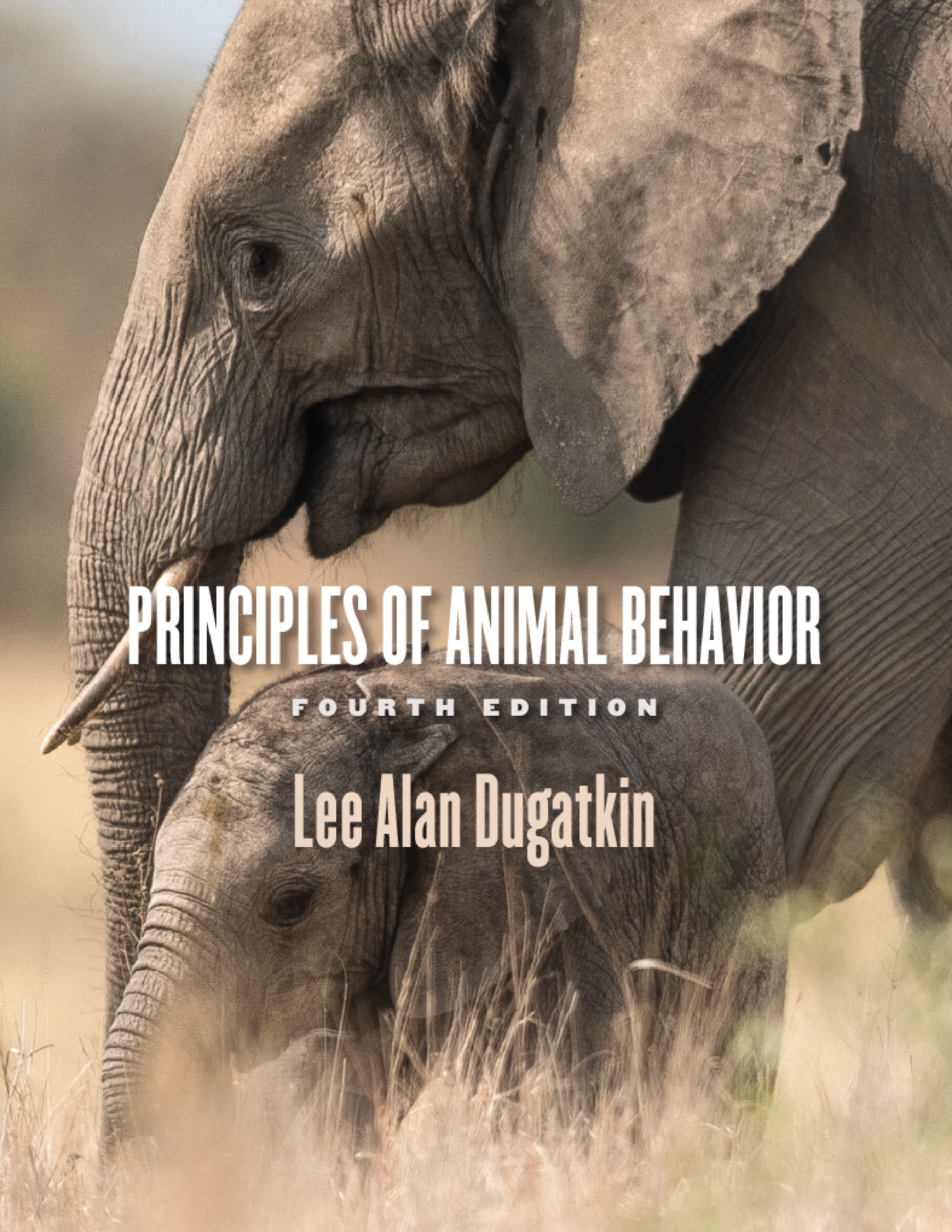

PRINCIPLES OF ANIMAL BEHAVIOR

FOURTH EDITION

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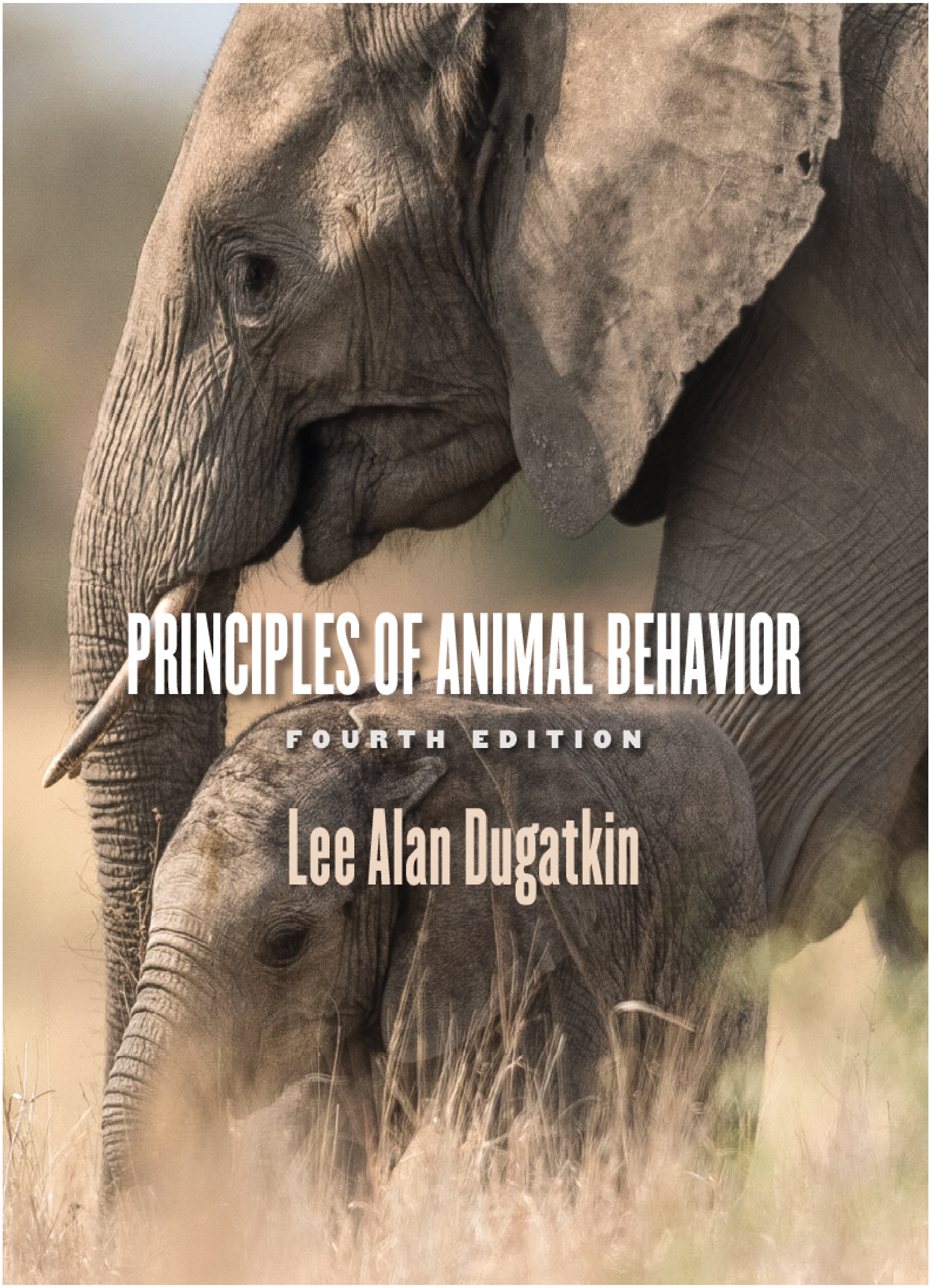

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FOURTH EDITION

Lee Alan Dugatkin

Principles of Animal Behavior

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Fourth Edition

Lee Alan Dugatkin

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For JERRAM *L. BROWN, my mentor and friend for the last three decades*

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Preface

So much has happened in the field of animal behavior since the last edition of this book was published in 2013, providing me with more than ample cutting-edge new work not only to update and expand on the studies presented, but also to reinforce the previous editions' focus on ultimate and proximate causation, as well as the book's unique emphasis on natural selection, learning, and cultural transmission. It's my long-held feeling that the tapestry of animal behavior is created from weaving all of these components into a beautiful whole.

A completely new feature in this edition is the Cognitive Connection boxes in chapters 2–17, designed to dig deep into the importance of the cognitive underpinnings to many types of behaviors we examine. Each box focuses on a specific issue related to cognition and the particular topic covered in that chapter. Another completely new feature in this edition is the "Science at Work" boxes in each chapter. Each of these focuses on one particular study discussed in a chapter and asks *What is the research question? Why is this an important question? What approach was taken to address the research question? What was discovered?* and *What do the results mean?*

Many students taking a course in animal behavior are interested in the course, in part, because they care about the natural world and the creatures that inhabit it. They want to make a difference, and some may even pursue careers in conservation biology. But most animal behavior textbooks barely touch on the subject of conservation biology, or they discuss it only in passing. The Conservation Connection boxes that were introduced in the third edition remain and have been updated here, giving the topic of conservation and animal behavior the space it deserves.

From the first edition of this book, my aim has been to explain underlying concepts in a way that is scientifically rigorous but, at the same time, accessible to students. Each chapter in the book provides a sound theoretical and conceptual basis upon which the empirical studies rest. The presentation of theory, sometimes in the form of mathematical models, is not meant to intimidate students but rather to illuminate the wonderful examples of animal behavior in that chapter. My goal has been to produce a book that students will actually enjoy and will recommend to their friends as a “keeper.” I also hope that instructors will find this book useful in their research programs, as well as in their courses.

Acknowledgments

I wish to thank my gifted editor at the University of Chicago Press, Christie Henry, for shaping this fourth edition. Her editorial skills took this edition to new heights. Christie has moved on to become director of all of Princeton University Press and she will be dearly missed. Miranda Martin, the assistant editor working with Christie, was of immense help on the day-to-day operations associated with a project of this scope. I would like to acknowledge the late Jack Repcheck, my editor on the first edition of this book, for all the time and effort that he invested in this project. Many thanks go to Michael Wright, who did a great job as editor for the second edition, and Betsy Twitchell, who edited the third edition. My thanks also go to Ryan Earley, who has been involved in all four editions of this book, producing a wonderful *Instructor's Manual* for each edition.

Each of the seventeen chapters in this book ends with an illuminating, in-depth interview with a leader in the field of animal behavior. I am deeply indebted to these seventeen brilliant (and busy) animal behaviorists who took time to allow me to interview them. So I extend a huge thank you on this front to E. O. Wilson, Alan Grafen, Geoffrey Hill, Gene Robinson, Sara Shettleworth, Cecilia Heyes, Anne Houde, Cathy Marler, Francis Ratnieks, Hudson Kern Reeve, John Krebs, Anne Magurran, Rufus Johnstone, Judy Stamps, Karen Hollis, Marc Bekoff, and Sam Gosling.

Dozens of my colleagues have read all or parts of *Principles of Animal Behavior*, and I extend my thanks to them all.

Reviewers for this and prior editions of the book were Noah Anderson, Andrea Aspbury, Marin Beaupré, Marc Bekoff, Thore Bergman, Samuel Beshers, Brett Beston, H. Jane Brockmann, Sarah F. Brosnan, Richard Buchholz, Terry Christenson, Anne B. Clark, Ann Cleveland, Cathleen Cox, Mary Dawson, Reuven Dukas, Fred Dyer, Susan Foster, Nick Fuzessery, George Gamboa, Robert Gerlai, Deborah Gordon, Harold Gouzoules, David Gray, Douglas Grimsley, Ann Hedrick, Peter Henzi, Geoff Hill, Kurt Hoffman, Teresa

Horton, Anne Houde, Melissa Hughes, Rudolph Jandler, Clint Kelly, Scott L. Kight, Eileen Lacey, Curt Lively, Catherine Lohmann, Suzanne E. MacDonald, John Maerz, Anne Magurran, Jill Mateo, Maria Maust, Jennifer Mather, Kevin McGraw, Roger Mellgren, Michael Mesterton-Gibbons, Manfred Milinski, Allen Moore, Peter Nonacs, Shawn Nordell, Dan Papaj, Geoff Parker, John Pastor, Aras Petrulis, Terry F. Pettijohn, David Pfennig, Naomi Pierce, Stephen Pruett-Jones, Jesse Purdy, Rick Relyea, Christoph Richter, Gwynne Rife, John Rosenkoetter, Locke Rowe, Olav Rueppell, Roger D. Santer, Andrea Schnitz, Bruce Schulte, Michelle Scott, Carol Shearer, Con Slobodchikoff, Joseph Sisneros, Mark Spritzer, John Swallow, Max Terman, Jeanette Thomas, Kaci Thompson, Elizabeth Tibbetts, Sean Veney, Carolyn Walsh, Scott R. Wersinger, David J. White, Stim Wilcox, Jerry Wilkinson, and Sarah Wooley.

The manuscript in each edition benefited from these reviewers' close reading and sound advice. Please credit these folks with all that is good about this book, and assign any problems you have to my hand.

Last, special thanks go to my wife, Dana, who helped with almost every aspect of this project, and to my son, Aaron, for being such a special young man, and for keeping me smiling. Also thanks to 2R, who knows who he is.

L.A.D.

1

Principles of Animal Behavior

I grew up in the heart of New York City. One animal that my family and I encountered on a fairly regular basis was the American cockroach (*Periplaneta americana*) (Figure 1.1). Much to my mother's chagrin, we seemed locked in a never-ending battle with this creature—a battle that we usually lost. And we probably lost because cockroaches have been subject to this sort of problem—other organisms trying to kill them—for tens of millions of years. As a result, they have evolved an exquisite set of antipredator behaviors, which have had the side effect of making them a thorn in the side of modern apartment dwellers.

Figure 1.1. American cockroach. The American cockroach, often thought of as a pest in households around the world. *(Photo credit: © Thomas Won)*

As a very young boy, I had, of course, never heard of the **scientific method**—which the *Oxford English Dictionary* defines as "scientific observation, measurement, and experiment, and the formulation, testing, and modification of hypotheses." Nevertheless, I was able to draw some inferences and formulate some hypotheses about cockroach behavior by watching my mother put out the roach traps. First, it seemed to me that roaches liked to spend their time in dark places, and second, it appeared that most roaches agreed on what was a good place for roaches to be, as we kept putting the traps out in the same place. These two thoughts on cockroach behavior could easily be developed into the following hypotheses: (1) cockroaches will choose dark places over light places, and (2) roaches will return to the same places over and over, rather than moving randomly through their environment. Of course, as a child, I didn't formally sit down and generate these hypotheses, and I surely didn't run the controlled experiments that a scientist studying animal behavior would run to test these ideas, but I was nonetheless dabbling with scientific hypotheses in **ethology**—the study of animal behavior.

Many people think like ethologists: from my mother, who understood roach behavior, to the farmer who has detailed knowledge about pigs, cows, chickens, and other domesticated farm animals. The girl who works to train her dog, and the outdoorsman who, on his camping vacation, searches for some animals and tries to avoid others, also think like ethologists. Indeed, humans have always thought and acted like ethologists. If our hunter-gatherer ancestors had not thought like ethologists, and hadn't, for example, understood the prey they were trying to catch, as well as the behavior of the predators that were trying to catch them, we wouldn't be here today.

The study of animal behavior appears to have been so important that the earliest cave paintings tended to depict animals. Early cave drawings might have focused on any number of things, but apparently understanding something about the other life forms surrounding our ancestors was fundamental enough that they chose animals as the subjects for the earliest art. This focus on animals, and their behaviors, continued as humans began developing other types of art. Artifacts from 4,000-year-old Minoan cultures suggest an advanced understanding of some aspects of animal behavior: for example, a golden pendant from a Cretan cemetery that depicts two wasps transferring food to one another (Figure 1.2). Masseti hypothesizes that this kind of knowledge of insect food-sharing behavior could only have come from people who observed and studied the details of wasp life (Masseti, 2000). A similar sort of argument has been made regarding a Minoan wall painting of "white antelopes.” This painting likely depicts gazelles in the early stages of an aggressive interaction (Figure 1.3), and it is the sort of art that is associated with an in-depth knowledge of the subject in question (Voultsiadou and Tatolas, 2005).

Figure 1.2. Art captures animal behavior. This pendant from the Chrysolakkos funeral complex in Crete suggests that some members of this ancient culture had a detailed knowledge of wasp behavior. *(From Gianni Dagli Orti/The Art Archive at Art Resource, NY)*

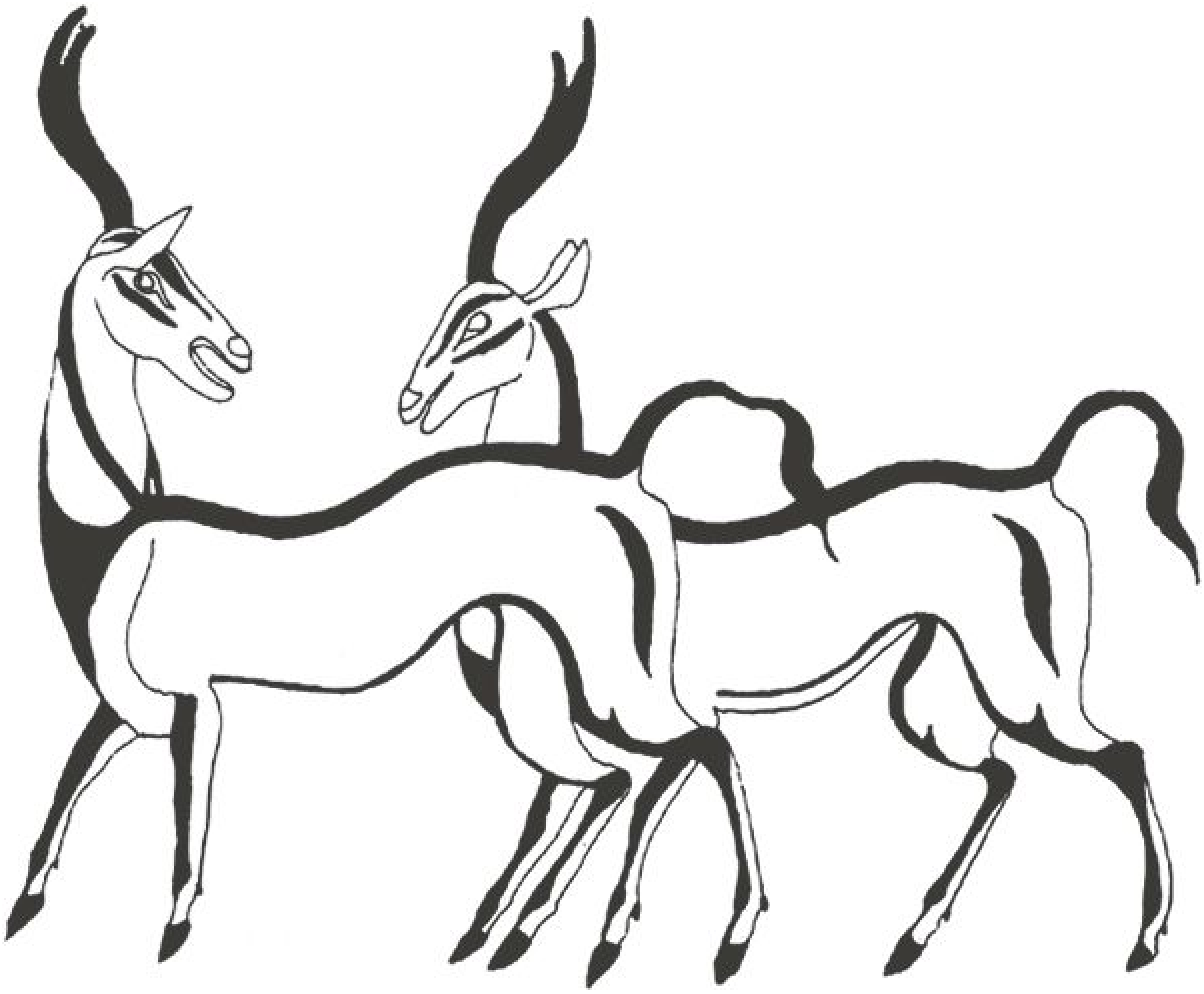

Figure 1.3. Minoan wall paintings of "white antelopes." The drawing may depict a "lateral intimidation" during an aggressive encounter between the animals. *(From Masseti. Courtesy Ministry of Culture, Hellenic Republic)*

Spanning the millennia between ancient Cretan civilization and the present, thousands of amateur and professional naturalists have made some contribution to the study of animal behavior. These contributions have enabled ethologists to draw on a rich trove of information that has greatly expanded our understanding of animal behavior (Figure 1.4). Aristotle's work on animals, for example, though 2,500 years old, is a treasure chest of ethological tidbits. Indeed, with Aristotle's books *Physics* and *Natural History of Animals*, the field of natural history was born. In these and other works, Aristotle distinguished among 500 species of birds, mammals, and fish, and he wrote entire tracts on the behavior of animals.

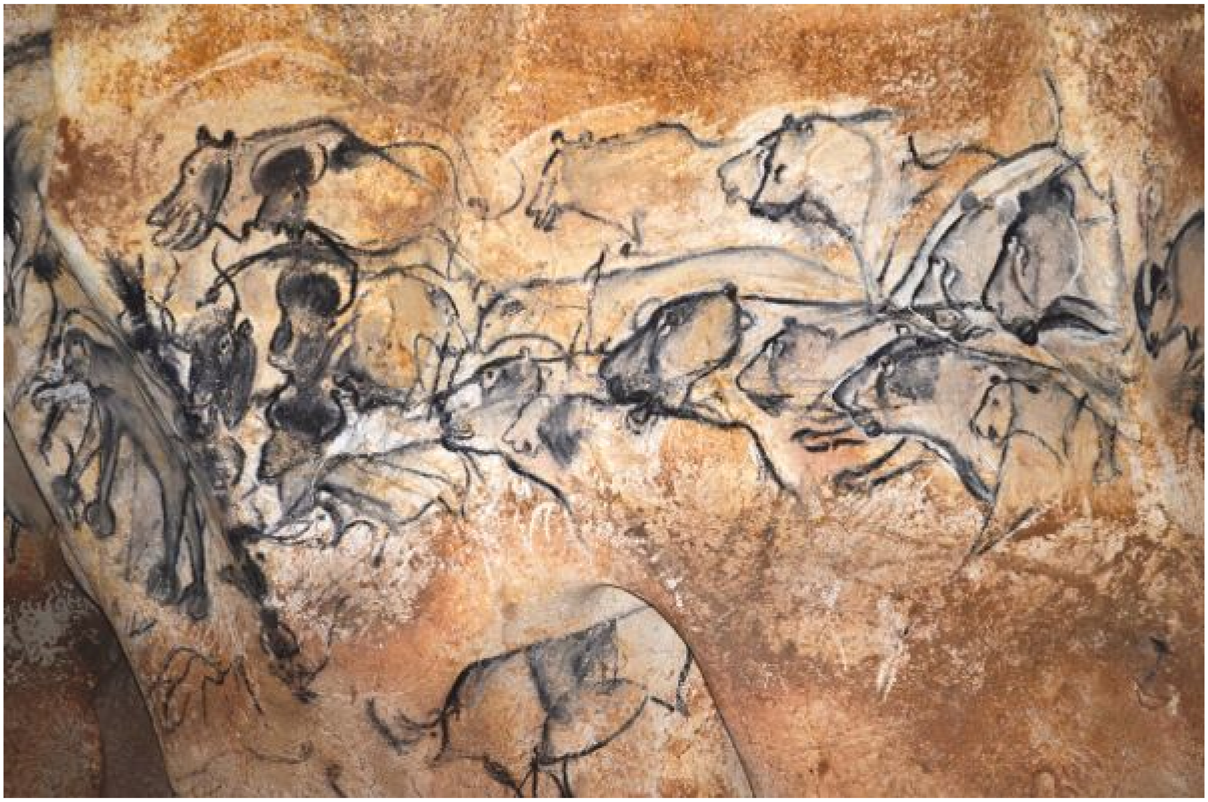

Figure 1.4. Images from a cave. A drawing of a herd of antelope found on the walls of a cave at Dunhuang, China. *(Photo credit: © Jean Clottes)*

In many ways, a course in animal behavior is where all the other biology and psychology classes that you have sat through up to this point in your academic career come together. Evolution, learning, genetics, molecular biology, development, neurobiology, and endocrinology congeal into one grand subject—animal behavior. The field of ethology is integrative in the true sense of the word, in that it combines the insights of biologists, psychologists, anthropologists, and even mathematicians and economists.

Types of Questions and Levels of Analysis

Ethologists have asked questions about almost every conceivable aspect of animal behavior—feeding, mating, fighting, and so on. At a broad level, ethologists pose four distinct *types of questions*, which Niko Tinbergen outlined in a classic paper entitled “On the Aims and Methods of Ethology” (N. Tinbergen, 1963; Bateson and Laland, 2013; Taborsky, 2014; Burkhardt, 2014; Dawkins, 2014; Strassmann, 2014; Lefebvre, 2015). These questions center on:

- Mechanism—What stimuli elicit behavior? What sort of neurobiological and hormonal changes occur in response to, or in anticipation of, such stimuli?
- Development—How does behavior change with the ontogeny, or development, of an organism? How does developmental variation affect behavior later in life?
- Survival value—How does behavior affect survival and reproduction?
- Evolutionary history—How does behavior vary as a result of the evolutionary history, or **phylogeny**? When did a behavior first appear in the evolutionary history of the species under study?

Thousands of studies have been undertaken on each of these four types of questions. Tinbergen's four questions can be captured in two different kinds of analyses—proximate analysis and ultimate analysis (Alcock and Sherman, 1994; Dewsbury, 1992, 1994; Hailman, 1982; Hogan, 1994; J. Huxley, 1942; Mayr, 1961; Orians, 1962; Reeve and Sherman, 1993; Haig, 2013). **Proximate analysis** focuses on *immediate causes*, whereas **ultimate analysis** centers on *evolutionary forces* that have shaped a trait over time. As such, proximate analysis incorporates Tinbergen's first two types of questions, and ultimate analysis covers the latter two types (Figure 1.5). We could ask, for example: Why do some bird chicks peck at red stimuli but not stimuli of other colors? Does red trigger a set of neuronal responses that are not triggered otherwise? If so, exactly which neurons and when? These are questions about proximate causation. An analysis at the ultimate level, on the other hand, would ask: What selective forces in the birds' evolutionary past would have favored individuals that had responses to red stimuli? Was the color red associated with a particular food source? Do other closely related bird species show similar responses to red stimuli?

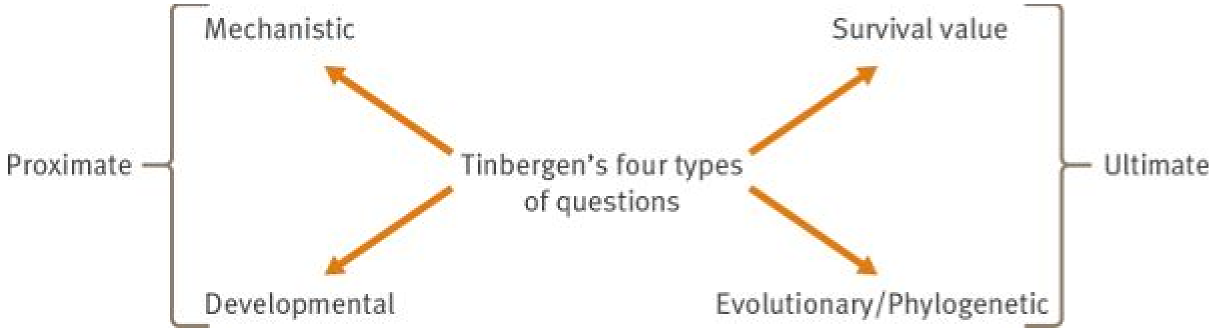

Figure 1.5. Tinbergen's four types of questions. A diagrammatic representation of the four different types of questions asked by ethologists. Two of these types of questions are proximate and two are ultimate.

Every chapter of this book examines animal behavior from both proximate and ultimate perspectives.

What Is Behavior?

