture) transponder code is unique, with over 34 billion combinations available.

Transponders are available in several sizes, ranging from 2 mm in diameter by 10 mm long (roughly the size of a grain of rice) to 3.5 mm in diameter by 32 mm long. The larger the transponder, the greater the distance from which it can be read. The read range for all the currently available transponders is very limited, ranging from less than 8 cm for the 2-by-10-mm transponders (Fagerstone and Johns 1987; Thomas et al. 1987; Schooley, Van Horne, and Burnham 1993) to approximately 16 cm for the 3.5-by-32-mm transponders. As the larger transponder sizes are unacceptable for many mammals and increase the read range by only centimeters, we recommend the smaller 2-by-10- to 12-mm transponders.

Prepackaged by the manufacturer in sterilized implanter needles, the transponder can be implanted in the muscle or under the skin. At the Bronx Zoo, we implant mammals subcutaneously. Transponder functionality should be verified both before and after implantation. After the implant site is cleaned with alcohol, loose skin is raised between the thumb and forefinger and the hair is spread to expose the skin. (We do *not* recommend shaving the site.) The implanter needle is placed bevel-up at an approximately 45° angle to the skin surface, and the skin is pierced with the needle. The implanter needle is then positioned almost parallel to the skin, and the transponder is injected under the skin. The needle should be carefully withdrawn and finger pressure applied to the implantation site for approximately 30 seconds. If necessary, the chip can be physically manipulated away from the point of insertion. The implantation site then should be scanned by the reader to verify both successful implantation and the transponder's unique code. Occasionally, the needle will leave a wound; if it does, we recommend sealing the wound with an adhesive skin bond (e.g. Nexaband). The site of implantation as well as the transponder's unique code should be carefully recorded.

When this technique has been properly applied, neither infection nor internal migration of the transponder implants has been a problem (Fagerstone and Johns 1987; Thomas et al. 1987; Ball et al. 1991). Since 1987 we have implanted over 2000 mammals at the Bronx Zoo with ID transponders and have had no known health problems associated with chip migration or infection.

Transponders fail through either lack of retention or malfunction at roughly the rate of 5% (Schooley, Van Horne, and Burnham 1993; Taylor, Emerson, and Wagner 1993; Harper and Batzli 1996; Braude and Ciszek 1998; Rogers, Hounsome, and Cheeseman 2002). While transponders can be retained and fail to function, or only read sporadically (Schooley, Van Horne, and Burnham 1993; Rogers, Hounsome, and Cheeseman 2002), most transponder failures are the result of lack of retention (Schooley, Van Horne, and Burnham 1993; Taylor, Emerson, and Wagner 1993; Harper and Batzli 1996; Braude and Ciszek 1998; Conill et al. 2000; Rogers, Hounsome, and Cheeseman 2002). Schooley, Van Horne, and Burnham (1993) found that most transponders that failed due to lack of retention were lost within 10 days of tagging. Transponder loss can be reduced by manipulating the chip away from the point of insertion or by closing the hole of insertion with surgical adhesive (Braude and Ciszek 1998).

Increasingly, transponder chips manufactured by different companies are becoming compatible; most chips now operate at 125 KHz and manufacturers are producing interchangeable readers. Some of the older chips do operate at 400 KHz. If an individual animal is transferred from one institution to another and the transponder systems are not compatible, this can considerably diminish the practical usefulness of the transponder as a permanent ID. The continued trend toward standardization of transponder equipment is critical to the usefulness of this identification technique.

Because of the limited read range of transponders, it is important to standardize and/or clearly record sites of implantation. At the Bronx Zoo, we implant most large mammals at the base of the left ear, and medium to small mammals between the shoulder blades to the left of center. There are some exceptions. The thick skin of species such as the slow loris, *Nycticebus coucang*, and rock hyrax, *Procavia capensis*, makes quick and relatively atraumatic scapular implantation difficult. We implant these animals on the left hip.

There are many methods used by zoos to ameliorate the limited read range of transponders. At the Denver Zoo, many species are trained to present the body part where the transponder has been inserted for reading of the chip (D. Leeds, personal communication). Likewise, callitrichids at the Bronx Zoo are trained to sit at their station while they are scanned with the reader wand (C. Wilson, personal communication). The low-frequency radio waves used to read transponders can penetrate most solid objects except those made of metal. Consequently, the San Diego Zoo reads transponders on mammals crated in wooden and plastic crates (C. Simerson, personal communication).

The major disadvantages of transponder identification are as follows:

1. The equipment is expensive. A basic transponder setup—implanting tool, scanner/reader, battery charger, and carrying case—costs approximately $800.00. The cost of an individual transponder chip varies from $5.00 to $9.00, depending on the supplier and the quantity purchased. Although by far the most expensive marking technique, the cost of PIT tagging has decreased over the last decade while performance has increased.
2. Transponders are not legible at a distance. Individual training, crating, or restraint of the animal is usually required to read them.
3. Transponders have a failure rate of about 5%. Careful implantation technique—insertion of the chip well away from the insertion hole—should reduce transponder loss. Those who depend solely on this method should probably implant transponders at 2 sites.

Transponder ID chips show the promise of providing a genuinely permanent marking method. They are humane and extremely inconspicuous.

EAR TAGGING

A variety of ear tags have been developed by the livestock industry and are useful for many wild ungulate species. Ear tags come in numerous sizes and colors and may have numbers printed on them or transponders encased inside. The catalogs provided by C. H. Dana and Nasco (see table A.2.2) give good descriptions of many tag types. Plastic tags (e.g. Rototag, All Flex, DuFlex) are typically made up of a front and a back piece, which may be different colors. One piece has a post with a sharpened point that pierces the ear as the tag is attached. The other piece has a hole to accept the post, and the 2 pieces lock together as the tag is applied. A special tool is used to align the 2 pieces and to provide the force necessary to pierce the ear and push the post into the hole. Numbered metal tags are also available in several sizes. These tags are applied with pliers that flatten a hollow rivet to secure the tag. Smaller metal tags designed for fish fingerlings have been used to mark such animals as rodents and bats (e.g. Twigg 1975; Stebbings 1978), and Le Boulenge-Nguyen and Le Boulenge (1986) have adapted surgical wound clips for marking these animals. Generally, plastic tags are preferable, as they seem to be less likely to result in infection.

On young animals with thin ears, the tag should be affixed to the thickest cartilage portion of the ear, such as the lower half, near the base. On the other hand, it may be difficult to pierce some parts of the ears of large, mature ungulates, in which case it may be necessary to attach the tag to a thinner section of the ear or to precut the puncture site with a clean scalpel. For ungulates of any age, care should be taken not to puncture any large blood vessels.

The selection of tags that are both legible at a distance and inconspicuous will depend on the circumstances. For example, large, 7.5-by-7-cm numbered black tags are quite inconspicuous on large, hairy-eared bovids such as American bison, *Bison bison*, or yak, *Bos grunniens*, but would be quite noticeable on the relatively hairless ears of gaur, *Bos gaurus*. Smaller numbered tags are less conspicuous, but may not be legible at a distance.

Several tagging strategies are possible. A unique color combination, such as red/blue or white/green, can identify each animal. If possible, one should avoid using 2 colors that may become difficult to distinguish if they fade, such as blue and green or yellow and orange. Colors should contrast with the surrounding area (e.g. avoid black on the inside of the ear of Thomson's gazelles, *Eudorcas thomsonii*). If numbered tags are used, a color that is inconspicuous against the surrounding area can be chosen. At the Bronx Zoo, the ear that is tagged indicates the sex of the individual: females are tagged in the left ear and males are tagged in the right. Another strategy is to use a different color each year so that the age of an individual can be verified at a glance. Tagging both ears with different color combinations increases the number of possible combinations. Alternatively, one may tag both ears with the same color combination so that even if the tag is lost from one ear, the animal can still be identified.

When properly applied, ear tags meet most of the criteria for the ideal marking method. They can be "read" at considerable distances (especially with the aid of binoculars); they are inexpensive, quick, and easy to apply; they cause little trauma; and they are usually ignored by the general public. The biggest problem with ear tags is their lack of permanence. They may be lost by being torn out or by falling out when the front and back pieces separate. Problems may ensue when adult-size tags are placed on newborn animals. These problems can be alleviated by waiting for tissues to mature. For instance, at the Bronx Zoo we ear-tag Himalayan tahr, *Hemitragus jemlahicus*, at an age of 6 to 8 weeks, rather than during the neonatal veterinary exam (at which time they are transpondered).

TATTOOING

Tattooing is another technique developed by the livestock industry that has found wide application in zoo and wildlife marking programs. A tattoo is made by rubbing ink into a superficial wound inflicted in the animal's skin. As the wound heals, the ink remains in the skin and is visible for many years. Areas of skin with little or no hair are usually chosen to facilitate tattooing and reading the tattoo. Common sites are the ear (usually the inside), the inside of a lip, the inside of a thigh, the chest, the bottom of a foot, or (on bats) the wing or tail membrane.

Tattoos may be applied with a small, battery-powered needle or with tattooing pliers. These pliers have interchangeable units (of various sizes) in which stout needles spell out letters or numbers. As the pliers are compressed, the needles puncture the skin. The pliers are then withdrawn and tattooing ink is rubbed into the holes. While tattoo pliers are effective and easy to use, one must have access to the back as well as the front of the tattoo site. They are quite effective for tattooing ears and wing membranes. Attempting to tattoo small ears, however, may result in extensive damage and atrophy of the ear (e.g. sugar gliders, *Petaurus breviceps*). On other parts of the body, tattoo pliers may be used if a fold of skin can be pulled up sufficiently to allow tattooing through the fold. In other cases, an electrically powered needle is employed to "write" the numbers or letters. Effective tattoo application with an electric needle requires practice. With the drill running, the tip of the needle is dipped into the ink, the drill is firmly pressed against the skin, and the numbers are "engraved" on the tattoo site.

In practice, tattooing is inexpensive, relatively permanent, generally acceptable from a humane standpoint, and inconspicuous. However, tattoos usually cannot be read from a distance, and the marks may fade with time, depending on the species. For instance, MacNamara et al. (1980) found that tattoos in wing membranes of fisherman bats, *Noctilio leporinus*, remained legible for more than 10 years, whereas those on hammer-headed bats, *Hypsignathus monstrosus*, were effaced after only a few months. Tattoos on young animals will grow with the animal. The larger symbols may be easier to read, but the ink will also diffuse somewhat, making the marks less distinct. The following stratagems should increase the life of a tattoo:

1. Either choose a relatively hairless tattoo site or closely shave or clip the hair.

2. Thoroughly clean the site with alcohol to remove all oil and wax.
3. Let the alcohol dry completely before applying the ink.
4. Use green ink. Green ink contrasts with the background on most ears and has proved to be the most readable over time. (It is tempting to use white ink on the black inner ears of ungulates such as blackbuck, *Antilope cervicapra*, but this has not proved effective.)
5. Apply ink before and after applying the tattoo instruments. Once the tattoo punctures have been made, thoroughly rub in the ink for at least one minute.
6. Hold the animal securely while applying the tattoo to prevent scratching the animal and blurring the tattoo.
7. Be certain that the opposite side of the pliers is padded to ensure adequate penetration of the needles.

EAR NOTCHING

Mammals can be permanently marked by cutting U- or wedge-shaped notches out of the ear margins. Special plier-punches are manufactured for this purpose. The numbers 1 through 99 can be coded by cutting one to 4 notches (fig. A2.1; Schmidt 1975). The numbers not shown in the figure are represented by the sum of 2 others (e.g. 1 + 4 = 5, 20 + 70 = 90), so that it is not necessary to notch either ear more than twice. When the notch representing 4 (or 40) is made, care should be taken to ensure that there is no possibility of confusing it with a notch for 7 (or 70), and vice versa. In small mammals, one strategy is to notch ears at only 3 sites (1, 2, and 4; 10, 20, and 40), thus eliminating this problem (C. R. Schmidt, personal communication). Some animals, such as saddleback tamarins, *Saguinus fuscicollis*, have ears with irregular margins, and this may cause difficulty in deciphering notches. According to C. R. Schmidt (personal communication), the European and North American ear notch systems are reversed with reference to which ear bears the notches representing 1–9 and which 10–90 (e.g. notches for 12 in Europe would be read as 21 in North America). Figure A2.1 shows the North American system.

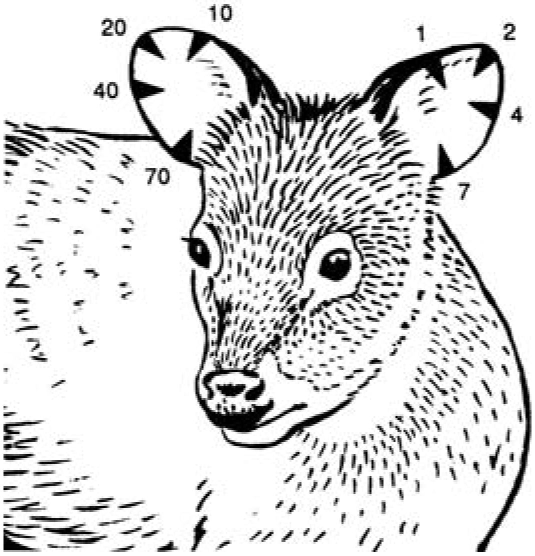

Fig. A2.1. Ear notch sites for numeric coding. With one or two notches per ear, the code number (1B99) is the sum of the notches for both ears. For example, (40 + 10) + (2 + 7) = 59.

The ear is cleaned with alcohol before notching, and on long-haired mammals, the hair at the notching site is clipped. The size of the notch will vary with the size and structure of the ear, the amount of hair on the ear margins, and the distance at which the notches need to be discerned. Judging the minimum size needed takes some experience, since the definition of notches decreases with time as the wound heals and hair (if any) grows in the notch. Schmidt (1975) recommends notches 7 mm in length for vicuña, *Vicugna vicugna*. Notching the ears of adult animals can lead to excessive bleeding, which can be curtailed by applying direct pressure, a coagulant such as ferric subsulfate (Moncel's) solution, hemostats, or versaclips (Carnio and Killmar 1983).

Ear notches are permanent, but may be obscured if subsequent injuries leave indentations in the ear margins. Notches cannot always be read at long distances, but they are inexpensive and inconspicuous. Ear notching may be objectionable on humane grounds. Injuring an animal in this or any other way also incurs the risk of infection or exposure to pathogenic agents.

COLLARING

Collars have been used to mark both wild and domestic animals. A wide variety of designs have been developed (Twigg 1975; Stonehouse 1978; Day, Schemnitz, and Taber 1980). Common techniques include color-coding the collars, painting them, or attaching numbers or other symbols to them.

The greatest advantage of collars is the ease with which they can be read. They are also inexpensive and humane. On the other hand, collars are often not permanent (on long-lived animals), and they are very conspicuous. For these reasons, collars are useful for animals that are the subject of observational study, but are not on public display. Snug collars made of dog-collar chain, coded with sections of aluminum and copper tubing, have been used to mark hanuman langurs, *Semnopithecus entellus*, at the San Diego Wild Animal Park, California (R. Massena, personal communication). Bats are occasionally collared at the Denver Zoo (D. Leeds, personal communication). Similarly at the Bronx Zoo, we use nylon-web puppy collars to identify off-exhibit ring-tailed lemurs, *Lemur catta*.

Collars should be carefully fitted—loose enough to not constrict the airway and snug enough that they cannot be slipped off. Collars of any type should be monitored regularly to ensure that they do not wear or cut into the skin.

TEMPORARY MARKING

Dyes (e.g. Nyanzol), bleach, colored plastic adhesive tape, paint sticks, spray paint, and guns that shoot a ball of paint up to 15 m are useful tools for temporarily marking animals. Horns and antlers can be marked with paint or colored adhesive tape, or paint can be applied directly to the hide or fur. Most of these mark the animal for less than a month, but serve well to mark animals for veterinary treatment and shipment. Site-specific hair clipping is also suitable for temporary marking. Human hair dye (i.e. Lady Clairol) has been used to dye the fur of pinnipeds, leaving a mark visible until the next molt (J. L. Dunn, personal communication). This technique is applicable to other species as well.

DEVELOPING MARKING METHODS

In this section we describe marking methods that show promise for use in zoos, but have not as yet seen widespread application.

FREEZE MARKING

Freeze marking, or cryobranding, is a permanent marking technique that is gaining acceptance among horse (*The Morgan Horse* 1982) and cattle owners (Newton 1978). It has been used on mammals ranging in size from neonatal mice, *Mus musculus*, to African elephants, *Loxodonta africana* (see table A2.3). This promising marking method is, however, still in the developmental stage in the zoo community. Indeed, surveys of marking techniques for wild animals in captivity (Jarvis 1968; Ashton 1978; Carnio and Killmar 1983) did not mention freeze marking.

Freeze marks can be small and intricate. Ear marking using a hard backing to support the ear while the mark is being applied has been successful (Pienaar 1970; Farrell and Johnston 1973). The mark may consist of letters, numbers, or other symbols. Farrell (Farrell and Johnston 1973) developed a numeric system based on a right-angle mark and a straight line. These symbols at different orientations plus an underlining bar can represent any integer (fig. A2.2). Farrell also developed an

TABLE A2.3. Summary of freeze branding techniques

Refrigerant	Animal	Duration	Reference
Dry ice and alcohol (−70°C)	African elephant	2 × 2 min	Pienaar 1970
	Cow (adult)	30 sec	Farrell, Kroger, and Winward 1966
	Dairy cow (age >18 mo)	30 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age >18 mo)	35 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age 9–18 mo)	25 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age 9–18 mo)	30 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age 4–8 mo)	20 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age 4–8 mo)	25 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age 2–3 mo)	15 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age 2–3 mo)	20 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age <2 mo)	10 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age <2 mo)	15 sec	Farrell, Hostetler, and Johnson 1978
	White-tailed and mule deer	20–30 sec	Day 1973
	White-tailed deer	20–25 sec	Newsom and Sullivan 1968
	Dog (adult)	10 sec	Farrell, Kroger, and Winward 1966
	Dog (adult)	4–10 sec	Farrell and Johnston 1973
	Dog (puppy)	3–6 sec	Farrell and Johnston 1973
	Wombat	30–45 sec	Dierenfeld, pers. comm.
	Cat	10 sec	Farrell, Kroger, and Winward 1966
	Fox squirrel	25–40 sec	Hadow 1972
	Abert's squirrel	25–40 sec	Hadow 1972
Dry ice and alcohol	Hooded rat	20–35 sec	Hadow 1972
	House mice (adult)	20–35 sec	Hadow 1972
	House mice (3–6 day)	7–10 sec	Hadow 1972
	Degu	28 sec	Rice and Kalk 1991
	Patagonian cavy	18 sec	Rice and Kalk 1991
	Mouflon	12 sec	Rice and Kalk 1991
	Pere David's deer	30 sec	Kalk, unpub.
	Mongolian Wild Horse	30 sec	Kalk, unpub.
Liquid nitrogen (−195°C)	Horse (adult)	ca 20 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age >18 mo)	20 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age >18 mo)	25 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age 13–18 mo)	15 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age 13–18 mo)	20 sec	Farrell, Hostetler, and Johnson 1978

(*continued*)

TABLE A2.3. continued

Refrigerant	Animal	Duration	Reference
	Dairy cow (age 10–12 mo)	12 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age 10–12 mo)	17 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age 6–9 mo)	10 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age 6–9 mo)	15 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age 2–5 mo)	7 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age 2–5 mo)	12 sec	Farrell, Hostetler, and Johnson 1978
	Dairy cow (age <2 mo)	5 sec	Farrell, Hostetler, and Johnson 1978
	Beef cow (age <2 mo)	10 sec	Farrell, Hostetler, and Johnson 1978
	Cow (age 2–10 weeks)	10 sec	Macpherson and Penner 1967a
Liquid nitrogen	Pony (adult)	35 sec	Farrell, Hostetler, and Johnson 1978
	Sheep and goats (adult)	ca 20 sec	Farrell, Hostetler, and Johnson 1978
	Sea lion	18–20 sec	Ensley, pers. comm.
	Seal (age 14 mo)	7 sec	Macpherson and Penner 1967b
	Seal (age 2 mo)	5 sec	Macpherson and Penner 1967b
	Dog (adult)	8 sec	Farrell, Hostetler, and Johnson 1978
	Beaver (6-10 mo)	20 sec	Zurowski 1970
	Beaver (adult)	2 × 20 sec	Zurowski 1970
	Wombat	20 sec	Dierenfeld, pers. comm
	Mouflon	8 sec	Rice and Kalk 1991
Freon 12 (−30°C)	Horse	9 sec	Farrell, Farrell, and Patterson 1974
	Brown lemur (juvenile)	6–8 sec	Miller, Berglund, and Jay 1983
	Dwarf mongoose	5–8 sec	Rood and Nellis 1980
	Rats	10 sec	Lazarus and Rowe 1975
	Mice	4–10 sec	Lazarus and Rowe 1975
Freon 22 (−41°C)	Horse	6 sec	Farrell, Farrell, and Patterson 1974
Liquid petroleum (−42°C)	Dog	5–6 sec	Farrell, Farrell, and Patterson 1974

Note: For scientific names, consult the appropriate references.