What do ethologists mean by the word *behavior*? It turns out that this is not a trivial question, and it is one that ethologists have grappled with for some time. Early on, ethologists like Tinbergen defined behavior as "the total movements made by the intact animal," but that definition seems far too general, incorporating almost everything an animal does. But if a definition proposed by Tinbergen—who shared a Nobel Prize as a founder of the study of animal behavior—doesn't work, how can a satisfactory definition be achieved?

One solution is to survey ethologists to get a discipline-wide view of the way the term *behavior* is employed. In a review paper on definitions of behavior, Daniel Levitis and his colleagues surveyed 174 members of three professional societies that focus on behavior to try to understand what researchers mean when they used the term *behavior* (Levitis et al., 2009). What they found was much variation among ethologists on how behavior should be defined. Based on their survey results, Levitis and his colleagues argued that many of the definitions that ethologists use can be captured by a few published, but quite dated, definitions already in the literature. These include Tinbergen's 1952 definition of behavior, as well as the following:

- "Externally visible activity of an animal, in which a coordinated pattern of sensory, motor and associated neural activity responds to changing external or internal conditions" (Beck et al., 1981).
- "A response to external and internal stimuli, following integration of sensory, neural, endocrine, and effector components. Behavior has a genetic basis, hence is subject to natural selection, and it commonly can be modified through experience" (Starr and Taggart, 1992).

- "Observable activity of an organism; anything an organism does that involves action and/or response to stimulation" (R. Wallace et al., 1991).
- "Behavior can be defined as the way an organism responds to stimulation" (D. Davis, 1966).
- "What an animal does" (Raven and Johnson, 1989).
- "All observable or otherwise measurable muscular and secretory responses (or lack thereof in some cases) and related phenomena such as changes in blood flow and surface pigments in response to changes in an animal's internal and external environment" (Grier and Burk, 1992).
- "Behavior is defined as the expression of the activity of the nervous system" (Hogan, 2015).

Each of these definitions has its pluses and minuses. If "behavior has a genetic basis," as it certainly does in many instances, does that mean that we should exclude all actions that have not been studied from a genetic perspective when we speak of behavior? Surely not. For any of the definitions above we could pose equally strong challenges. That said, I needed to adopt a consistent definition of behavior in this book, and I will use one that is a slight modification of a suggestion by Levitis and his colleagues—namely, that behavior is the coordinated responses of whole living organisms to internal and/or external stimuli. This definition is appropriate for a number of reasons (all of which are admittedly somewhat subjective): (1) it seems to capture what most modern ethologists and behavioral ecologists mean when they use the term behavior, (2) it works fairly well for the behaviors covered in detail in chapters 6–17 of this book, and (3) it makes an important distinction between organism and organ. What this third point means is that, as Levitis and his colleagues note, sweating in response to increasing body temperature is not generally thought of as a behavior per se. But when an animal moves to the shade in response to heat and its own sweating, most ethologists would agree that this is a behavioral response.

Three Foundations

Incredible tales and fascinating natural history make a textbook on animal behavior different from a textbook on organic chemistry or molecular genetics. What links animal behavior to all scientific endeavors, however, is a structured system for developing and testing falsifiable hypotheses and a bedrock set of foundations on which such hypotheses can be built. Throughout this book, the force of natural selection, the ability of animals to learn, and the power of transmitting learned information to others (cultural transmission) will serve as the foundations upon which we build our approach to ethology.

In his classic, *On the Origin of Species*—widely regarded as the most important biology book ever written—Charles Darwin laid out general arguments for how evolutionary change has shaped the diversity of life and how the primary engine of that change is a process that he dubbed **natural selection** (Darwin, 1859). In a nutshell, Darwin argued that any trait that could be transmitted across generations (i.e., is heritable) and provided an animal with some sort of reproductive advantage over others in its population would be favored by natural selection. Natural selection is, then, the process whereby traits that confer the highest relative reproductive success on their bearers increase in frequency over generations.

Whereas natural selection changes the frequency of different behaviors over the course of many generations, **individual learning** can alter the frequency of behaviors displayed within the lifetime of an organism. Animals learn about everything from food and shelter to predators and familial relationships. If we study how learning affects behavior *within the lifetime* of an organism, we are studying learning from a proximate perspective. If we study how natural selection affects the *ability* of animals to learn, we are approaching learning from an ultimate perspective. Later in this chapter we will examine a study on learning and foraging (feeding) behavior in grasshoppers. When we ask what sort of cues grasshoppers use to learn where to forage, we are addressing learning from a proximate perspective. When we examine how a grasshopper's ability to learn about food sources affects its reproductive success, and how selection might favor such abilities, we are studying learning from an ultimate perspective.

Cultural transmission also affects the type of behavior animals exhibit and the frequency with which behaviors occur. While definitions vary widely across disciplines, this book uses the term *cultural transmission* to mean a transmission system in which animals learn through various forms of **social learning**. Cultural transmission can allow newly acquired traits to spread through populations at a very quick rate, as well as permit the rapid transmission of information across generations. As with individual learning, natural selection can also act on animals' ability to transmit, acquire, and act on culturally transmitted information.

NATURAL SELECTION

Darwin recognized that his theory of natural selection applied to behavioral traits as well as morphological, anatomical, and developmental traits. Indeed, morphological traits are often the physical underpinning for the production of behavior, so morphology and behavior are linked at many levels. More detail about this linkage is provided below and throughout the book, but for the moment, the key point is that Darwin's ideas on evolution, natural selection, and behavior were revolutionary, and ethology today would look very different were it not for the ideas that Darwin set forth in *On the Origin of Species*. A fascinating example involving mating and parasites in Hawaiian crickets illustrates how natural selection operates on animal behavior in the wild.

In the evening on the Hawaiian Islands, male crickets sing to attract their mates. This "singing" results when the male cricket rapidly moves the smooth scraper on the front of one wing against the serrated file on the other wing. Females cue in on male songs, and they typically will not mate with males that do not produce songs. But as with many behavioral traits associated with attracting mates, male singing is not cost free. Just as females are attracted to male song, so too are potentially dangerous parasites (Zuk and Kolluru, 1998).

Marlene Zuk and her colleagues have been studying this trade-off in male song production—between attracting females and attracting parasites—in the field cricket *Teleogryllus oceanicus* (Zuk et al., 2006). These crickets are parasitized by the fly *Ormia ochracea*, who are attracted to singing males. If a fly finds a singing cricket, it lays its eggs on the cricket, and then the fly larvae burrow their way into the cricket and grow. Emergence of the flies from the larvae kills the cricket.

Parasitic flies are found on three of the Hawaiian Islands—Oahu, Hawaii, and Kauai—that are also home to *T. oceanicus*. The flies are most common on the island of Kauai, where 30 percent of the crickets are parasitized. Zuk and her team have been studying the relationship between crickets and parasitic flies since 1991, and over time, they noted what appeared to be a significant decline in the cricket population on Kauai. Over the years, they heard fewer and fewer singing males on this island, and they assumed that the parasitic fly was slowly causing the extinction of *T. oceanicus* on Kauai. Indeed, in 2003 they heard only a single male singing. But when they got down on their hands and knees and searched for crickets, Zuk and her team found *T. oceanicus* in abundance. How could they explain these seemingly contradictory findings?

What Zuk and her team found was that most of the males on Kauai had modified wings that were not capable of producing song (Figure 1.6). The file section of the wings of these Kauai males (called “flatwing males”) was significantly reduced compared to that of normal males, and its position on the wings changed, such that song production was no longer possible. These changes were likely the result of mutations of one, or possibly, a few genes associated with wing development and song production. Once such mutations arose, natural selection should strongly favor such flatwing males, that would virtually never be parasitized by very dangerous flies. Or should it?

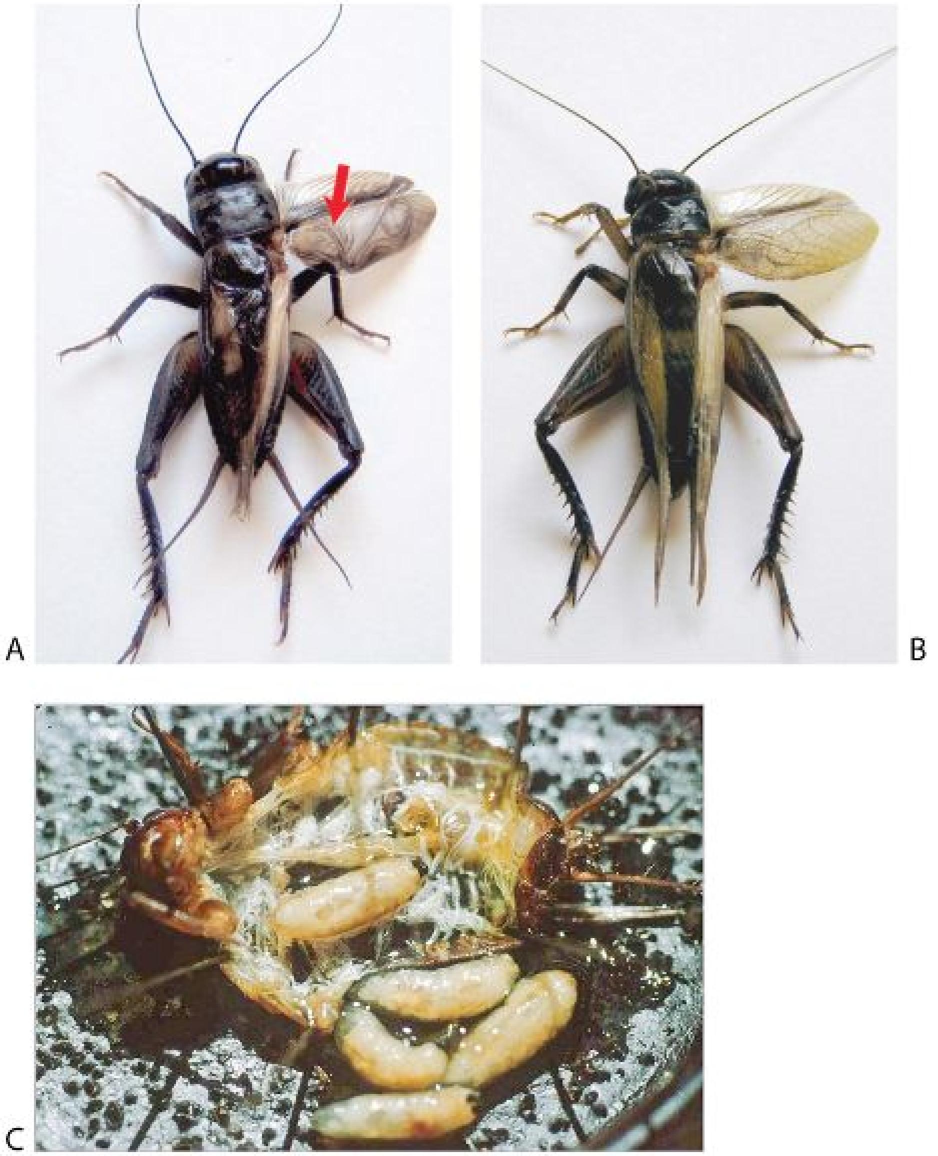

Figure 1.6. Natural selection in crickets. Marlene Zuk and her colleagues have been studying the field cricket *Teleogryllus oceanicus*. Pictured here are (A) a field cricket with normal wings (the arrow points to the file on its outstretched wing); (B) a field cricket with flat wings, in which the file section on the outstretched wing has evolved to a much smaller size and is visible only under a high-powered microscope; and (C) fly larvae in a parasitized cricket. *(Photo credits: Robin Tinghitella; John Rotenberry)*

Flatwing males should have a huge survival advantage, but they might also be at a disadvantage with respect to attracting females that hone in on singing males as potential mates. For flatwing males to be favored by natural selection, they must somehow still secure opportunities to mate. Zuk and her colleagues hypothesized that flatwing males do this by staying near the handful of singing males still on Kauai, and mating with females as they approach singers. This sort of “satellite” male mating behavior has been seen in many *T. oceanicus* populations (Tinghitella et al., 2009). To test their hypothesis, they collected 133 Kauai males—121 of which were flatwings, and 12 of which were singers. They then used “playback” experiments, in which male songs were broadcast over loudspeakers. What they found was that flatwing males were drawn to playbacks more strongly than normal males, suggesting that flatwing males stay near singer males in order to secure chances to mate with females drawn in by the singers. With both a huge survival advantage and the continued ability to obtain matings, flatwing males should be strongly favored by natural selection. And indeed, Zuk and her colleagues suggest that the mutation(s) leading to the loss of song occurred only fifteen to twenty generations ago and has quickly increased in frequency, so that now most males on Kauai are flatwing males (Rotenberry et al., 2015; Rotenberry and Zuk, 2016). Remarkably, on the nearby Hawaiian island of Oahu, Zuk and her team have found an independent, parallel, case of the evolution of flatwing males, and they are currently tracking the success of flatwings on that island (Pascoal et al., 2015). We will delve more deeply in this sort of **convergent evolution** in subsequent chapters.

As a second example of natural selection acting on animal behavior, let’s examine how individuals in social groups respond to strangers. For animals that live in stable groups, strangers—unknown individuals from outside your group—represent a threat. Such individuals may compete for scarce resources (including food and mates), disrupt group dynamics that have long been in place, and so on. Because of such costs, ethologists have examined whether animals from group-living species display **xenophobia**—a fear of strangers. In particular, ethologists hypothesize that xenophobia may be especially strong when resources are scarce, since competition for such resources will be intense then, and keeping strangers away may have an especially strong impact on the lifetime reproductive success of group members.

To examine the effect of resource scarcity on the evolution of xenophobia, Andrew Spinks and his colleagues examined xenophobia in the common mole rat (*Cryptomys hottentotus*) (Spinks et al., 1998; Figure 1.7). Common mole rats live in South Africa in underground colonies made up of two to fourteen individuals. They are an ideal species in which to examine xenophobia and its possible connection to resource availability for two reasons: First, all populations of common mole rats are “tightly knit” in the sense that each group typically has a single pair of breeders that produce most of the offspring in a colony, which means that most group members are genetic relatives (J. M. Bishop et al., 2004). Second, populations of common mole rats differ in terms of the amount of resources in their environments. Some common mole rat populations live in moderately moist (mesic) environments that present only mild resource limitations, while other populations live in dry (arid) environments and face intense limitations on their resources. Variation in resource availability between arid and mesic populations is largely due to the fact that mesic environments have about four times as much rainfall as arid environments.

Figure 1.7. Common mole rat. This xenophobic common mole rat (*Cryptomys hottentotus*) is showing an aggressive stance in response to a stranger. *(Photo credit: Chris and Tilde Stuart/FLPA/Minden Pictures)*

Spinks and his colleagues examined whether populations from arid areas were more xenophobic than those from mesic environments, as one might predict based on the discussion above about natural selection, resources, and xenophobia. To do so, they conducted 206 trials in which two mole rats—one from the arid and one from the mesic environment—were placed together, and aggression was recorded. When the pair of individuals were both males or both females, aggression toward such strangers was much more pronounced in the common mole rats from the arid environment, where resources were limited, than it was in the common mole rats from the mesic environment. This result was not a function of individuals from arid populations just being more aggressive in general. Control experiments demonstrated that when two individuals that knew each other from the arid population were tested together, aggression disappeared—it was the identification of a stranger that initiated the aggression. Natural selection has favored stronger xenophobic responses in common mole rats whose resources are more limited.

The ecology of common mole rats is such that some individuals leave their home colony to find a mate. What this means is that some strangers that are encountered by members of a social group are potential mates, and perhaps worth tolerating. Natural selection then should not simply favor all xenophobia, but a xenophobia that is sensitive to the sex of the stranger. In trials in which the two individuals tested were a male and a female, Spinks and his colleagues found that while aggression was still observed in the low-resource, arid population, the level of aggression decreased dramatically when compared with aggression in same-sex interactions (Figure 1.8). Natural selection has favored common mole rats that temper their fear of strangers as a function of both where they live and the sex of the strangers.

(Figure 1.9).

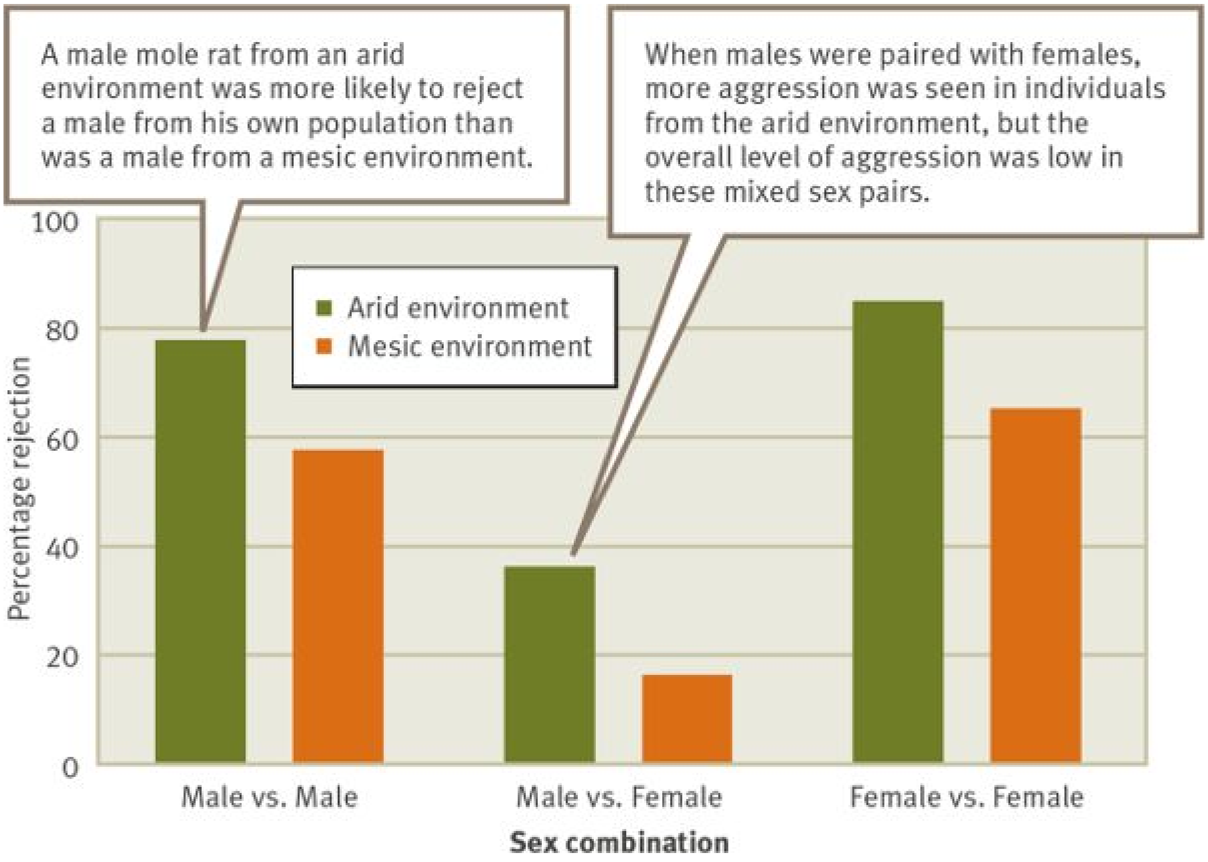

Figure 1.8. Xenophobia in common mole rats. Spinks and his colleagues found that mole rats from an arid environment (green bars) were more likely to reject a potential partner from their own population than were mole rats from a resource-rich mesic environment (orange bars). *(From Spinks et al., 1998, p. 357)*

INDIVIDUAL LEARNING

As chapter 5 explores in much greater detail, individual learning can take many forms. Let's begin our discussion by considering a hypothetical case of learning and mate choice. Suppose that we are studying a species in which female birds mate with numerous males throughout the course of their lifetime and females are able to keep track of how many chicks fledged their nest when they mated with male 1, male 2, male 3, and so forth. If we found that females changed their mating behavior as a result of direct personal experience, preferring to mate with males that fathered the most successful fledglings, such results would suggest that learning had changed the behavior of an animal within the course of its lifetime (Figure 1.9).

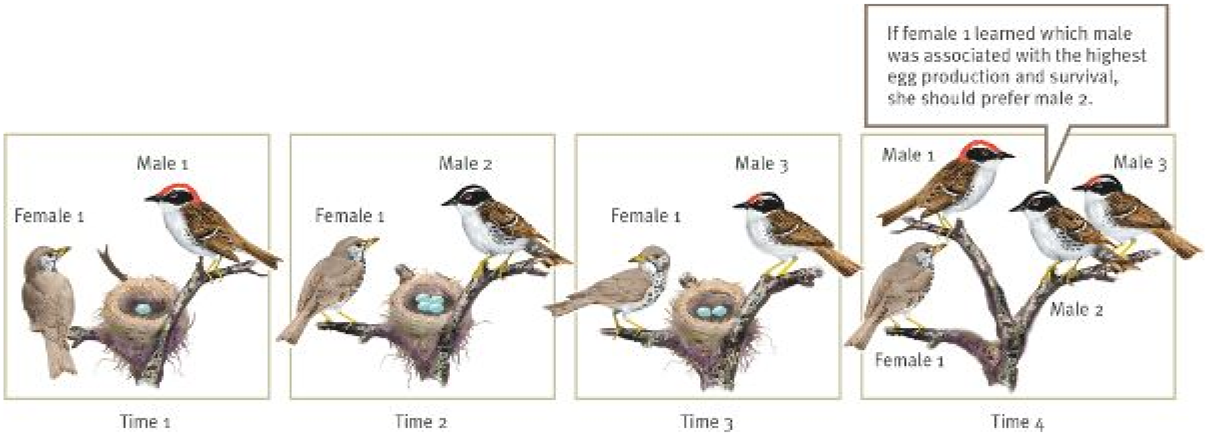

Figure 1.9. A role for learning. Imagine a female that mates with different males over the course of time. Such a female might learn which male is a good mate by keeping track of the number of eggs she laid after mating with each male.

The learning example above highlights an important relationship between learning and natural selection. In our example, females changed their preference for mates as a result of prior experience, and so learning affected mating behavior within a generation. But just because the use of a behavior is changing within the course of an individual's lifetime does not mean that natural selection is not occurring. It is certainly possible for natural selection to operate on the *ability* to learn. That is, natural selection might favor the ability to learn which individuals make good mates over, say, the lack of such an ability. If this were the case in the example above, learning would change behaviors within a generation, and natural selection might change the frequency of different learning rules across generations.

Learning and natural selection are tied together nicely in Reuven Dukas and Elizabeth Bernays's ingenious experiment examining the fitness consequences of learning in insects (Dukas and Bernays, 2000). While learning in insects is well documented, documenting the potential fitness-related benefits of learning has proved to be more difficult (Dukas, 2006). To address the question of learning-related benefits directly, Dukas and Bernays examined the potential fitness-related benefits of learning in the context of feeding behavior in the grasshopper, *Schistocerca americana* (Figure 1.10).

Figure 1.10. Some components of foraging in grasshoppers are learned. *Schistocerca americana* grasshoppers learned to associate various cues with food sources. *(Photo credit: American bird grasshopper, © Maria de Bruyn;* https://mybeautifulworldblog.com/)

In their experiment, they placed two food dishes in a grasshopper's cage. The food in one dish provided a "balanced diet (b)" that included proteins and carbohydrates—a diet that promotes maximal growth rates in *S. americana*. The food in a second dish was labeled a "deficient diet (d)." This diet contained flavoring and protein, but no carbohydrates. Specific odors and colors were associated with each of the two diets. Diets were supplemented with either citral (odor 1) or coumarin (odor 2), and food dishes were placed near either a brown-colored card (color 1) or a green-colored card (color 2). This created an opportunity for the grasshoppers to pair balanced and deficient diets with both odor cues and color cues.

Dukas and Bernays's experiment contained a "learning" treatment and a "random" treatment (Figure 1.11). In the learning treatment, the balanced diet dish was always paired with one specific odor and one specific colored card. Twice a day, a grasshopper was presented with the two food dishes and allowed to choose one from which to feed. For example, grasshopper A might be placed in a cage in which the balanced diet was always paired with the brown color and the odor of coumarin. In principle, grasshopper A could learn that together the cues coumarin and brown color are associated with a food dish that contained the balanced diet. In contrast, in the random treatment, the odor and color cues associated with the balanced diet were randomly assigned. For example, in the morning, grasshopper B might have the balanced diet dish paired with the color green and the odor of coumarin, but in the afternoon, the balanced diet dish might be paired with the color green and the odor of citral, while the next morning the balanced diet dish might be paired with the color brown and the odor of coumarin. In this treatment, the grasshopper could not learn to pair the balanced diet with specific color and odor cues.

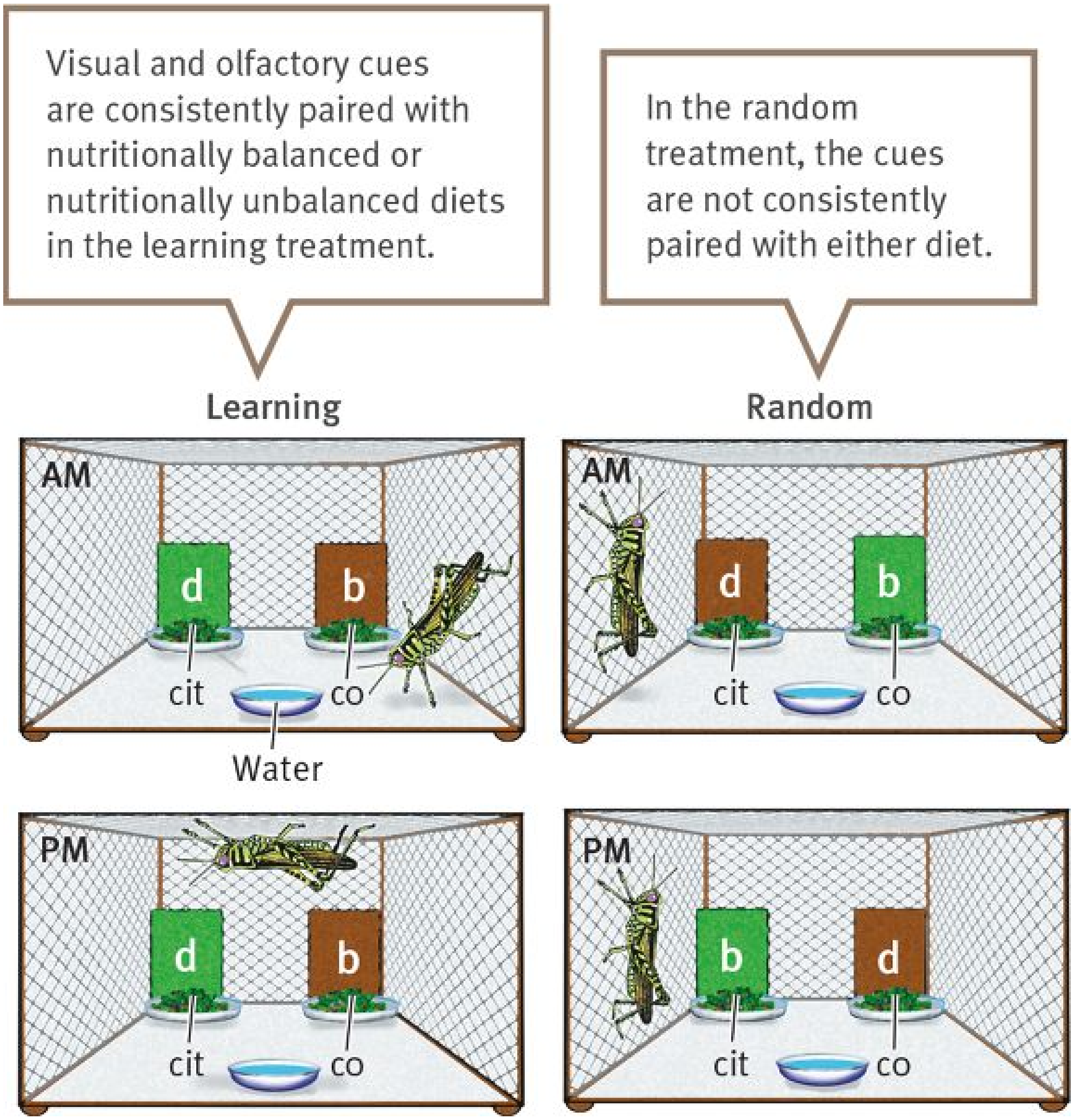

Figure 1.11. Learning, foraging, and fitness in grasshoppers. A schematic of the set-up showing the learning and random conditions. In the learning condition, the set-up consisted of a water dish in the center of the cage and a nutritionally balanced dish (b) on one side of the cage and a nutritionally deficient dish (d) on the other side of the cage. Each dish was paired with one odor (citral [cit] or coumarin [co]) and one colored card (brown or green). *(Based on Dukas and Bernays, 2000)*

Significant differences between the grasshoppers in the learning and random treatments were uncovered. Grasshoppers in the learning treatment ate a greater proportion of their food from the balanced diet dish than did the grasshoppers in the random treatment (Figure 1.12): they learned to pair diet type with color and odor cues when the situation allowed for such learning. Over the course of the experiment, individuals in both treatments increased the proportion of time they spent feeding on the balanced diet, but grasshoppers in the learning treatment did so more quickly than did those in the random treatment. This difference was most likely due to the fact that grasshoppers in the learning treatment went to the balanced diet dish almost immediately when feeding, while those in the random treatment ended up at the balanced diet dish, but only after much sampling of the deficient diet dish. Perhaps most important of all, the individuals in the learning treatment had a growth rate that was 20 percent higher than that of the grasshoppers in the random treatment (Figure 1.13).