"anatomical dot" system for coding numbers (fig. A2.3; Farrell, Milleson, and Reynolds n.d.)

Freeze marking is accomplished by cooling the skin to such a degree that the melanocytes in the hair follicles are permanently destroyed. As a result, subsequent hair growth in these areas lacks pigmentation (i.e. the hairs are white). The skin is cooled by immersing a marking instrument in liquid nitrogen or a mixture of crushed solid carbon dioxide and 95% alcohol (ethyl, methyl, or isopropyl) and then applying the instrument to the skin of the animal. Rice and Kalk (1991) found that the dry ice and alcohol refrigerant had a broader exposure latitude and produced better marks. Alternatively, the skin may be cooled by exposure to freon or liquid petroleum (Farrell, Farrell, and Patterson 1974). The use of freon, however, is not recommended, considering the potential for degradation of the atmospheric ozone layer.

Freeze marking is most commonly done with a copper instrument, although brass and bronze can also be used (fire brands are not suitable; Farrell, Hostetler, and Johnson 1978). The instrument should have a depth of at least 2 to 3 cm. It is immersed in the refrigerant bath held in a suitable container (styrofoam for dry ice and alcohol, urethane or insulated metal for liquid nitrogen). When the refrigerant stops boiling and only a stream of bubbles rises from the instrument, the instrument has reached the temperature of the bath. The site to be marked is prepared by clipping the hair and wetting the area with alcohol. Farrell, Hostetler, and Johnson (1978) recommend close-clipping blades (no. 40 Oster or E8-1-SUR Sunbeam) for dry ice and alcohol marking and coarser clipping (no. 10 Oster or 83-84AU Sunbeam) when liquid nitrogen is used. The instrument is usually applied to a well-fleshed area such as the hip or shoulder to ensure even contact (uneven contact results in distorted, broken marks). Application time varies greatly among species (table A2.3). Excessive application time kills the hair follicles rather than just the melanocytes, and the mark becomes a scar that may or may not be legible. Insufficient contact time results in a patchy mark (if any).

Immediately after the instrument is removed, the affected skin appears frozen. As the tissue thaws, the mark fades and a reddened swelling appears. This remains for one to 2 days, after which a scruffy, blistered mark develops. After about 3 weeks the hair and superficial epidermis are shed, leaving a bare mark. Depending on the hair growth cycle of the animal, white hair should appear after one to 3 months.

The major disadvantages of freeze marking are as follows:

1. Combinations of proper refrigerant and application time are not yet well established for a broad range of species.

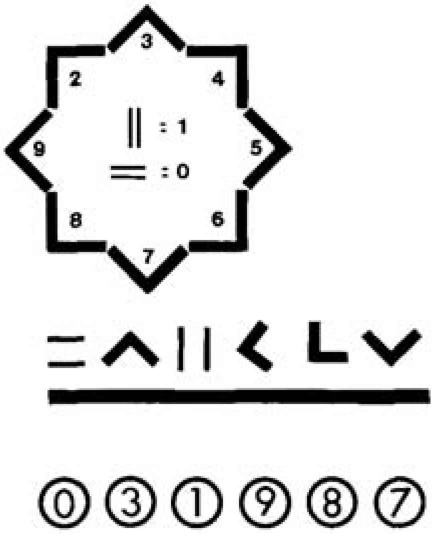

Fig. A2.2. The angle code for freeze marking. The orientation of the angle or parallel bars represents an integer (*above*), as shown in example (*below*). (Adapted from Farrell and Johnston 1973.)

2. The animal must be restrained for the duration of the contact time. A good mark depends on proper restraint.
3. Commercially marketed marking instruments often make marks that are too large to be inconspicuous in a zoo.
4. The equipment necessary for containing the refrigerant is cumbersome.

These problems will diminish as the method becomes more refined. Conservatively used, the symbols developed by Farrell (Farrell and Johnston 1973) can appear to be random natural markings to the zoo visitor. As techniques for the application of pressurized refrigerants and liquid petroleum become better established, the need for bulky equipment may be eliminated.

Freeze marking has the potential of meeting many of our ideal marking method criteria. It is permanent, can be legible at a distance, and is thought to be painless; the rapid freezing of the skin acts as a local anesthetic (Farrell and Johnston 1973) and inactivates local nerve endings for about 4 weeks (Farrell, Hostetler, and Johnson 1978). The dry ice–alcohol and freon refrigerants are inexpensive.

CHARACTER PRINTS

A number of external morphological characters that are unique to individuals can be transferred to paper or other media to provide a permanent record, as is done with the dermal ridges (e.g. fingerprints) of humans. Phillips-Conroy, Jolly, and Nystrom (1986) review methods for recording dermatoglyphs (handprints and footprints) of primates. They recommend smearing the skin surface sparingly with powdered graphite and pressing wide cellophane tape onto it. The tape is then peeled off and stuck to a labeled index card. Solis and Maala (1975) describe a method for taking ink prints of the skin patterns of cows, *Bos taurus primigenius*, and water buffalo, *Bubalus bubalis arnee*. Comparable prints can be made of hair growth patterns, such as the whorl (cowlick) on the forehead of a horse. Baclig (1952) notes 23 common locations of such patterns on horses. A method for diagramming the location of cowlicks is given in *The Morgan Horse* (1984).

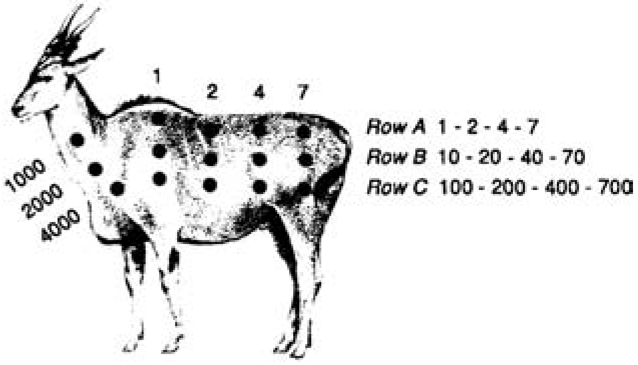

Fig. A2.3. The anatomical dot code system for freeze marking. As with ear notches (fig. A2.1), the sites marked are summed to give the code number. (Adapted from Farrell, Milleson, and Reynolds, n.d.).

The characters mentioned above are permanent, but they are not discernible at a distance. Taking the prints is inexpensive in terms of materials but is time consuming, since most animals have to be immobilized. The procedures are not objectionable on humane grounds, and since they involve natural characters, conspicuousness is not a concern. For these reasons, character prints may be useful for long-term records of individual identity, but are not suitable for daily recognition.

SUMMARY AND CONCLUSIONS

The lack of a universally suitable technique has resulted in an array of methods for recognizing individual animals. Each method has its strengths and weaknesses, and the selection of the most suitable method(s) will depend on the species and the circumstances. Recognition by natural marks is particularly well suited to small collections of animals with easily distinguished characters. Over the last decade, transponders have become a widely employed marking technique. They can be used to mark every order of mammal. Transponders and tattoos meet most of our criteria for the ideal marking method. Transponder chips have begun to replace tattoos because of their greater permanence. At present, neither transponders nor tattoos can be read from a distance, so they are often used in combination with other methods, such as ear tags. If the logistical difficulties involved in freeze marking are surmountable, it should find wide application in zoos.

Freeze marking may also be the best method for species such as pinnipeds and cetaceans that are difficult to mark by other means, although ear tags can be attached to the flippers (or fins) of these species (Norris and Pryor 1970; J. L. Dunn, personal communication). Bats are another group of animals that is difficult to mark.

As with most aspects of zoo animal husbandry, there is a great need for systematic investigations of marking methods.

Most marking techniques have been adopted on the basis of subjective assessment, thus confounding actual performance with other subjective factors such as personal bias. Such investigations require a long-term commitment, because permanence is a major criterion of a good marking method.

The thermodynamics and physiology of freeze marking warrant further research. Trials with domestic animals indicate a correlation between body size and exposure time, but there is also considerable variation among and within species (see table A2.3). In the context of zoos, conducting freeze-marking trials for animals of various ages of all species is impractical. Systematic investigation of the various factors influencing effective freeze marking is needed to allow appropriate exposure times to be predicted. Such factors include hair density, skin thickness, follicle structure, subcutaneous fat thickness, width of the instrument, and ambient temperature. Coupled with knowledge of the histological changes that occur with freeze marking, these factors could be incorporated in a thermodynamic model suitable for determining exposure times.

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Appendix 3

Records, Studbooks, Regional Zoo Associations, and ISIS

Laurie Bingaman Lackey

INTRODUCTION

Wild animals have been held in captivity in zoological gardens for hundreds of years. Yet until relatively recently, records of any sort, much less the detailed data necessary to modern management practices, were not maintained. Wild animals were considered unlimited resources, and more were captured as needed. Few older zoos can produce precise specimen data from the beginning of the twentieth century. Where records do exist, they are tantalizingly incomplete—for example, a California condor, *Gymnogyps californianus*, was held at a North American zoo for 45 years, but was never sexed—at least in the record.

Many zoos today have difficulty retrieving detailed data for specimens held during the 1950s and 1960s. Often, these animals may form the founder genetic base for zoos' current populations and may lead to uncertainty about the relationships between current collection animals. This situation has been improving greatly in recent years, and must continue to improve. Contemporary zoo-based species conservation programs are critically dependent on quality specimen records.

RECORD KEEPING

Record keeping must be an integral part of all zoological husbandry programs. Many captive populations are now "insurance policies" against extinction in the wild. Dwindling wild populations also means that most future zoological exhibit specimens will descend from today's captive populations. With increasingly more stringent regulations concerning interstate and international shipping, disease monitoring, and endemic species policies, some species can no longer be acquired easily, if at all. Any specimens held now and their future descendants are the only possibilities for future display, so they must be carefully managed in order that these populations persist.

In 1990, two-thirds of ISIS-registered zoological mammal specimens were captive bred (ISIS 1990). By 2007, this amount had risen to 89% (ISIS 2007). Only permanent record systems on individually identified specimens will tell us what we have and what its pedigree is.

Prior to 1974 and the founding of the International Species Information System (ISIS), record-keeping standards varied widely, even though many national regulatory agencies require retention of accurate records and documents related to interstate and international commerce in and transportation of animals. In many instances, critical data on zoological specimens were known only by the director, curator, or keepers involved with the events and were never recorded. Accordingly, the accuracy of these unwritten "data" faded over time or was lost following personnel changes. There were no uniform record-keeping procedures among zoos, and in the case of very large facilities, data maintained by divisions within a single institution were often contradictory.

As a matter of standard best practice, every specimen entering a collection, even if only for a few days, should be formally accessioned, permanently identified, and documented, with special attention given to information on its original provenance. This includes specimens acquired from other institutions and those accepted from the public as well as those born within the collection or captured in the wild. Furthermore, the records should include all captive-born young, regardless of whether they survive to maturity, are stillborn, die shortly after birth, or are represented only by abortions or premature fetuses. Such data may be the first indication of problems stemming from inbreeding or management. For similar reasons, information on clutch sizes, fertility, and hatch rates should be recorded and retained for egg-laying species.

CRITICAL DATA

Specimen identification. Each specimen should receive a unique accession number individually identifying it within the zoological collection. Accession numbers should be entirely numeric to facilitate computerization. When possible, these numbers should be sequential, i.e. begin with specimen 1 to indicate the first animal entering the collection and progress through 2, 3, 4, 5 . . . *n* to the present. Use of alphabetical or other non-numeric characters is not recommended, as these have often caused confusion (i.e. O-Oh versus 0-Zero, B versus 8) and sorting difficulties. Encoding other information such as species, sex, or age into the accession number is generally not desirable. Attempts to keep the numbers in strictly chronological order should be avoided—this was necessary in early pencil-and-paper records systems simply to allow finding the animal, but modern computerized systems allow manipulation of the data in many ways.

Sex. The sex of all specimens should be noted, even if only to indicate that no determination has yet been made. Where sex is confirmed surgically or by laboratory analysis, this should be noted, including dates and methods used. If the sex is found to have been incorrectly determined, record the correction, but do not remove the old information.

Parentage. The accession numbers and associated institutions for sires and dams of captive-born offspring should be recorded, regardless of whether they were born at the current holding institution or at another location. In this way, pedigrees can be constructed when genealogies need to be examined. When a studbook exists for the taxon, the assigned studbook numbers of the parents should also be recorded, for the same reason.

If there are multiple possible candidates for parentage, i.e. a species kept in a herd situation, all possible parents should be recorded. If known, also record notes with the parent IDs on likelihoods, such as "current herd sire" or "dominant female" or "seen nursing."

Age. The specimen's age on arrival should be recorded, along with an indication of whether it is accurately known or is an estimate. If the actual birth date is known, this is all the information that is necessary. If the date is an estimate, indicate the basis, such as size or pelage. If no reasonable estimate can be made, even to within a several-year time frame, then indicate the current life stage (i.e. juvenile). Age data are necessary for the important demographic analyses applied to captive populations.

Source and provenance. If the specimen is acquired as the result of a birth or hatch into the collection, this should be recorded. As previously stated, it is very important that all reproductive events be documented, no matter at what stage they terminate.

The origin and date of arrival for wildlife acquired from other locations should be recorded. Whenever possible, it is vital to record accession numbers and any other identifiers assigned to this same specimen by previous institutions. It is also important to record information on any dealers, brokers, or transport firms that may have handled the specimen; this may be the only clue available to confirm the origin or identity of an animal.

Whenever possible, data on the geographic origin of specimens, whether wild caught or captive bred, should be obtained and recorded. Institutions will know what they have only when specimens can be traced through any captive pedigree back to the place of wild capture of their ancestors. This is especially important when both pure and hybridized specimens of a species are held. Some hybrid young are intermediate in appearance between their 2 parents and may be easily distinguished from them. The young of other species may not be distinguished readily from either parent and, after multiple generations, become impossible to distinguish from pure specimens.

Disposition. The destination and date of shipment for wildlife sent to other locations should be recorded. If possible, the accession number and/or other identifiers assigned by the receiving institution should be recorded, both to confirm that the animal sent was the animal that arrived, and to use later in specimen tracing.

If disposition is by death, the circumstances of death and any causal information or necropsy findings should be recorded, along with the names and accession numbers of any museums, educational institutions, or other facilities receiving all or parts of the specimen (skin, skull, skeleton, etc).

Additional data. Some important data are specific to particular taxa. Among the more common categories of information vital to both identification and management are the types and locations of transponders, tattoos, tags, and bands; house names, such as "Twiga"; exhibit locations, which will allow linking to possible mates or disease contacts; and regional and international studbook numbers. Important behavioral considerations, especially rearing techniques (i.e. parent or hand reared), should be noted. The certificate number of any international, national, state, or provincial permits used to acquire or remove the wildlife should be listed for ease of reference.

STUDBOOKS

HISTORY

An important exception to the generally poor record-keeping practices of the past has been the compilation and maintenance of international and regional species studbooks. *The General Stud Book for the Thoroughbred Horse* was the world's first studbook, published in 1791 by James Weatherby. It included the pedigrees of 387 thoroughbred mares, each of which could be traced back to one of 3 foundation sires: the Darley Arabian, the Godolphin Arabian, or the Byerly Turk. This studbook is still published in England by Weatherby and Sons, Secretaries to the English Jockey Club.

In 1930, the last wild populations of the Caucasian subspecies of the European bison, *Bison bonasus caucasicus*, were extirpated, just a few years after the loss of the nominate race, *B. b. bonasus*, which was extinguished by poachers in Poland in 1922 (Slatis 1960). Fearing that the captive population of Europe's only remaining wild bovid would suffer a similar fate without careful monitoring, European zoo directors established an international studbook in 1924 with data obtained after World War I by Heinz Heck Sr. (Mohr 1968). This pedigree was first published in 1932 (von der Gröben) and became the first studbook designed specifically for the zoological park community. In 1959, a similar studbook for the Asian wild horse, *Equus przewalskii*, also extinct in the wild, was published by Mohr (1959). Since 1965, studbooks have become an integral part of the management of endangered species living in zoological parks.

DEFINITION

It is fortunate and noteworthy that the zoological community studbook standard also contains date-of-death information not normally included in domestic-breed registries. Because of this important addition, zoological studbooks contain the minimum critical data necessary for both genetic and demographic management of small populations.

A studbook and a registry are not the same. A studbook numerically identifies individual specimens and tracks them throughout their entire lifetime. A registry may only summarize the inventory at various locations, may not distinguish between individual animals, and does not include death information. As a result, the quality and usefulness of the data in a registry are significantly inferior to those in a studbook.

Studbook keeping involves the compilation of genealogical and demographic data covering a species' history in captivity. This task includes identifying each individual specimen, to permanently record data on

- origin and date of arrival from the wild;
- possible relationships to other animals captured at the same time;
- parentage and date of birth (if captive born);
- sex;
- dates of transfer to subsequent owners and holders;
- address and contact information for these facilities;
- important locally assigned identifiers, including accession numbers, house names, transponders, tags, etc.; and
- date and cause(s) of death.