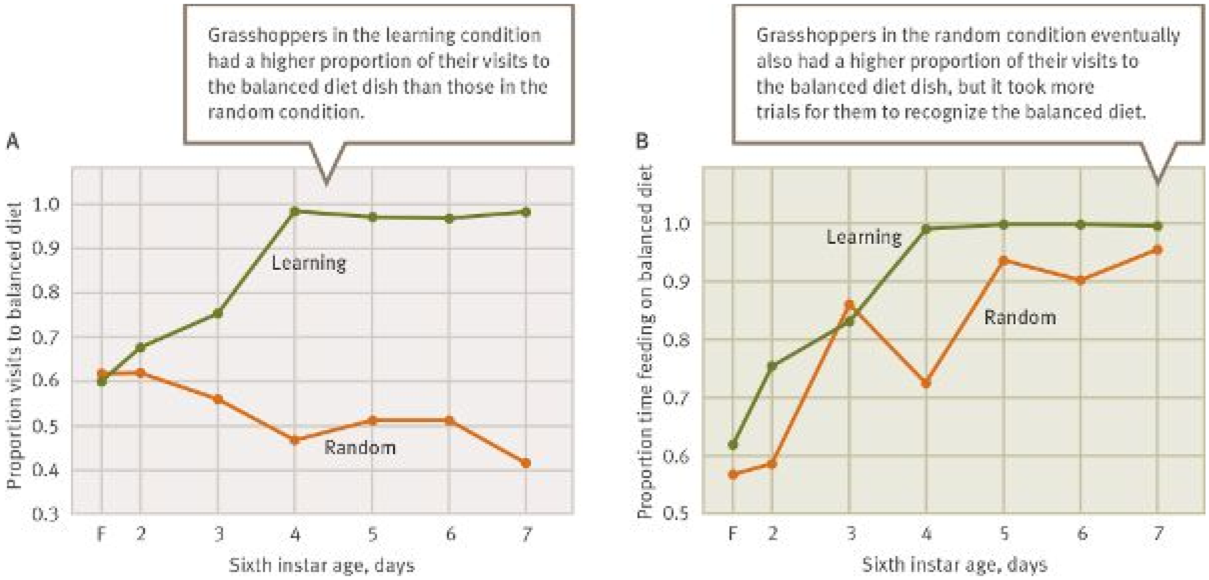

Figure 1.12. A balanced diet in grasshoppers. Grasshoppers in the sixth instar stage of insect development were given a choice between a balanced diet or a deficient diet, and researchers recorded the proportion of visits and feeding times of those in a learning treatment and those in a random treatment. In the learning condition, the food was presented in a way in which grasshoppers could learn to associate colored background cards and odors with balanced and unbalanced diets. In the random condition, food was presented in such a manner that grasshoppers could not make such associations. *(From Dukas and Bernays, 2000)*

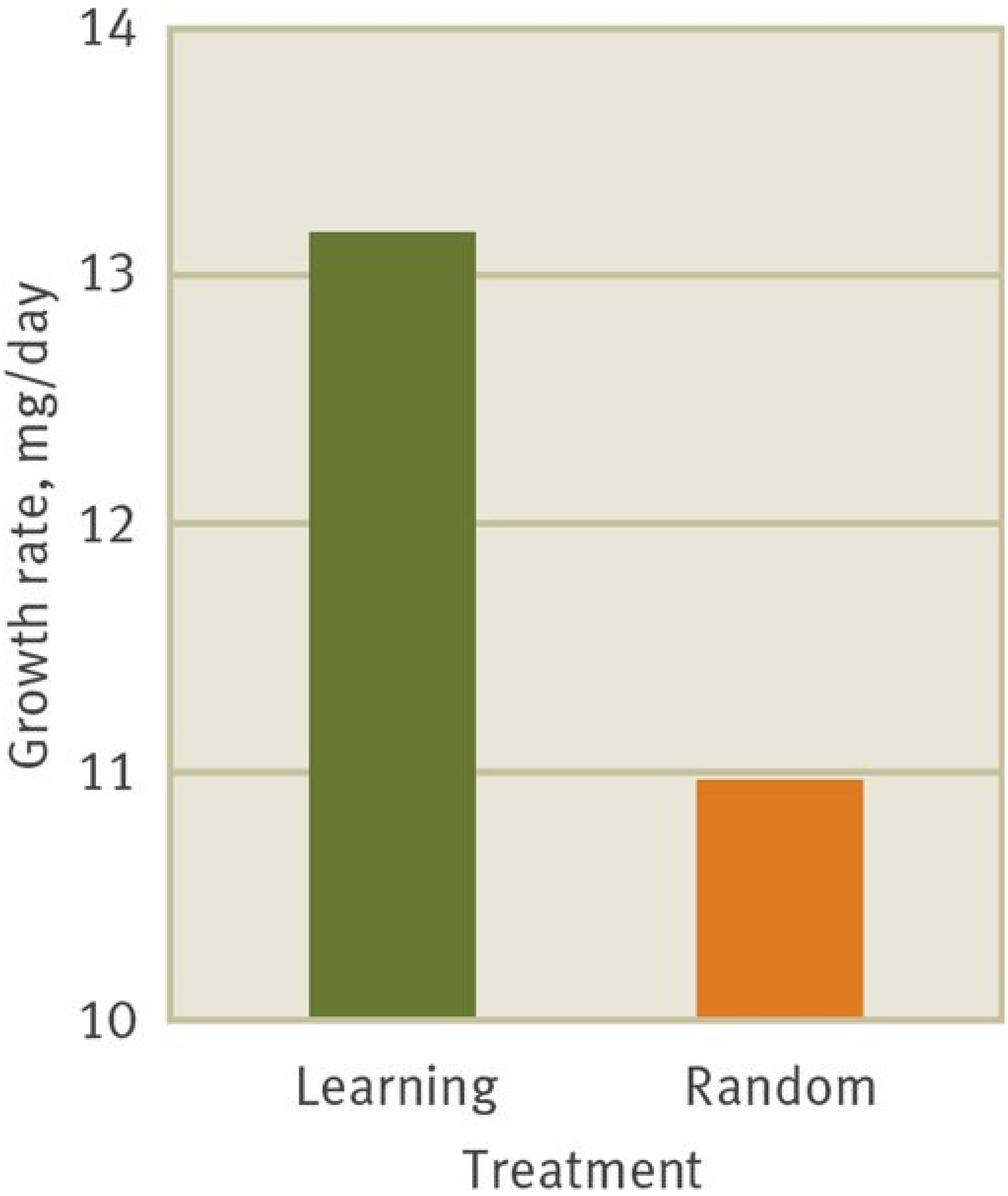

Figure 1.13. Fitness and foraging. Not only did grasshoppers in the learning condition approach the balanced diet dish more often, but this translated into quicker growth. Growth rate in grasshoppers is positively correlated with egg size and number. *(From Dukas and Bernays, 2000)*

The ability to learn about food in *S. americana* translated into an important fitness gain: a significant increase in growth rate observed in individuals in the learning treatment. This difference in growth rate likely translates into greater reproductive success later in life, as growth rate is positively correlated with the number and size of eggs laid over the course of an individual’s life (Atkinson and Begon, 1987; Slansky and Scriber, 1985).

CULTURAL TRANSMISSION

Cultural transmission has received much less attention in the ethological literature than natural selection or individual learning, but work in this area is growing quickly (Danchin et al., 2004; Galef and Laland, 2005; Galef et al., 2005; Kendal et al., 2005; Mesoudi et al., 2006; Whiten et al., 2012; Laland and Galef, 2009: Mesoudi, 2011; Henrich, 2015).

For an interesting case study illustrating the importance of cultural transmission and social learning in animals, let’s examine Jeff Galef’s work on foraging behavior in rats. Rats are scavengers and often encounter new foods (Figure 1.14A). This has probably been true for most of the rat’s long evolutionary history, but it has been especially true over the last few thousand years, during which time humans and rats have had a close relationship. Scavenging presents a foraging dilemma. A new food source may be an unexpected foraging bounty for rats, but it may be dangerous, either because it contains elements inherently bad for rats, or because rats have no experience with the odor of that food, so they may not be able to tell if some piece of this new food type is fresh or spoiled. One possible way to get information about new food types is through the cultural transmission of information.

Figure 1.14. Scavenging rats and cultural transmission. (A) When a rat scavenges in the trash, it may encounter new food items that are dangerous or spoiled and that can lead to illness or even death. (B) Smelling another rat provides olfactory cues about what it has eaten. This transfer of information from one rat to another about safe foods is a form of cultural transmission. *(Photo credits: Paul Hobson/npl/Minden Pictures; Joe Blossom / Alamy Stock Photo)*

Galef began his study of cultural transmission and food preferences in rats by testing what is known as the information-center hypothesis, which posits that foragers may learn critical pieces of information about the location and identity of food by interacting with others that have recently returned from foraging bouts (Figure 1.14B; Ward and Zahavi, 1973). Galef and his colleagues tested this hypothesis in the Norway rat (Galef and Wigmore, 1983). To examine whether cultural transmission via social learning played a role in rat foraging, rats were divided into two groups—observers and demonstrators (also known as tutors). The critical question that Galef examined was whether observers could learn about a novel, distant food source by interacting with a demonstrator that had recently encountered such a food source.

After the observer and demonstrator had lived together in the same cage for a few days, a demonstrator rat was removed and taken to another experimental room, where it was given one of two novel diets—either rat chow flavored with Hershey's cocoa (eight demonstrators) or rat chow mixed with ground cinnamon (eight demonstrators). The demonstrator was then brought back to its home cage and allowed to interact with the observer for fifteen minutes, at which time the demonstrator was removed from the cage. For the next two days, the observer rat—that had no personal experience with either of the novel foods, and had never *seen* the demonstrator eat anything—was given two food bowls, one with rat chow and cocoa, the other with rat chow and cinnamon. Galef found that through the use of olfactory cues, observer rats were influenced by the food their tutors had eaten, and they were more likely to eat that food (Figure 1.15).

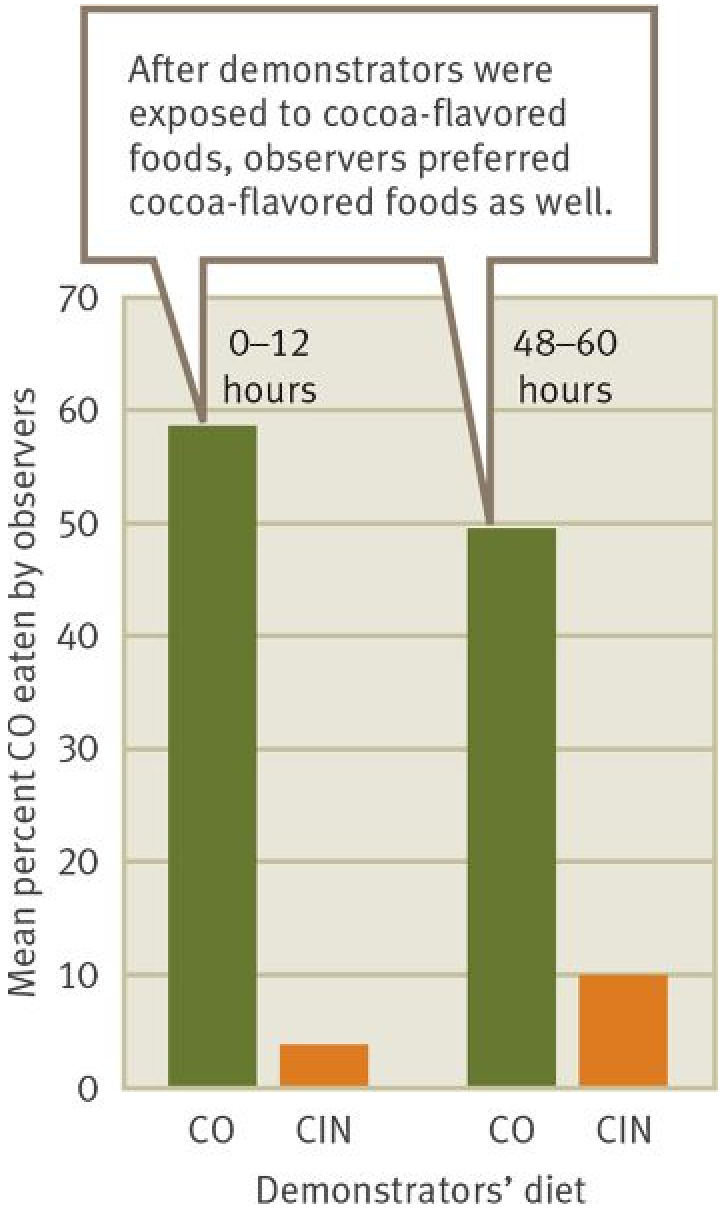

Figure 1.15. Social learning and foraging in rats. Observer rats had a “tutor” (demonstrator) that was trained to eat rat chow containing either cocoa (CO) or cinnamon (CIN) flavoring. After the observer rats had time to interact with a demonstrator rat, the observer rats were more likely to add their tutor’s food preferences to their own. *(From Galef and Wigmore, 1983)*

Cultural transmission is more complicated than individual learning. The information acquired via individual learning never makes it across generations. In contrast, with cultural transmission, if a single animal’s behavior is copied, it can affect individuals many generations down the road (see chapter 6).

Suppose adult rat A (in generation 1) adopts a novel, formerly uneaten, type of food into its diet after it smelled this food on a nestmate. Now suppose young individuals (generation 2) in the same colony as rat A add this new food to their diet after they smell it on rat A. When individual A dies, the cultural transmission chain it began may still be in force, as the young individuals that copied rat A will still be around: a culturally learned preference in generation 1 may make it to generation 2 (Figure 1.16). If generation 3 individuals learn from generation 2 individuals, then the culturally derived preference will have been transmitted across two generations, and potentially so on down the generations (Mesoudi et al., 2006). Cultural transmission itself, in other words, has both within- and between-generation effects (see chapter 6). Understanding the dynamics of cultural transmission can be very complicated. In addition to the within- and between-generation effects just discussed, if there is variation in the tendency to copy the behavior of others, and that variation is due to certain types of genetic variation, then natural selection can act on the tendency to use culturally transmitted behavior as well.

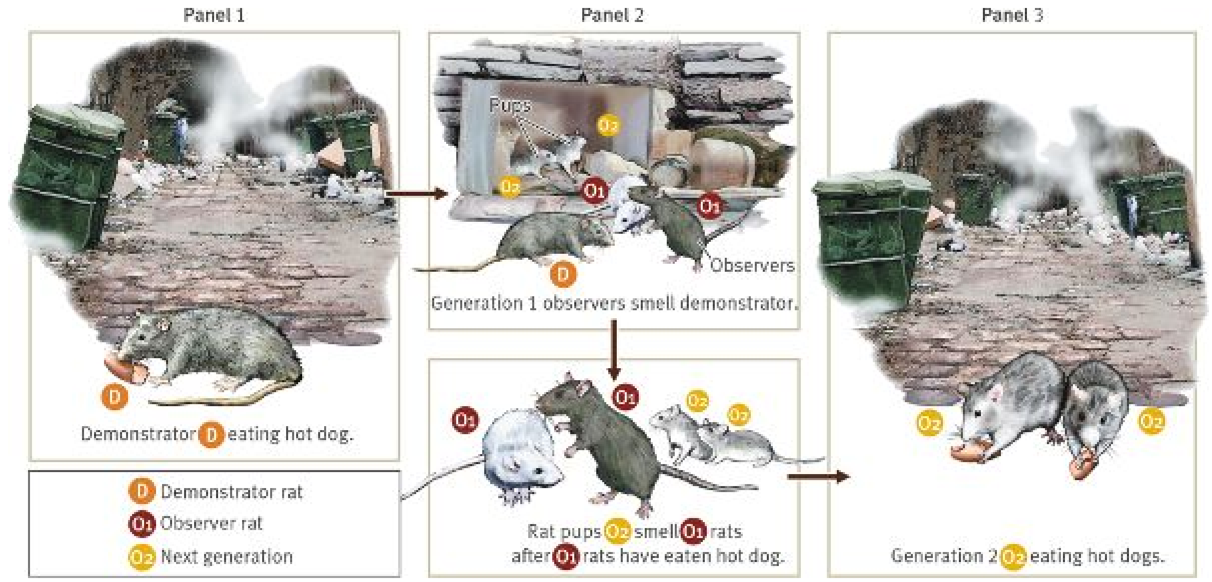

Figure 1.16. A role for cultural transmission. In panel 1, a rat eats a new food type (hot dog). When this rat (D for demonstrator rat) returns to its nest (panel 2), observer rats (O_1) smell the rat and then are more likely to add hot dogs to their diet when they encounter such an item. Multigenerational cultural transmission occurs when rats from the next generation (O_2) smell generation O_1 rats after they have eaten hot dogs and subsequently add hot dogs to their own diet (panel 3).

Conceptual, Theoretical, and Empirical Approaches

As in all sciences, in ethology, every question can be studied using conceptual, theoretical, and empirical approaches (Dugatkin, 2001a, 2001b; Figure 1.17): the best studies tend to use all three of these approaches to one degree or another. In addition to the focus on natural selection, learning, and cultural transmission, the empirical/theoretical/conceptual axis also plays an important role in almost every chapter of this book.

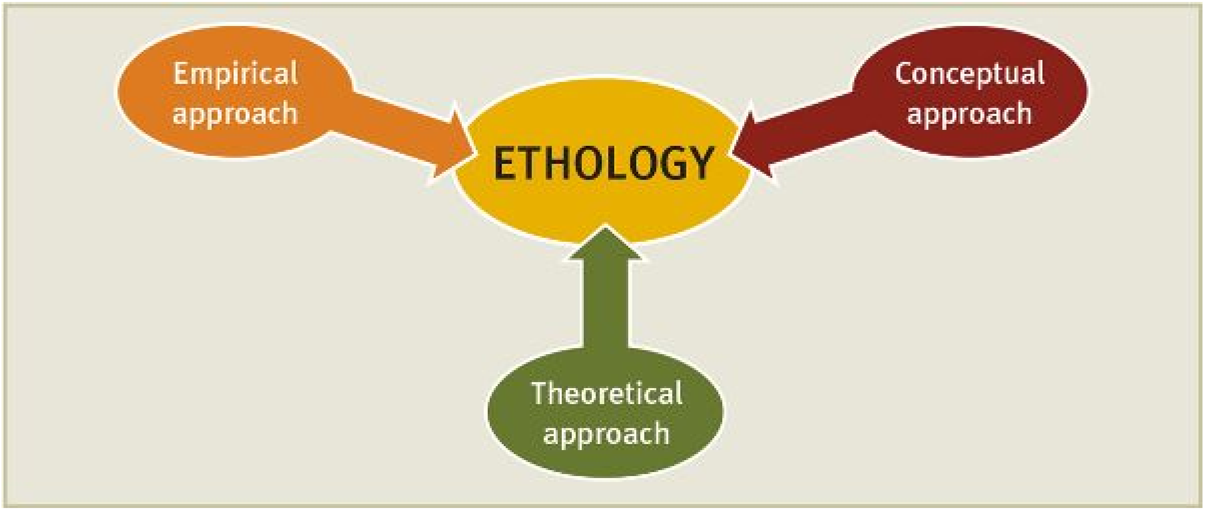

Figure 1.17. Different approaches to ethology. Ethology can be studied from a conceptual, theoretical, or empirical approach.

CONCEPTUAL APPROACHES

Conceptual approaches to ethology involve integrating formerly disparate and unconnected ideas and combining them in new, cohesive ways. Generally speaking, natural history and experimentation play a role in concept generation, but a broad-based concept itself is not usually directly tied to any specific observation or experiment.

Major conceptual advances tend not only to generate new experimental work, but also to reshape the way that a discipline looks at itself. One conceptual breakthrough that has made animal behaviorists rethink the basic way they approach their science is W. D. Hamilton's ideas on **kin selection** (chapter 9). Kin selection expanded the bounds of classic natural selection models by demonstrating that natural selection not only favors behaviors that increase the reproductive success of individuals expressing that behavior, but also favors behaviors that increase the reproductive success of those individuals' close genetic kin (Figure 1.18). Hamilton's work has a strong theoretical component to it as well, but here we will focus on the conceptual nature of this idea.

Figure 1.18. Kin selection and the mother-offspring bond. In many species, like the vervets shown here, mothers go to extreme lengths to provide for and protect their young offspring. W. D. Hamilton's kin selection ideas provided a conceptual framework for understanding the special relations between close genetic relatives. *(Photo credit: © Vlasenko / Dreamstime)*

Hamilton hypothesized that individual 1's fitness is not simply the number of viable offspring it produces (Hamilton, 1964; Figure 1.19). Instead, Hamilton proposed that fitness is composed of two parts: direct fitness and indirect fitness. **Direct fitness** is measured by the number of viable offspring produced, plus any effects that individual 1 might have on the direct descendants of its own offspring: for example, any effect individual 1 might have on the reproductive success of its grand-offspring. **Indirect fitness** effects are measured by the increased reproductive success of individual 1’s genetic relatives—not including its offspring and any lineal descendants of offspring—that are *due to individual 1’s behavior*. These actions *indirectly* get copies of individual 1’s genes into the next generation. An individual’s **inclusive fitness** is the sum of its direct and indirect fitness (J. L. Brown, 1980; Hamilton, 1964).

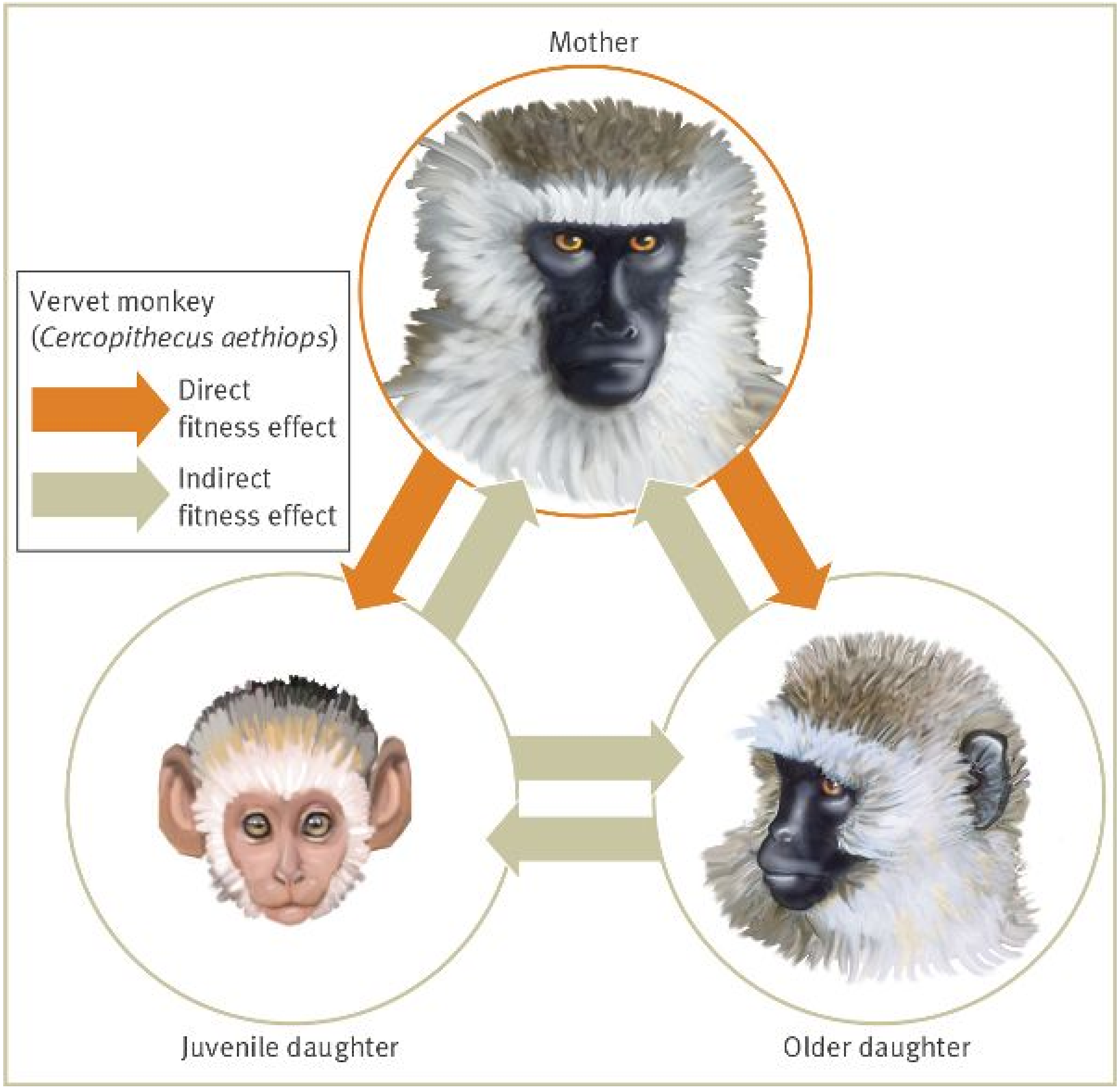

Figure 1.19. Two components to fitness. Three vervet monkeys—a mother, her juvenile offspring, and her older female offspring. Mother helping either daughter would be an example of a direct fitness effect. Siblings helping each other, or helping their mother, would represent indirect fitness effects. *(Based on J. L. Brown, 1987)*

Chapter 9 explores the logic of inclusive fitness in detail, but the kernel of this powerful idea is that, evolutionarily speaking, close genetic relatives are important because of their shared genes—genes inherited from some common ancestor. Imagine for a moment a Mexican jay, a species of birds that has been the subject of much work on inclusive fitness (J. L. Brown, 1987). A jay's inclusive fitness is a composite of the number of offspring it has, plus some fraction of the number of offspring it helps a relative raise. Let’s say that a jay helps its parents raise an additional brood of two siblings, above and beyond what its mother and father could have raised on their own. Our helper is related to its siblings by a value of 0.5 (see chapter 9 for more on this calculation). By helping its mother (and perhaps father) raise two additional offspring, it has contributed 2 × 0.5 or the equivalent of 1 offspring to its inclusive fitness. If this is the only help that it gives, our jay’s inclusive fitness is calculated by adding its indirect fitness (from helping its parents to raise its siblings) to its direct fitness.

Today, one of the first things that ethologists consider when studying social behavior is whether the individuals involved are close genetic kin. This is a direct result of Hamilton’s conceptual breakthrough.

THEORETICAL APPROACHES

In the late 1960s and early 1970s, ethologists’ understanding of how natural selection operates on animal behavior was greatly advanced with the appearance of sophisticated, usually mathematical, models of the evolution of social behavior in animals and humans. This work is most closely associated with George C. Williams, John Krebs, William D. Hamilton, John Maynard Smith, Robert Trivers, and Richard Alexander. The models that these animal behaviorists developed revolutionized the way that ethologists look at almost every type of behavior they study.