Some studbooks also include supplementary information, such as rearing technique, levels of inbreeding, and so forth. International studbooks must be updated annually and republished in their entirety every 3 years. Regional studbook standards are often even more stringent, but vary with the region.

Because captive population sizes and fecundity rates and the number of facilities involved vary greatly from species to species, the task of keeping a studbook ranges from the simple and easy to the large and very challenging. Studbooks may include data on animals not held in a zoological setting—many species are held and managed by private facilities and individual breeders—and will require communicating with a number of people. The advent of e-mail has greatly simplified this process.

All studbooks benefit from computerization, allowing better quality control, greater efficiency in publishing and distribution, and the ability to conduct sophisticated genetic and demographic analyses of the population. Coordinated population management requires extensive demographic and genetic analysis of the data set represented by the studbook. The SPARKS (Single Population Analysis and Record Keeping System) program, developed by ISIS, is recommended for zoological studbook and population analysis. All save a scant handful of studbooks are now fully computerized.

COORDINATION AND INITIATION

When studbooks were first developed, most were directed at species that were highly endangered or extinct in the wild. Current studbooks are often maintained for species that still may be common in the wild but may be seldom or completely unavailable from nature. In a similar vein, early studbooks were directed toward large, charismatic species, but today smaller, less charismatic species have begun to receive this level of treatment. Studbooks are now maintained for mammals, birds, reptiles, amphibians, fish, and invertebrates. The first studbooks were organized at the international level, but many of these are now augmented by regional studbooks, or encompass only captive populations within a single region.

As of 2009, approximately 1480 studbooks have been published by over 850 studbook keepers representing 380 zoological institutions in 56 countries (fig. A3.1). These volumes comprise 810,000 individuals of 502 mammal, 295 bird, 134 reptile/amphibian, and 28 fish and invertebrate species. A number of species have an international studbook and/or multiple regional studbooks assigned. About 175 of these studbooks are now in archive status, as there is either no further need for the studbook or no captive animals left to track.

Worldwide, international studbooks are overseen by a coordinator (originally Peter Olney, followed by Dr. Chris West, Dr. Peter Dollinger, and now Dave Morgan) under the auspices of IUCN (International Union for Conservation of Nature: www.iucn.org) and WAZA (World Association of Zoos and Aquariums, formerly IUDZG [International Union of Directors of Zoological Gardens]: www.waza.org). IUCN policy on studbooks is developed and expressed through CBSG (Conservation Breeding Specialist Group of the Species Survival Commission of IUCN: www.cbsg.org). International studbooks must receive official endorsement from these organizations.

Regional zoo associations. Studbook keeping is further regulated by the various regional zoo associations around the world, which act as liaisons between the international stud-

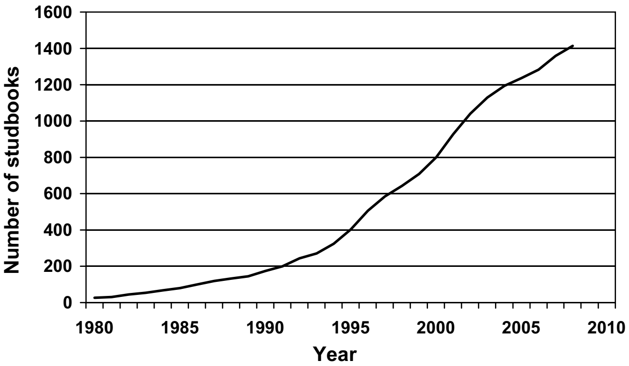

Fig. A3.1. Increase in the number of published studbooks since 1980.

book office and regional studbook keepers. To assist interested parties in developing a studbook petition, many of these associations have developed documents providing advice on selecting a species, application procedures and petition requirements, and standards for preparing a studbook.

Standards for format and timeliness of studbook publication have been developed based on much experience. Persons desiring further information on studbook keeping or managed species should contact their regional association.

There are over 30 regional associations as of December 2008, including

- Africa—PAAZAB: African Association of Zoos and Aquaria (www.paazab.com)
- Australasia—ARAZPA: Australasian Regional Association of Zoological Parks and Aquaria (www.arazpa.org.au)
- Austria—OZO: Austrian Zoo Association (www.ozo.at)
- Brazil—SZB: Sociedade de Zoológicos do Brasil (www.szb.org.br)
- Britain and Ireland—BIAZA: British and Irish Association of Zoos and Aquariums (www.biaza.org.uk/)
- Canada—CAZA: Canadian Association of Zoos and Aquaria (www.caza.ca)
- China—CAZG: Chinese Association of Zoos (www.cazg.net)
- Colombia—ACOPAZOA: Colombian Association of Zoos and Aquariums (http://acopazoa.org/)
- Czech Republic and Slovakia—UCSZ: Union of Czech and Slovak Zoos (www.zoopark.cz/ucsz)
- Denmark—DAZA: Danish Association of Zoological Parks and Aquaria (www.dazaportal.dk)
- Europe—EAZA: European Association of Zoos and Aquaria (www.eaza.net)
- Europe—EUAC: European Union of Aquarium Curators (www.euac.org)
- France—ANPZ: Association Nationale Française des Parcs Zoologiques (no Web site yet)
- Germany—VDZ: German Federation of Zoo Directors (www.zoodirektoren.de)
- India—CZAI: Central Zoo Authority of India (www.cza.nic.in)
- Indonesia—IZPA: Indonesian Zoological Parks Association (no Web site yet)
- Italy—UIZA: Italian Union of Zoos and Aquaria (www.uiza.org)
- Japan—JAZA: Japanese Association of Zoos and Aquariums (www.jazga.or.jp/english/index.html)
- Latin America—ALPZA: Latin-American Zoo and Aquarium Association (no Web site yet)
- Malaysia—MAZPA: Malaysian Association of Zoological Parks and Aquaria (www.mazpa.org.my)
- Mesoamerica—AMACZOOA: Mesoamerican and Caribbean Zoo and Aquaria Association (www.amaczooa.org)
- Mexico—AZCARM: Mexican Association of Zoos and Aquariums (www.azcarm.com.mx)
- Middle East—MEZA: Middle East Zoo Association (no Web site yet)
- Netherlands—NVD: Dutch Zoo Federation (www.nvdzoos.nl)
- North America—AZA: Association of Zoos and Aquariums (www.aza.org)
- Russia and Eastern Europe—EARAZA: Eurasian Regional Association of Zoos and Aquariums (www.zoo.ru)
- South Asia—SEAZARC: South Asian Zoo Association for Regional Cooperation (www.zooreach.org)
- Southeast Asia—SEAZA: Southeast Asian Zoo Association (www.seaza.org)
- Spain and Portugal—AIZA: Iberian Association of Zoos and Aquaria (www.aiza.org.es)
- Sweden—SAZA (SDF): Swedish Association of Zoological Parks and Aquaria (www.svenska-djurparksforeningen.nu)
- Switzerland—Zooschweiz: Swiss Association of Scientific Zoos (www.zoos.ch)
- Taiwan—TAZA: Taiwan Aquarium and Zoological Park Association (no Web site yet)
- Venezuela—FUNZPA: National Foundation of Zoological Parks and Aquaria (www.funpza.org.ve)

COORDINATED MANAGEMENT

Studbooks now serve as the databases for a growing number of captive management programs that not only focus on individual-species studbooks, but also coordinate higher-level management. Taxon Advisory Groups (TAGs) try to balance populations of animals so that the optimum numbers of species may be successfully managed. For example, the number of spaces allotted to one tiger subspecies should not preclude a successful program for another tiger subspecies. Similarly, tiger management plans should not overwhelm the spaces needed for other large cat programs. TAGs are usually organized at family level; i.e., each major regional program has established TAGs for antelope, felids, primates, penguins, parrots, snakes, and lizards, among others.

These programs include the North American Species Survival Plan (SSP), the Joint Management of Species Plan (JMSP) of zoos in the British Isles, the continental European zoos' European Endangered Species Programme (EEP), the Australasian zoos' Species Management Plan (ASMP), the Japanese Species Survival Committee (SSCJ), and developing programs elsewhere. This makes studbook accuracy and timeliness even more important than before.

ISIS

The International Species Information System (ISIS) grew out of widespread recognition that a central, timely source for pooled captive-specimen data was needed, and that zoological specimen records needed improvement. In 1973, Drs. Ulysses S. Seal and Dale G. Makey proposed that such a system be started. Development funds were raised from grant agencies and foundations, a computer system constructed, and invitations distributed to major zoos worldwide. ISIS began operations in 1974, with 51 North American and 4 European institutions participating. The IUDZG (now WAZA) endorsed ISIS shortly after operations commenced. The network

TABLE A3.1. Types and specimens of animals registered in ISIS as of December 2008

	Types	Specimens
Mammals	6251	914,459
Birds	7553	995,698
Reptiles	2951	285,768
Amphibians	863	78,620
Fish	4160	25,774
Terrestrial invertebrates	684	10,760
Marine invertebrates	477	3859
Totals	22,939	2,314,938

of ISIS-participating institutions expanded steadily, reaching 100 by 1979, 400 as of 1990, and 835 as of July 2009.

Today, ISIS is an international nonprofit association, governed by an international board of directors elected by members. These 835 institutions (22 African, 16 Southeast Asian, 63 Indian, 37 Australasian, 22 Central and South American, 364 European, 12 Japanese, 11 Middle Eastern, 288 North American) in a total of 80 countries on 6 continents participate in ISIS. They have registered over 2 million specimens of 22,939 types of animals, as depicted in table A3.1 (ISIS 2008).

ISIS is recognized by a number of national and international regulatory agencies, such as IUCN and CITES (Convention on International Trade in Endangered Species). ISIS is one of 10 international conservation organizations and programs of IUCN that together form BCIS—the Biodiversity Conservation Information System www.biodiversity.org. Their common goal: to support environmentally sound decision making and action by facilitating access to biodiversity data and information.

ISIS supports its operations primarily through members' fees. Development efforts, such as improvement of software and services, have been supported by granting agencies and private foundations as well as by donations from participant institutions.

ISIS AND ZOOLOGICAL RECORDS

Data collection began in 1974 by zoos completing and mailing standardized, archive-quality, multipart specimen records forms. The handwritten data sent to ISIS was keypunched and assembled in a mainframe computer. Various standardized reports were printed and mailed back to participating institutions. Over 1 million of these forms were completed over the next decade and contributed substantially to improving the quality and standardization of zoological records within institutions.

Beginning in 1985, ISIS developed an alternative to paper forms. Called ARKS, for Animal Records Keeping System, this software package was designed for in-house use by zoological facilities on desktop computers. ARKS produces reports and analyses for use by the facility, and automates participation in ISIS by automatically collecting relevant data and allowing regular data submission. Taxon reports produced by ARKS have greatly simplified participation in studbooks for many facilities. All ISIS members now use the ARKS program, the paper forms having been discontinued in 2001. ARKS has evolved through a number of versions as computer technology changed over the years; the current version is ARKS4. There are 16 language modules available: English, French, German, Spanish, Italian, Portuguese, Czech, Slovak, Hungarian, Russian, Norwegian, Swedish, Danish, Dutch, Japanese, and Ukrainian.

ISIS has focused on assembling individual institutions' specimen data necessary to create pooled inventories and for genetic and demographic population management, the same information collected for a much smaller number of species in studbooks. While nutritional and behavioral data is collected at the individual institution level, it has not yet been pooled in any standardized form.

The data are collected and disseminated based on individually identified specimens and on groups of animals, where the zoo has been unable to identify individuals (i.e. bat colonies, schools of fish, insect swarms). Individual specimen data is a far more powerful management tool than data on groups; ISIS strongly encourages identification and marking of individual specimens.

When a specimen is transferred to another institution, it is normally assigned a new accession number (specimen ID) by the new institution. ISIS assembles a specimen's history using primarily this chain of sequential specimen IDs. It is therefore vital that each successive acquiring institution report to ISIS the specimen ID used by the previous facility.

ISIS SERVICES

The main function of ISIS is to provide information based on the pooling of records across participating institutions. Major services available at present include the following.

ISIS Web site. This Web site, www.isis.org, is where member institutions can access specimen reports and pedigrees for any animal in the database. Species Holdings shows currently living animals in collections, organized by taxon and location. A number of data quality reports are available to improve various aspects of individual collections' records, especially as they interact with other collections' data. A detailed query tool allows users to freely query the entire database.

ARKS4 (Animal Records Keeping System, version 4). This is a powerful animal records software package for use in collections management at one site. It is used by individual institutions to record, maintain, and analyze data for the various animal species that are in their collections. ARKS4 produces numerous reports for use by the facility (specimen, taxon, collection inventory, transactions, local inbreeding, age pyramids, life tables, local pedigrees, reproductive history, siblings, enclosures, etc.) and also automates participation in ISIS by collecting and transmitting relevant data. These data are then available to all ISIS members at the ISIS Web site.

ISIS specimen reference DVD. The DVD contains historical and pedigree information on all the nearly 2 million specimens in the ISIS database. It is updated and distributed to ISIS members every 6 months.

MedARKS. The medical records companion system to ARKS, MedARKS was first offered in 1992. It offers a means for recording general clinical data and parasitology, treatment, prescription, anesthesia, cryopreservation, and clinical lab and pathology data. MedARKS is in use at over 500 institutions.

CD of ISIS reference ranges for physiological values in captive wildlife. This information is updated and republished every few years. It contains nearly 5300 pages of pooled reference values and clinical norms derived from the databases of hematology, blood chemistry, body temperatures, body weights, and hormonal values maintained by ISIS. The 2002 edition contained data on 111,000 sample records from 1105 species, contributed by 148 participating institutions from the information collected by MedARKS. Separate sets of reference values are calculated for various sex and age groups if the scope of data allows.

SPARKS (Single Population Analysis and Records Keeping System). This powerful software package is used to maintain and produce studbooks that record information on a single type of animal held at a number of institutions. It also performs the demographic and genetic analyses necessary for coordinated species management programs. SPARKS is an important tool for developing more efficient interchange of data between ISIS and studbook sources, as has been recommended by Glatston (1986) and others.

Partial studbooks. Pseudostudbooks are available in SPARKS format from ISIS for any ISIS-registered taxon. These include birth, move, and death information for all individuals in the taxon recorded with ISIS. These are of course limited to the information submitted by ISIS participants, and are typically current to within 1–2 months. For the 95% of captive species without a formal studbook available, these are the only existing sources of such information, and are the only available international data sets for tracing pedigree relationships or performing genetic or demographic analyses of the captive population. When new formal studbooks are initiated, the ISIS information offers a very good start, as it is already compiled.

Studbook library. The ISIS/WAZA Studbook and Husbandry Manual DVD has been published yearly since 1996. Many zoos use it as their primary means of publishing the studbooks for which they are responsible, at an estimated savings of over $2.5 million in printing and postage costs. The 2008 edition contains almost 1440 regional and international studbooks, 235+ husbandry manuals, and related resources and reference documents pertaining to captive animal data records and population management.

EGGS. EGGS supports record-keeping and egg clutch management and augments collection records for egg-laying species in both the ARKS and SPARKS programs.

REGASP (Regional Animal Species Collection Plan). REGASP is institutional collection-planning software, which is distributed to ISIS members under license from the Australasian Regional Association of Zoological Parks and Aquaria. Zoos determine the species and number of specimens they plan to include in their collections, including plans for the future. They enter this information into their local REGASP system and submit it to the central pool of global planning data, accessible by all REGASP users. Institutions using REGASP have direct access to collection plans from other collections, allowing users to coordinate placement or acquisition of specimens.

ZIMS (Zoological Information Management System). ZIMS is the next generation of ISIS software. Following the first systematic review of zoological data standards in 30 years, development began in 2002 to produce a comprehensive, integrated, current, Web-based zoological information management system. ISIS, working with almost 500 experts from zoological institutions worldwide, is combining and improving the functionality of all current ISIS software applications.

ZIMS will have unique lifetime animal identification numbers, replacing the current practice of a single specimen accruing a new ID at each successive institution. It will allow tracking animals beginning at egg laying or pregnancy, through the animal's lifetime and on into necropsy, pathology, and museum records. Moreover, it will automate much of the data collection for studbook keepers, eliminating the need for them to reenter institutional data, thereby allowing them to focus on data quality and analysis. Aquariums will be able to track water quality and environmental systems parameters and deal effectively with information for groups of animals.

ZIMS will meet modern veterinary and epidemiological needs, allowing evidence-based diagnosis and treatment. Access to additional information on population management, nutrition, behavior, and enrichment will allow building and querying a data warehouse that can support managers and researchers in setting best-practice husbandry standards.

The ZIMS Project is one of the largest international Web-based projects of its kind. The database is expected to come online in spring 2010.

SUMMARY

Specimen records have always been important, but the rapid conversion of many zoological populations to dependence on captive breeding for replacement stock makes them even more so. Both the studbook and ISIS mechanisms help meet these needs.

Collecting comprehensive specimen data institution by institution, as ISIS does, complements the studbook approach of collecting data taxon by taxon. As ISIS continues to expand its capabilities, coverage, and services, improved interaction, communication, and data interchange with the formal studbooks will result. This interchange should be mutually beneficial, and should contribute to sound captive population management and international animal conservation.

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Appendix 4

Annotated Bibliography of Books, Journals, and Web Sites on Captive Management

Kay Kenyon Barboza and Linda L. Coates

INTRODUCTION

The following annotated bibliography of books, journals, and Web sites is designed to complement and expand on the information presented in the individual chapters of this book. It is not comprehensive, but offers a balanced selection of authoritative titles for different levels of interest and different professions within the captive mammal community.

Following the layout of this book, the section of annotated books is divided into the following categories: General Reference, Ethics and Animal Welfare Standards for Captive Mammals, Basic Mammal Management, Nutrition, Exhibitry, Conservation and Research, Behavior, and Reproduction. When a book is also available in digital format, the online location is provided in the Web site section. The subject matter of some books may be relevant to other sections, so it is advisable to look over the entire list.

The list of journals reflects the most relevant and authoritative titles for information on captive mammals. Most are readily available, and many can be found online. Your library may have an institutional subscription.

Web site addresses are subject to change, and those selected for this list appear to be the most stable. Web site sections have been divided into the following headings: General Mammal Resources and Fact Sheets, Resources on Mammal Species and Families, Directories and Bibliographic Resources, Regulations and Guidelines, Husbandry, Enrichment, Veterinary Care, Nutrition, Exhibitry, Conservation, and Organizations. Again, the subject matter of the sites overlaps.

GENERAL REFERENCE

Allen, G. A. 1938–40. *The mammals of China and Mongolia*. 2 vols. (*Natural history of Central Asia*, vol. 11.) New York: American Museum of Natural History.

The only authoritative and complete treatment of the mammalian fauna of this region published in English to date.

Alterman, L., Doyle, G. A., and Izard, M. K., eds. 1995. *Creatures of the dark: The nocturnal prosimians*. New York: Plenum Press. 571 pp.

Contains life histories, taxonomy, captive behavior, social organization, locomotion, and conservation.

Armati, P., Dickman, C. R., and Hume, I., eds. 2006. *Marsupials*. New York: Cambridge University Press. 373 pp.

Covers evolution and classification of marsupials, genetics, reproduction and lactation, nutrition and digestion, the nervous and immunolymphatic systems, ecology and life histories, behavior, conservation, and management.

AZA *Annual Conference Proceedings* and *Regional Conference Proceedings*. Silver Spring, MD: Association of Zoos and Aquariums.

Each volume contains papers presented by zoo and aquarium personnel at both regional and annual conferences. Topics include animal behavior, husbandry, welfare, enrichment, zoo management, exhibits, conservation, and research.

Balfour, D., and Balfour, S. 1991. *Rhino*. Cape Town: Struik. 176 pp.

A good basic overview of the 5 species of rhinos.

Corbet, G. B., and Hill, J. E. 1991. *A world list of mammalian species*. 3rd ed. New York: Oxford University Press. 243 pp.

A great deal of information is packed into a small volume. Simple alphabetical index of species within a genus is accompanied by geographic range, status, and habitat preference.

Dagg, A. I., and Foster, J. B. 1976. *The giraffe: Its biology, behavior and ecology*. Melbourne, FL: Krieger. 232 pp.

A good overview of the giraffe.

Dawson, T. J. 1995. *Kangaroos: Biology of the largest marsupials*. Ithaca, NY: Cornell University Press. 208 pp.

From topics on the evolution of the kangaroo to kangaroo ranching, this is an excellent overview of the 6 species and 4 subspecies of the red and gray kangaroo. Suitable for the specialist and the general reader.

DeBoer, L. E. M., ed. 1982. *The orang utan: Its biology and conservation*. The Hague: Dr. W. Junk. 353 pp.

Results of a workshop held in 1979 in Rotterdam, the Netherlands. Contributors present a very good overview of the orangutan.

Dixson, A. F. 1981. *The natural history of the gorilla*. New York: Columbia University Press. 202 pp.

An update of Schaller's classic 1963 work. Integrates new research from zoos and primate centers with earlier information. Important sections on intelligence, behavior and ecology, reproduction, and infant development are included. Although written some time ago, the basic information is still the same.

Eisenberg, J. F., and Redford, K. H. 1989–99. *Mammals of the neotropics*. 3 vols. Chicago: University of Chicago Press. (Vol. 1, 1989, 449 pp.; vol. 2, 1992, 430 pp.; vol. 3, 1999, 624 pp.). Volume 1 (*The northern neotropics*) covers mammals of Panama, Colombia, Venezuela, Guyana, Suriname, and French Guiana. Volume 2 (*The southern cone*) covers mammals of Chile, Argentina, Uruguay, and Paraguay. Volume 3 (*The central neotropics*) covers mammals of Ecuador, Peru, Bolivia, and Brazil.

In all 3 volumes, species accounts include description, distribution, natural history, measurements, range, and habitat. Drawings and maps included. A monumental and thorough reference work. The fourth and final volume of this series will cover the mammals of Mexico and Central America.

Estes, R. D. 1991. *The behavior guide to African mammals*. Berkeley and Los Angeles: University of California Press. 611 pp.

A unique, comprehensive survey of the taxonomy, distribution, and description as well as the ecology and behavior of large African mammals. The section on ungulates is particularly thorough.

Feldhamer, G. A., Thompson, B. C., and Chapman, J. A., eds. 2003. *Wild mammals of North America: Biology, management, and conservation*. 2nd ed. Baltimore: Johns Hopkins University Press. 1216 pp.

Revises and updates Chapman's 1982 *Wild Mammals of North America: Biology, Management, and Economics*. Provides detailed species accounts on the distribution, physiology, ecology, behavior, commercial value, and viability of nongame species and big game species.

Gautier-Hion, A., [et al.], eds. 1988. *A primate radiation: Evolutionary biology of the African guenons*. New York: Cambridge University Press. 567 pp.

Topics include the African environment, genetic and phonetic characteristics, ecology, and social behavior. Extensive maps and tables included.

Gittleman, J. L., ed. 1989. *Carnivore behavior, ecology and evolution*. 2 vols. Ithaca, NY: Comstock. (Vol. 1, 620 pp.; vol. 2, 644 pp.)

A comprehensive 2-volume text on all aspects of carnivore biology. Papers in volume 1 discuss such topics as the role of odor in the social lives of carnivores, mating tactics and spacing patterns of solitary carnivores, adaptations for aquatic living, and physiology and evolution of delayed implantation. Papers in volume 2 discuss such topics as reintroduction efforts for the black-footed ferret and the red wolf, differential rates of mortality in the giant panda, and genetic techniques of DNA fingerprinting of the African lion.

Groves, C. 2001. *Primate taxonomy*. Washington, DC: Smithsonian Institution Press. 350 pp.

Addresses the theory of primate taxonomy and its practical application. Various groups of primates are discussed, including Malagasy lemurs, lorisiformes, tarsiiformes, playtyrrhini, Old World monkeys, and hominids.

Grzimek, B. 2003. *Grzimek's animal life encyclopedia*. Vols. 12–16, *Mammals*, ed. M. Hutchins, D. G. Kleiman, V. Geist, and M. C. McDade. Detroit: Gale.

Updates the 1990 edition with a different publisher and authors. This is still a major comprehensive reference on the biology of mammals. Excellent color photos, drawings, maps, and comparative charts summarizing the differences between related species.

Harrison, D. L., and Bates, P. J. J. 1991. *The mammals of Arabia*. 2nd ed. Sevenoaks, Kent, UK: Harrison Zoological Museum. 354 pp.

Systematics, geographic variation, distribution, ecology, and biology of the terrestrial mammals of Arabia. A comprehensive, well-researched work.

Heltne, P. G., and Marquardt, L. A., eds. 1989. *Understanding chimpanzees*. Cambridge, MA: Harvard University Press. 407 pp.

Topics include social behavior and ecology of chimpanzees in the wild, behavior in captivity, the differences in cultural traditions between wild populations, and the cognitive abilities of captive chimpanzee in language acquisition.

Hoelzel, A. R., ed. 2002. *Marine mammal biology: An evolutionary approach*. Malden, MA: Blackwell Science. 432 pp.

Broad in scope, this text considers all aspects of the biology of marine mammal species in light of their adaptation to aquatic habitats. Topics include anatomical and physiological adaptations, vocal communication, social behavior, problem solving and memory, reproductive strategies, patterns of movement, population genetics, and conservation and management.

International Zoo Yearbook. Vols. 1–. 1959–. London: Zoological Society of London.

This is an annual collection of articles on captive management and new developments in the zoo world (husbandry, breeding, building, exhibits, etc.). Appendices list captive animals bred, rare animals in captivity, and available studbooks. Periodically, a volume will also include a world directory of zoos and aquariums. A very important resource for the animal manager.

Kingdon, J. 1971–82. *East African mammals: An atlas of evolution in Africa*. 7 vols. San Diego, CA: Academic Press.

This 7-volume reference work provides a natural-history account for each species of mammal living in East Africa. Distribution maps and many excellent drawings are included.

Kingdon, J. 1997. *The Kingdon field guide to African mammals*. San Diego, CA: Academic Press. 464 pp.

More than a handbook, this guide provides full information on identification, distribution, ecology, evolutionary relationships, and conservation status.

Lee, A., and Martin, R. 1988. *The koala: A natural history*. Kensington: New South Wales University Press. 102 pp.

A very readable overview of the biology of the koala. Covers the diet, digestion, reproduction, life history, behavior, and management. Both authors are highly regarded in koala research.

Lindburg, D., and Baragona, K., eds. 2004. *Giant pandas: Biology and conservation*. Berkeley and Los Angeles: University of California Press. 323 pp.

A team of international scientists and conservationists, including Chinese researchers, come together and discuss evolutionary history, biology, habitat, and conservation of the giant panda.

Long, J. L. 2003. *Introduced mammals of the world: Their history, distribution and influence*. Collingwood, Victoria, Australia: CSIRO. 589 pp.

Provides accounts for 337 species of mammals. Details include date of introduction, person or agency responsible, the source population, the location of release, the fate of the introduction, and the impact on native biota. Distribution maps included.

Macdonald, D., ed. 2006. *The encyclopedia of mammals*. 3 vols. 2nd ed. New York: Facts on File. 976 pp.

This comprehensive reference work has been updated to include the latest scientific developments since the first edition. Written by internationally acclaimed experts, entries contain facts on animal evolution, behavior, conservation, and ecology for all mammalian species and species groups. Beautiful color photographs and drawings supplement the text.

Mitchell-Jones, A. J., [et al.], eds. 1999. *The atlas of European mammals*. London: T. and A.D. Poyser. 484 pp.

Species descriptions with world distribution and geographic variations. Included for each species is its conservation status and important references to the literature.

Napier, J. R., and Napier, P. H. 1985. *The natural history of primates*. Cambridge, MA: MIT Press. 200 pp.

General survey of primate morphology, evolution, and ethology, with brief descriptive accounts for each genus.

Nowak, R. M. 1999. *Walker's mammals of the world*. 6th ed. 2 vols. Baltimore: Johns Hopkins University Press. 1936 pp.

This sixth, revised and expanded edition provides basic natural history facts and descriptions for over 1192 living mammalian genera and 4809 species. Photographs or drawings are provided for each species. A real classic.

Perrin, W. F., Wursig, B., and Thewissen J. G. M., eds. 2002. *Encyclopedia of marine mammals*. San Diego, CA: Academic Press. 1414 pp.

Alphabetically arranged, over 280 articles provide a complete source of information on marine mammals. Suitable for the general public as well as the specialist. Topics include anatomy, physiology, life history, human-animal interaction, population biology, and research methodology.

Prater, S. H. 1980. *The book of Indian animals*. 3rd ed. Bombay: Bombay Natural History Society. 324 pp.

Considered a classic in the literature of the mammalian fauna of India, Pakistan, Sri Lanka, and the surrounding borders. An introduction to each family covered includes its natural history, physical characteristics, behavior and habitats, and interactions with other species. Well illustrated.

Reynolds, J. E. III, and Rommel, S. A. 1999. *Biology of marine mammals*. Washington, DC: Smithsonian Institution Press. 578 pp.

Ten review chapters by leading marine biologists present a comprehensive overview of marine mammals. Detailed topics include behavior, communication and cognition, sensory systems, reproduction, feeding, physiological adaptations, and marine toxicants.

Rowe, N. 1996. *The pictorial guide to the living primates*. New York: Pogonias Press. 263 pp.

Contains color pictures of all 234 species of primates, plus descriptive characteristics, habitat, diet, life history, and behavior.

Rylands, A. B., ed. 1993. *Marmosets and tamarins: Systematics, behaviour, and ecology*. New York: Oxford University Press. 396 pp.

This multiauthored book addresses the systematics, distribution, behavior, and reproduction of the Callitrichidae. Detailed information is provided on scent marking, habitat preference, feeding ecology, communal infant care, group size, and structure.

Seidensticker, J., and Lumpkin, S., eds. 1991. *Great cats*. Emmaus, PA: Rodale Press. 240 pp.

A good basic resource for feline species. Covers a wide variety of topics, from cats in zoos to preserving cats in the wild. Over 200 full-color photographs and illustrations included.

Shoshani, J., ed. 2000. *Elephants*. Rev. ed. New York: Checkmark Books. 240 pp.

Good overview of the African and the Asian elephant. Covers evolution and biology in great detail as well as the elephants' relationship with humans.

Sikes, S. K. 1971. *The natural history of the African elephant*. London: Weidenfeld and Nicholson. 397 pp.

Although dated, still a classic on information pertaining to the African elephant.

Smithers, R. H. N. 2005. *The mammals of the southern African subregion*. 3rd ed. Cambridge, MA: Cambridge University Press.

An authoritative and comprehensive reference on the mammals of Namibia, Botswana, Zimbabwe, Mozambique, and the Republic of South Africa. Each entry is provided with a complete natural history and a color illustration.

Sowls, L. K. 1997. *Javelinas and other peccaries: Their biology, management, and use*. 2nd ed. College Station: Texas A&M University Press. 325 pp.

A wealth of information on the 3 species of piglike creatures that inhabit the Americas.

Spinage, C. A. 1986. *The natural history of antelopes*. New York: Facts on File. 203 pp.

A general overview of African antelopes. Addresses their complicated taxonomy and provides information on habitat, feeding, migration, breeding territoriality, and social organization. An appendix contains synopses of various species.

Stirling, I., ed. 1993. *Bears: Majestic creatures of the wild*. Emmaus, PA: Rodale Press. 240 pp.

A good basic resource on bears by bear experts. Contains descriptions and comparisons of all 8 species of bear, including the giant panda. Lots of good photos.

Strahan, R., ed. 1995. *Mammals of Australia*. Rev. ed. Washington, DC: Smithsonian Institution Press. 756 pp.

A basic reference source on every species of native and introduced mammal of Australia and Tasmania. Range maps and color photographs are provided.

Sunquist, M., and Sunquist, F. 2002. *Wild cats of the world*. Chicago: University of Chicago Press. 452 pp.

Behavior and ecology of the 36 wild cat species with photos, distribution maps, and extensive bibliographies.

Susman, R. L., ed. 1984. *The pygmy chimpanzee: Evolutionary biology and behavior*. New York: Plenum Press. 435 pp.

A comprehensive resource on the pygmy chimpanzee. Part 1 details the molecular biology, systematics, and morphology. Part 2 deals with behavior and includes habitat utilization, feeding ecology, social organization, and reproduction.

Tattersall, I. 1982. *The primates of Madagascar*. New York: Columbia University Press. 382 pp.

An authoritative guide to the lemurs. Addresses the origins of the Malagasy primates, the members of the Lemuridae, Lepilemuridae, Indriidae, Daubentoniidae, and Cheirogaleidae families. Discusses phylogeny and classification, morphology, and adaptation, behavior, and ecology.

Taylor, A. B., and Goldsmith, M. L., eds. 2003. *Gorilla biology: A multidisciplinary perspective*. New York: Cambridge University Press. 508 pp.

Covers morphology, genetics, behavioral ecology, and conservation of the gorilla.

Walton, D. W., and Richardson, B. J., eds. 1989. *Fauna of Australia*. Vol. 1B, *Mammalia*. Canberra: Australian Government Publishing Service. 1224 pp.

Comprehensive description of the morphology, physiology, and ethology of the Australian mammal families, with extensive bibliographies.

Wemmer, C. M. 1987. *Biology and Management of the Cervidae, A symposium held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution in 1982*. Washington, DC: Smithsonian Institution Press. 577 pp.

A thorough review of the Cervidae by more than 60 experts in the field. Topics addressed include their evolutionary history and radiation, anatomy and physiology, including antler development and neuroendocrine regulation, all aspects of behavior and reproduction, interspecific relationships, and management, both in captivity and in the wild.

Whitehead, G. K. 1993. *The Whitehead encyclopedia of deer*. Stillwater, MN: Voyageur Press. 597 pp.

Covers the world's deer species, their distribution and every aspect of their biology, mythology, and iconography.

Wilson, D. E., and Cole, F. R. 2000. *Common names of mammals of the world*. Washington, DC: Smithsonian Institution Press. 204 pp.

Provides a single, unique English common name for all 4629 mammal species recognized by Wilson and Reeder (1993) and, when appropriate, for genera, families, and orders.

Wilson, D. E., and Mittermeier, R. A., eds. 2009–16. *Handbook of the mammals of the world.* 8 vols. Barcelona, Spain: Lynx Editions.

A comprehensive reference book covering detailed information on morphology, biology, ecology, and conservation of each mammal species. Extensive introductions to each mammal family are included. Distribution maps, color illustrations, and color photos are outstanding.

Wilson, D. E., and Reeder, D. M., eds. 2005. *Mammal species of the world: A taxonomic and geographic reference.* 3rd ed. Baltimore: Johns Hopkins University Press. 2142 pp.

A 2-volume checklist of the world's mammal species. Each species account provides scientific name and authority, type locality, distribution, and comments. Protected status is also given for some. Also available free online.

Wilson, D. E., and Ruff, S., eds. 1999. *Smithsonian book of North American mammals.* Washington, DC: Smithsonian Institution Press. 750 pp.

Beautifully illustrated species accounts for mammal species north of Mexico. Includes range maps.

ETHICS AND ANIMAL WELFARE STANDARDS FOR CAPTIVE MAMMALS

Appleby, M. C. 1999. *What should we do about animal welfare?* Malden, MA: Blackwell Science. 192 pp.

The author gives a clear and balanced account of the science and ethical issues of animal welfare. A good introduction.

Appleby, M. C., and Hughes, B. O., eds. 1997. *Animal welfare*. Oxon, UK: CABI. 316 pp.

Written by a diverse group of international behavioral scientists. Although slanted toward farm animals, it provides information that can be applied or adapted to wild species.

Austen, M., and Richards, T. 2000. *Basic legal documents on international animal welfare and wildlife conservation.* Boston: Kluwer Law International. 696 pp.

A thorough compilation of important international agreements designed to protect wild animals. It includes everything from large, multilateral agreements such as CITES to much smaller agreements protecting individual species and companion animals.

Beck, B. B., Arluke, A., and Stevens, E. F., eds. 2001. *Great apes and humans: The ethics of coexistence.* (Zoo and Aquarium Biology and Conservation Series). Washington, DC: Smithsonian Institution Press. 388 pp.

Discusses human responsibilities toward gorillas, chimpanzees, bonobos, and orangutans in captivity and in the wild from a wide range of viewpoints (zoo managers, conservationists, and behavioral scientists).

Bekoff, M., and Meaney, C. A., eds. 1998. *Encyclopedia of animal rights and animal welfare*. Westport, CT: Greenwood Press. 446 pp.

Provides a comprehensive overview in an A–Z encyclopedic format. Topics include genetic engineering, hunting, pain, reproductive control, and zoos. Appendixes include related organizations, Internet sites, comprehensive bibliography, and index.

Bostock, S. St. C. 1993. *Zoos and animal rights: The ethics of keeping animals.* New York: Routledge. 227 pp.

Explores the history as well as current ethical issues of keeping wild animals in zoos. Such topics include human cruelty, human domination over animals, the well-being of wild animals outside their natural habitat, and the nature of wild and domestic animals.

Broom, D. M., and Johnson, K. G. 1993. *Stress and animal welfare*. Chapman and Hall Animal Behaviour Series. New York: Chapman and Hall. 211 pp.

An excellent resource for studies on animal welfare and stress. Analyzes the systems regulating the body and brain and an animal's limits to adaptation.

Burghardt, G. M., Bielitzki, J. T., Boyce, J. R., and Schaeffer, D. O., eds. 1996. *The well-being of animals in zoo and aquarium sponsored research*. Greenbelt, MD: Scientists Center for Animal Welfare. 137 pp.

Considers the ethical issues of research for conservation, environmental enrichment, and the role of IACUC (Institutional Animal Care and Use Committee) in zoos and aquariums.

Carbone, L. 2004. *What animals want: Expertise and advocacy in laboratory animal welfare policy*. New York: Oxford University Press. 304 pp.

A scholarly look at the history of animal rights in the laboratory, written by a veterinarian at a major research university. The author advocates balancing both biomedical progress and animal welfare.