A **theoretical approach** to animal behavior often entails the generation of some sort of mathematical model of the world. During the formative years of modern ethology, much theoretical work focused on animal foraging behaviors (Kamil et al., 1987; Stephens and Krebs, 1986). One foraging-related question of particular interest was “which food items should an animal add to its diet, and under what conditions?” To tackle this question, a mathematical tool called optimality theory was used (see chapter 11). Optimality theory searches for the best (optimal) solution to a particular problem, given that certain constraints exist in a system.

For example, one might be interested in building a model that examines how animals choose which prey to add to their diet to maximize the amount of energy they take in per unit time foraging. In that case, the amount of daylight could be a constraint (for some foragers), and your mathematical model could include the total amount of time an animal has to search for food (let's label that T_s), the energy (*e*) provided by a prey type, the time it takes to handle (*h*) the prey (e.g., to kill and then eat it), and the rate at which prey are encountered (λ). You would then examine how these variables affect foraging decisions made by animals (Figure 1.20). These variables are then built into an algebraic inequality, and solving this inequality produces numerous testable, and often counterintuitive, predictions (see chapter 11). For example, one such model predicts that the decision to add certain prey types into a forager's diet does not depend on how often a predator encounters that prey, but on how often it encounters more preferred prey types.

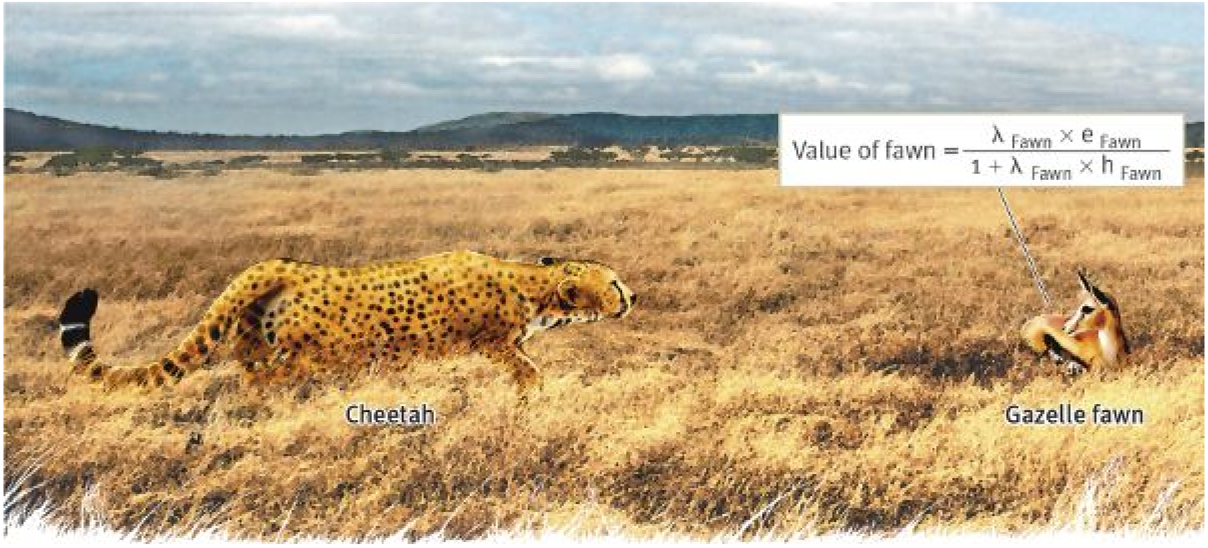

Figure 1.20. Mathematical optimality theory and foraging. Cheetahs can feed on many different prey items, including a gazelle fawn. Ethologists have constructed mathematical models of foraging that determine which potential prey items should be taken. The value assigned to each prey is a composite of energy value (*e*), handling time (*h*), and encounter rate (λ).

It is important to realize that theoreticians, including those who work on ethological questions, are not interested in mimicking the natural world in their models, but rather in condensing a difficult, complex topic to its barest ingredients in an attempt to make specific predictions. In that sense, the criticism that a particular theory doesn't match the details of any given system will often be true, but irrelevant. A good theory will whittle away the details of specific systems, but just enough to allow for general predictions that can apply to many systems.

EMPIRICAL APPROACHES

Much of this book is devoted to empirical studies. Empirical work in ethology can take many forms, but essentially it can be boiled down to one of two types—either observational or experimental studies. Both have been, and continue to be, important to the field of animal behavior.

While empirical studies in ethology preceded the work of Karl von Frisch, Niko Tinbergen, and Konrad Lorenz, modern ethological experimentation is often associated with these three Nobel Prize winners, each of whom was an extraordinary naturalist who had a fundamental understanding of the creatures with whom he worked and the world in which these creatures lived. They were able to ask fundamentally important questions about animal behavior—questions that could be addressed by a combination of observation and experimentation.

Observational work involves gathering data on what animals do, without attempting to manipulate or control any ethological or environmental variable. For example, I might go out into a marsh and record every action that I see red-winged blackbirds doing from 9 a.m. to 5 p.m. I might record information on foraging behavior, encounters with predators, the feeding of nestlings, and so forth, and be able to piece together how red-winged blackbirds in my study population spend their time. Next, from my observations, I might hypothesize that red-winged blackbirds seem to make fewer foraging bouts when predators are in the vicinity. To empirically examine the relationship between foraging and predation pressure, I might make detailed observations on how much food red-winged blackbirds eat and how many predators I can spot. I could then look for a relationship between these two variables and test the hypothesis that they are correlated.

Let’s say that when I graph foraging behavior against predation pressure, I find that they are correlated. Redwings do increase and decrease their foraging behavior as a function of the number of predators in their environment. During periods when lots of predators are around, redwings forage infrequently, but when predators are few and far between, redwings forage significantly more often. What then can I conclude? Is it fair to say that increased predation pressure causes decreased foraging? No, the data we have so far do not demonstrate causation. I can say that predation and foraging are correlated, but from the existing data, I can’t speak to the subject of what caused what—correlation does not equal causation. It might be that some other variable is causing both greater predation pressure and less redwing foraging behavior. For example, it might be that when the temperature rises, redwing predators become more active, but redwings themselves become less active, and so forage less frequently. Increased predation pressure and foraging would still be correlated, but now the former wouldn’t be seen as causing the latter; rather, they would both be associated with changes in weather.

In order to examine causality, I must experimentally manipulate the system. I might, for example, experimentally increase the number of redwing predators in area 1, but not in area 2, and see how redwing foraging is affected in these populations (Figure 1.21). I might do so by using trained predators or by simulating increased predation pressure by flying realistic predator models in area 1, but not in area 2. In either case, if redwing foraging behavior decreases in area 1 but not in area 2, I would more confident that increased predation pressure causes decreased foraging in red-winged blackbirds.

Figure 1.21. Observation and experimentation. Imagine your observations led you to predict that red-winged blackbirds will decrease foraging when under predation pressure. To experimentally examine causality, you could allow a trained falcon to fly over a red-winged blackbird area and observe how its presence affects the amount of foraging.

Before completing this section on conceptual, theoretical, and empirical perspectives in ethology, we need to address one more question—whether there is any natural ordering when it comes to the theoretical and empirical approaches. Does theory come before or after empirical work? The answer is, “It depends.” Good theory can precede or postdate data collecting. On some occasions, an observation or experiment will suggest to a researcher that the results obtained call for a mathematical model of behavior to be developed. Models of reciprocity and cooperation, for example, originally emerged from observations that many animals appeared to sacrifice something in order to help others. Given that natural selection should typically eliminate such unselfish actions, the observations cried out for mathematical models to explain their existence. Mathematical models were then developed, and they provided some very useful insights on this question, as well as stimulating more empirical work.

In turn, theoretical models can inspire empirical studies. The foraging models discussed earlier in the chapter preceded the large number of empirical studies on foraging that ethologists and behavioral ecologists continue to undertake. While it is true that ethologists have long studied what and when animals eat, controlled experimental work designed to test specific predictions about foraging were initially spurred on by the theoretical work in this area. Regardless of whether theoretical work predates or postdates empirical work, however, a very powerful feedback loop typically emerges wherein advances in one realm (theoretical or empirical) lead to advances in the other realm.

An Overview of What Is to Follow

Following this chapter are five "primer" chapters that provide an overview of natural selection, phylogeny, and animal behavior (chapter 2); hormones, neurobiology, and animal behavior (chapter 3); molecular genetics, development, and animal behavior (chapter 4); learning and animal behavior (chapter 5); and cultural transmission from an ethological perspective (chapter 6). The topics reviewed in the primer chapters are intertwined in the remaining eleven chapters, which cover sexual selection (chapter 7), mating systems (chapter 8), kinship (chapter 9), cooperation (chapter 10), foraging (chapter 11), antipredator behavior (chapter 12), communication (chapter 13), habitat selection and territoriality (chapter 14), aggression (chapter 15), play (chapter 16), and animal personalities (chapter 17). In addition, studies of our own species, *Homo sapiens*, are woven into the fabric of many chapters. In this way, the reader receives a truly integrative view of animal (nonhuman and human) behavior.

Interview with Dr. E. O. Wilson

The 25th anniversary edition of your classic book *Sociobiology*, a landmark book in the field of animal behavior, was published in 2000. What prompted you to write *Sociobiology*?

In the 1960s, as a young researcher working in the new field of population biology, which covers the genetics and ecology of populations of organisms, I saw the logic of making that discipline the foundation of the study of social behavior in animals. At that time a great deal was known about societies of bees, ants, fish, chimpanzees, and so forth, but the subject largely comprised descriptions of each kind of society in turn, and with few connections. There had been little effort to tie all that information together. I had the idea of analyzing animal societies as special kinds of populations, with their characteristics determined by the heredity of behavior of the individual members, the birth rates of the members, together with their death rates, tendency to emigrate or cluster, and so forth—in other words, all the properties we study and put together in analyzing ordinary, nonsocial populations.

Sociobiology as a discipline grew from this idea and was born, not in my 1975 book with that name (*Sociobiology: The New Synthesis*), but in my 1971 *The Insect Societies*. In this earlier work I synthesized available knowledge of the social insects (ants, termites, the social bees, and the social wasps) on the base of population biology. I defined the term *sociobiology* that way, and predicted that if made a full unified discipline it would organize knowledge of all animal societies, from termites to chimpanzees. In *Sociobiology: The New Synthesis* I added the vertebrates to the social insects (and other invertebrates) to substantiate this view, then in the opening and closing chapters, the human species. In the latter chapters, I suggested that sociobiology could (and eventually would) serve as a true scientific foundation for the social sciences. This was a very controversial notion then, but it is mainstream today.

What do you see as *Sociobiology's* legacy to date?

The legacy of *Sociobiology*, which took hold and generated interest and discussion as *The Insect Societies* never could, is indeed the discipline of sociobiology, with journals and many new lines of research devoted to it. This advance was greatly enhanced by the rapid growth of studies on animal communication, behavioral ecology, and, in population genetics, kin selection. Of ultimately equal and probably even greater importance, it showed how to create a link of cause-and-effect explanation between the natural sciences, including especially the study of animal social behavior on the one side and the social sciences on the other.

What sort of debt do ethologists owe Charles Robert Darwin?

Ethologists owe an enormous debt to Darwin, by encouraging the deep and now well-established concept that instincts are biological traits that evolved by natural selection. A word on terminology is worth introducing here. *Ethology* is the systematic (i.e., scientific) study of the behavior of animals (including, by extension, humans) under natural conditions. *Sociobiology* is the study of the biological basis of all forms of social behavior and social organization in all kinds of organisms, including humans, and organized on a base of ethology and population biology. *Evolutionary psychology* is a spin-off of both ethology and sociobiology, including both social and nonsocial behavior with special links to traditional studies of psychology.

After Darwin, whose work has had the most profound impact on the scientific study of animal behavior?

In 1989 the Fellows of the International Animal Behavior Society voted *Sociobiology: The New Synthesis* the most influential book on animal behavior of all time. The most important individual discoveries of all time would have to include sign stimuli, ritualization, the multiple modalities of nonhuman communication, the neurological and endocrinological basis of many forms of behavior, and the amazingly diverse and precise manifestations of kin selection.

Why should a talented undergraduate studying biology care about animal behavior?

Animal behavior is of course a fundamental and extraordinarily interesting subject in its own right. But it is also basic to other disciplines of biology, all the way from neuroscience and behavioral genetics to ecology and conservation biology.

Why should social scientists pay attention to what is happening in the field of animal behavior? What can they gain by doing so?

The social sciences desperately need biology as their foundational discipline, in the same way and to the same degree as chemistry needed physics and biology needed chemistry. Without biology, and in particular genetics, the neurosciences, and sociobiology, the social sciences can never penetrate the deep wells of human behavior; they can never acquire the same solidity and explanatory power as biology and the other natural sciences.

You and Bert Hölldobler won a Pulitzer prize for *The Ants*. Why have you devoted so much time and effort to studying this taxa?

There are two kinds of biologists: those who select a scientific problem and then search for the ideal organism to solve it (such as bacteria for the problems of molecular genetics), and those who select a group of organisms for personal aesthetic reasons and then search for those scientific problems which their organisms are ideally suited to solve. Bert Hölldobler and I independently acquired a lifelong interest in ants as children, and added science to that fascination later.

You have written much on the subject of conservation biology. How does work in animal behavior affect conservation biology studies, and vice versa?

The understanding of animal behavior is crucial to conservation biology and its applications. Consider how important to ecosystems and species survival are the behaviors of mating, territorial defense, dispersal, pollination, resource searching, and predation. To be successfully grasped, these phenomena have to be studied in an organized, scientific manner, not just added haphazardly to conservation strategies.

What do you believe will be the most important advance in animal behavior in the next twenty-five years?

My prediction: the complete linkage of a number of complex behavior patterns from genes to proteonones to sensors and neuron circuits to whole patterns of behavior. Biologists will learn how to scan the whole range of levels of organization to account for each animal behavior in turn.

Will animal behavior be a discipline fifty years from now, or will it be subsumed by other disciplines?

Today the study of animal behavior is the broad gateway to a wide array of different modes of study. But in fifty years—who knows? It may well be subsumed by other disciplines, some as yet undefined.

Dr. E. O. Wilson is an emeritus professor at Harvard University and a member of the National Academy of Sciences. He is the recipient of two Pulitzer prizes, and his book *Sociobiology* (Harvard University Press, 1975) is regarded as one of the most important books on evolution and behavior ever written.

SUMMARY

1. The scientific study of animal behavior, which dates back hundreds (if not thousands) of years, is called *ethology*.
2. The process of natural selection, the ability of animals to learn, and the process of cultural transmission are all important concepts for developing an integrative view of animal behavior.
3. Niko Tinbergen suggested that ethologists ask four types of questions: What are the immediate causes of behavior? How does behavior change as an animal develops and matures? How does behavior affect survival and reproduction? How does behavior vary as a function of evolutionary history?
4. Ethologists examine behavior from a proximate perspective by examining immediate causes of behavior, and from an ultimate perspective by examining evolutionary factors responsible for a behavior.
5. Work in ethology, like in all scientific fields, can be conceptual, theoretical, or empirical. Empirical work can be further subdivided into observational and experimental studies.

DISCUSSION QUESTIONS

1. Take a few hours one weekend day and focus on writing down all the behavioral observations you've made, as well as any, even indirect, behavioral hypotheses you have constructed over the last 24 hours. Think about your interaction with both humans and nonhumans. How has your very brief introduction into ethology reshaped the way you observe behavior?
2. Why do we need a science of ethology? What insights does this discipline provide both the scientist and the layperson?
3. Imagine that you are out in a forest, and you observe that squirrels there appear to cache their food only in the vicinity of certain species of plants. Construct a hypothesis for how this behavior may have been the product of (a) natural selection, (b) individual learning, and (c) social learning.
4. Why do you suppose that mathematical theories play such a large part in ethology? Couldn't hypotheses be derived in their absence? Why does mathematics force an investigator to be very explicit about his or her ethological hypotheses?
5. Discuss the pros and cons of each of the bulleted definitions of behavior in this chapter.

SUGGESTED READING

Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, *5*, 325–383. This paper, published just before E. O. Wilson's *Sociobiology*, provides the reader with a good overview of how one approaches behavior using "natural selection thinking."

Dewsbury, D. (Ed.) (1985). *Studying animal behavior: Autobiographies of the founders*. Chicago: University of Chicago Press. A fascinating introduction to the lives of early ethologists.

Galef, B. G. (2009). Strategies for social learning: Testing predictions from formal theory. *Advances in the Study of Behavior*, *39*, 117–151. In this review, Galef formalizes

predictions from social learning models, and puts those models to the test.

Levitis, D. A., Lidicker, W. Z., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*, *78*, 103–110. A review of different definitions of the word *behavior*.

Strassmann, J. E. (2014). Tribute to Tinbergen: The place of animal behavior in biology. *Ethology*, *120*, 123–126. An modern overview of proximate and ultimate causation as applied to behavior.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift fur Tierpsychologie*, *20*, 410–440. A classic paper that outlines Niko Tinbergen's approach to animal behavior.

2

The Evolution of Behavior

The Bahamas archipelago, with its islands within islands within islands, provides animal behaviorists with a natural laboratory. The thousands of smaller rock islands (Figure 2.1), often just a few hundred square meters in size, allow ethologists and ecologists an amazing opportunity for observation, experimental manipulation, and replication in natural populations of animals. Jonathan Losos, Thomas Schoener, and their colleagues have been using the rock islands associated around Snake Cay on the Island of Greater Abaco, Bahamas, to study the effects of lizard predators on the behavior and morphology of their lizard prey (Schoener et al., 2001; Losos et al., 2004).

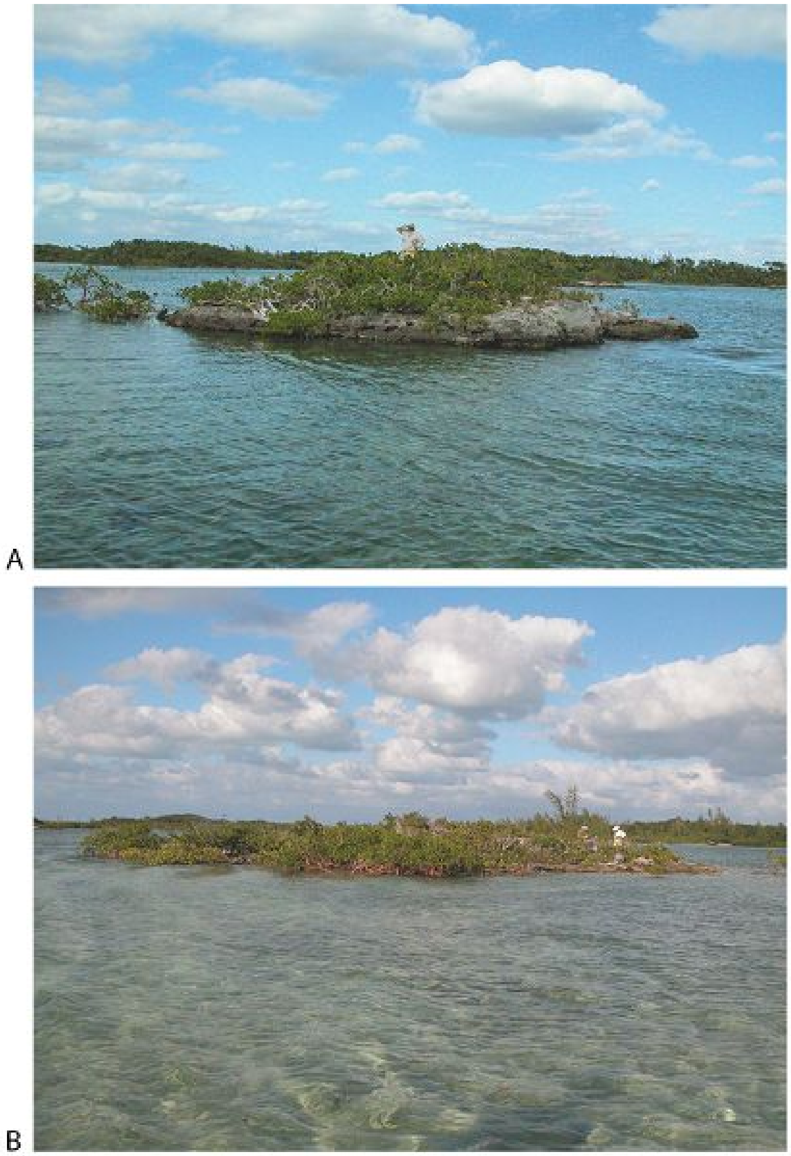

Figure 2.1. **Natural laboratories.** Two of the small islands in the Bahamas used to test hypotheses about how predators affect the behavior and morphology of prey. Photos courtesy of Jonathan Losos.

Lizards abound on many of these rock islands. One of the prey items of the curly-tailed lizard (*Leiocephalus carinatus*) is the smaller brown anole lizard (*Anolis sagrei*; Figure 2.2). The power of examining predator-prey dynamics in *L. carinatus* and *A. sagrei* on the rock islands of Greater Abaco is that dozens of these rock islands are of similar size and vegetation, and while many are home to *A. sagrei*, only a subset of those also have curly-tailed lizards. This sets the stage for experimentally introducing the predators to a series of rock islands where they are otherwise absent, and examining both the short-term and long-term effects of the introduction on prey behavior and prey morphology.

Figure 2.2. **Predator and prey on the rock islands.** (A) The prey species, the brown anole lizard, and (B) one of its main predators, the curly tailed lizard. Photos courtesy of Jonathan Losos.

In April 1997, Losos and his colleagues experimentally introduced curly-tailed lizard predators onto five rock islands where they were absent, but brown anoles were present. As controls, they observed brown anoles on islands of similar size and vegetation, but which had no curly-tailed lizard predators added. Not surprisingly, one effect of the predator introduction was that brown anole populations decreased, typically to half the size of the control populations: years later, when Hurricane Floyd struck, brown anole populations on islands that had predators added, and where population size had plummeted, were much more likely to experience local extinction than control anole populations.

Brown anoles responded behaviorally to the addition of predators as well, in a quick and dramatic fashion (Schoener et al., 2001). On the control islands, brown anoles typically were found in vegetation about 10 cm above the ground. On islands to which predators had been added, brown anoles moved to higher, thinner branches, presumably to avoid the new danger present. This behavioral response occurred within a year of the experimental manipulation (Figure 2.3).

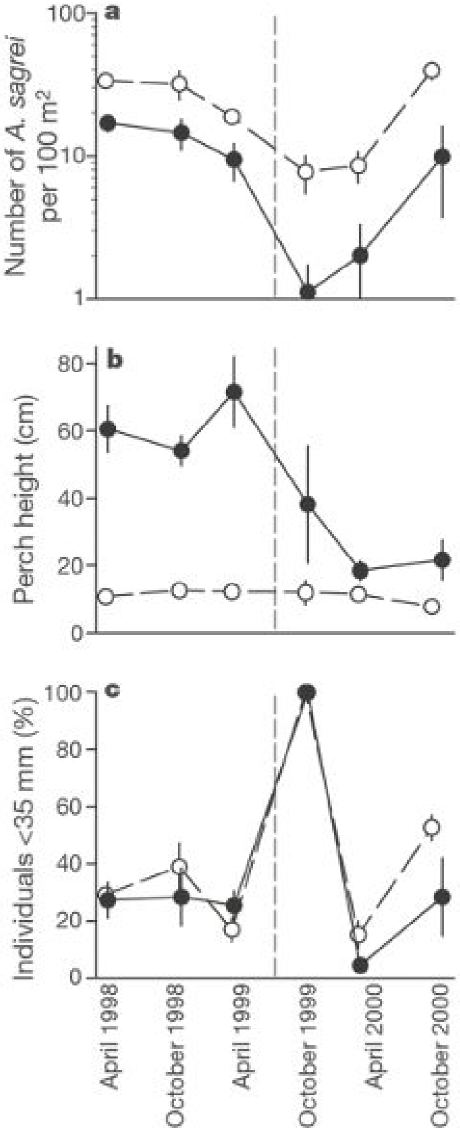

Figure 2.3. **Behavioral response to predator introduction.** Brown anoles moved to higher (and thinner) perches when predators were added (open circles = controls, closed circles = predator added). Reprinted by permission from Macmillan Publishers Ltd. © 2011. *(From Schoener et al., 2011)*

These results allowed the researchers to examine a long-standing question regarding evolution and behavior: if a behavioral change occurs as a result of predatory pressures, will natural selection be weaker or absent on any additional morphological traits that might be important with respect to predators? In the case of the rock islands, does the behavioral shift to higher perches mean that selection will be weak or absent on morphology in prey, since the prey have moved to safer areas? Losos and his colleagues tackled this question in an experiment in which, again, they compared islands with only brown anoles and islands where they added curly-tailed lizard predators (Losos et al., 2004).

As in their earlier work, they found that brown anoles moved to higher perches when predators were present. But this time they measured various physical traits of the brown anoles across control and experimental islands. Strong evidence for natural selection acting on morphology, even after behavioral changes, was uncovered. Selection on islands with experimentally introduced predators selected for males with longer limbs who were faster at escaping from predators, and larger females, who were both faster at escaping predators and harder for predators to consume should they be caught.

* * *

Every biology and psychology student should read Charles Darwin's *On the Origin of Species*, considered one of the greatest, if not *the* greatest, science books ever written. What may surprise you most about Darwin's book is not only the ease with which it can be read, but also the subject material of the first chapter. The opening chapter of the most significant book ever written in biology talks at some length about pigeon breeding in Victorian England. Victorians and others, Darwin noted, had bred many varieties of pigeons that looked and behaved dramatically differently from one another. Indeed, he himself was a pigeon breeder, noting "I have kept every breed [of pigeon] I could purchase or obtain." (p. 23). Some of these various breeds have exquisite color and very elaborate tail feathers (Figure 2.4).

Figure 2.4. Natural and artificial selection. Both natural and artificial selection have produced many morphological varieties of the pigeon, including (A) bright colors and (B) elaborate tail feathers. *(Photo credits: © Budimir Jevtic / Shutterstock; © Martina_L / Shutterstock)*

Darwin was fascinated by both the morphological and the *behavioral* varieties of pigeons. “Tumbler” pigeons seem to somersault over themselves as they fly; homing pigeons can be released long distances from home yet somehow find their way back (Figure 2.5). These morphological and behavioral varieties of pigeons were the product of many generations of breeding, primarily by amateur pigeon breeders.

Figure 2.5. Artificial selection on pigeon behaviors. Pigeon breeders have selected for behavioral varieties of pigeons, including (A) tumbler pigeons (here one bird tumbles as it flies) and (B) homing pigeons. *(Photo credits: © Mircea Costina / Shutterstock; © givaga / Shutterstock)*

The reason for this seemingly odd subject matter for the opening chapter of *On the Origin of Species* was strategic—Darwin was preparing the reader for what was to come. He knew that his readers would feel at home with a discussion of pigeon breeding, a popular pastime in Victorian days. If he could convince them that the process leading to extraordinary breeds of pigeons was similar to the process leading to *new varieties and species* in nature, his task would be a little simpler. The process leading to new pigeon breeds—tumbler pigeons, homing pigeons, and so on—is called **artificial selection**, which is defined as the process of humans deliberately choosing certain varieties of an organism over others by implementing breeding programs that favor such varieties. Darwin's discussion of artificial selection led directly to his introducing readers to his ideas on natural selection.

Rather than artificial selection, the evolutionary process leading to the extraordinary variation—including behavioral variation—that we see in nature is called natural selection, which, you will recall from chapter 1, is the process whereby traits conferring the highest reproductive success to their bearers increase in frequency over time. This chapter serves as an introduction or "primer" to the manner in which ethologists think about evolution and animal behavior.

Once Darwin's ideas were integrated into the heart of biology during what is called "the modern synthesis" (J. Huxley, 1942), animal behaviorists possessed a theory that helped explain not only *what* animals do, but *why* they do it. These sorts of "why" questions—that is, questions that deal with how evolutionary processes shape traits—are often also labeled "ultimate" questions (see chapter 1). The term "ultimate" does not imply a greater importance attached to such questions than to any other questions in animal behavior. Instead, *ultimate* in this context simply refers to a focus on evolutionary forces per se.