Cavalieri. P. 2004. *The animal question: Why nonhuman animals deserve human rights*. New York: Oxford University Press. 192 pp.

A clearly written, concise argument on why we should extend basic human rights to nonhuman animals.

Cohen, C., and Regan, T. 2001. *The animal rights debate*. Lanham, MD: Rowman and Littlefield. 323 pp.

Two highly influential philosophers present opposing sides of the animal rights debate very thoroughly and articulately.

Dawkins, M. S., and Gosling, M. 1992. *Ethics in research on animal behaviour: Readings from animal behaviour*. London: Academic Press. 64 pp.

Whether studying animals in the field or in captivity, this guide provides information on the number of subjects used in experiments, on assessing pain, and on the ethical issues raised by studies of predation and aggression.

Dolan, K. 1999. *Ethics, animals, and science*. Malden, MA: Blackwell Science. 287 pp.

A clear and balanced introduction on the ethical issues associated with using animals for research.

Margodt, K. 2000. *The welfare ark: Suggestions for a renewed policy in zoos*. Brussels: VUB University Press. 158 pp.

Deals with the role of zoos in animal welfare and the conservation of endangered wildlife. Discusses the physical, social, and psychological welfare issues of zoo enclosures, and considers zoo education and research and their role in the future of wildlife.

Moberg, G. P., and Mench, J. A., eds. 2000. *The biology of animal stress: Basic principles and implications for animal welfare*. New York: Oxford University Press. 392 pp.

Contributors bring together a wide range of perspectives on animal stress from biomedical research. New approaches to alleviating stress are also discussed.

Mullan, B., and Marvin, G. 1999. *Zoo culture*. 2nd ed. Urbana: University of Illinois Press. 172 pp.

A provocative study of what zoos and zoo animals mean to humans. Topics include anthropomorphism, containment and control, zoo architecture, exhibition, and zoos in evolution.

National Research Council. 1998. *The psychological well-being of nonhuman primates.* Washington, DC: National Academy Press. 168 pp.

Results of a 1985 amendment to the Animal Welfare Act. Examines what is known about the psychological needs of primates. Clearly written and useful, it discusses in detail a daily care program, which includes housing and sanitation, social companionship, and activities.

Norton, B. G., Hutchins, M., Stevens, E. F., and Maple, T. L., eds. 1995. *Ethics on the Ark: Zoos, animal welfare, and wildlife conservation.* Zoo and Aquarium Biology and Conservation Series. Washington, DC: Smithsonian Institution Press. 330 pp.

An important book on issues of animal conservation, wel-

fare, and rights facing the zoo community. Much of the focus of these papers is on ethical issues associated with captive breeding programs, such as research, reintroductions, and Species Survival Plans.

Regan, T. 2004. *The case for animal rights*. 2nd ed. Berkeley and Los Angeles: University of California Press. 474 pp.

A scholarly classic written by the intellectual leader of the animal rights movement. Very thorough and persuasive argument for the end of animal exploitation.

Rollin, B. E. 1998. *The unheeded cry: Animal consciousness, animal pain, and science*. Expanded ed. Ames: Iowa State University Press. 330 pp.

Discusses the morality of using animals for scientific research.

Silverman, J., Suckow, M. A., and Murthy, S., eds. 2007. *The IACUC Handbook*. 2nd ed. Boca Raton, FL: CRC Press. 652 pp.

In a question-and-answer format, the authors offer their interpretation of proper animal care and use in research laboratories based on federal regulations in the United States. Topics include IACUC (Institutional Animal Care and Use Committee) protocol forms, euthanasia, surgery, and the inspection of animal housing areas. Appendixes include the Animal Welfare Act and Animal Welfare Act regulations.

U.S. Office of Federal Register. Annual. *Code of federal regulations. Title 8: Animals and animal products*. 2 vols. *Title 50: Wildlife and fisheries*. 2 vols. Washington, DC: Government Printing Office. Also available online.

The primary source for current government regulations dealing with animals. *Title 8* contains regulations on animal health, interstate transportation, quarantine, and animal welfare. *Title 50* is the current list of regulations on wildlife possession, selling, trapping, importing, exporting, etc. A mandatory tool for the zoo manager.

BASIC MAMMAL MANAGEMENT

American Association of Zoo Keepers. 1994. *Zoo infant development notebook*. Volume 1: *Marsupialia-Carnivora*. Volume 2: *Tubulentata-Artiodactyla*. Topeka, KS: American Association of Zoo Keepers.

Two loose-leaf binders include contributions from keepers at many institutions concerning hand-rearing techniques. Infant development data sheets document the nursing position, frequency of nursing, tooth eruption ages, introduction of solids, preferred solids, and weaning.

———. 2003. *Biological information on selected mammals*. 4th ed. Topeka, KS: American Association of Zoo Keepers. 1396 pp. CD-ROM version.

A handy and informative CD-ROM containing biological data on 590 species of mammals. Included are common name, scientific name, geographic range, normal adult size and weight, estrus cycle, breeding, gestation period, number of young, weaning, sexual maturity, and pulse and respiration rate.

———. [2005]. *AAZK enrichment notebook*. 3rd ed. Topeka, KS: American Association of Zoo Keepers. 455 pp. CD-ROM version.

Presents zoo management, and gives practical ways to improve the environment of zoo animals, including a list of browse plants, toxic plants, treats, enrichment suppliers, and cookbook recipes for enrichment.

American Association of Zoo Veterinarians. 1976–. *Annual Proceedings*. Atlanta: American Association of Zoo Veterinarians.

Papers of the Annual Meeting of the American Association of Zoo Veterinarians. Covers all aspects of zoological medicine dealing with captive and free-ranging wild animals.

Asa, C. S., and Porton, I. J., eds. 2005. *Wildlife contraception: Issues, methods, and applications*. Zoo and Aquarium Biology and Conservation Series. Baltimore: Johns Hopkins University Press. 288 pp.

This is a comprehensive book on contraception. Provides zoo and aquarium wildlife managers information on the latest research developments in this area.

Brent, L. 2001. *The care and management of captive chimpanzees*. Special Topics in Primatology, vol. 2. San Antonio, TX: American Society of Primatologists. 306 pp.

Encompasses a wide range of topics written by the top experts in the field. Covers facility design, health care and contraception, regulations, training, and the forming and managing of social groups. A thorough review of scientific literature.

Cheville, N. F. 2006. *Introduction to veterinary pathology*. 3rd ed. Ames, IA: Blackwell. 370 pp.

Although this book is intended for the beginning student of veterinary pathology, it is also of value to curators and managers. Provides basic principles of general and molecular pathology for nonhuman vertebrate animal species. It is clearly written and exceptionally well illustrated.

Clubb, R., and Mason, G. 2002. *A review of the welfare of zoo elephants in Europe*. London: Royal Society for the Prevention of Cruelty to Animals. 303 pp. Also available free online at the RSPCA Web site.

A report that addresses the history of elephants in captivity, their general husbandry, the social aspects of the zoo environment, training, reproduction, behavior problems, and mortality. There are special appendixes on dietary recommendations and foot problems.

Crandall, L. S. 1964. *The management of wild mammals in captivity*. Chicago: University of Chicago Press. 761 pp.

No one involved in the management of captive wild mammals should miss this classic. General management information is provided for each mammal species, such as general care, diet, history in captivity, exhibit techniques, and breeding methods, and specific information on gestation periods and longevity is given.

Csuti, B., Sargent, E. L., and Bechert, U. S., eds. 2001. *The elephant's foot: Prevention and care of foot conditions in captive Asian and African elephants*. Ames: Iowa State University Press. 163 pp.

This book is a useful guide to the prevention, care, and treatment regimens of foot conditions in captive Asian and African elephants. Black-and-white photos included.

Dierauf, L. A., and Gulland, F. M. D., eds. 2001. *CRC handbook of marine mammal medicine*. 2nd ed. Boca Raton, FL: CRC Press. 1120 pp.

Broad in scope, this book covers information on anatomy and physiology, infectious diseases, medical treatment, surgery, pathology, conservation medicine, feeding and housing, husbandry, stranding, and rehabilitation of cetaceans, pinnipeds, manatees, sea otters, and polar bears. An excellent reference for the veterinarian as well as the animal-husbandry person.

Ettinger, S. J., and Feldman, E. C., eds. 2005. *Textbook of veterinary internal medicine*. 6th ed. 2 vols. Philadelphia: W. B. Saunders. 2208 pp. Comes with either a CD-ROM or access to online edition with updates.

An encyclopedic resource covering pathophysiology, diagnosis, and treatment of diseases affecting dogs and cats. This classic textbook is useful to all professionals concerned with diseases of mammals.

Field, D. A., ed. 1998. *Guidelines for environmental enrichment*. West Sussex, UK: Association of British Wild Animal Keepers. 1 vol. (loose-leaf). 250 pp.

A variety of authors provide detailed descriptions of enrichment devices and ideas for all vertebrate groups, from fish to great apes.

Fowler, M. E. 1995. *Restraint and handling of wild and domestic animals*. 2nd ed. Ames: Iowa State University Press. 383 pp.

Through text and illustrations, this book provides guidelines for humane and practical handling, both physically and chemically, of wild and domestic animals.

Fowler, M. E., and Cubas, Z. S., eds. 2001. *Biology, medicine, and surgery of South American wild animals*. Ames: Iowa State University Press. 536 pp.

For the non-veterinarian and/or zoo manager. Covering reptiles to mammals, topics include reproduction, nutrition, captive management, public health, pests, and nuisance animals in zoos.

Fowler, M. E., and Miller, R. E., eds. 2003. *Zoo and wild animal medicine*. 5th ed. Philadelphia: W. B. Saunders. 942 pp.

Thoroughly revised and organized by species in a user-friendly format, this is the most up-to-date authoritative text on veterinary medicine for captive exotic animals. The authors have contributed their knowledge and expertise on each animal's biology, anatomy, physiology, restraint and handling, special housing requirements, diseases, etc. Highly recommended for those who work with exotics.

Gage, L. J., ed. 2002. *Hand-rearing wild and domestic mammals*. Ames: Iowa State University Press. 279 pp.

Illustrated, detailed guide of instructions, tips, and advice on raising and caring for over 50 species of domestic, farm, wild, and zoo mammals. Topics include housing, common medical problems, expected weight gains, diets, and weaning techniques.

Gibbs, E. P. J., and Bokma, B. H., eds. 2002. *The domestic animal/wildlife interface: Issues for disease control, conservation, sustainable food production, and emerging diseases*. Annals of the New York Academy of Sciences, vol. 969. New York: New York Academy of Sciences. 369 pp.

Results of a conference and workshop held in 2001 in South Africa for the Society for Tropical Veterinary Medicine and the Wildlife Disease Association. It addresses the problems of disease in both wild and domestic animals, and the transmission of disease between the 2 populations.

Gosden, C. 2004. *Exotics and wildlife: A manual of veterinary nursing care*. New York: Elsevier. 256 pp.

A practical guide to nursing exotic pets, with example case histories in each chapter.

Grandin, T. 2007. *Livestock handling and transport*. 3rd ed. Cambridge, MA: CABI. 386 pp.

Research data and practical information on animal handling. Scientific information on stress physiology of animals during transport.

Griner, L. A. 1983. *Pathology of zoo animals: A review of necropsies conducted over a fourteen-year period at the San Diego Zoo and San Diego Wild Animal Park*. San Diego, CA: Zoological Society of San Diego. 608 pp.

Provides good, basic physiological information for a wide variety of mammals. Discusses stress, trauma, malnutrition, and systemic disease.

Hand, S. J., ed. 1997. *Care and handling of Australian native animals: Emergency care and captive management*. Chipping Norton, NSW, Australia: Surrey Beatty. 210 pp.

A practical guide to animal care, including emergency first aid, caging and enclosure requirements, diets, breeding, handling, marking, and diseases and parasites. Nicely illustrated with numerous drawings and photos.

Hediger, H. 1964. *Wild animals in captivity*. New York: Dover. 207 pp.

This classic text provides the foundation for studying zoo biology. Discusses animal behavior and the basic principles of managing captive wild animals in terms of space requirements, diet, and animal-human relationships.

Hugh-Jones, M. E., Hubbert, W. T., and Hagstad. H. V. 2000. *Zoonoses: Recognition, control and prevention*. Ames: Iowa State University Press. 369 pp.

A good introduction to the problems of zoonoses. Topics covered are recognition of agents and diseases, development of control, prevention, and eradication strategies, the process of disease reporting, and issues for the future.

International Conference on Environmental Enrichment. 1993–. *Conference Proceedings*. Biannual. Several are available at *Shape of Enrichment*'s Web site.

These conference proceedings are concerned exclusively with enrichment and animal welfare. Important for those dealing with captive mammals.

Jackson, S. M. 2003. *Australian mammals: Biology and captive management*. Collingwood, Victoria, Australia: CSIRO. 524 pp.

Complete comprehensive guide to the husbandry of Australian marsupials and other mammals. Information is provided on biology, housing, capture and restraint, transport, diet, breeding, artificial rearing, behavior, and behavioral enrichment.

Kirkwood, J. K., and K. Stathatos. 1992. *Biology, rearing, and care of young primates*. New York: Oxford University Press. 154 pp.

A practical manual that provides detailed information for managing neonate and young primates. Discusses such topics as social structure, breeding age, seasonality, gestation, milk and milk intake, lactation and weaning, feeding, physical and behavioral development, disease and mortality, preventive medicine, indications for hand rearing and reintegration.

Kleiman, D. G. [et al.], eds. 1996. *Wild mammals in captivity: Principles and techniques*. Chicago: University of Chicago Press. 639 pp.

Although a bit dated, most parts are still very useful for those working directly with wild mammals in captivity or concerned generally with mammal conservation and management. It is the first edition of the present volume.

McKenzie, A. A., ed. 1993. *The capture and care manual: Capture, care, accommodation and transportation of wild African animals*. Pretoria, South Africa: Wildlife Decision Support Services, South African Veterinary Foundation. 729 pp.

Practical guide by 26 wildlife specialists to using drugs on, capturing and handling, and transporting wild animals. Chapters discuss carnivores, primates, antelopes, and other herbivores such as elephants, rhinos, hippos, and giraffes.

Neilson, L. 1999. *Chemical immobilization of wild and exotic animals*. Ames: Iowa State University Press. 400 pp.

A practical and thorough treatment for those called on to capture and restrain wild animals. Includes information on history, ethics, drug delivery equipment, techniques, pharmacology, postcapture management, emergency procedures, and human safety. Included is an extensive account of species-specific characteristics, and drug recommendations for over 300 common species of mammals, birds, and reptiles. Nicely illustrated.

Poole, T., ed. 1999. *The UFAW handbook on the care and management of laboratory animals*. Vol. 1, *Terrestrial Vertebrates*. 7th ed. Malden, MA: Blackwell Science.

A practical reference source for keeping laboratory animals healthy and in a favorable environment. Thirty chapters are devoted to mammals. Topics include biology, disease, feeding, handling, breeding, and life history.

Quesenberry, K. E., and Carpenter, J. W., eds. 2003. *Ferrets, rabbits and rodents: Clinical medicine and surgery* (*includes sugar gliders and hedgehogs*). 2nd ed. Philadelphia: W. B. Saunders. 461 pp.

Useful reference for those who work with small mammals. Coverage includes basic biology, husbandry, and routine care. Chapters also on disease management, surgery, and radiology.

Ramirez, K., ed. 1999. *Animal training: Successful animal management through positive reinforcement*. Chicago: Shedd Aquarium. 578 pp.

Produced for professional animal trainers and animal behavior/husbandry students, this collection of articles focuses on sound operant conditioning and training principles. Ramirez obtained permission to reprint more than 100 articles by more than 150 experts.

Reinhardt, V., and Reinhardt, A., eds. 2002. *Comfortable quarters for laboratory animals*. 9th ed. Washington, DC: Animal Welfare Institute. 114 pp. Online free version found at AWI Web site.

Illustrated manual for those planning to build, remodel, or re-equip their animal quarters.

Rollefson, I. K., Mundy, P., and Mathias, E. 2001. *A field manual of camel diseases: Traditional and modern veterinary care for the dromedary*. Rugby, Warwickshire, UK: ITDG. 232 pp.

Details 90 major camel ailments. Provides information on the symptoms of the disease, the causes, and simple prevention and treatment methods. Includes both Western treatments as well as those used by native healers and herders. Illustrated with line drawings.

Samuel, W. M., Pybus, M. J., and Kocan, A. A. 2001. *Parasitic diseases of wild mammals*. 2nd ed. Ames: Iowa State University Press. 559 pp.

Revised edition of *Parasitic Diseases of Wild Animals* by J. W. Davis, 1971. Provides information on parasitic diseases of both captive and free-ranging mammals. Parasites and parasitic groups covered are ecotoparasites, helminths or endoparasites, and protozoans. Serves as a benchmark reference for all animal health professionals.

Shepherdson, D., Mellen, J., and Hutchins, M., eds. 1998. *Second nature: Environmental enrichment for captive animals*. Zoo and Aquarium Biology and Conservation Series. Washington, DC: Smithsonian Institution Press. 350 pp.

A guidebook on how to structure environmental enrichment programs for captive animals in laboratories, marine parks, and zoos. The authors discuss theoretical basics of enrichment, animal conservation and welfare, and captive management, husbandry, and training. Heavy on the mammals from leopards to whales.

Williams, E. S., and Barker, I. K. 2001. *Infectious diseases of wild mammals*. 3rd ed. Ames: Iowa State University Press. 558 pp.

Seventy-one contributors provide diagnosis and treatment of infectious diseases in free-ranging and captive wild mammals. Each disease discussed includes information on history, distribution, etiology, epidemiology, immunity, transmission, clinical signs, pathology, diagnosis, treatment, and control.

Woodford, M. H., ed. 2001. *Quarantine and health screening protocols for wildlife prior to translocation and release into the wild*. Paris: Office International des Espizooties (OIE). 99 pp.

A booklet that provides descriptions of possible disease risks which can accompany wildlife translocation projects. Written by more than 30 wildlife veterinarians worldwide.

Young, R. J. 2003. *Environmental enrichment for captive animals*. UFAW Animal Welfare Series. Oxford: Blackwell Science. 228 pp.

Discusses the history of animal keeping, legal issues, and ethics. Explores in detail various environmental enrichment methods and whether they actually work, and how to design and manage enrichment programs. Both theoretical and practical. Great for zoos.

NUTRITION

American Zoo and Aquarium Association. Animal Health Committee. 1994. *Infant diet notebook*. Rev. ed. Silver Spring, MD: American Zoo and Aquarium Association.

A loose-leaf manual containing diets and information on hand-rearing techniques for infant wild mammals. Covers such topics as when to "pull" animals, composition of selected formulas, growth curves, any feeding apparatus or enclosure requirements, and the weaning process.

———. Nutrition Advisory Group. 1997. *Nutrition advisory group handbook*. Silver Spring, MD: American Zoo and Aquarium Association.

Easy-to-read fact sheets on all aspects of zoo animal nutrition, such as hay and feedstuff quality, vitamins, and fish as food. The diets of elephants, leaf-eating primates, and Asian small-clawed otters are specifically addressed.