This chapter outlines, step-by-step, how ethologists tackle ultimate questions. Following Darwin's strategy, we begin with artificial selection. From there, we will move directly to the discussion of natural selection and animal behavior, and then delve into the role of phylogenetic history in understanding behavioral evolution.

Artificial Selection

For more than 10,000 years, humans have used the process of artificial selection to shape the way that animals and plants look, and the way that animals behave. When we select some varieties of wheat, corn, and rice over others, and systematically plant their seeds, and when we choose horses that are faster and more agile generation after generation, we are involved in artificial selection. The same can be said of our systematic preference for breeding certain varieties of dogs, cats, cattle, goats, pigs, sheep, and so many others, including the pigeon breeds that so obsessed Darwin in *On the Origin of Species*.

With respect to artificial selection in dogs, the process began with wolf populations about 15,000 years ago (perhaps even longer and perhaps on numerous independent occasions) and continues to this day, having produced the stunning array of dog breeds we see around us (Frantz et al., 2016). The process of artificial selection is the same in all of these cases, although *what* we specifically select for in dog breeds—companionship, hunting skills, sentinel behavior, etc.—will be different. For example, suppose we wish to produce a variety of collie that is an especially good herder, circling around our flocks of sheep, forcing the sheep to stay in a herd, and keeping predators away from our economically valuable flock. We would test which male and female collies were best at herding sheep and keeping flocks safe, and then preferentially breed those individuals. If we had evidence that herding skills were heritable, then in the next generation we would continue to sort the dogs we had, selecting those that met our criteria associated with herding ability and allowing them to breed, while denying breeding opportunities to those dogs that failed to meet our criteria. Repeating this, generation after generation, produces individuals that come closer and closer to our ideal herder. We can answer the question, “Why do we see the herding breeds of dog we see today?” only by referring to a selection process—in this case, artificial selection (Figure 2.6).

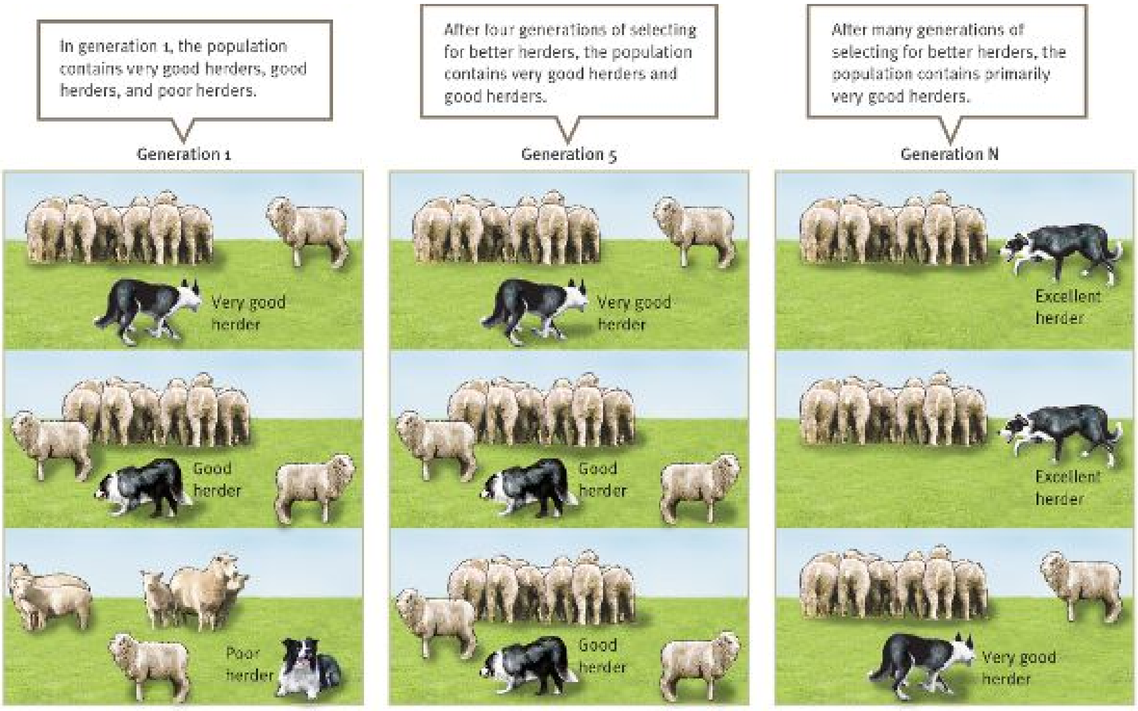

Figure 2.6. Artificial selection on herding behavior. An example of how herding behavior might be selected in dogs. In each generation, the dogs that displayed the herding behaviors that a breeder was interested in would be allowed to breed, with preferential access to breeding given to the best herders. Over many generations, breeding can lead to dogs that are excellent herders—dogs that will circle around a flock of sheep, keeping the sheep together and also keeping predators away from the flock of sheep. *(© Jabruson / NaturePl)*

Let's move to a more concrete example of artificial selection—an ongoing domestication experiment that has been underway since the late 1950s, in which a team of Russian scientists, led by Dmitri Belyaev and Lyudmila Trut, has been systematically selecting the tamest, most docile foxes from an experimental population of foxes they have in Siberia. In each generation, they allow only the tamest individuals—those that are calmest and most prosocial toward humans—to breed and parent the next generation. The results have been remarkable: this artificial selection program has produced foxes that not only can be held and petted by humans, but who seek out human contact (Figure 2.7; Trut, 1999; Trut et al., 2009).

Figure 2.7. **Selection for tame foxes.** (A) Two domesticated silver foxes. (B) A researcher with a tame silver fox pup. Photos courtesy of Aaron Dugatkin; Lyudmila Trut and the Institute of Cytology and Genetics.

The silver fox domestication experiment addresses a long-standing question in the area of artificial selection and domestication: Why is it that so many domesticated species display a suite of traits—called the domestication syndrome—that include mottled coloration, floppy ears, curly tails, and more juvenile characteristics? Belyaev hypothesized that all of these traits are the byproduct of selection for tame behavior. He proposed that humans always directly or indirectly selected the tamest animals when domesticated, and that all of the other traits in the domestication syndrome are somehow genetically linked to changes in tameness (Belyaev, 1979).

Results from the fox experiment are in line with Belyaev's hypothesis. Tame foxes have mottled color and wagging curly tails, and they retain their juvenile appearance as adults. They also have lower levels of stress hormones and their skull shape has been remolded. Differences in gene expression patterns in the forebrains of tame foxes have also been documented (Kukekova et al., 2011). These changes occurred even though the only criteria Belyaev and Trut used to select which foxes would breed was how tame they were. But why?

Richard Wrangham and his colleagues have proposed that neural crest cells may be key in explaining how tameness is linked to the domestication syndrome (Wilkins et al., 2014; Wrangham et al., 2014). Very early on in vertebrate embryonic development, these cells move along what is known as the neural crest—a concentration of cells in the middle of the developing embryo—and migrate to different parts of the body, such as the forebrain, skin, jaws, teeth, larynx, ears, and cartilage. Wrangham and his team hypothesize that selection for tameness may lead to a reduction in the number of neural crest cells and affect many of the traits associated with the domestication syndrome (Box 2.1).

Box 2.1. SCIENCE AT WORK

What is the research question? How have we domesticated animals?

Why is this an important question? For the last 15,000 years humans have been domesticating animals for sources of protection, food, conveyance, companionship, and more. Understanding the process of domestication will shed light on the evolutionary history of species we have come to rely on for many aspects of our day-to-day lives, and which our recent ancestors relied on to an even greater extent.

What approach was taken to address the research question? To mimic the domestication of dogs from wolves, for the last 59 years a team of Russian geneticists have been selecting the tamest foxes to parent the next generation in their population. Foxes are chosen strictly on the extent of their prosocial behavior toward humans.

What was discovered? Behavioral selection for tameness operated very quickly. In less than ten generations, the average degree of tameness in the foxes increased dramatically. In addition, a suite of other traits, none of which had been selected by the experimenters, also were found in these tame foxes. These include the mottled color patterns, floppy ears, and curly tails that are common to many domesticated species.

What do the results mean? Behavioral selection for tameness may have been key to how our ancestors domesticated many species, including dogs. Many of the other associated traits appear to be genetically linked to tameness, perhaps through the effect that tameness has on neural crest cell development.

With a basic understanding of artificial selection and behavior in hand, we, like Darwin’s original readers, are ready to move on to natural selection and animal behavior.

Natural Selection

Darwin came up with his theory of natural selection before Mendel's work on genetics was disseminated. But Darwin didn't need to know about genes per se for his theory to work; all he needed to realize was that behavioral traits that affected reproductive success were passed from parents to offspring (G. Bell, 1997; Darwin, 1859, 1871; Endler, 1986; Williams, 1966). Any Victorian naturalist would have known that offspring resemble their parents, and Darwin was an excellent naturalist (Darwin, 1845).

SELECTIVE ADVANTAGE OF A TRAIT

Consider any trait—height, weight, fur color, foraging behavior, mating behavior, and so on—and instead of humans as the selective agent, allow the selective agent to be nature itself. When nature is the selective agent, traits, including behavioral traits, increase or decrease in frequency as a function of how well they suit organisms to their environments. If one variety of a trait helps individuals survive and reproduce better in their environment than another variety, and if the trait can be passed down across generations, then natural selection will operate to increase its frequency over time. To see this, let's examine how natural selection might have favored "pack hunting" behavior in wild dogs (*Lycaon pictus*). Modern wild dogs tend to hunt in packs of about ten individuals, but what would a hypothetical scenario for the evolution of the trait "hunt in packs" look like (Creel, 2001; Figure 2.8)? First, imagine a simplified scenario during the early stages of wild dog evolution, in which two types of foragers existed: one type that tended to hunt in packs, and one type that tended to hunt prey alone.

Figure 2.8. Group hunting in wild dogs. Wild dogs are ferocious predators and often hunt in groups. Here they are shown capturing a wildebeest. *(Photo credit: © Bruce Davidson/naturepl.com/ARKive)*

Hunting behavior—alone or in groups—represents one component of a wild dog's **phenotype**, typically defined as the observable properties of an organism. An individual's phenotype is the result of its **genotype**—that is, its genetic makeup—and the way that a particular genotype manifests itself in the environment. In our wild dogs hunting scenario, suppose that in the evolutionary past, individuals that hunted as part of a group got more meat, on average, than wild dogs that hunted alone, and that the more food a wild dog took in, the more offspring it could produce (Figure 2.9). If wild dogs that prefer to hunt in groups produce offspring that also like to hunt in groups, this behavioral variant will increase in frequency over time, helping us to understand why modern wild dogs display this behavior. This increase will occur even if group-hunting behavior produces only a very slight advantage in terms of the number of offspring an individual raises. To see why, we need to think about the implication of small fitness differences that are magnified over long periods of evolutionary time.

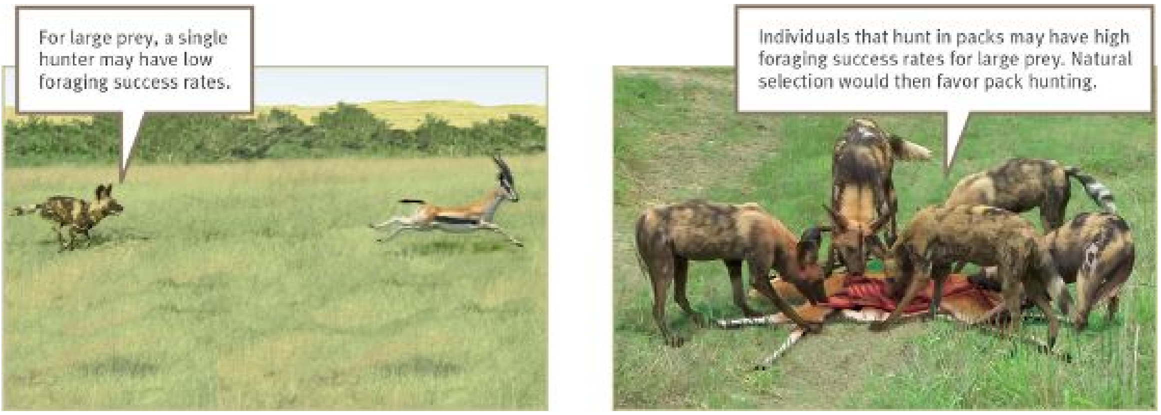

Figure 2.9. Natural selection for group hunting. A schematic of how natural selection could favor wild dogs that prefer to hunt in groups.

Even a fitness advantage of 1 percent per generation is sufficient for one behavioral variant to replace another over evolutionary time. For example, for the sake of simplicity, let's assume that hunting preference —alone or in groups—is controlled by a single gene. In reality, of course, there are probably dozens of genes affecting this trait. This logic would work equally well for traits controlled by dozens of genes, but the math would be more difficult.

If an **allele**—that is, a gene variant, one of two or more alternative forms of a gene—that codes for group hunting provides its possessors with an average of just 1 percent more offspring per generation than the allele associated with solo hunting, then all else being equal, the group-hunting allele will eventually increase in frequency to the point where virtually all dogs in the population have it. Natural selection will result in a population of individuals that hunt in groups, because the fitness advantage conferred by group hunting makes those with our hypothetical group-hunting allele more likely to survive and produce offspring. These offspring, that in turn will have the allele coding for hunting in groups, are more likely to survive and reproduce. Each generation the process is the same. Over evolutionary time, small differences in fitness can accumulate into large changes in gene frequencies (Table 2.1.)

Table 2.1. Fitness benefits and frequency of traits. When a fitness benefit to group hunting exists the frequency of wild dogs that hunt in groups will increase and, all else equal, they will eventually make up close to 100 percent of the population. In this model, we are assuming

a population size of 100, no mutation, and no migration in or out of our population. The number of generations for group hunting to go to 100 percent is calculated as follows: (2/the selective advantage to group hunting) the natural log of population size. *(Based on Carroll, 2007)*

Fitness benefit to group hunting	Population size	Generations before group hunting reaches 100% of population
1%	100	1,060
5%	100	212
10%	100	106
20%	100	53

In a breeding population of about 100 wild dogs, if group hunting provided a fitness benefit of just 1 percent, it would increase to a frequency of 100 percent in 1,060 generations. If we assume an average generation time of about five years for a wild dog, that amounts to just 5,300 years. If the selective advantage were 5 percent—that is, if those that hunted in groups had reproductive success that was 5 percent higher than that of other individuals—in just 212 generations, or about 1,060 years, our entire hypothetical population of wild dogs would be composed of animals that hunted in groups.

HOW NATURAL SELECTION OPERATES

The example of hunting in groups gives us a sense for how natural selection operates on behavior. But what exactly does it take for the process of natural selection to operate, and what is the end product of this process (G. Bell, 1997; Endler, 1986; Mousseau et al., 1999; Williams, 1966)?

To understand how natural selection operates, the first thing any ethologist needs to do is to be specific about which behavior is being studied. We don’t so much speak of “natural selection” as we do of “natural selection operating on foraging behavior,” or “natural selection operating on fighting behavior,” and so on. Once a trait is specified, the process of natural selection requires three prerequisites to be met:

- Variation in the trait—different varieties of the trait.

- Fitness consequences of the trait—different varieties of the trait must affect reproductive success and/or longevity differently.
- A mode of inheritance—a means by which the trait is passed down to the next generation.

Let’s follow the process of natural selection with respect to a specific behavioral trait: how quickly an animal approaches a novel object in its environment—a behavior that has been well studied in many taxa, including birds (Drent et al., 2003; van Oers, Drent, de Goede, et al., 2004; van Oers, Drent, de Jong, et al., 2004; van Oers et al., 2005). “Object” here is used in the broadest sense—for example, a novel object might be a previously unencountered food type or an individual from a species that has not been encountered before or a trap put out by humans or a new type of food in the environment. Approaching novel objects can be dangerous (if they turn out to be predators), but it might also yield benefits (if the novel object is a new type of prey). For simplicity, let’s call the time from when the object is first spotted to the time the animal interacts with this object, the “approach” score.

We now examine approach behavior by stepping through the three prerequisites mentioned—variation, fitness consequences, and mode of inheritance. Although we will focus on a hypothetical population, as we will see the details of both novel object approach behavior in birds and group hunting in wild dogs (discussed earlier) have been well studied by ethologists in more complicated experiments.

Variation

For natural selection to act, there must be variation in the trait under investigation (Mousseau et al., 1999). If every animal in our hypothetical population of birds displayed the same approach score, there would be nothing for natural selection to select between (Dingemanse et al., 2002). For natural selection to act, individuals in our population must differ in their approach scores (Figure 2.10).

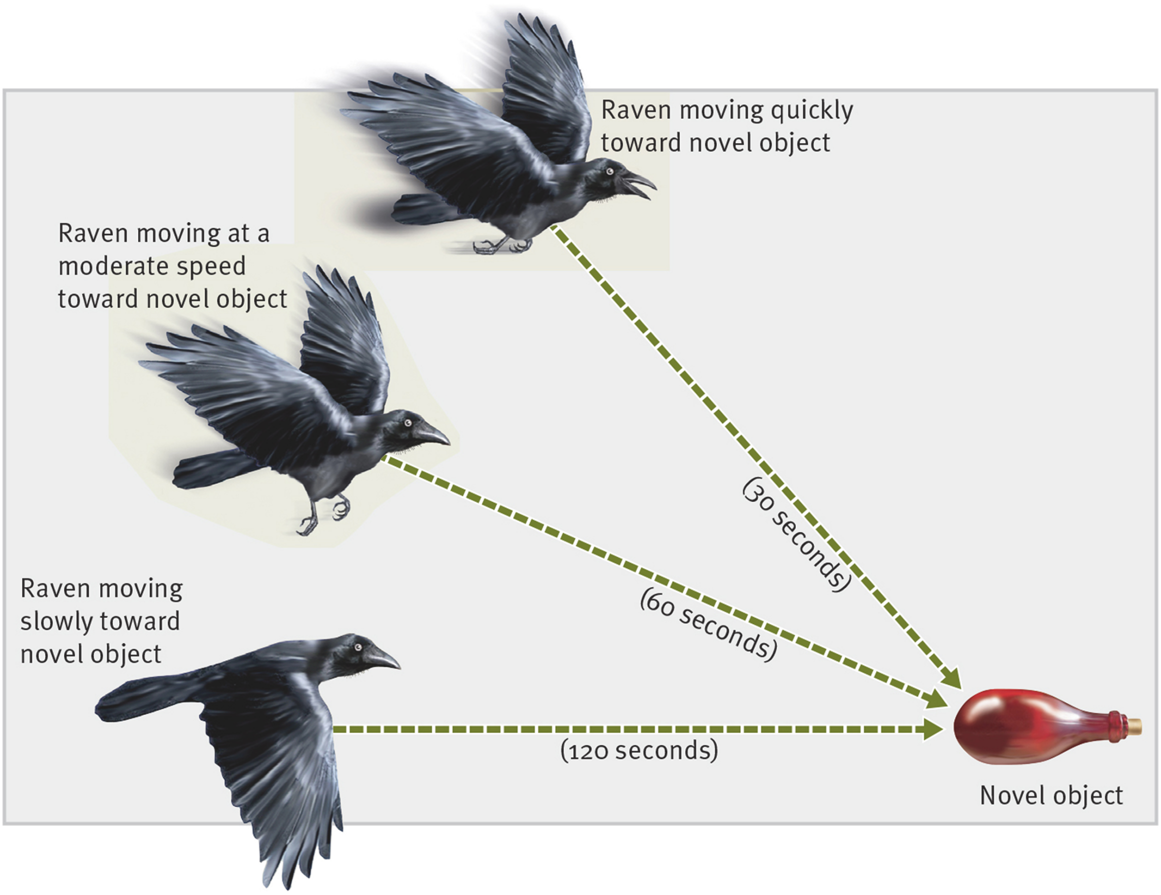

Figure 2.10. Natural selection and variation. For natural selection to act on a behavior, behavioral variation must be present in the population under study. In the case of novel object approach behavior, different birds may approach an object they have not previously encountered slowly (taking 120 seconds to reach the object), moderately slowly (taking 60 seconds to reach the object), or quickly (taking 30 seconds to reach the object).

Variation in a trait can be caused by either environmental or genetic factors. We shall return to these two different forms of variation a bit later, but here we focus on **genetic variation**—in our case, behavioral variation in approach score that correlates with genetic differences between birds in our population. Genetic variation in a population can be generated in a number of ways. For example, **mutation**—which is defined as any change in genetic structure—creates new variation in a population.

Mutations can occur in many different ways. Addition and deletion point mutations occur when a single nucleotide is either added or deleted from a stretch of DNA. Because genes often code for the production of enzymes and other kinds of proteins (which are made up of amino acids), this type of mutation typically causes the production of an inactive enzyme, which may, in turn, affect an animal's behavior. Base mutations occur when one base in a nucleotide replaces another. Many base mutations can potentially affect protein function, and so they may have an impact on an individual's reproductive success often, but certainly not always, by affecting behavior. Some base mutations do not cause changes in which amino acids are produced. These mutations are known as silent mutations.

In addition to mutation, another factor that produces variation in a population is **genetic recombination**. In sexually reproducing organisms, when pairs of chromosomes line up during cell division, sections of one chromosome may "cross over" and swap positions with sections of the other chromosome. This swapping creates new genetic variation. Crossing-over points are essentially random, and so virtually any crossover between a pair of chromosomes is possible in principle. As such, crossing over creates huge amounts of new genetic variation—including genetic variation in behavioral traits—in sexually reproducing organisms.

Although it may sound paradoxical, new genetic variants of a trait can enter a population via nongenetic pathways. The most common way for this to occur is through **migration**. Migration can increase genetic diversity in a given population because individuals coming from other populations can introduce new trait variants. In our bird population, the range of approach scores is from 30 to 120 seconds, but suppose that in a neighboring population some birds have approach scores of 150 seconds. If the differences in approach scores between the migrants and those in our population are a function of underlying genetic differences, then migration can increase genetic variation in the time it takes to approach novel objects. When migrants mate with individuals in their new population, this generates even more genetic variation.

Fitness Consequences

Genetic variation alone is not enough; that variation must have fitness consequences (Darwin, 1859; Dejong, 1994; Endler, 1986; Kingsolver et al., 2001).

The **fitness** consequences of a trait refer to the effect of a trait on an individual's lifetime reproductive success—for example, the difference in reproductive success associated with slow versus fast approach behavior (R. A. Fisher, 1958; Grafen, 1988; Reeve and Sherman, 1993; Williams, 1966). In later chapters, when we discuss inclusive fitness, we shall broaden this definition, but for now, reproductive success refers to the mean number of reproductively viable offspring an individual produces.

In our novel object/approach score example, variation in approach score must map onto differences in reproductive success, even if only weakly. Without this translation from variation in a trait to fitness differences associated with such variation, natural selection cannot act on approach behavior (or any trait). To understand why, think about it like this: If we have behavioral variation, but all variants have the same effect on reproductive success, there is nothing for natural selection to select between. Suppose we have 100 birds, and let's imagine that 50 of them show approach scores of 30 seconds, and 50 display approach scores of 120 seconds—in this population, we clearly have variation in approach score. Let's assume that individuals with approach scores of 30 seconds produce an average of 4 offspring, and birds with approach scores of 120 seconds also produce an average of 4 offspring. Since individuals with different approach scores produce the same average number of offspring, variation in approach score (30 versus 120 seconds) does not translate into variation in fitness, and natural selection cannot act on approach score. In contrast, if all individuals with lower approach scores of 30 had greater reproductive success than all individuals with higher approach scores, then behavioral variation does translate into fitness differences (Figure 2.11).

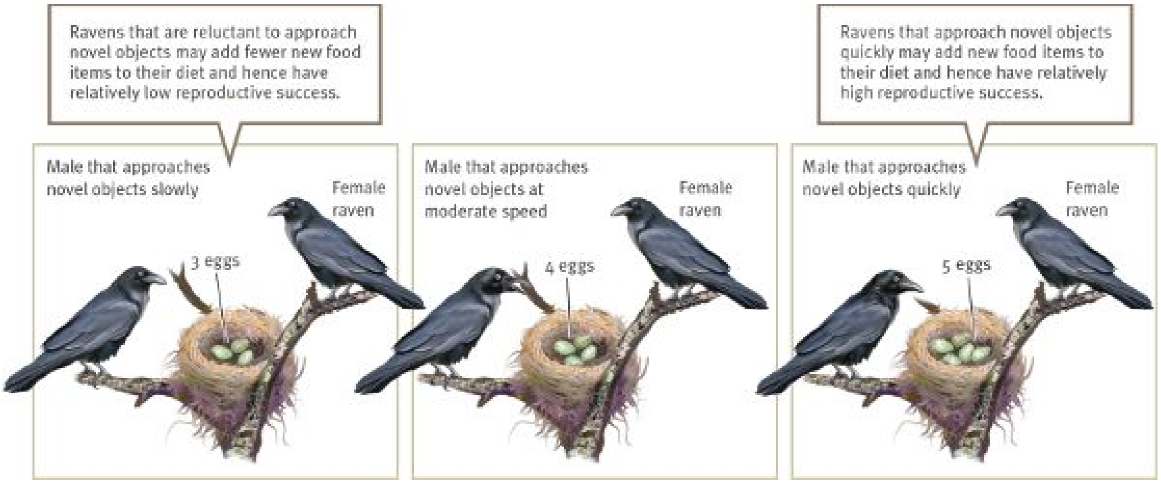

Figure 2.11. **Natural selection and fitness consequences.** If approaching novel objects quickly enables a bird to be the first to reach a new food source, this may contribute to its survival, as it may get more of that food than birds with slower approach times. This variation in approach time will have fitness consequences if it leads to those approaching quickly having more eggs and hence more offspring.

Experimental work in ethology has found that fitness differences are ubiquitous between behavioral variants. The odds that two behavioral variants would have the exact same effect on reproductive success are very low, and we have already seen that over evolutionary time, even small differences in reproductive success can have important consequences on the evolution of behavior.

Mode of Inheritance

In addition to variation and fitness consequences, there must be some mode of inheritance in place for natural selection to act on a trait. Without a mode of inheritance, any fitness differences that exist within one generation are washed away, and natural selection cannot act. To understand why, imagine that birds with approach scores of 30 seconds have (on average) five offspring and that birds with approach scores of 120 seconds have (on average) three offspring. In this case, both variation and fitness consequences are associated with behavioral variation. If there is no mode of inheritance in place, however, offspring will not resemble their parents with respect to approach score. Without a mode of inheritance, individuals that have low approach scores are no more likely to produce offspring with low approach scores than are individuals that have high approach scores, and vice versa. Any fitness associated with approach score would be lost in the next generation and natural selection would not be able to operate on this behavior.

Because genes are passed down from generation to generation, they are the most obvious candidate for a method of transmission of a trait from one generation to then next. We focus on genetic transmission here, holding off a discussion of other modes of transmission until an in-depth discussion of cultural transmission in chapter 6.

One way to study genetic transmission is by calculating narrow-sense **heritability**—a measure of the proportion of variance in a trait that is due to what is known as additive genetic variance (Hartl and Clark, 2006; Mousseau and Roff, 1987). Recall that for natural selection to operate on a trait, there must be variation in that trait—in our example, variation in approach scores. But these *differences* in approach scores—indeed, in any behavior—can come about in many ways. Individuals displaying different approach scores may have been raised on different diets, exposed to different learning opportunities, and so on. Behavioral differences can also be the result of genetic differences. It is this genetic variance that is measured in heritability experiments.

Truncation Selection

One way for measure narrow-sense heritability is through a **truncation selection experiment**. In step 1 of a truncation selection experiment examining heritability in approach scores, we measure the approach score of every bird in our population when it reaches twelve months of age. Suppose this gives us a mean approach score of 60 seconds for generation 1. Let's label this mean value x_0. Step 2 of our experiment is to *truncate*, or cut off, the population-level variation in approach scores by allowing only those individuals with approach scores greater than some value—for example, 80 seconds—to breed. We then calculate the mean approach score of those individuals that we have allowed to breed. Let's label that mean as x_1 and suppose that x_1 equals 90 seconds (Figure 2.12).

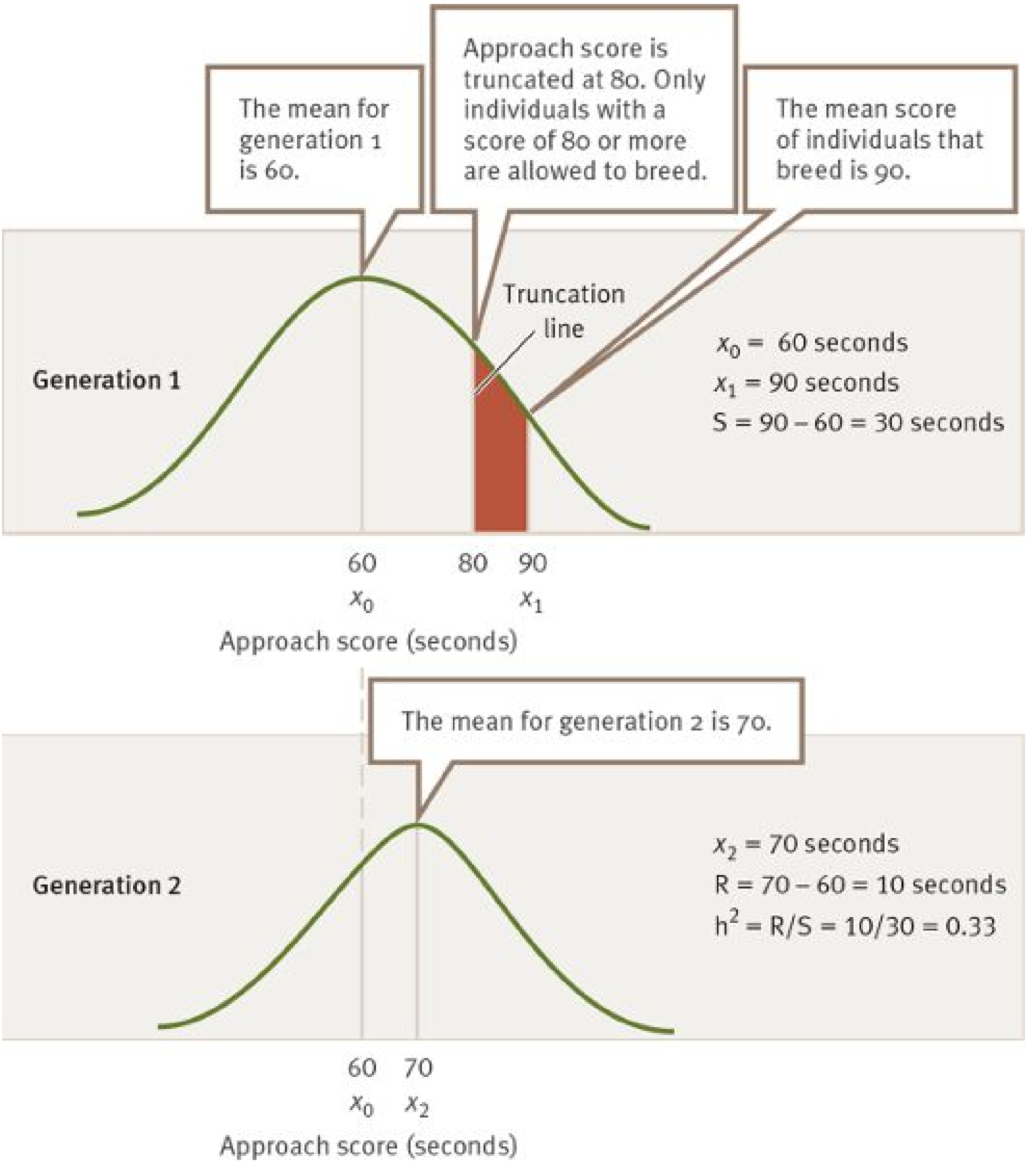

Figure 2.12. Heritability of novel object approach. Hypothetical results from a heritability experiment on novel object approach. The mean of *all* generation 1 individuals (60 seconds) is labeled x_0, and the mean of those generation 1 individuals that were allowed to breed (90 seconds) is labeled x_1. The mean of *all* generation 2 individuals (70 seconds) is labeled x_2. S = $x_1 – x_0$ = 30 seconds, R = $x_2 – x_0$ = 10 seconds, h^2 = R/S = 0.33.

The difference between x_1 and x_0 is referred to as the selection differential, or S. In our case, S = 30 seconds. One way to think about S is as the maximal amount we could expect natural selection to change approach scores—the amount of change that we might expect if all the variation in approach score was genetic variation upon which natural selection could act.

In step 3 of our truncation selection protocol, we raise the offspring produced by the generation 1 birds that were allowed to breed under conditions identical to those experienced by their parent, until they have reached twelve months of age, and then we measure their approach scores. Let's label the mean approach score of these generation 2 individuals as x_2, and for argument's sake, suppose this value is 70 seconds. The difference between this mean (x_2) and the mean of the entire population in the first generation (x_0) is referred to as the response to selection, or R. It is a measure of how much truncation selection has changed approach scores across generations 1 and 2. In our case, R = 10 seconds. Heritability is defined as R/S, so in our population of birds, the heritability of approach is 10/30 or about 0.33. In other words, one-third of all the variance in approach is due to genetic variance upon which natural selection can act.

Work in evolutionary biology, population genetics, and animal behavior all suggest that many traits—ranging from morphological to behavioral—show low (0.0 to 0.1) to moderate (0.1 to 0.4) heritability (Hoffmann, 1999; Mousseau and Roff, 1987; T. Price and Schulter, 1991; Weigensberg and Roff, 1996).

The same protocol we have employed for measuring variability, fitness, and heritability of approach scores can be used for any number of behaviors. This is not to say that obtaining concrete experimental evidence that natural selection operates on animal behavior *in the wild* is an easy task—it isn't, and it often takes years and years of effort to do so (Endler, 1986; Mousseau et al., 1999). Many studies *infer* how natural selection has operated on behavior in the wild, but experimental studies that measure natural selection in the field are very difficult to design and implement.

Parent-Offspring Regression

In addition to the truncation selection method, narrow-sense heritability can also be measured through **parent-offspring regression**. The idea here is simple. Parents pass on genes to their offspring, so when narrow-sense heritability is high, the behavioral variation in the offspring should map onto the behavioral variation observed in parents. The greater the role environmental variance—differences between the environments experienced by parents and offspring in relation to diet, location, and so forth—plays in determining variance in behavior, the lower the narrow-sense heritability of that behavior. To see how parent-offspring analysis can help us understand behavioral variance, consider Charles and Mary Brown's work on behavior in cliff swallows (*Petrochelidon pyrrhonota*; Figure 2.13) in which they used parent-offspring regression to dissect the behavioral variance in an individual's preference for living in larger or smaller groups.

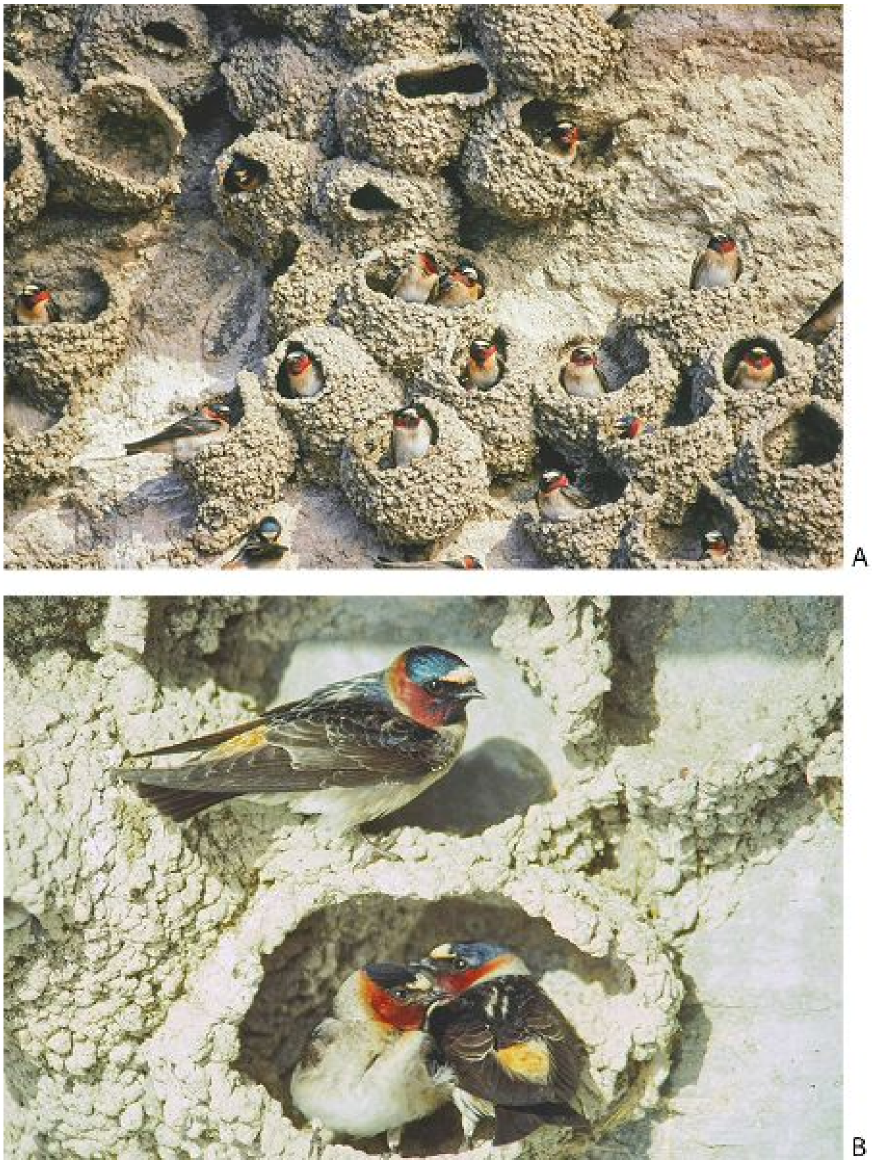

Figure 2.13. Cliff swallows in their nests. In cliff swallows, preference for group size is a heritable trait. (A) Cliff swallow nests are often clustered together. (B) A closeup of one nest with chicks, and the mother standing next to the nest. *(Photo credits: © Charles R. Brown)*

For more than thirty years, the Browns have conducted field studies of cliff swallow birds—a species in which group size affects survival, for example, by affecting rates of parasitic infection (C. R. Brown and Brown, 2004a, 2004b). Using five clusters of cliff swallow colonies, and a sample of 2,581 birds, they found that the group size in which individual swallows lived was statistically similar to the group size in which their parents lived (Brown and Brown, 2000). This was true for birds that bred at the same site as their parents, as well as for offspring that emigrated elsewhere, suggesting that the correlation between parent and offspring was not a function of habitat per se (Figure 2.14). If the correlation in group-size preference was due to parents and their offspring living in the same environment—that is, if this variance in group size was due to environmental variation—we would expect that correlation to disappear when offspring emigrated and lived in different environments from their parents. But Brown and Brown found that the correlation held, suggesting that preference for group size might be a heritable trait.

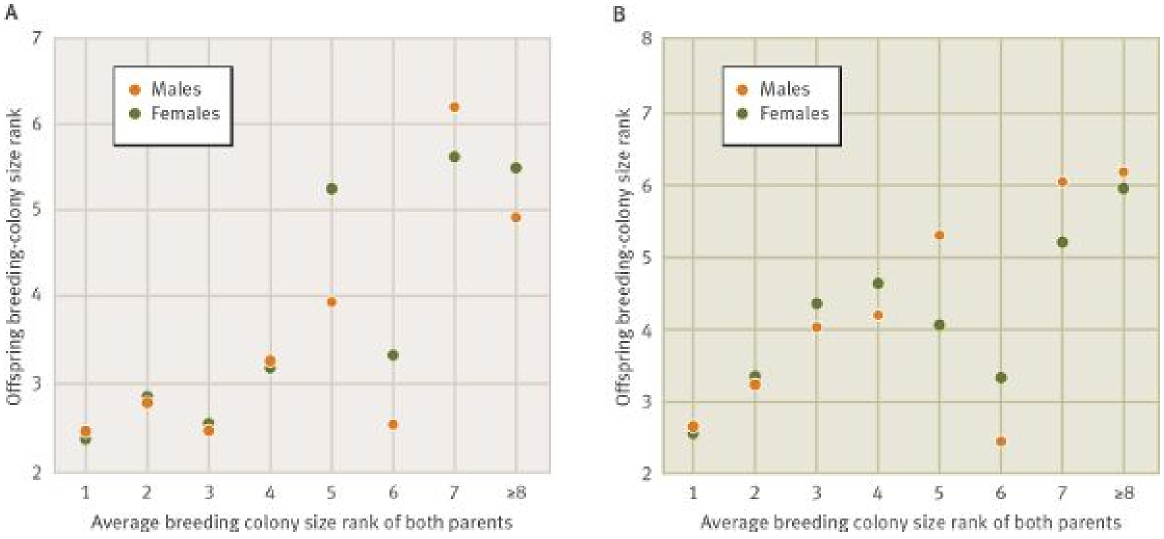

Figure 2.14. Breeding colony size in parents and offspring. There is a positive correlation between breeding colony size in parents and offspring in cliff swallows. Charles and Mary Brown sampled thousands of birds in their native habitat and found a strong correlation between parent and offspring colony size. This held true for all offspring (A), as well as for offspring that bred away from their natal site (B). To calculate heritability for a parent-offspring graph like this, the “line of best fit” for a set of data points is drawn (not shown here). If the line of best fit has a slope significantly greater than zero, the narrow-sense heritability is significant. *(From C. Brown and Brown, 2000)*

In a second experiment, Brown and Brown used nestlings from two *large* and five *small* colonies. Half the young from the nests in the large colonies were removed (the other half remained in the nest), and the young from small colonies were placed in their stead. Likewise, half the young in small colonies were replaced by young from large colonies. In all their manipulated nests, then, Brown and Brown had offspring from both large and small colonies. This sort of design is referred to as a **cross-fostering experiment**, and of the almost 2,000 birds in this experiment, 721 were recaptured and used for a parent-offspring regression on preference for group size.

When examining the preference for group size in cross-fostered offspring, the Browns found a positive correlation with the group-size preferences of their genetic parents; a negative correlation was uncovered when group-size preferences of offspring and foster parents were compared. In other words, even after the cross-fostering, the young displayed the same group-size preference as their genetic parents (not their foster parents), indicative of a significant narrow-sense heritability for this complex behavioral trait (Box 2.2).

Box 2.2. SCIENCE AT WORK

What is the research question? Is the preference for group size heritable in cliff swallows?

Why is this an important question? For a trait to be subject to the process of natural selection, it must be heritable.

What approach was taken to address the research question? Two techniques were used: a parent-offspring regression to calculate narrow-sense heritability, and a cross-fostering experiment using swallows from colonies in which individuals displayed different group size preferences.

What was discovered? Both the parent-offspring regression and the cross-fostering experiment suggest that group size preference is a heritable trait.

What do the results mean? Even complex behavioral traits such group size preference can be heritable and subject to the process of natural selection.

Sociobiology, Selfish Genes, and Adaptation

Sociobiology is the study of the evolution of social behavior (Wilson, 1975). The sociobiological notion that genes—in our case, genes associated with behavior—are the units upon which natural selection acts, is often referred to as the “selfish gene” approach to ethology. The phrase “selfish genes” was popularized by Richard Dawkins in 1976. As Dawkins makes clear, genes aren’t “selfish” in any emotional or moral sense. But, genes can sometimes be treated as though they were selfish in that the process of natural selection favors those alleles that increase the expected relative reproductive success of their bearers (Dawkins, 2006; Grafen and Ridley, 2006). (The Conservation Connection in Box 2.3 shows how this approach can inform conservation biology studies.)

Box 2.3. CONSERVATION CONNECTION

Conservation Biology and Symmetry as an Indicator of Risk

One goal of conservation biology is to detect populations under risk. But it is often difficult to identify which environments are stressful, and in which environments populations are at especially high risk. In some cases, of course, changes to an environment may be so extreme that it clearly can no longer support a population. But ideally, conservation biologists want to identify these stressful environments before so much damage is done that it might be irreversible. What tools does “natural selection thinking” offer conservationists in such situations?

One approach is to look for certain generalizable traits that can be used as indicators of the genetic quality of an individual. Evolutionary biologists and ethologists have long searched for traits that indicate the ability to respond to the changing (and often adverse) conditions that animals face throughout their development. If such indicator traits exist and are heritable, animals might use such indicator traits to select their mates.

A number of studies suggest that one trait that may serve as an indicator of genetic quality is the symmetry of the left and right side on an individual (Figure 2.15). Research suggests that symmetry is a cue that an individual has fared well in responding to the changing conditions that it faces during its development (Leamy and Klingenberg, 2005; Swaddle, 2003).

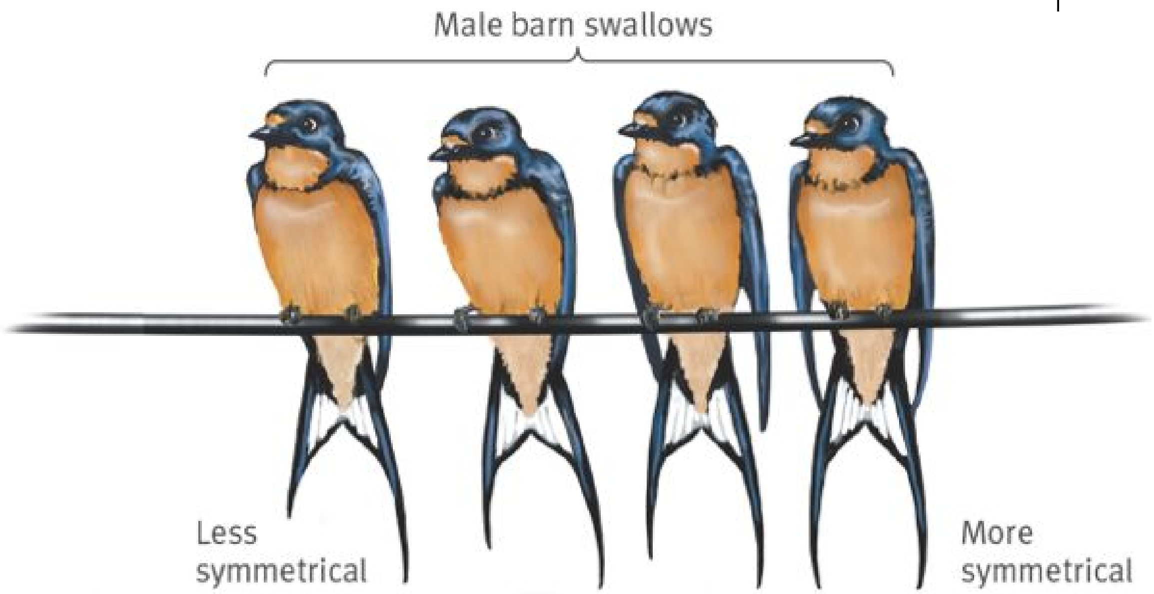

Figure 2.15. Symmetry. Male barn swallows differ in how symmetric their tail feathers are.

What are the implications of this for conservation biology? If symmetry is an indicator of the ability to handle development stress, then as we move from less stressful to more stressful environments we would expect to see more asymmetry in traits. Luc Lens and his colleagues have proposed that conservation biologists can use asymmetry as an early warning system for detecting populations under risk (Lens et al., 2002).

To test this idea, Lens et al. examined symmetry and survival in three populations of Taita thrushes (*Turdus helleri*). This species lives in forests in Kenya, and their forests have been fragmented by human activity since the 1960s. Fragments in this forest have been classified by conservation biologists as "low degeneration" (least damage, most similar to undisturbed forest), moderate degeneration, and high degeneration. Lens and his team studied one population of thrushes in each type of fragment. Not surprisingly, they found decreased rates of survival as they moved from the low-degeneration to high-degeneration sites. But as the researchers captured and marked each bird, they also measured the symmetry of the left and right tarsus. They found that symmetry decreased as forest degeneration increased: individuals in the high-degeneration areas had higher levels of asymmetry than those in low-degeneration areas (Figure 2.16). Symmetry of the left and right tarsus bone in these thrushes appears to be an early warning signal that conservation biologists could use to identify populations at high risk. Rather than wait for the grim differences in survival between high- and low-degeneration forests to manifest themselves, conservation biologists could proactively take measures in populations showing high measures of asymmetry. For example, researchers could pay special attention to populations showing high measures of asymmetry, conducting more periodic inspections in such populations by surveying population size and growth rate.

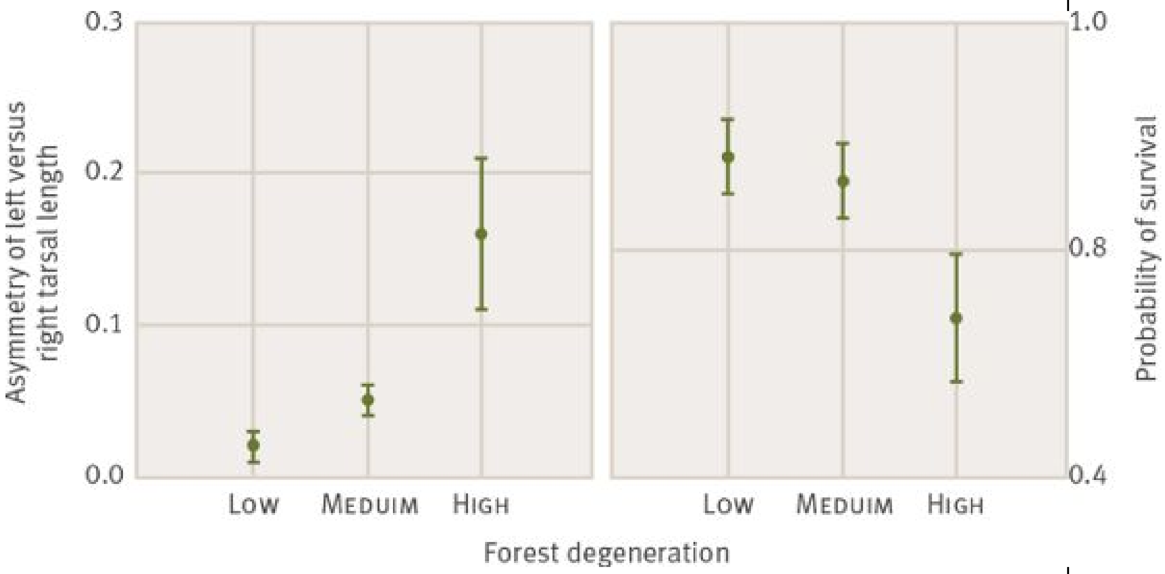

Figure 2.16. Symmetry as an early warning cue. In Taita thrushes (*Turdus helleri*), asymmetry of the left and right tarsus bone may be an early warning signal that researchers can cue in on to identify populations at high risk. As forest degeneration increases, survival decreases and asymmetry (in the length of left and right tarsus bones) increases. *(From Lens et al., 2002)*

Any allele that codes for a trait that increases the fitness of its bearer above and beyond that of others in the population will increase in frequency. So natural selection often, but not always, produces genes that *appear* to be selfish. Apply this approach to animal behavior, particularly animal social behavior, and you have one of the main ways in which ethologists think about genetics and animal behavior (Alexander and Tinkle, 1981; J. L. Brown, 1975; Grafen and Ridley, 2006; E. O. Wilson, 1975). Thinking of a gene as “selfish” provides a convenient means to conceptualize some problems in animal behavior.

We need a term for traits that natural selection molds, and that often match organism to environment so exquisitely. Such traits are typically referred to as **adaptations**, a term that is defined in many ways in the literature (Mayr, 1982; Mitchell and Valone, 1990; Reeve and Sherman, 1993; Sober, 1987). We will define *adaptations* as traits associated with the highest relative fitness in a given environment (Reeve and Sherman, 1993). Natural selection is the primary process producing adaptations.

Let’s examine two case studies of adaptation: (1) antipredator behavior in guppies, and (2) cooperative behavior in naked mole rats.

ANTIPREDATOR BEHAVIOR IN GUPPIES

The guppy (*Poecilia reticulata*) has been the subject of many studies on the evolution of behavior (Houde, 1997; Magurran, 2005). Not only do guppies breed quickly, facilitating multigenerational studies, but their population structure is also ideal for studies of natural selection and behavior. Most guppy studies use fish from the Northern Mountains of Trinidad and Tobago. In many of these streams, guppies can be found both upstream and downstream of a series of waterfalls (Houde, 1997; Magurran, 2005; Seghers, 1973; Figure 2.17). These waterfalls act as a barrier to many of the guppies’ predators. Upstream of waterfalls, guppies are typically under only weak predation pressure from one small species of fish, but downstream of the waterfalls, guppies are often under severe predation pressure from numerous piscine (fish) predators.

Figure 2.17. Guppy habitats. (A) An upstream, low-predation stream in Trinidad, and (B) a downstream, high-predation stream. Guppies in these streams have been subject to different natural selection pressures with respect to predation. *(Photo credits: © Joshua F. Goldberg)*

High-predation and low-predation sites in the same streams are often only kilometers apart (and sometimes much less), but there is little gene flow between high- and low-predation sites, so if the type of predators differ dramatically based on site, then natural selection should favor different traits in upstream and downstream guppy populations. And indeed, between-population comparisons in guppies have found differences with respect to many traits, including antipredator behavior, male coloration, number of offspring in a female's clutch, size of offspring, and age at reproduction (Endler, 1995; Houde, 1997; Magurran, 2005; Reznick, 1996; Figure 2.18). Recent genome-wide scans of guppies from many sites have found "genetic signatures" indicative of natural selection favoring different sets of alleles linked to behavioral traits at high- and low-predation sites (Willing et al., 2010).

Figure 2.18. Male color patterns. Male guppies have unique color patterns. Males at low-predation sites are more colorful than males at high-predation sites. *(Photo credit: Paul Bentzen)*

Using a combination of field and laboratory experiments, David Reznick and his colleagues have found that guppies from high-predation sites mature faster, produce more broods of smaller offspring, and tend to channel more resources to reproduction when compared to guppies from low-predation sites (Figure 2.19). Why? At high-predation sites, predators who feed on guppies tend to be much larger and can eat a guppy no matter how large it gets. At these sites, producing many smaller fish should be favored by natural selection, as this is akin to buying lots of lottery tickets and hoping that one is a winner. Low-predation sites are home to a single small fish predator (*Rivulus hartii*) of guppies. If guppies can get past a certain size threshold, they are safe from *R. hartii*. As such, natural selection should favor females producing fewer, but larger, offspring that can quickly grow large enough to be out of the zone of the danger associated with *R. hartii*, and this is precisely what we see in these populations (Reznick, 1996).