Barboza, P. S., Parker, K. L., and Hume, J. D. 2009. *Integrative wildlife nutrition*. Berlin: Springer-Verlag. 341 pp.

A general reference work that applies the basic principles of nutrition to mammals and other animals in their natural environments. Well illustrated with photos, graphs, and drawings.

Carey, D. P., Norton, S. A., and Bolser, S. M., eds. 1996. *Recent Advances in Canine and Feline Nutritional Research: Proceedings of the 1996 Iams International Nutrition Symposium*. Wilmington, OH: Orange Frazer Press. 284 pp.

Discusses the importance of diet to gastrointestinal health, neonatal and reproductive health, and renal health. Provides information on nutrition for the physically stressed dog.

Cheeke, P. R. 2004. *Applied animal nutrition: Feeds and feeding*. 3rd ed. Upper Saddle River, NJ: Prentice Hall. 624 pp.

Describes the properties of feedstuffs and feeding practices for a variety of domestic and exotic animals. A good introduction on this topic.

Comparative Nutrition Society. 1998–. *Symposia of the Comparative Nutrition Society*. Silver Spring, MD: Comparative Nutrition Society.

Symposia held biennially by the Comparative Nutrition Society bring together laboratory and field scientists from various disciplines with interests in comparative nutrition. Papers cover the disciplines of nutrition, physiology, metabolism, biochemistry, animal science, wildlife and marine biology, ecology, and all taxa, including mammals.

D'Mello, J. P. F., and Devendra, C., eds. 1995. *Tropical legumes in animal nutrition*. New York: Oxford University Press. 352 pp.

Discusses the use of tropical browse, pasture, and grain legumes in animal nutrition. Written by leading international authorities.

Dr. Scholl Nutrition Conference. 1980–91. *Proceedings of the Annual Dr. Scholl Nutrition Conference on the Nutrition of Captive Wild Animals*. 1st–9th. Chicago: Lincoln Park Zoological Society.

Subjects covered in these annual proceedings range from general nutrition of exotic animals to requirements of individual species and families. One of the few sources of information about nutrition of exotic animals.

Engel. C. 2002. *Wild health: How animals keep themselves well and what we can learn*. Boston: Houghton Mifflin. 276 pp.

In this engaging book, the author investigates how animals (mammals and birds) self-medicate themselves to stay healthy. She has compiled laboratory studies and field observations to separate scientifically verifiable fact and hard data from folklore.

Fidgett, A., [et al.], eds. 2003. *Zoo animal nutrition*. Vol. 2. Furth: Filander Verlag. 278 pp.

This volume presents a selection of the papers that would have been presented at the 2nd Zoo Animal Nutrition Conference, had it not been cancelled due to an outbreak of foot-and-mouth disease. It is a useful reference on the nutrition of both free-ranging and captive ungulates.

Hudson, R. J., and White, R. G. 1985. *Bioenergetics of wild herbivores*. Boca Raton, FL: CRC Press. 314 pp.

Topics include digestion, thermoregulation in ungulates, maintenance metabolism, and pregnancy and lactation as they relate to herbivores. A classic for the nutritionist.

Hume, I. D. 1999. *Marsupial nutrition*. New York: Cambridge University Press. 434 pp.

Discusses how the digestive systems and metabolism of marsupials, from small insectivores to large folivores, are designed to cope with very different food types, such as nectar, fungus, tree sap, grass, insects, and eucalyptus foliage. Applicable to all mammals. Excellent reference for wildlife biologists and veterinarians.

Jung, H-J. G., and Fahey, G. C. Jr., eds. 1999. *Nutritional Ecology of Herbivores: Proceedings of the 5th International Symposium on the Nutrition of Herbivores*. Savoy, IL: American Society of Animal Science. 836 pp.

A series of papers on factors affecting digestion and metabolism in a wide range of wild and domestic herbivores.

Kellems, R. O., and Church, D. C. 2001. *Livestock feeds and feeding*. 5th ed. Upper Saddle River, NJ: Prentice Hall. 654 pp.

A good introduction to the nutrition and feeding of livestock, including the chemical composition and animal utilization of feedstuffs. Species chapters discuss the management and feeding practices that are unique to those species.

Montgomery, G. G., ed. 1978. *The ecology of arboreal folivores*. (A symposium held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, May 29–31, 1975.) Washington, DC: Smithsonian Institution Press. 574 pp.

Papers given at a symposium that addressed plant ecology and animal adaptations for feeding on leaves. A guide to the captive management of mammals such as monkeys and koalas. Although dated, still useful for zoos.

National Research Council. *Nutrient requirements of domestic animals*. Washington, DC: National Academies Press. The following are also available full text at the National Academies Press Web site:

Nutrient requirements of beef cattle. 7th rev. ed. 1996. 248 pp.
Nutrient requirements of dogs and cats. Rev. ed. 2006. 398 pp.
Nutrient requirements of goats: Angora, dairy, and meat goats in temperate and tropical countries. 1981. 91 pp.
Nutrient requirements of horses. 6th rev. ed. 2007. 341 pp.
Nutrient requirements of mink and foxes. 2nd rev. ed. 1982. 72 pp.
Nutrient requirements of nonhuman primates. 2nd rev. ed. 2003. 308 pp.
Nutrient requirements of rabbits. 2nd rev. ed. 1977. 17 pp.
Nutrient requirements of sheep. 6th rev. ed. 1985. 99 pp.
Nutrient requirements of small ruminants: Sheep, goats, cervids, and new world camelids. 2007. 362 pp.
Nutrient requirements of swine. 10th rev. ed. 1998. 210 pp.

Nijboer, J [et al.], eds. 2000. *Zoo animal nutrition*. Furth: Filander Verlag. 324 pp.

Provides an overview of nutrition research in zoos and addresses nutritional problems specific to captive animals. Papers on marsupials, bats, gorillas, monkeys, lemurs, otters, babirusa, okapis, and giraffes. Infant diet requirements of cats, otters, and wild pigs are provided.

Perlman, J., and MacLeod. A. *Wildlife feeding and nutrition*. 1st ed. Oakland, CA: International Wildlife Rehabilitation Council. 42 pp.

Topics in the publication include dietary patterns, nutrients, digestion, feeding captive adult wildlife, energy requirements, principles of formulating diets, feeding neonate and juvenile animals, emaciation, malnutrition, and enrichment.

Pond, W. G., Church, D. C., and Pond, K. R. 1995. *Basic animal nutrition and feeding*. 4th ed. New York: John Wiley. 615 pp.

Good introductory resource covering the principles of animal nutrition. Identifies all the nutrients required in animal diets for growth, reproduction, and maintenance.

Robbins, C. T. 1994. *Wildlife feeding and nutrition*. 2nd ed. San Diego, CA: Academic Press. 352 pp.

Reviews on the basic principles of nutrition for free-ranging and captive wild animals. A valuable reference for the zoo nutritionist and manager.

Stevens, C. E., and Hume. I. D. 1995. *Comparative physiology of the vertebrate digestive system*. 2nd ed. New York: Cambridge University Press. 416 pp.

Discusses energy and nutrient requirements and how they vary across vertebrate groups. Chapters cover motor activity, digestion and absorption, microbial fermentation, secretions, and neuroendocrine control.

Van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. 2nd ed. Ithaca, NY: Comstock. 476 pp.

Classic on fiber and the rumen and tropical forages.

EXHIBITRY

Association of Zoological Horticulture. 1998. *Animal browse survey*. New Orleans: Audubon Institute. 172 pp. CD-ROM version available from AZH entitled *2003 Animal Browse and Enrichment Survey*. Requires MS access 2000 or later version.

Provides a list of plants used as feed and/or enrichment for various zoo animals. The information is organized in a number of different ways to ensure easy access.

Association of Zoological Horticulture and American Association of Zoo Veterinarians. 1992. *1992 toxic plant survey*. Asheboro: North Carolina Zoo/Association of Zoological Horticulture. 502 pp.

Gathers zoo expertise and experience together in one resource. An extensive plant index indicates the toxic parts of the plant, and the animal's reaction. A separate animal index provides a list of plants toxic to individual species. An extensive bibliography is included.

Bailey, L. H. 1976. *Hortus third: A concise dictionary of plants cultivated in the United States and Canada*. Hoboken, NJ: John Wiley. 1290 pp.

Still recognized as one of the best plant encyclopedias. Includes 23,979 entries with descriptions for families, genera, and species. Notes on plant use, culture, and propagation. Excellent for planning exhibits and landscapes.

Bell, C. E., ed. 2001. *Encyclopedia of the world's zoos*. 3 vols. Chicago: Fitzroy Dearborn. 1577 pp.

A 3-volume set providing a comprehensive overview of the world's major zoos, their history, development, operating budgets, conservation activities, and strategic plans. Species accounts are provided for key animals, along with their exhibit and collection history. Many black-and-white photos of exhibits and architectural drawings are included.

Burrows, G. E., and Tyrl, R. J. 2001. *Toxic plants of North America*. Ames: Iowa State University Press. 1342 pp.

A comprehensive reference of plants toxic to both humans and animals found in North America. Information includes plant morphology and distribution, toxicants, associated disease problems, and treatment. Arranged alphabetically, with black-and-white drawings and range maps.

Graf, A. B. 1992. *Hortica: Color cyclopedia of garden flora in all climates and indoor exotic plants*. Farmingdale, NJ: Roehrs. 1216 pp.

Extensive number of high-quality color photographs (8100). Excellent source for identifying and choosing garden and indoor plants for exhibits. Includes hardiness zone maps and detailed descriptions of more than 10,000 ornamental plants.

———. 2003. *Tropica: Color cyclopedia of exotic plants and trees for warm-region horticulture, in cool climate, the summer garden, or sheltered indoors*. 5th ed. Farmingdale, NJ: Roehrs. 1152 pp.

Excellent source for identifying and choosing tropical and

indoor plants for exhibits and gardens. Illustrated with 7000 color photographs.

Hancocks, D. 1971. *Animals and architecture*. New York: Praeger. 200 pp.

A history of zoological garden architecture. Well illustrated with drawings and photographs of exhibits, from old farm buildings and menageries to state-of-the-art exhibits of the time. Includes a chapter on animal architecture. Stresses naturalistic enclosures. Though older, it is a classic in this small field of literature.

———. 2001. *A different nature: The paradoxical world of zoos and their uncertain future*. Berkeley and Los Angeles: University of California Press. 279 pp.

While exploring the history of zoos and their role in society worldwide, the author focuses on zoo exhibits and zoo design. He advocates for humane environments for captive animals. Well illustrated.

Hanson, E. 2002. *Animal attractions: Nature on display in American zoos*. Princeton, NJ: Princeton University Press. 243 pp.

A historical look at how American zoos have designed and displayed their animal collections in their efforts to promote nature appreciation.

International Symposium on Zoo Design and Construction. 1975, 1976, 1980, 1989, 1999. *Zoo Design 1, 2, 3,4, and 5*. (Proceedings of the International Symposium on Zoo Design and Construction held at Paignton Zoological and Botanical Gardens and Oldway Mansion, Paignton, Devon, England.)

The 1989 symposium is titled *Zoo Design and Construction*, and the 1999 symposium is titled *Conservation Centres for the New Millennium*. Papers address general principles of zoo design, quarters for large mammals, indoor exhibits, and the use of glass; designing for animal welfare; facilities for visitors; the use of plants; building zoos in regions of extreme temperatures; and redesigning old zoos.

Polakowski, K. J. 1987. *Zoo design: The reality of wild illusions*. Ann Arbor: University of Michigan Press. 193 pp.

A compendium of zoo design concepts from professionals who participated in a landscape architecture design course. Discussed are such topics as design philosophies of the past and present, carrying out goals of the zoo through design of exhibits, long-range development planning, presenting themes in exhibits, and using plants for both animals and people.

Sausman, K., ed. 1982. *Zoological parks and aquarium fundamentals*. Wheeling, WV: American Association of Zoological Parks and Aquariums. 356 pp.

Contributors to this volume provide basic information for the successful design, development, and overall operation of the modern zoo and aquarium. Although published in 1982, much of the information is still relevant. A valuable source of information for the zoo manager.

Serrell, B. 1996. *Exhibit labels: An interpretive approach*. Walnut Creek, CA: Alta Mira Press. 261 pp.

Provides a complete overview on writing visitor-friendly interpretive labels. Analyzes the different visitor learning styles and gives advice on making words and images work together. Discusses typographic design, production, and fabrication.

Wemmer, C. M., ed. 1992. *The Ark evolving: Zoos and aquariums in transition*. Front Royal, VA: Conservation and Research Center, National Zoological Park. 288 pp.

Addresses the evolution of zoo animal exhibits, the stylistic trends affecting modern exhibit design, and the messages that zoos and aquariums should be conveying.

CONSERVATION AND RESEARCH

American Zoo and Aquarium Association. *AZA Annual Report on Conservation and Science* (*ARCS*). 1993/94–2006. Silver Spring, MD: American Zoo and Aquarium Association. Available only for AZA members online: 2003–6.

Annual summaries of AZA member institutions' contributions to wildlife and habitat conservation.

———. 1994. *AZA Manual of Federal Wildlife Regulations*. Vol. 1: *Protected Species*. Vol. 2 A and B: *Laws and Regulations*. Silver Spring, MD: American Zoo and Aquarium Association.

A guide to all federal and internationally protected wildlife species.

Bolton, N., ed. 1997. *Conservation and the use of wildlife resources* Conservation Biology Series. New York: Chapman and Hall. 278 pp.

Provides a contemporary perspective on conservation issues. Topics include the impact of human, technological, urbanization, and cultural change, sustainability, use of protected areas, zoos and their roles, and ecotourism. A number of international case studies are included.

Bookhout, T. A., ed. 1996. *Research and management techniques for wildlife and habitats*. 5th ed. Bethesda, MD: Wildlife Society. 740 pp.

An extremely comprehensive resource. It covers research and experimental design, data analysis, capture, handling and marking of wildlife, populations analysis and management, and habitat analysis and management.

Bothma, J. du P., ed. 1996. *Game ranch management*. 3rd ed. Pretoria, South Africa: J. L. van Schaik Publishers. 639 pp.

A multiauthored, practical resource on all aspects of game ranching, such as planning, guiding principles, wildlife selection, disease, habitat management, and sustainable use of resources.

Caro, T., ed. 1998. *Behavioral ecology and conservation biology*. New York: Oxford University Press. 582 pp.

Each chapter discusses conservation problems and conservation intervention programs. Topics include behavior, mating systems, dispersal and inbreeding avoidance, and effective population size. Useful for designing research and reintroduction programs.

Caughley, G., and Gunn, A. 1996. *Conservation biology in theory and practice*. Cambridge, MA: Blackwell Science. 459 pp.

An authoritative, practical guide to conserving endangered species. Includes numerous case histories of extinctions and near extinctions to illustrate population dynamics, risk assessment, and diagnosis and treatment of declines. Discusses the importance of economics and international and national legislation.

Clark, T. W., Reading, R. P., and Clarke, A. L., eds. 1994. *Endangered species recovery: Finding the lessons, improving the process*. Washington, DC: Island Press. 461 pp.

Case studies of prominent species recovery programs are presented in an attempt to explore and analyze their successes, failures, and problems. Provides practical solutions to improve recovery programs.

Conover, M. R. 2002. *Resolving human-wildlife conflicts: The science of wildlife damage management*. Boca Raton, FL: CRC Press. 440 pp.

Discusses issues facing wildlife managers and anyone else who deals with the interaction of wildlife and humans. Covers such topics as philosophy, history, zoonoses, economics, environment damage by exotic species, management techniques (lethal control, fertility control, translocation, chemical repellents, etc.), and human perspectives. Well organized, with case studies.

Conway, W. G., [et al.], eds. 2001. *The AZA field conservation resource guide*. Silver Spring, MD: American Zoo and Aquarium Association. 323 pp.

A practical manual that discusses the possible options for field

conservation in zoos and aquariums as well the costs and benefits of each.

Cowlishaw, G., and Dunbar, R. I. M. 2000. *Primate conservation biology*. Chicago: University of Chicago Press. 498 pp.

Gives detailed overviews of the diversity, life history, ecology, and behavior of primates; discusses the current threats, such as habitat destruction and hunting; and reviews conservation strategies and managing practices.

Dinerstein, E. 2003. *The return of the unicorns: The natural history and conservation of the greater one-horned rhinoceros*. New York: Columbia University Press. 316 pp.

This is a fascinating book about the author's efforts to save the one-horned rhinoceros in the Royal Chitwan National Park in Nepal. Its program of protection, habitat planning, public awareness, and economic incentives serve as a successful example of large mammal conservation.

Entwistle, A., and Dunstone, N., eds. 2000. *Priorities for the conservation of mammalian diversity: Has the panda had its day? Conservation Biology*, no. 3. New York: Cambridge University Press. 455 pp.

A review of modern conservation approaches as they relate to mammals. Researchers and conservationists discuss justifying mammal conservation, setting priorities, and the promising new approaches and techniques for future mammal protection.

Feinsinger, P. 2001. *Designing field studies for biodiversity conservation*. Washington, DC: Island Press. 212 pp.

A common-sense approach to scientific inquiry, such as framing questions and designing the study; understanding the natural history of plants, animals, and landscapes; and interpreting results.

Festa-Bianchet, M., and Apollonio, M., eds. 2003. *Animal behavior and wildlife conservation*. Washington, DC: Island Press. 380 pp.

Explores how knowing individual animal behavior can play a key role in the effectiveness of conservation programs.

Frankham, R., Ballou, J. D., and Briscoe, D. A. 2004. *A primer of conservation genetics*. New York: Cambridge University Press. 234 pp.

Introductory text that stresses the importance of genetic studies to conservation. Topics covered are genetic diversity, genetics consequences of small population size, and captive breeding and reintroduction.

Friedmann, Y., and Daly, B., eds. 2004. *Red data book of the mammals of South Africa: A conservation assessment*. Parkview, South Africa: Conservation Breeding Specialist Group, Southern Africa/International Union for Conservation of Nature; Endangered Wildlife Trust. 722 pp.

A comprehensive scientific evaluation of the conservation status of 295 terrestrial and marine species and subspecies of mammals in South Africa. Includes distribution, habitat, population status and trends, breeding characteristics, distribution maps for terrestrial species, and all available references and research findings. Provides recommendations for conserving and managing all mammals in South Africa and their habitat.

Gales, N., Hindell, M., and Kirkwood, R., eds. 2003. *Marine mammals: Fisheries, tourism and management issues*. Collingwood, Victoria, Australia: CSIRO. 446 pp.

Papers presented at the Southern Hemisphere Marine Mammal Conference of 2000. Sixty-eight leading scientists from 12 countries discuss human-wildlife interaction. They examine such topics as culling, how fisheries and aquaculture interact with mammal populations, and the effects of whale-, dolphin-, and seal-watching industries on wildlife.

Ganslosser, U., Hodges, J. K., and Kaumanns, W. 1995. *Research and captive propagation*. Furth: Filander Verlag. 338 pp.

This book provides a comprehensive overview of the biological and veterinary techniques for keeping and breeding endangered species. Areas covered include systematics, genetics, reproductive biology, nutrition and metabolism, behavior, ecology, veterinary medicine, and evolutionary biology. Excellent for zoos.

Gibbons Jr., E. F., Durrant, B. S., and Demarest, J., eds. 1995. *Conservation of endangered species in captivity: An interdisciplinary approach*. Albany: State University of New York Press. 810 pp.

The book is organized by taxonomic group, and includes marine mammals, primates, and other mammals. For each group, discussion is centered on conservation, reproductive physiology, behavior, and captive design. Conservation chapters summarize the status of the taxonomic group, both in the wild and in captivity.

Gibbons Jr., E. F., Wyers, E. J., and Waters, E., eds. 1994. *Naturalistic environments in captivity for animal behavior research*. Albany: State University of New York Press. 387 pp.

Addresses all aspects of naturalistic environments for animals in captivity. It integrates animal care regulations, design, construction, and operation of animal facilities and the impact of these elements on animal behavior. For regulatory and animal care personnel as well as for the researcher and student of animal behavior.

Gipps, J. H. W., ed. 1991. *Beyond captive breeding: Reintroducing endangered mammals to the wild. Symposia of the Zoological Society of London*, no. 62. Oxford: Clarendon Press. 284 pp.

An examination of the theory and practice of reintroduction, with detailed case studies of the Arabian oryx, red wolf, and black-footed ferret. One of the first books on this expanding field.

Gittleman, J. L., Funk, S. M., Macdonald, D. W., and Wayne, R. K., eds. 2001. *Carnivore conservation*. (*Conservation Biology*, no. 5.) New York: Cambridge University Press. 690 pp.

International contributors review and summarize current problems, limitations, and opportunities of carnivore conservation, such as introduced species, hybridization, and competition for habitat between humans and carnivores. Approaches and solutions are also considered for future research and applied management, such as carnivore reintroductions, monitoring terrestrial carnivore populations, and new methods for obtaining and analyzing genetic data.

Gosling, L. M., and Sutherland, W. J. 2000. *Behaviour and conservation. Conservation Biology*, no. 2. Cambridge: Cambridge University Press. 438 pp.

Contributors discuss how their work on the behavior of an animal can contribute to its conservation. This book is important in the efforts being made to conserve endangered species.

Griffiths, H. I., ed. 2000. *Mustelids in a modern world: Management and conservation aspects of small carnivore; Human interactions.* Leiden: Backhuys. 342 pp.

Chapters include conservation of wolverines in Scandinavia, recovery of the polecat in Britain, conservation implications of hybridization between polecats, ferrets, and European mink, and monitoring the rare pine martin populations in England and Wales.

Hearn, J. P., and Hodges, J. K., eds. 1985. *Advances in animal conservation. Symposia of the Zoological Society of London*, no. 54. New York: Oxford University Press. 282 pp.

Proceedings of a symposium held at the Zoological Society of London. The volume is divided into 4 major sections: conservation in the wild, conservation in captivity, conservation and comparative medicine, and government and conservation.

Hoage, R. J., and Moran, K,. eds. 1998. *Culture: The missing element in conservation and development.* Dubuque, IA: Kendall/Hunt. 160 pp.

Papers presented at a symposium held at the National Zoological Park, Washington, DC, and follow-up discussions. Topics include participation of local people in the design and implementation of conservation projects, the rights of indigenous peoples in natural resource management, and cultural considerations in the design of conservation, public awareness, and education campaigns.

Kleiman, D. G., and Rylands, A. B., eds. 2002. *Lion tamarins: Biology and conservation*. Zoo and Aquarium Biology and Conservation. Washington, DC: Smithsonian Books. 384 pp.

This book describes the extraordinary efforts made to save 4 lion tamarin species (golden, golden-headed, black-faced, and black) from extinction, first in captivity and then in the wild. Good scientific, management, and educational principles contributed to developing a good recovery and conservation program.

Macdonald, D. W., and Sillero-Zubiri, C., eds. 2004. *The biology and conservation of wild canids*. Oxford: Oxford University Press. 450 pp.

Summation on current research of the 36 species of wolves, dogs, jackals, and foxes. Included are papers on their biology, natural history, management, diseases, population genetics, and conservation.

Maehr, D. S., Noss, R. F., and Larkin, J. L., eds. 2001. *Large mammal restoration: Ecological and sociological challenges in the 21st century*. Washington, DC: Island Press. 375 pp.

Written by conservation biologists, this book brings together detailed case studies of restoring large mammals in North America, such gray wolves to Yellowstone National Park and bison herds to the Great Plains. A valuable resource for those involved in conservation and reintroductions.

Mazur, N. A. 2001. *After the Ark? Environmental policy making and the zoo*. Carlton South, Victoria, Australia: Melbourne University Press. 262 pp.

Discusses how well modern zoos are fulfilling their aims of conservation, education, research, and recreation, and concludes that more needs to be done. Although it focuses on Australian zoos, the scope is international. An appendix describes strategies relevant to the role of zoos in conservation. Illustrations, charts, and bibliography included.

Morrison, M. L. 2002. *Wildlife restoration: Techniques for habitat analysis and animal monitoring*. Washington, DC: Island Press. 209 pp.

A concise guide to understanding wildlife and habitats in hopes of restoring it. Topics include captive breeding, monitoring programs, designing a reserve, and working with wildlife managers. Useful for reintroduction programs.

O'Brien, S. J. 2003. *Tears of the cheetah: And other tales from the genetic frontier*. New York: Thomas Dunne Books/St. Martin's Press. 287 pp.

Easily understood by the nonexpert, this is a wonderfully fast-paced book of genetic detective stories about such species as the cheetah, humpback whale, and giant panda. Shows the importance of genetics to the field of conservation.

Olney, P. J. S., Mace, G. M,. and Feistner, A. T. C., eds. 1994. *Creative conservation: Interactive management of wild and captive animals*. New York: Chapman and Hall. 517 pp.

Thirty-one authors discuss the relationships between breeding endangered species in captivity and preserving and managing species in the wild. Issues such as population structure and disease risk are discussed. Case studies include canids, ferrets, primates, and bats.

Pullin, A. S. 2002. *Conservation biology*. New York: Cambridge University Press. 358 pp.

This beautifully illustrated textbook introduces the field of conservation biology, the science of preserving biodiversity. Among other topics, it discusses the problems of habitat loss and fragmentation, habitat disturbance, and nonsustainable species exploitation.

Seidensticker, J., Christie, S., and Jackson, P., eds. 1999. *Riding the tiger: Tiger conservation in human-dominated landscapes*. New York: Cambridge University Press. 383 pp.

For the general reader, this is a well-illustrated scientific account of the reasons for the decline of and possible solutions for saving a large carnivore—the tiger.

Soulé, M. E., and Orians, G. H., eds. 2001. *Conservation biology: Research priorities for the next decade*. Washington, DC: Island Press. 307 pp.

This volume is a result of a gathering of leading conservation biologists in 2000. Its 10 articles, introduction, and conclusion serve as a guide to what research is needed in the years to come so that conservation can be effective.

Stanley Price, M. R. 1989. *Animal re-introduction: The Arabian oryx in Oman*. New York: Cambridge University Press. 291 pp.

A classic conservation success story, this book is a scientific account of the planning, problems, and successes of the first 7 years of the Arabian oryx reintroduction project in Oman. Maps, drawings, graphs, and references are included. Important example for future reintroduction.

Twiss Jr., J. R., and Reeves, R. R., eds. 1999. *Conservation and management of marine mammals*. Washington, DC: Smithsonian Institution Press. 471 pp.

In this edited volume, 31 scholars, researchers, and conservationists discuss such topics as legislation and policy, conflicts between humans and animals, marine pollution, marine mammals in captivity, and endangered marine species such as the Hawaiian monk seal, the Florida manatee, and the North Atlantic right whale.

Wallis, J., ed. 1997. *Primate conservation: The role of zoological parks*. Special Topics in Primatology, vol. 1. Chicago: American Society of Primatologists. 252 pp.

Provides details of primate conservation projects conducted or sponsored by U.S. zoological parks. A valuable resource for conservationists, zoo personnel, and all primatologists working to save threatened or endangered primates.

Western, D., and M. C. Pearl. 1989. *Conservation for the twenty-first century*. New York: Oxford University Press. 365 pp.

This book brings together diverse views on the topic of conserving nature from an international group of experts. Centering on the subject of wildlife and its habitat, it is organized around 4 themes—tomorrow's world, conservation biology, conservation management, and conservation realities. A classic on this topic.

Wiese, R. J., and Hutchins, M. 1994. *Species Survival Plans: Strategies for wildlife conservation*. Wheeling, WV: American Zoo and Aquarium Association. 64 pp.

A concise introduction to the conservation mission of zoos and aquariums. The importance of Species Survival Plans to accomplishing that mission is explained, and numerous examples of research projects are given.

World Association of Zoos and Aquariums. 2005. *Building a future for wildlife: The world zoo and aquarium conservation strategy*. Bern, Switzerland: World Association of Zoos and Aquariums Executive Office. 118 pp.

An international effort that provides a common conservation philosophy for zoos and aquariums around the world as well as standards and policies to support their conservation goals. This document can also be used to articulate to the general public what zoos and aquariums are doing for conservation.

BEHAVIOR

Barrows, E. M. 2000. *Animal behavior desk reference: A dictionary of animal behavior, ecology, and evolution*. 2nd ed. Boca Raton, FL: CRC Press. 936 pp.

A valuable and easy-to-use reference book. Contains over

5000 alphabetically arranged, annotated entries on animal behavior, biogeography, evolution, ecology, genetics, and other related sciences. Appendixes contain taxonomic tables; companies, organizations and societies; and numerous references.

Benyus, J. M. 1992. *Beastly behaviors: A zoo lover's companion; What makes whales whistle, cranes dance, pandas turn summersaults, and crocodiles roar; A watcher's guide to how animals act and why*. Menlo Park, CA: Addison-Wesley. 366 pp.

A well-illustrated, easy-to-read guide to the behavior of captive animals.

Boinski, S., and Garber, P. A., eds. 2000. *On the move: How and why animals travel in groups*. Chicago: University of Chicago Press. 811 pp.

Leading scholars discuss animal communication, cognition, and memory as they relate to how animals organize their group movements. The emphasis is on primates.

Burghardt, G. M. 2005. *The genesis of animal play: Testing the limits*. Cambridge, MA: MIT Press. 488 pp.

The author examines the origins and evolution of play in humans and animals, and how it can help our understanding of evolution, the brain, and psychology.

De Waal, F. B. M., and Tyack, P. L., eds. 2003. *Animal social complexity: Intelligence, culture and individualized societies*. Cambridge, MA: Harvard University Press. 616 pp.

Data are presented on topics such as cooperative strategies, social cognition, communication, and cultural transmission. Case studies take in a variety of animals such as primates, hyenas, dolphins, and sperm whales.

Eisenberg, J. F., and Kleiman, D. G., eds. 1983. *Advances in the study of mammalian behavior*. Special Publication of the American Society of Mammalogists, no. 7. Stillwater, OK: American Society of Mammalogists. 753 pp.

A collection of papers delivered at a conference held in 1980 at the National Zoological Park's Conservation and Research Center, Fort Royal, Virginia. A good introduction of the many subdisciplines of behavioral studies and their applications.

Evans, C. 2003. *Vomeronasal chemoreception in vertebrates: A study of the second nose*. London: Imperial College Press. 265 pp.

This book deals with the nature of the vomeronasal organ and the chemical signals that convey information from one individual to another.

Ewer, R. F. 1968. *Ethology of mammals*. New York: Plenum. 418 pp.

Discusses basic principles of mammalian behavior based on structure and relationship to the environment. Chapters are on such subjects as expression and communication, courtship and mating, parent and child, and play.

Fagen, R. 1981. *Animal play behavior*. New York: Oxford University Press. 684 pp.

An in-depth look into the biology of animal play. This excellent book is extremely well researched and provides references to earlier literature. Appendixes explain scientific notations and provide common and scientific names, a list of vocabulary terms, and more.

Geist, V., and Walther, F., eds. 1974. *The behaviour of ungulates and its relation to management*. 2 vols. IUCN Publications, n.s., no. 24. Morges, Switzerland: International Union for Conservation of Nature.

A series of papers presented at an international symposium held at the University of Calgary, Alberta, Canada, November 1971. Volume 1 deals primarily with social behavior and ecology, classification, and taxonomy. Volume 2 focuses on ecology and management. A technical treatment, well illustrated, aimed at captive and wild management.

Goodall, J. 1986. *The chimpanzees of Gombe*. Cambridge, MA: Harvard University Press, Belknap Press. 673 pp.

A detailed account of Goodall's landmark chimpanzee studies. Provides insight into the ape's learning processes, cognitive abilities, and problem solving. Every aspect of chimpanzee behavior is covered: feeding, social structure, aggression, hunting, grooming, dominance, and communication.

Goodenough, J., McGuire, B., and Wallace, R. A. 2000. *Perspectives on animal behavior*. 2nd ed. New York: John Wiley. 542 pp.

A balanced, integrated, and thorough treatment of animal behavior. Chapters discuss the various approaches taken in studying behavior, the relationship between genes and behavior, development and environmental factors, behavior of groups, social behavior, and much more.

Gubernick, D. J., and Klopfer, P. H., eds. 1981. *Parental care in mammals*. New York: Plenum Press. 459 pp.

A well-balanced treatment of this important topic. Includes why parental care evolved and the evolution of various parental strategies. The mother-infant relationship, male parental care, allomothering, sibling interactions, and the social context of parental care are addressed.

Hauser, M. D. 2000. *Wild minds: What animals really think*. New York: Henry Holt. 315 pp.

The author guides us through field and laboratory scientific studies of the brain to reveal the intellectual and emotional lives of animals. Species such as primates, monkeys, crows, and white-crowned sparrows serve as examples.

Hediger, H. 1968. *The psychology and behaviour of animals in zoos and circuses*. New York: Dover. 166 pp.

This collection of essays on animal psychology is based on the author's own experiences and observations. Included is the daily behavior of animals in the wild as well as that of animals in zoos and circuses. Useful for anyone dealing with exotic animals.

Krebs, J. R., and Davies, N. B., eds. 1997. *Behavioural ecology: An evolutionary approach*. 4th ed. Cambridge, MA: Blackwell Science. 456 pp.

Contributors discuss recent developments such as individual behavior, social systems, life histories, phylogenies, and populations.

Lawrence, A. B., and Rushen, J., eds. 1993. *Stereotypic animal behaviour: Fundamentals and applications to welfare*. Tucson, AZ: CAB International. 212 pp.

The forms and neurobiological basis of stereotypic behavior are discussed in this volume.

Lehner, P. N. 1996. *Handbook of ethological methods*. 2nd ed. New York: Cambridge University Press. 672 pp.

A practical approach to the study of animal behavior. The book is clearly written and well illustrated, and presents a logical, meaningful, and practical approach to ethology. Sections include design of research, data collection methods and equipment, and statistical tests, as well as interpretation and presentation of results.

Mann, J., Connor, R. C., Tyack, P. L., and Whitehead, H., eds. 2000. *Cetacean societies: Field studies of dolphins and whales*. Chicago: University of Chicago Press. 433 pp.

A comprehensive synthesis and review of cetacean behavior. It discusses the history of cetacean scientific behavioral research; provides information on the most studied species: humpback whales, sperm whales, bottlenose dolphins, and killer whales; and concludes with several chapters on general topics of cetacean group living, reproductive strategies, communication, and conservation.

Maple, T. L. 1980. *Orang-utan behavior*. New York: Van Nostrand Reinhold. 268 pp.

Detailed behavior study of the orangutan in captivity and in the wild.

Maple, T. L., and Hoff, M. P. 1982. *Gorilla behavior*. New York: Van Nostrand Reinhold. 290 pp.

Integrates the findings of field and captive research. Special sections on the general behavior patterns of the gorilla, its expression of intelligence and emotions, its sexual behavior, and its birth and parental behavior.

Martin, P. 1986. *Measuring behaviour: An introductory guide*. New Rochelle, NY: Cambridge University Press. 200 pp.

This book provides a comprehensive review of the principles and techniques used for measuring animal and human behavior. It discusses how to record direct observations, and analyses data. Useful for the zoo researcher.

Maynard Smith, J., and D. Harper. 2003. *Animal signals*. Oxford: Oxford University Press. 166 pp.

The authors review theories on the reliability of animal signals, especially those of mammals. For those interested in animal communication, behavior, and evolution.

Mittermeier, R. A., and Coimbra-Filho, A. F., eds. 1981. *Ecology and behavior of neotropical primates*. Vol. 1. Rio de Janeiro: Academica Brasileira de Ciencias. 496 pp.

Ecology and behavior for Goeldi's monkeys, night monkeys, titi monkeys, squirrel monkeys, capuchin monkeys, saki monkeys, and the uakaris.

Mittermeier, R. A., Coimbra-Filho, A. F., and Fonseca, G. A. B., eds. 1988. *Ecology and behavior of neotropical primates*. Vol. 2. Washington, DC: World Wildlife Fund. 610 pp.

Ecology and behavior for marmosets, tamarins, howling monkeys, spider monkeys, woolly monkeys, and muriquis.

Pearce, J. M. 1997. *Animal learning and cognition: An introduction*. 2nd ed. Hove, East Sussex, UK: Psychology Press. 333 pp.

Reviews the main principles and experimental findings from a century of research on animal intelligence. Topics covered include learning, conditioning, memory, communication, and language.

Poole, T. B. 1985. *Social behaviour in mammals*. New York: Chapman and Hall. 248 pp.

A good summary of research on mammalian behavior in natural environments. Discusses competitive behavior, such as fighting, threat, and submission, and cooperative interactions, such as mating and parental care.

Reader, S. M., and Laland, K. N., eds. 2003. *Animal innovation*. New York: Oxford University Press. 300 pp.

This collection of essays discusses how individual animals invent new behavior patterns, which then spread throughout a population. This flexibility of behavior patterns is important in the survival of species, especially those that are endangered.

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T., eds. 1987. *Primate societies*. Chicago: University of Chicago Press. 578 pp.

A review of field studies on nonhuman primates. General descriptions of taxonomic groups with emphasis on social behavior are followed by essays on socioecology and communication in primates.

Tomasello, M., and Call, J. 1997. *Primate cognition*. New York: Oxford University Press. 517 pp.

A comprehensive overview. Covers social knowledge and interaction, tool use, problem solving, behavioral traditions in the wild, and current and past theory and research.

Walther, F. R. 1984. *Communication and expression in hoofed mammals*. Bloomington: Indiana University Press. 423 pp.

Topics covered include advertising, marking, signals in mother-offspring relations, displays of threat, dominance, courtship, and submission, and interspecific communication. Well illustrated. Includes a 30-page table of behavioral occurrences listed by species.

Wrangham, R. W., McGrew, W. C., deWaal, F. B. M., and Heltne, P., eds. 1994. *Chimpanzee cultures*. Cambridge, MA: Harvard University Press. 424 pp.

The information in this volume is the result of long-term field studies on chimpanzees, bonobos, and occasionally gorillas. Noted scientists present their findings and explain the relationships between the biology, ecology, and behavior of these great apes.