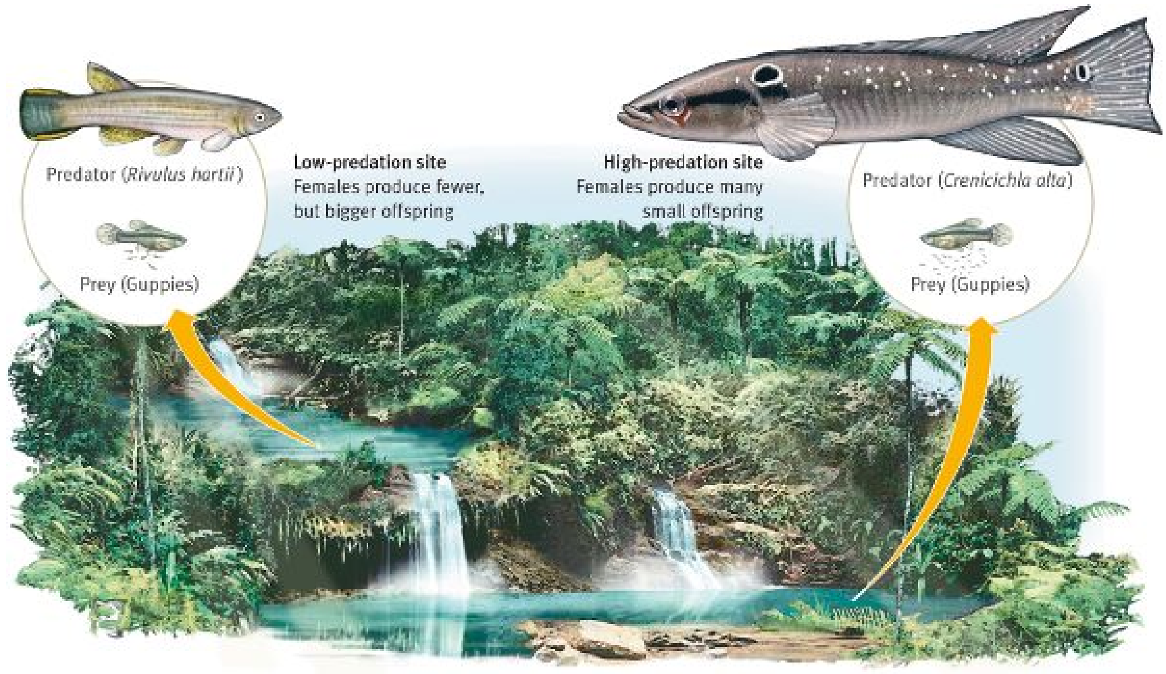

Figure 2.19. Natural selection and predation. Natural selection acts differently on guppy populations from high-predation sites (with *Crenicichla alta*) and low-predation sites (with *Rivulus hartii*). At high-predation sites, natural selection favors guppies producing many small young, but at low-predation sites, natural selection pressure favors fewer, but larger, offspring. Offspring are pictured below female guppies in left and right circles above.

Natural selection has also operated on various aspects of guppy *behavior* (Endler, 1995; Houde, 1997; Magurran, 2005; Reznick, 1996). Antipredator behaviors have been studied extensively in natural populations of guppies (Magurran, 2005; Magurran et al., 1995; Seghers, 1973). Depending upon whether they evolved in populations under heavy or light predation pressure, guppies (as well as sticklebacks and minnows) have a very different suite of antipredator behaviors (Table 2.2).

Table 2.2. The effects of predation. An abbreviated list of some behaviors that differ across populations as a function of predation pressure in guppies (*P. reticulata*), sticklebacks (*G. aculeatus*), and minnows (*P. phoxinus*). *(Adapted from Magurran et al., 1993)*

Behavior	At areas of high predation pressure	Species
Schooling	Larger and more cohesive schools	*P. reticulataP. phoxinus*

Behavior	**At areas of high predation pressure**	**Species**
Evasion tactics	More effectively integrated in high-risk populations	*P. reticulataG. aculeatusP. phoxinus*
Inspection and predator assessment	Increase in inspection frequencyIncrease in inspection group size	*G. aculeatusP. phoxinusP. phoxinus*
Habitat selection	Remain near surface and seek cover at edge of river	*P. reticulata*
Foraging	Increased feeding tenacity	*P. reticulata*
Female mating choice	Preference for less brightly colored males	*P. reticulata*
	Avoidance of sneaky mating attempts	*P. reticulata*
Male mating tactics	Increased use of sneaky mating tactics	*P. reticulata*

Two components of antipredator behavior—shoaling and predator inspection—have been studied in detail by animal behaviorists. Shoaling, or swimming together in a group (also referred to as schooling), is a measure of group cohesiveness (Keenleyside, 1955; Pitcher, 1986), whereas **predator inspection** behavior refers to the tendency for individuals to move toward a predator to ascertain various types of information about this presumptive danger (Dugatkin and Godin, 1992; George, 1960; Pitcher, 1992; Pitcher et al., 1986).

Because research from many fish species has found that swimming in large groups provides more protection from predators than swimming in small groups, ethologists have hypothesized that guppies from high-predation sites would shoal more tightly, and in greater numbers, than guppies from low-predation sites (Houde, 1997; Magurran, 2005; Magurran et al., 1995). The data from the field are in line with this prediction. Furthermore, guppies from high-predation sites inspect a predator more cautiously, but more often, than their low-predation counterparts. This difference, too, is likely the result of contrasting natural selection pressures at high- and low-predation sites—inspecting a threat cautiously, but frequently, should be more strongly favored in areas of high versus low predation.

In the early 1990s, Anne Magurran and her colleagues discovered a unique opportunity to examine a “natural experiment” on the evolution of antipredator behavior in guppies. In 1957, one of the original researchers on guppy population biology, C. P. Haskins, transferred 200 guppies from a high-predation site (in the Arima River) to a low-predation site (in the Turure River) that had been unoccupied by guppies. Magurran realized that this was an opportunity to examine natural selection on antipredator behavior. If natural selection, via predation, shapes antipredator responses, then the lack of predation pressure in the Turure should have led to selection for weakened antipredator behavior in guppy descendants studied in the 1990s.

Magurran and her colleagues sampled numerous sites in the Turure (Magurran et al., 1992; Shaw et al., 1992; Sievers et al., 2012). Genetic analysis suggested that the high-predation fish transferred from the Arima River back in 1957 had indeed spread all around the previously guppy-free site in the Turure River. More to the point, as a result of strong natural selection pressures, the descendants of the Arima River fish showed shoaling and predator inspection behaviors that were more similar to those of guppies at low-predation sites than they were to the behaviors of their ancestors from the dangerous sites in the Arima River. This sort of result has also been found in other transplant experiments that had examined shifts in morphology and life history (Reznick, 1996; Reznick et al., 1990; Figure 2.20).

Figure 2.20. Transplants and natural selection. One way to examine natural selection in the field is to do reciprocal transplant experiments, which reverse selection pressures. Here, some guppies from high-predation sites (with *C. alta*) are transplanted to low-predation sites, and vice versa. Over the course of several generations, as a result of new selection pressures, transplanted guppy populations converge on the characteristics of the fish in the populations into which they were transplanted.

Magurran's group uncovered another curious finding. In addition to colonizing the low-predation areas of the Turure River (located upstream, where there is weak predation), over the course of time the descendants of the Arima River fish moved downstream in the Turure River, back into areas of greater predation pressure. When tested, these fish showed antipredator behavior similar to that of their ancestors from the original high-predation site in the Arima River. One possible explanation is that the original colonizers spread fast, and since their antipredator behavior was beneficial when they reached high-predation sites in the Turure River, natural selection simply maintained such behavior. A more tantalizing, but to date untested, hypothesis is that the Arima River fish and their descendants colonized their new habitat at a much slower rate. If this were the case, natural selection may have shifted the colonizers and early descendants one way—toward the norm for low-predation sites—and then, later on, shifted the late descendants back in the opposite direction—toward the norm for fish from high-predation sites.

In addition to nicely illustrating how ethologists study the evolution of behavior, the guppy example illustrates that while natural selection may take hundreds of thousands of years to shape some traits, it can act much more quickly. Upstream and downstream guppy populations have been separated from one another for less than 10,000 years, yet as a result largely of differences in predation pressure, natural selection has produced significant differences in behavior in guppy populations over this fairly brief evolutionary time period (Endler, 1995). Indeed, both Magurran's and Reznick's work on transfer experiments demonstrates that natural selection can act on antipredator behavior in wild populations on the time scale of years to decades.

KINSHIP AND NAKED MOLE RAT BEHAVIOR

By definition, genetic relatives (siblings, parents and offspring, cousins, and so on) share copies of the same alleles. Because of this genetic similarity between kin, we expect natural selection to favor more cooperative and altruistic behavior among kin than among unrelated individuals. In fact, as discussed in chapter 9, the more related individuals are, the more we expect to see cooperative and altruistic behaviors (Hamilton, 1964). To see how genetic relatedness can effect the evolution of cooperative and altruistic behaviors, here we will look into the fascinating life of naked mole rats (*Heterocephalus glaber*; Figure 2.21).

Figure 2.21. Naked mole rats. Naked mole rats show very high within-colony relatedness. This maps nicely onto numerous cooperative and altruistic behaviors common to this species, such as digging tunnels, sweeping dirt or debris out of the tunnels, grooming the queen, or defending against predators. Here, workers are in the process of digging a tunnel. Naked mole rats use their sharp teeth to break up the dirt and then move it back through the tunnel to a worker that throws it out of the tunnel. *(Photo credit: Gregory G. Dimijian/Photo Researchers, Inc.)*

Few mammals have captured the fancy of both scientists and laypersons to the extent of the naked mole rat (Jarvis, 1981; Sherman et al., 1991). These small, hairless rodents of tropical Africa display **eusociality**, an extreme form of sociality that is present in many social insect groups (Table 2.3). Naked mole rats were the first vertebrates discovered to display the three characteristics associated with this extreme form of sociality, namely:

- A reproductive division of labor in which individuals in certain castes reproduce and individuals in other castes do not.
- Overlapping generations, such that individuals of different generations are alive at the same time.
- Communal care of young.

Table 2.3. The relationship between social behavior in naked mole rats and social insects. Comparisons between naked mole rats and eusocial insects indicate similarities in such characteristics as reproductive division of labor, overlapping generations, and communal care of young. *(From Lacey and Sherman, 1991)*

Species	SIMILARITIES TO NAKED MOLE RATS	DIFFERENCES FROM NAKED MOLE RATS
Paper wasp	Single breeding female per colony	All female workers
(*Polistes fuscatus*)	Aggressive domination of other colony members by reproductive female	Haplodiploid genetics
		New nests each spring
	No permanent sterility in subordinate foundresses	Outcrossing promoted by dispersal of reproductives from nest site
	Size-based subdivision of nonbreeding caste	Carnivore
	Similar colony sizes (20–100 workers)	
	Slightly larger size in queens than in workers	
Honeybee	Single breeding female per colony	All female workers
(*Apis mellifera*)	Colony reproduction by fissioning (swarming)	Haplodiploid genetics
	Change in behavior with age in nonreproductives	Primarily chemical, not behavioral, reproductive suppression of workers
	Slightly larger size in queens than in workers	Permanently “sterile” nonreproductive females
		Vastly larger colonies in honeybees
		Outcrossing promoted by aerial mating aggregations
		Nectarivore
Wood termite(*Kalotermes flavicollis*)	Single breeding female per colony	Chemical, not behavioral, reproductive suppression
	Diploid genetics	Vastly larger colonies in termites
	Male and female workers	Queens many times larger than workers

Species	SIMILARITIES TO NAKED MOLE RATS	DIFFERENCES FROM NAKED MOLE RATS
	Delayed caste determination	Outcrossing promoted by aerial mating aggregations
	Division of labor among nonbreeders	
	Extremely long life of reproductives	
	Diet of plant material; breakdown of cellulose by gut endosymbionts	
	Eating of feces	
	Opportunity for workers to become reproductive	
	Working behavior begins before adulthood	

Naked mole rats are the longest-living rodent species, and their genome has recently been sequenced, shedding light on their longevity (Kim et al., 2011). They live in large groups in which a *queen* and between one and three males are the only individuals that mate and reproduce in the entire colony. Although within-colony aggression occurs, cooperative behavior is much more common (Reeve, 1992; Reeve and Sherman, 1991; Stankowich and Sherman, 2002). Nonreproductive male and female naked mole rats, which live much shorter lives than reproductive individuals, undertake a wide variety of cooperative behaviors, such as digging new tunnels for the colony, sweeping debris, grooming the queen, and defending against predators (Lacey and Sherman, 1991; Pepper et al., 1991). But why do individuals yield exclusive reproduction to a single queen and a few males, as well as work for the colony? How could natural selection have favored such behaviors? The answer in part centers on the high genetic relatedness between individuals within naked mole rat colonies.

Because kinship theory suggests that the more genetically related individuals are, the more cooperation they will show with each other, Hudson Kern Reeve and his colleagues hypothesized that naked mole rats are very cooperative with others in their colony, in part because they are close genetic relatives (Reeve et al., 1990).

To test this idea, Reeve's group sampled the DNA of fifty naked mole rats and then employed a molecular technique called DNA fingerprinting to examine the genetic relatedness among colony members (DeSalle and Schierwater, 1998; Jeffreys et al., 1985). Using DNA from liver, muscle, and brain samples, they created three DNA "probes" to isolate three distinct DNA fragments for each mole rat. These probes produced a series of prominent black bands (consisting of between 1.6 and 1.8 kilobytes of DNA). Individuals had an average of about twenty-nine such distinct bands, and these bands together represented the **DNA fingerprint** of that mole rat. DNA fingerprints of different individuals could then be compared—the more closely the bands matched up, the more closely related were the individuals (Reeve et al., 1992).

Reeve and his colleagues found that because of very high levels of inbreeding—a result of mating between relatives—the average genetic relatedness in their colonies of naked mole rats was extremely high, as predicted by kinship theory (see Braude, 2000, for an alternative view). The exact value they came up with was an average relatedness of 0.81 within naked mole rat colonies. To put this number in context, unrelated individuals have a value of 0 for this indicator, siblings score (on average) 0.5, and the most related of all individuals, identical twins, score 1.0 (Figure 2.22). Thus, naked mole rat individuals, on average, fall between normal siblings and identical twins on a relatedness scale, and they even lean toward the identical twins' side of the equation. The cooperative and altruistic behavioral adaptations seen in naked mole rats are then largely driven by the high degree of genetic relatedness seen within colonies.

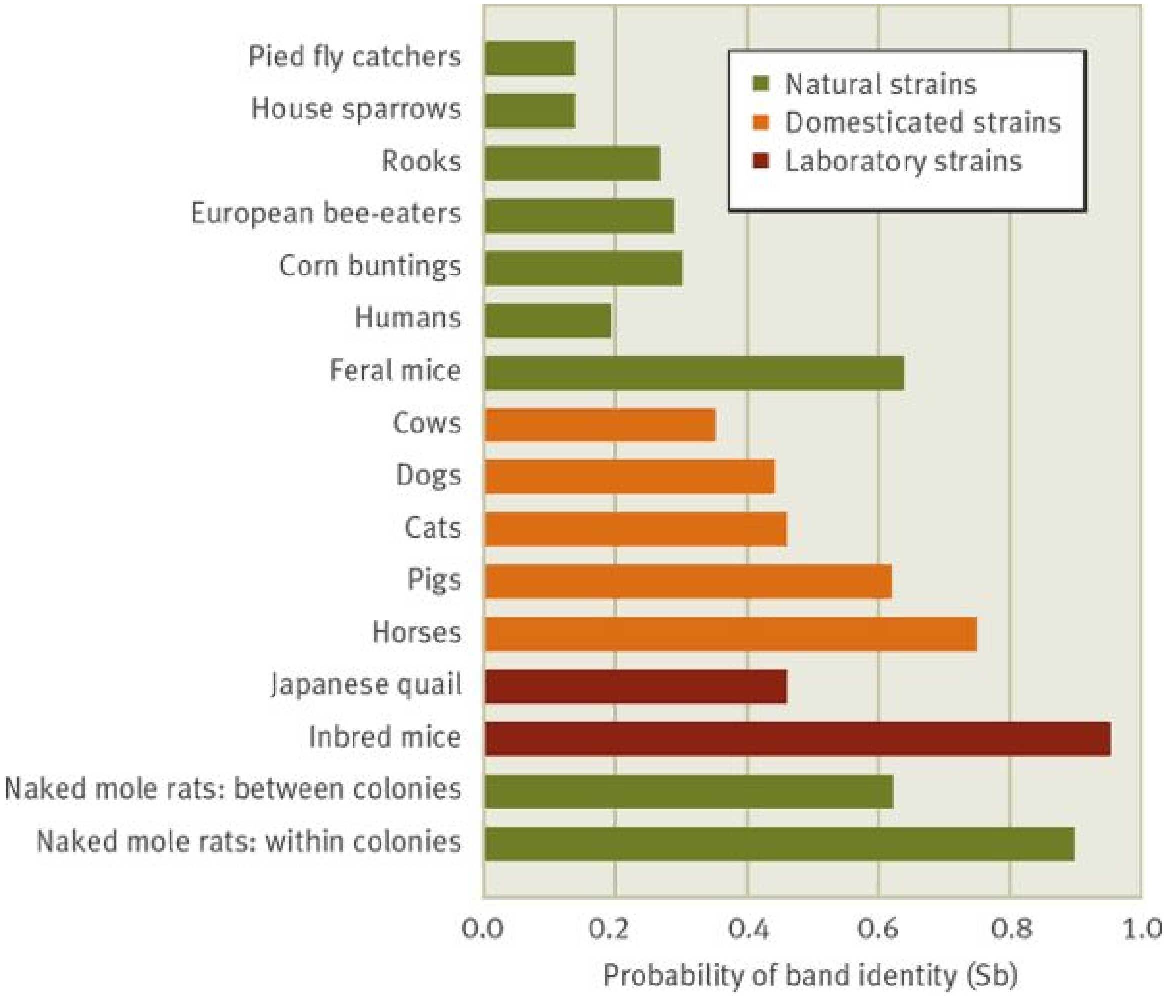

Figure 2.22. Naked mole rats show high levels of genetic relatedness. Naked mole rats in a colony are more genetically related to one another than any non-inbred strain of animal known. *(From Reeve et al., 1990)*

Phylogeny and the Study of Animal Behavior

In *On the Origin of Species*, Darwin summarized his ideas on evolution in “two great laws” that centered on (1) conditions of existence, and (2) common ancestry. When Darwin spoke of the “conditions of existence,” he meant the living (biotic) and nonliving (abiotic) environment that sets the stage on which natural selection operates. The effect that a given variant of a trait has on reproductive success is not absolute, but depends on the environment in which an organism finds itself—on the conditions of existence. The first part of this chapter has been devoted to examining animal behavior and natural selection. Here we turn to Darwin’s other great law—common ancestry—as it applies to the study of ethology.

PHYLOGENETIC TREES

To study common ancestry, evolutionary biologists construct phylogenetic trees, which depict the evolutionary history of a group of species, genera, families, and so forth. These trees graphically depict the phylogeny of the groups of organisms in question. The term “phylogeny” was first introduced by a German contemporary of Darwin, Ernst Haeckel, who was deeply involved in disseminating ideas on evolution throughout Europe. Although Darwin himself did not use the word *phylogeny* until the fifth edition of *On the Origin of Species*, he was clearly thinking about phylogenetic trees as early as 1837, twenty-two years before the publication of the first edition (Dayrat, 2005). Figure 2.24A depicts a hypothetical tree that Darwin included as the *only* figure in the first edition of *On the Origin of Species*. Figure 2.24B shows one of the first sketches of a phylogenetic tree from Darwin’s early notebooks.

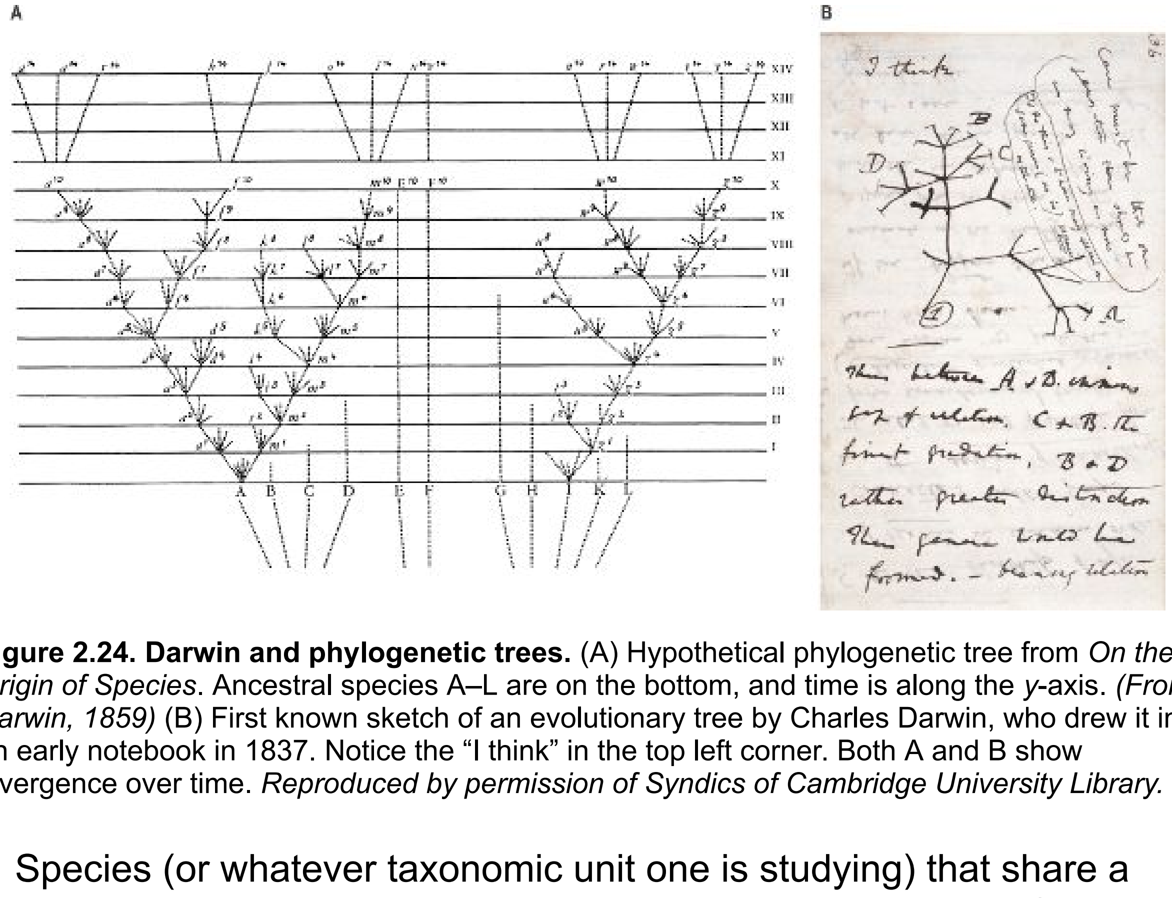

Figure 2.24. Darwin and phylogenetic trees. (A) Hypothetical phylogenetic tree from *On the Origin of Species*. Ancestral species A–L are on the bottom, and time is along the *y*-axis. *(From Darwin, 1859)* (B) First known sketch of an evolutionary tree by Charles Darwin, who drew it in an early notebook in 1837. Notice the “I think” in the top left corner. Both A and B show divergence over time. *Reproduced by permission of Syndics of Cambridge University Library.*

Species (or whatever taxonomic unit one is studying) that share a recent common ancestor tend to have many traits in common for the very reason that they share a common ancestor. For Darwin, common ancestry was important because it helped explain “that fundamental agreement in structure which we see in organic beings in the same class, and which is quite independent of their habits of life” (Darwin, 1859). For example, from an ethological perspective, suppose that squirrel species 2 and squirrel species 3 descended from a recent common ancestor, squirrel species 1. If species 2 and 3 display the same set of antipredator behaviors, one possible reason—but not the only possible reason—for this similarity is that both species 2 and 3 possess this suite of traits because their common ancestor, species 1, possessed it.

Reading a Phylogenetic Tree

The tree shown in Figure 2.25 depicts the evolutionary relationships among vertebrates. In this figure, each branch tip represents a group of related organisms or taxa—birds, crocodilians, mammals, and so on. Figure 2.25 illustrates two different ways of showing the same information: on the left side, the phylogeny is drawn in *tree format*; on the right side, the same phylogeny is illustrated in a slanting structure known as *ladder format* (Novick and Catley, 2007). These two ways of drawing a phylogeny are interchangeable. The orientation of the tree *does not matter*: phylogenetic trees can be drawn with the root at the left and the branch tips at the right or, equivalently, with the root at the bottom and the branch tips at the top—it makes no difference to the meaning of the tree.

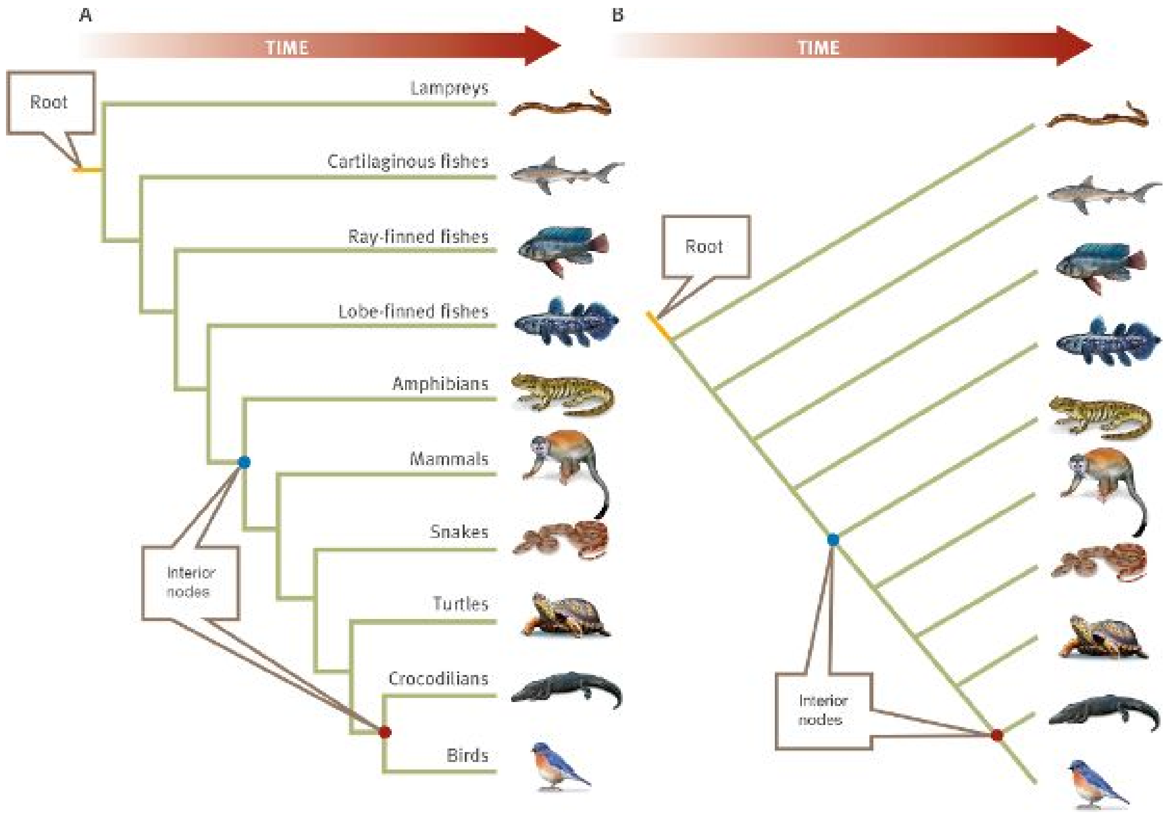

Figure 2.25. Two ways of drawing a phylogeny. The two phylogenies of the vertebrates shown illustrate exactly the same information. The phylogeny on the left (A) is referred to as a *tree* representation; the one on the right (B) is termed a *ladder* representation. In each, time flows from left (older) to right (more recent), so that the branch tips at the right represent current groups, whereas the *interior nodes* (nodes on the inner section of the tree) represent ancestral populations. The red dot indicates the common ancestor of birds and crocodilians, whereas the blue dot indicates the common ancestor to all tetrapods. The yellow line segment is the root of the tree. *(From Bergstrom and Dugatkin, 2012)*

The points where a tree splits—the **nodes**—represent common ancestors to the groups that come after the splitting or branching point. All branch tips arising from a given branching point are descendants of the common ancestor at that branching point. For example, a red dot highlights the node representing the common ancestor to birds and crocodilians, and a blue dot indicates the common ancestor to all tetrapods. Notice that the hypothesized common ancestor to tetrapods would not have been identical to any currently living tetrapod. Rather, evolutionary change has occurred along every branch leading from this ancestor to the species we currently observe on earth.