Wyatt, T. D. 2003. *Pheromones and animal behaviour: Communication by smell and taste*. New York: Cambridge University Press. 391 pp.

A clearly written, good introduction to chemical communication of animals.

REPRODUCTION

Austin, C. R., and Short, R. V. eds. 1985. *Reproduction in mammals*. Vol. 4, *Reproduction fitness*. 2nd ed. Cambridge: Cambridge University Press. 256 pp.

This volume pays particular attention to genetic, environmental, behavioral, and immunological mechanisms that can contribute to an animal's overall reproductive fitness.

Bearden, H. J., Fuquay, J. W., and Willard. S. T. 2004. *Applied animal reproduction*. 6th ed. Upper Saddle River, NJ: Pearson Prentice Hall. 427 pp.

A general comprehensive text that covers basic physiology related to reproduction in livestock species. Topics include artificial insemination, anatomy, function, and regulations. For animal scientists, reproductive physiologists, caretakers, and herd managers.

Bronson, F. H. 1989. *Mammalian reproductive biology*. Chicago: University of Chicago Press. 325 pp.

An overview of the way mammals reproduce, especially how environmental factors regulate reproduction. Ecological and physiological factors are also considered, such as food availability, photoperiod, and social cues.

Concannon, P. W., [et al.], eds. 1993. *Fertility and Infertility in Dogs, Cats and Other Carnivores: Proceedings of the 2nd International Symposium on Canine and Feline Reproduction. Journal of Reproduction and Fertility* 47. Cambridge, UK: Society for Reproduction and Fertility. 569 pp.

This volume summarizes reproductive research in canid, felid, and related species, including fox, mink, and exotic cats. It focuses on basic reproductive biology, infertility problems, and the application of reproductive technologies such as semen evaluation, artificial insemination, estrus induction, and pregnancy termination.

———. 2001. *Advances in Reproduction in Dogs, Cats and Exotic Carnivores: Proceedings of the 4th International Symposium on Canine and Feline Reproduction. Journal of Reproduction and Fertility Supplement* no. 57. Cambridge: Society for Reproduction and Fertility. 450 pp.

Contains 60 research reports and reviews for clinicians, breeders, and researchers. Examples of topics include clinical management of natural breeding, monitoring pregnancy and parturition of domestic species, and pregnancy termination and nonsurgical contraception in exotics.

Crichton, E. G., and Krutzsch, P. H., eds. 2000. *Reproductive biology of bats*. San Diego, CA: Academic Press. 510 pp.

An in-depth, highly technical look at the anatomical, physiological, chronological, and behavioral aspects of bat reproduction. Lists of references are included at the end of each chapter.

Dixson, A. F. 1998. *Primate sexuality: Comparative studies of the prosimians, monkeys, apes, and human beings*. New York: Oxford University Press. 546 pp.

Comprehensive synthesis of our knowledge of the sexual behavior (combining evolutionary biology and physiological basis) of primates, from prosimians to humans. Topics covered include mating systems, sex selection, sperm competition, evolutionary dimorphism, hormonal mechanism, and the ovarian cycle.

Hundreds of drawings and more than 2000 references are included.

Graham, C. E., ed. 1981. *Reproductive biology of the great apes: Comparative and biomedical perspectives*. New York: Academic Press. 437 pp.

This is a review of all aspects of great ape reproduction, geared to management of captive breeding. Most captive documentation is taken from primate centers. One of the few texts on this subject; an important tool for husbandry and research.

Hayssen, V., Van Tienhoven, A., and Van Tienhoven, A. 1993. *Asdell's patterns of mammalian reproduction: A compendium of species-specific data*. Ithaca, NY: Cornell University Press. 1023 pp.

Information such as breeding season, gestation period, litter size, physiology of reproduction, and age of puberty is provided for each species. The list of literature cited is quite extensive.

Holt, W. V., Pickard, A. R., Rodger, J. C., and Wildt, D. E., eds. 2003. *Reproductive science and integrated conservation.* (*Conservation Biology*, no. 8). New York: Cambridge University Press. 409 pp.

Explores factors that influence the reproduction of wildlife species and how they can affect conservation efforts. Topics include genetics, behavior and nutrition, environmental chemicals, inbreeding, captive breeding, predator control, embryo technologies, and genetic resource banks.

Kirkpatrick, J. F., ed. 2002. *Fertility Control in Wildlife: Proceedings of the 5th International Symposium on Fertility Control in Wildlife. Journal of Reproduction and Fertility Supplement* no. 60. Cambridge: Society for Reproduction and Fertility. 209 pp.

Forty-five scientists present the latest advances in wildlife contraceptive research. Among topics discussed are ethical issues, contraceptive steroids, population modeling, and actual field applications of wildlife contraceptives.

Knobil, E., and Neill, J. D., eds. 1994. *Physiology of reproduction*. 2 vols. 2nd ed. New York: Raven Press. 3250 pp.

A comprehensive scholarly classic for those with a serious interest in mammalian reproductive physiology and reproductive behavior.

Loudon, A. S. I., and Racey, P. A., eds. 1987. *Reproductive Energetics in Mammals: The Proceedings of a Symposium Held at the Zoological Society of London. Symposia of the Zoological Society of London*, no. 57. New York: Oxford University Press. 371 pp.

Discusses the energy costs of pregnancy and lactation in mammals and how it relates to food supply, growth, and survival of offspring.

Meredith, M. J., ed. 1995. *Animal breeding and infertility*. Veterinary Health Series. Cambridge, MA: Blackwell Science. 508 pp.

A practical veterinary resource for information on reproduction and infertility of farm livestock and horses. Includes cytogenetics, reproductive endocrinology and pharmacology, and breeding and infertility in cattle, goats, horses, pigs, and sheep. A final chapter, on biotechnology in animal breeding, deals mainly with embryo technologies, embryo stem cell manipulation, gene transfer, and the use of transgenic livestock.

Small, M. F. 1993. *Female choices: Sexual behavior of female primates*. Ithaca, NY: Cornell University Press. 245 pp.

A survey of female sexual activities in prosimians, monkeys, and apes that range from solitary orangutans, to social baboons, to promiscuous bonobos. Topics include estrus, bonding, grooming, friendship, and parental care.

Smith, G. R., and Hearn, J. P. 1988. *Reproduction and disease in captive and wild animals. Symposia of the Zoological Society of London*, no. 60. Oxford: Clarendon Press. 209 pp.

A series of papers that present the results of research on wild and captive animals in the areas of reproduction and diseases as applied to animal management. Topics include natural suppression of fertility, effects of chemicals on gamete production, and viruses transmitted between wild and domestic animals.

Solomon, N. G., and French, J. A., eds. 1997. *Cooperative breeding in mammals*. New York: Cambridge University Press. 390 pp.

Cooperative breeding behavior is when individuals of a social group invest in the care of the offspring of others. This phenomenon is explored in a wide variety of mammals, including primates, canids, rodents, and viverrids.

Tyndale-Biscoe, H., and Renfree, M. 1987. *Reproductive physiology of marsupials*. Monographs on Marsupial Biology. Cambridge: Cambridge University Press. 476 pp.

A good reference on marsupial reproduction. Discusses breeding biology by family and then by subject, such as anatomy of the reproductive parts, lactation, hormonal control, placenta, etc.

Wolf, D. P., and Zelinski-Wooten, M,. eds. 2001. *Assisted fertilization and nuclear transfer in mammals*. Totowa, NJ: Humana Press. 305 pp.

Provides a historical overview of mammalian in vitro fertilization (IVF), and then discusses the latest technical aspects of IVF and cloning. Application to preservation of endangered species is mentioned. Includes ultrasound images and photomicrographs of eggs.

Youngquist, R. S., and Threlfall, W. R., eds. 2007. *Current therapy in large animal theriogenology*. 2nd ed. St. Louis: Saunders Elsevier. 1061 pp.

Extensive reference for veterinarians regarding the reproductive processes of several species of large animals, including horses, cows, goats, sheep, pigs, camels, and llamas. 145 contributors.

JOURNALS

African Journal of Ecology (formerly *East African Wildlife Journal*). Quarterly. 1963–. Published for the East African Wild Life Society. Oxford: Blackwell.

[Available also by subscription via the Internet.]

American Journal of Primatology. 12/year. 1981–. Official journal of the American Society of Primatologists. Hoboken, NJ: Wiley-Liss.

[Available also by subscription via the Internet.]

Animal Behaviour. 12/year. 1953–. A publication of the Association for the Study of Animal Behaviour. New York: Elsevier.

[Available also by subscription via the Internet.]

Animal Conservation. Quarterly. 1998–. Cambridge: Cambridge University Press. Published on behalf of the Zoological Society of London.

[Available also by subscription via the Internet.]

Animal Keeper's Forum. Monthly. 1974–. Topeka, KS: American Association of Zoo Keepers.

Animal Welfare. Quarterly. 1992–. South Mimms, Potters Bar, Hertfordshire, UK: Universities Federation for Animal Welfare.

[Available also by subscription via the Internet.]

Behavioral Ecology and Sociobiology. 12/yr. 1976–. Heidelberg: Springer-Verlag.

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Behaviour. Bimonthly. 1947–. Leiden, The Netherlands: Brill.

[Available also by subscription via the Internet.]

Conservation Biology. Bimonthly. 1987–. Journal of the Society for Conservation Biology. Oxford: Blackwell.

[Available also by subscription via the Internet.]

Ethology (formerly *Zeitschrift für Tierpsychologie*). Monthly. 1937–. Oxford: Blackwell.

[Available also by subscription via the Internet.]

Folia Primatologica. 6/year. 1963–. Basel, Switzerland: S. Karger.

[Available also by subscription via the Internet.]

International Journal of Primatology. 6/year. 1980–. Official journal

of the International Primatogical Society. New York: Springer Science 1 Business Media B.V.
[Available also by subscription via the Internet.]
International Zoo News. 8/year. 1953–. Chester, UK: North of England Zoological Society.
[Available also via the Internet.]
Journal of Mammalogy. 6/year. 1919–. Lawrence, KS: American Society of Mammalogists.
[Available also by subscription via the Internet.]
Journal of Medical Primatology. Bimonthly. 1972–. Oxford: Blackwell.
[Available also by subscription via the Internet.]
Journal of the American Veterinary Medical Association (*JAVMA*). Semimonthly. 1915–. Schaumburg, IL.: American Veterinary Medical Association.
[Available also by subscription via the Internet.]
Journal of Wildlife Diseases. Quarterly. 1965–. Lawrence, KS: Wildlife Disease Association.
[Available also by subscription via the Internet.]
Journal of Wildlife Management. Quarterly. 1937–. Bethesda, MD: The Wildlife Society.
[Available also by subscription via the Internet.]
Journal of Zoo and Wild Animal Medicine (formerly *Zoo Animal Medicine*). Quarterly. 1970–. Lawrence, KS: American Association of Zoo Veterinarians.
[Available also by subscription via the Internet.]
Journal of Zoology. 12/year. 1830–. Published for the Zoological Society of London. New York: Cambridge University Press.
[Available also by subscription via the Internet.]
Mammalia. Quarterly. 1936–. Text in French and English, summaries in both languages. Paris: Musee National D'Histoire Naturelle.
[Available also by subscription via the Internet.]
Mammalian Biology. (Continues *Zeitschrift für Saugetierkunde*.) 6/year. 1926–. Text in German and English. Jena: Urban and Fischer.
[Available also by subscription via the Internet.]
Mammal Review. Quarterly. 1970–. Published for the Mammal Society, London. Oxford: Blackwell.
Marine Mammal Science. Quarterly. 1985–. Published for the Society for Marine Mammalogy. Lawrence, KS: Allen Press.
Oryx, the International Journal of Conservation. Quarterly. 1903–. Published for Fauna and Flora International. Cambridge, UK: Cambridge University Press.
[Available also by subscription via the Internet.]
Primates. Quarterly. 1957–. Tokyo: Springer-Verlag.
[Available also by subscription via the Internet.]
Ratel: Journal of the Association of British Wild Animal Keepers. Quarterly. 1973–. Sponsored by the Edinburgh Zoo. Edinburgh: Association of British and Irish Wild Animal Keepers.
Reproduction: The Journal of the Society for Reproduction and Fertility (continues *Journal of Reproduction and Fertility* and *Reviews of Reproduction*). Monthly. 1960–. Bristol, UK: BioScientifica Ltd.
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Thylacinus. Quarterly. 1976–. Melbourne, Victoria, Australia: Australasian Society of Zoo Keeping.
Wildlife Research. 8/year. 1974–. Collingwood, Victoria, Australia: CSIRO.
[Available also by subscription via the Internet.]
Zoo Biology. Bimonthly. 1982–. Published in affiliation with the Association of Zoos and Aquariums. Hoboken, NJ: Wiley-Liss.
[Available also by subscription via the Internet.]
Zoologische Garten. 6/year. 1859–. Published for the Federation of German Zoo Directors. Text in English, French, German. Heidelberg: Elsevier.
[Available also by subscription via the Internet.]

WEB SITES

GENERAL MAMMAL RESOURCES AND FACT SHEETS

African Animals. African Wildlife Foundation
http://www.awf.org/section/wildlife/gallery
African Mammals Databank
http://mercury.ornl.gov/metadata/nbii/html/ma/www.nbii.gov_metadata_mdata_Millennium_nbii_wdc_ma_d_africanmamldb.html
American Society of Mammalogists Resources. Links to state lists of indigenous species
http://www.mammalsociety.org/aboutmammals/index.html
Animal Info—Information on endangered mammals
http://www.animalinfo.org/
Animal Planet News—click Animals A to Zoo section
http://animal.discovery.com/news/news.html
BBC Nature Wildfacts. Basic information on many different animals, including mammals
http://www.bbc.co.uk/nature/wildfacts/
BIOSIS Guide to Mammals. Information about databases, journals, etc.
http://www.biosis.org/
Digital Library of the U.S. Fish and Wildlife Service. Collection of public-domain still photos
http://images.fws.gov/
Electronic Zoo. A wide range of electronic resources related to animals
http://netvet.wustl.edu/e-zoo.htm
eNature. Includes field guides to many North American animals and plants
http://www.enature.com/
Encyclopedia Smithsonian
http://www.si.edu/Encyclopedia_si/
Fact Sheets on Animals. Zoological Society of San Diego Library
http://www.sandiegozoo.org/animalbytes/index.html
Intute, a U.K. gateway to the best resources in the life sciences
http://www.intute.ac.uk/healthandlifesciences/
Mammal Species of the World, a taxonomic database. D. E. Wilson and D. M. Reeder, eds. Smithsonian Institution
http://vertebrates.si.edu/mammals/msw/
Mammalia Directory-Google
http://directory.google.com/Top/Science/Biology/Flora_and_Fauna/Animalia/Chordata/Mammalia/
Mammalian Species. Species account files
http://www.science.smith.edu/departments/Biology/VHAYSSEN/msi/
Names for Mammals and other Animals (collective nouns, plural, etc.)
http://www.anapsid.org/beastly.html
Northern Prairie Wildlife Resources Center (U.S. Geological Survey). Includes articles on mammals
http://www.npwrc.usgs.gov/resource/resource.htm
Sciencenews for kids. Articles on animals
http://www.sciencenewsforkids.org/pages/search.asp?catid52
World Wildlife Fund Species Programme. Animals close to extinction
http://www.panda.org/about_wwf/what_we_do/endangered_species/

RESOURCES ON MAMMAL SPECIES AND FAMILIES

African Elephant Database
http://www.elephant.chebucto.ns.ca/

Armadillo Online
http://www.msu.edu/user/nixonjos/armadillo/index.html
Bat Conservation International—Click “Discover”
http://www.batcon.org/
Bears. International Association for Bear Research and Management. Species descriptions, links, etc.
http://www.bearbiology.com/
Canids. Links recommended by the Canid Specialist Group (International Union for Conservation of Nature/Species Survival Commission)
http://www.canids.org/csglinks.htm#indspp
Cat Specialist Group. (International Union for Conservation of Nature)
http://www.catsg.org/catsgportal/20_catsg-website/home/index_en.htm
Chimpanzee Cultures. Behaviors from long-term study sites in Africa
http://biologybk.st-and.ac.uk/cultures3/
DeerNet. University of Alberta
http://www.deer.rr.ualberta.ca/index.html
Elephant Information Repository
http://elephant.elehost.com/index.html
Lemur Conservation in Madagascar, Center for. St.Louis Zoo.
http://www.stlzoo.org/wildcareinstitute/lemursinmadagascar/
Livestock Breeds. Oklahoma State University
http://www.ansi.okstate.edu/breeds/
Otternet
http://www.otternet.com/index.htm
Primate Info Net. Wisconsin Regional Primate Center
http://pin.primate.wisc.edu/
Rhinoceroses
http://www.rhinos-irf.org/
Tapir Gallery
http://www.tapirback.com/tapirgal/
Ultimate Ungulate. Guide to the World’s Hoofed Mammals
http://www.ultimateungulate.com/

DIRECTORIES AND BIBLIOGRAPHIC RESOURCES

AGRICOLA: National Agricultural Library’s article citation database
http://agricola.nal.usda.gov/
Association of Zoos and Aquariums (AZA) Resource Center
Register for access using your membership number
http://members.aza.org/index.cfm?Log_Check5True&myPath5/
Canadian Wildlife Service publications online
http://www.cws-scf.ec.gc.ca/publications/index.cfm?lang5e
Directory of Public Aquaria
http://fins.actwin.com/dir/public.php
Federal register documents (regulations, permits, recovery plans, habitat preservation plans)
http://www.fws.gov/policy/library/frindex.html
Federal register (Government Printing Office access). Full-text articles on North American species
http://www.gpoaccess.gov/fr/index.html
Findarticles. Free articles from such journals as *National Wildlife*, *International Wildlife*, and *Natural History*
http://www.findarticles.com/
Google Scholar. Articles from peer-reviewed papers, theses, books
http://scholar.google.com
International Directory of Primatology
http://pin.primate.wisc.edu/idp/index.html
Journal abbreviations sources for biosciences journals
http://www.abbreviations.com/#Biosciences
PrimateLit. A bibliographic database for primatology
http://primatelit.library.wisc.edu/
Rhino Resource Center. International Union for Conservation of Nature/Species Survival Commission. Includes rhino bibliography
http://www.rhinoresourcecenter.com/
Science.gov. Searches all online scientific sources (EPA, USDA, Dept. of Interior, etc.)
http://www.science.gov/
SCIRUS. A comprehensive science-specific search engine
http://www.scirus.com/srsapp/
U.S. Fish and Wildlife Service Publications Unit
http://training.fws.gov/library/pubunit.html
World Wide Web Virtual Library: Zoos
http://www.mindspring.com/~zoonet/www_virtual_lib/zoos.html
World Wildlife Fund publications
http://www.worldwildlife.org/news/index.cfm
ZooGoer. Fourteen years of full-text articles from the Friends of the National Zoo’s magazine
http://nationalzoo.si.edu/Publications/ZooGoer/
Zoo Home Pages. Links from the Association of Zoos and Aquariums Web site
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