Box 2.4. COGNITIVE CONNECTION

Tool Use in New Caledonian Crows

Historically, the study of “cognitively sophisticated” behaviors in nonhumans has followed a pattern: we want to think of ourselves as unique, somehow separate from all other animals, and so we search for things that we see as being “uniquely human.” We then build a “humans only” fence around these traits—tool use, culture, etc.—and as a result very few researchers look for these phenomena in nonhumans. Eventually, a few people stumble upon examples of this “uniquely human” behavior, whatever it is, in nonhumans, thereby breaking this loop, and we begin to remember what evolutionary biologists since Darwin have been saying; namely, that many complex traits are found, albeit in different and sometimes more rudimentary forms, across the animal kingdom.

Tool use provides a nice example of this. During the “uniquely human” phase of thinking about tool use we tended to equate tools with wheels, gears, pulleys, and the like. If that is going to be our criteria for tool use, it will likely be something we see in no other species. But there is no conceptual reason to limit tool use to this: it just so happens that wheels, gears, and pulleys are central to human tool use. More generally, tools are things manipulated and crafted to serve some function. This more general meaning does not, a priori, make it impossible for nonhumans to craft and use tools. Stripping a branch bare, so it can be used to probe a termite mound, as we see in many chimpanzee populations, is creating a tool. And chimps are not the only nonhumans to use tools.

New Caledonia crows (*Corvus moneduloides*) extract prey from under tree bark using tools constructed from twigs and leaves, often from the *Pandanus* shrubs and trees, whose leaves have small sharp barbs running along their edges (Rutz and St. Clair, 2013; Hunt, 2014). Their tool making has even been captured by a series of “crow cams” placed into their environment (Trosianko and Rutz, 2016). When prey react and grab the inserted twig or leaf, the crows pull it out, then feed on the prey or give them to offspring. Crows learn to make these tools during their first two years of life by watching older toolmakers. Novice toolmakers begin by constructing simple tools—twigs from which they simply strip leaves (like chimpanzees do)—and as they mature, they start to build more complex tools, such as twigs with hooks on their ends (Figure 2.23). This involves choosing a branch that is forked into two branches, and biting one of the branches off right above the base of the fork, so that the remaining branch now has a small “v” at the end, after which they whittle the v with their bills, sharpening it in the process. Remarkably, they also safeguard their best and favorite tools to reuse (Klump et al., 2015).

Figure 2.23. **Avian toolmakers.** (A) New Caledonian crows shape complex tools from twigs. Here we see a crow holding a “crochet” tool with a hook at the end. From Hunt et al., 2001. Reprinted by permission from Macmillan Publishers Ltd. © 2001. (B) A Pandanus leaf from which a tool was made. *(From Hunt, 2014)*

Gavin Hunt has found an interesting similarity between tool use in humans and New Caledonian crows. Most human tools have been made for the right hand. Until Hunt’s work, there was no evidence of handedness in animal tool making, but he found that New Caledonian crows remove their tools-to-be preferentially from the left edges of leaves (Hunt, 2000; Hunt et al., 2001). This is not due to the structure of the leaf or its positioning on the tree, but instead is due to the crows primarily using their right eye and the right side of their bill to make tools.

Why crows have evolved their complex tool-making expertise is the subject of much discussion and active research. One hypothesis is that a combination of low competition from other birds for food and low predation rates provide New Caledonian crows time to experiment with tools, and the relatively very long developmental period of these birds offers youngsters ample opportunity to learn the skills from their parents and other adults.

At the base of the tree, in yellow, is the **root**—the common lineage from which all species indicated on a tree are derived. To find the most recent common ancestor of two or more species, trace backward along the tree until the branches leading to these species converge. Figure 2.26 illustrates this process.

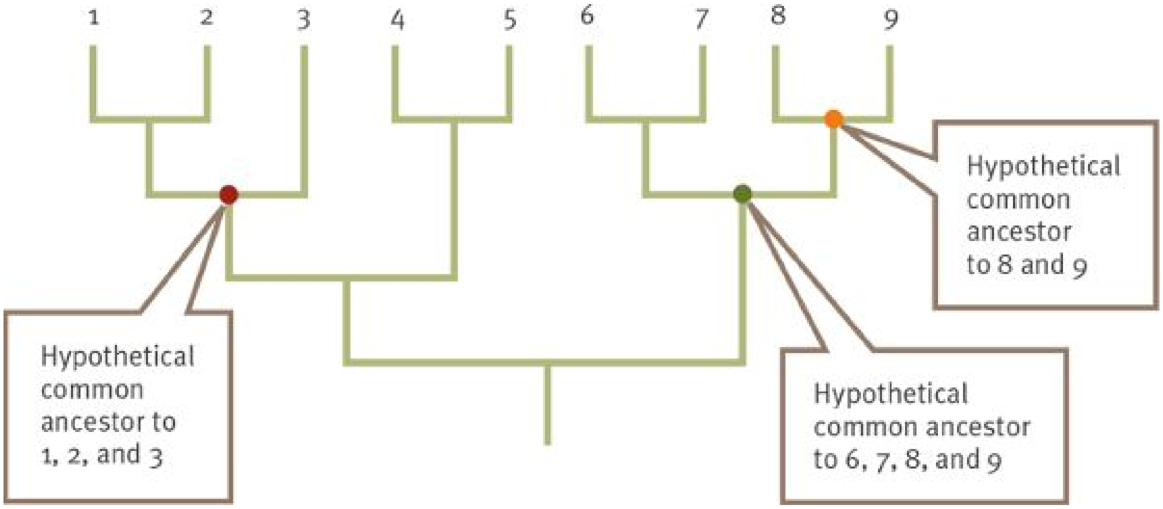

Figure 2.26. Finding common ancestors on a tree. Finding the common ancestor for a group involves tracing backward in time. Follow the dashed lines to see the common ancestors of different groups in this phylogeny. *(From Bergstrom and Dugatkin, 2012)*

Building a Phylogenetic Tree

The first step in building a phylogenetic tree is to measure some set of traits, often referred to as characters, in the organisms under study. Traits can, for example, be structural, developmental (embryological), molecular, or behavioral. Or a trait can instead be a measure of a number of related structures, such as jaw shape, the relative position of a group of bones, and so forth.

Until the molecular revolution of the 1970s, almost all trait measurements were morphological or anatomical—bone length, tooth shape, and so on—and many of them were gathered from fossil evidence. With the advent of molecular genetics, many “traits” measured today are DNA sequences, sometimes whole genomic sequences, and evolutionary biologists can use these molecular genetic maps to build phylogenies by comparing and contrasting sequences across different species.

Not all traits are equally valuable in constructing phylogenies. To understand why, we need to distinguish between two basic types of traits—homologies and homoplasies. A **homology** is a trait shared by two or more species because they share a common ancestor. For example, all female mammals produce milk for their young, and they all possess this homologous trait because mammals share a common ancestor that produced milk.

A **homoplasy** is a trait that is shared between two or more species, not because they share a common ancestor, but natural selection has acted independently on each species. A classic example of a homoplasy is the wings of birds, mammals (for example, bats), and insects (Figure 2.27). Superficially, wings found in these different groups are constructed in a similar manner, but not because wings were present in a common ancestor of birds, mammals, and insects. In the case of wings, natural selection pressures in the three taxa were similar enough that an appendage associated with flight would have some of the same basic characteristics. Such homoplasies—the result of shared natural selection pressure—are also referred to as **analogies**, and the process leading to the production of analogous traits is called **convergent evolution**.

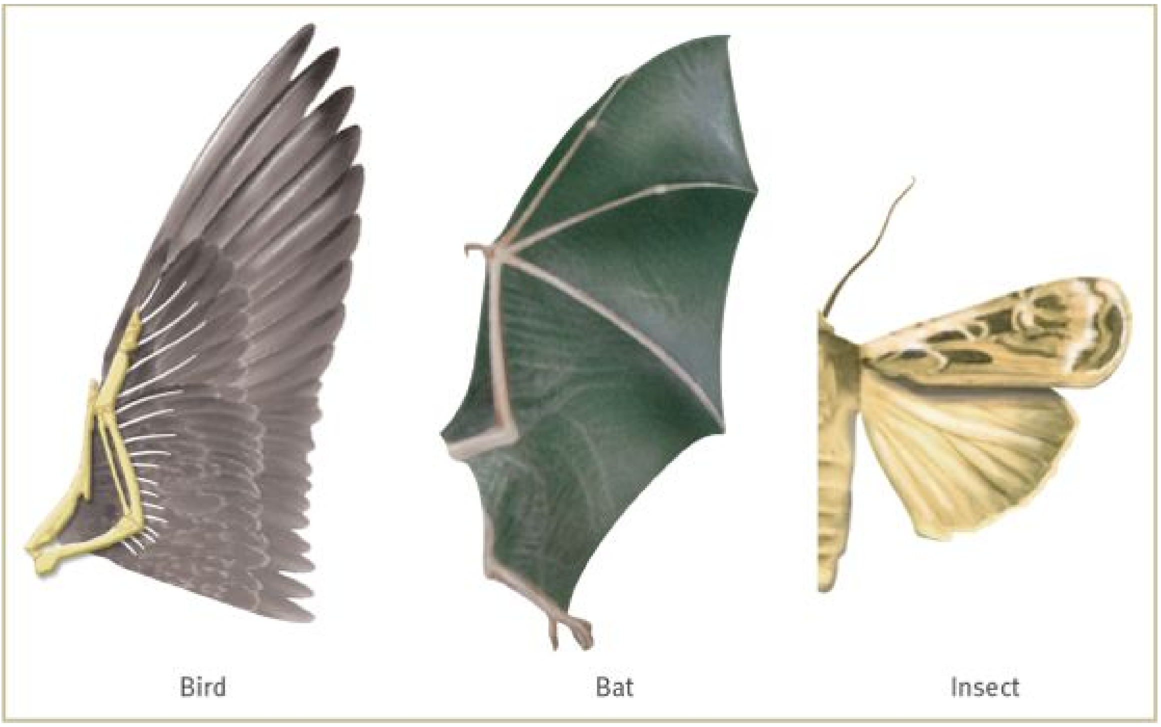

Figure 2.27. Convergent evolution in wing structure. Convergent evolution has led to wings in birds, bats, and insects. Wings in these groups are a homoplasy—an analogous trait.

Homologous traits are used in phylogeny building because they reflect shared evolutionary histories. Homoplasies, on the other hand, while they do shed light on natural selection, do not reflect the historical relationships between species and, in fact, distort and misrepresent these relationships when used in phylogenetic tree building. Ideally, evolutionary biologists would like to be able to build phylogenetic trees by including homologies but eliminating homoplasies, and they have developed many techniques for distinguishing between these two types of traits (Bergstrom and Dugatkin, 2016).

When constructing phylogenetic trees, we need a method to ascertain which varieties of a trait appeared first—that is, which are ancestral—and which varieties are derived from these ancestral states. When we study the historic order in which different varieties of a trait appear, we are examining what is referred to as **polarity**, or the direction of historical change in a trait.

Evolutionary biologists have many ways for determining polarity, including using the fossil record in conjunction with techniques for dating fossils. Indeed, for most of the history of evolutionary biology, the fossil record was the primary source for adding a temporal component to phylogenetic trees. The oldest state of a trait found in the fossil record is assumed to represent the oldest true state—what is called the ancestral or primitive state of the trait.

Today, molecular genetic data can be used to help date major changes that occur on phylogenetic trees. To do so, DNA sequences from different species are compared against one another at the nucleotide level. Complex mathematical models that include an estimate of the rate of molecular genetic change can then be used to calculate the amount of time that would be required to produce the nucleotide differences we have measured. In essence, even in the absence of information from the fossil record, these molecular genetic data allow us to work backward from extant (present-day) species to build and date phylogenetic trees.

When evolutionary biologists use the techniques described above, they often end up with many possible phylogenetic trees, each of which *might* represent the true phylogenetic history of the taxa they are studying. But, of course, there is only one actual phylogenetic history for any taxon, so we need a method for distinguishing between candidate trees. Researchers have developed a number of techniques to handle the problem of distinguishing between possible phylogenetic trees (Felsenstein, 2004; Hillis et al., 1992). The most common of these techniques is **parsimony analysis**. The concept of parsimony is most often associated with the ideas of a fourteenth-century philosopher named William of Ockam (sometimes spelled Occam), who argued that “entities are not to be multiplied beyond necessity.” This is now referred to as Ockam’s razor, and within evolutionary biology it has been taken to mean that the phylogenetic tree that requires the least number of evolutionary changes is the most likely to be correct.

Every phylogenetic tree is a *hypothesis* of the evolutionary history of the groups under study. When two different types of analyses (for example, morphological and molecular genetic) produce similar phylogenetic trees, our confidence increases that our phylogenetic tree is correct. In addition, as more morphological, molecular genetic, and fossil evidence is uncovered in the future, we can examine whether the new data are consistent with our phylogenetic tree. If they are, we gain confidence that our tree accurately reflects the evolutionary history of the taxa we are studying.

Phylogeny and Independent Contrasts

Ethologists use phylogenetic trees in many ways. In some cases, phylogenies are built from behavioral data, but this is relatively rare. A second, more common way for ethologists to use phylogenetic trees is to find an already established phylogenetic tree for the taxa and then to superimpose the behavioral data they have—let’s say data on mating systems—onto the phylogenetic tree to examine the evolutionary history of mating systems. Then, animal behaviorists can ask questions such as: Which of the mating systems seen today are derived? Which are ancestral? For example, employing parsimony analysis we can use statistical techniques to calculate which ancestral state (of mating system) would require the fewest number of evolutionary changes to produce the mating systems that we see in our extant species. These calculations help them make inferences about the mating systems of species that predated those they are studying, even if they are extinct.

Ethologists can also use existing phylogenetic trees to make inferences about natural selection. Once we know something about the phylogenetic history of the group we are studying, we can ask whether certain selection pressures consistently favor one combination of traits or another *independent of phylogenetic history*, or whether the co-occurrence of the traits in certain species is the result of a common ancestry for those species. Imagine we are interested in understanding whether natural selection consistently favors organisms that display both nocturnal activity and an arboreal (tree-based) lifestyle

(Felsenstein, 2004). We can address this question by collecting information on both of these traits in a number of species and using the **comparative method**. Suppose we find the pattern of characters shown in Figure 2.28. At first glance, this figure appears to offer strong support for the hypothesis that nocturnal and arboreal lifestyles go hand in hand. One interpretation here would be that natural selection has independently favored this combination of traits, over and over.

Figure 2.28. Relationship between nocturnal and arboreal behavior in ten species. Nocturnal is shaded in red, diurnal in orange, arboreal in green, and terrestrial in yellow. Nocturnal and arboreal co-occur often, as do diurnal and terrestrial. *(Adapted from Feselstein, 2004)*

But there is a problem here, in that we are not accounting for any shared evolutionary history among these species. What if we discover that the phylogenetic history of these species is as depicted in Figure 2.29A? From this phylogeny, we can infer the evolutionary changes that most likely gave rise to the characters we observe. This is shown in Figure 2.29B. With this information in hand, we might take a different view of the character pattern that we have observed. Rather than natural selection favoring a pairing of nocturnal and arboreal habits in ten independent cases, the entire pattern has likely arisen from a *single pair* of evolutionary changes, one for the diurnal/nocturnal trait and one for the arboreal/terrestrial trait.

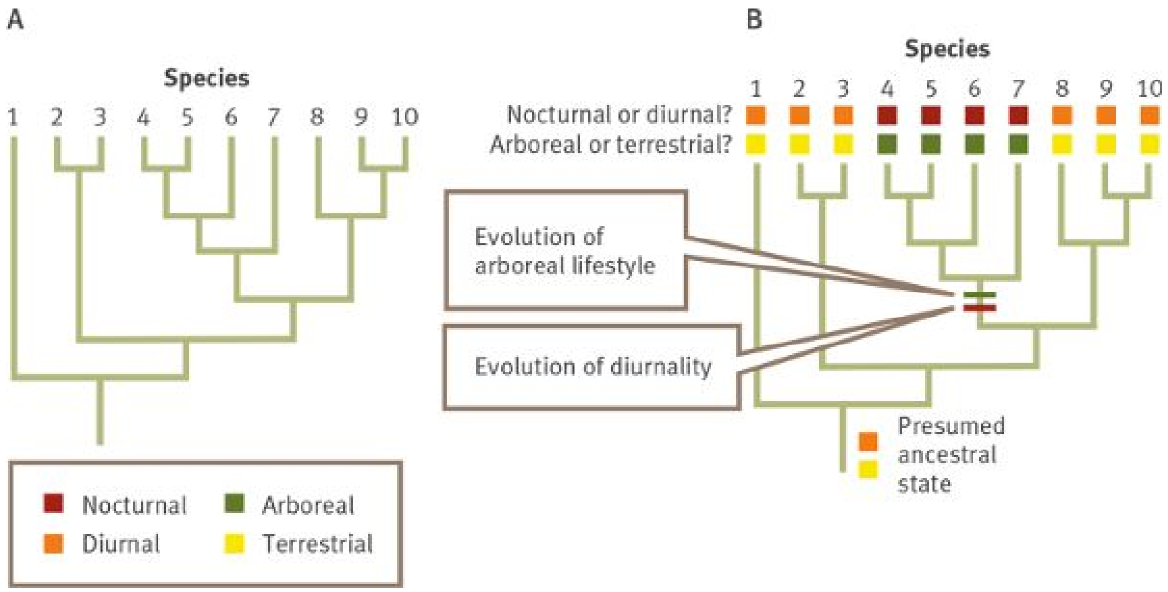

Figure 2.29. Relationship between nocturnal and arboreal behavior is not independently favored in different lineages. (A) The phylogenetic relationships among the ten species. (B) Nocturnal behavior and arboreal behavior evolved just one time each along one branch of our tree. *(Adapted from Feselstein, 2004)*

To further delve into how using analyses that correct for shared phylogenetic history can be used to show how natural selection has shaped animal behavior, consider this interesting fact: there is a huge amount of variation in how much time animals spend sleeping, or more specifically, how much time they spend in both REM (rapid eye motion) and non-REM sleep. Donkeys sleep, on average, 3.8 hours per day, chimpanzees 9.7 hours per day, and armadillos a remarkable 20 hours per day (Figure 2.30).

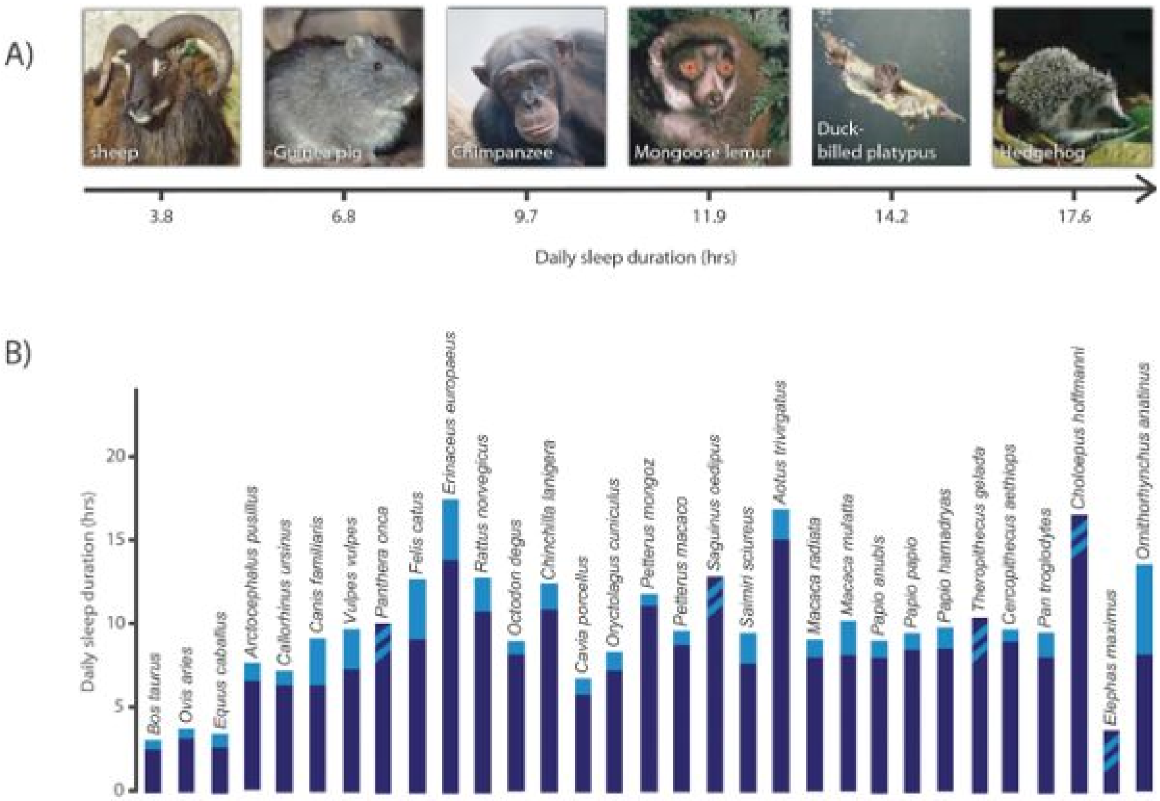

Figure 2.30. **Sleep across mammals.** (A) A few examples of the number of hours spent sleeping each day. (B) A taxonomic representation of sleep patterns across mammals. REM = rapid eye motion, NREM = non–rapid eye motion. *(From Preston et al., 2009)*

What explains such dramatic differences in sleep across species? It was once thought that sleep correlates positively with body size, but an analysis that corrected for shared phylogenetic history showed that the data do not support this idea (if anything the correlation is negative). Some researchers have proposed that sleep is linked to cognitive functions associated with learning and memory, in particular with what is known as "memory consolidation," yet some studies find that adult brain mass does not correlate with sleep when shared phylogenetic history is taken into account (Capellini et al., 2008).

While variation in adult brain mass does not explain variation in sleep, Isabella Capellini, Charles Nunn, and their colleagues suggested that sleep may still be linked to cognitive function, but in a more nuanced way. Adult brain mass is a coarse measure of any cognitive function—one that ignores the fact that some *regions* of the brain are associated with learning and memory across species. In particular, in mammals, the amygdala, neocortex, and hippocampus have been found to be involved in memory consolidation (Sterpenich et al., 2007; Pare et al., 2003; Buzsaki, 1998). Capellini et al.'s analysis, correcting for shared phylogenetic history of more than a dozen species of mammals, found no evidence for correlation between these brains and REM sleep, but a positive correlation between relative amygdala size and non-REM sleep. While much work remains to be done on any positive relationship between cognitive function and sleep, this study provides some evidence for this link in mammals (Capellini et al., 2008; Figure 2.31).

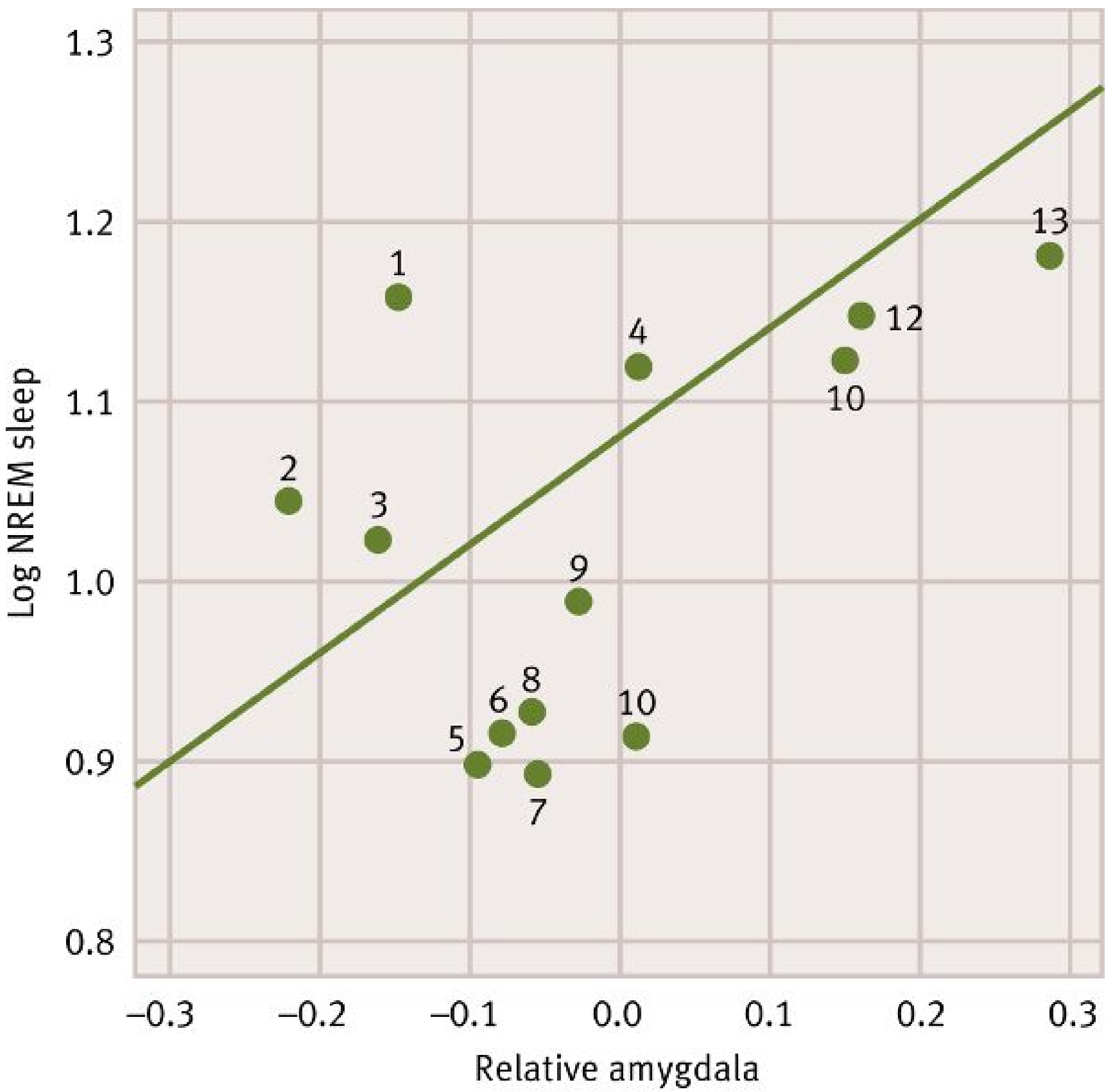

Figure 2.31. **Amygdala size and non-REM sleep in mammals.** Relative amygdala size helps explain some of the variance seen in 13 different species of mammals. (1) *Microcebus murinus*, (2) *Rattus norvegicus*, (3) *Nannospalax ehrenbergi*, (4) *Tupaia glis*, (5) *Callithrix jacchus*, (6) *Pan troglodytes*, (7) *Saimiri sciureus*, (8) *Papio hamadryas*, (9) *Erythrocebus patas*, (10) *Macaca mulatta*, (11) *Tenrec ecaudatus*, (12) *Erinaceus europaeus*, (13) *Aotus trivirgatus*. *(From Capellini et al., 2009)*

While variation in amygdala size may help explain some of the variance in sleep in mammals, other factors may also play a role, perhaps a large role, in helping us understand the evolution of sleep. One hint regarding this comes from clinical work that has found that sleep may strengthen the immune system, perhaps because energy that is invested in our activities when we are awake can be diverted to boost the immune system during sleep (Preston et al., 2009). For example, clinical studies have found that infected rabbits who sleep longer recover more quickly, infected rats that are sleep deprived suffer more severe symptoms, and our own antibody responses are compromised when we are sleep deprived (Bryant et al., 2004; Lange et al., 2003; Toth, 1995; Toth et al., 1993; Spiegel et al., 2002) .

Using published data on twenty-six mammalian species, Brian Preston, Charles Nunn, and their team examined the hypothesis that sleep strengthens the immune system, employing the number white blood cell as a measure of the strength of the immune system. White blood cells are produced in bone marrow, as are red blood cells and platelets. But while white blood cells are directly involved in immune system function, red blood cells and platelets are not, and so Nunn et al. used the latter two types of cells as controls, hypothesizing that after accounting for shared phylogenetic history (and a number of other variables such as body size), white blood cell count and sleep would be positively correlated, while red blood cell and platelet count and sleep would not be. Their analyses found just that pattern (Figure 2.32A, new). Follow-up analyses found support for the positive relationship between immune system and sleep for four of the five other immune cell types they examined.

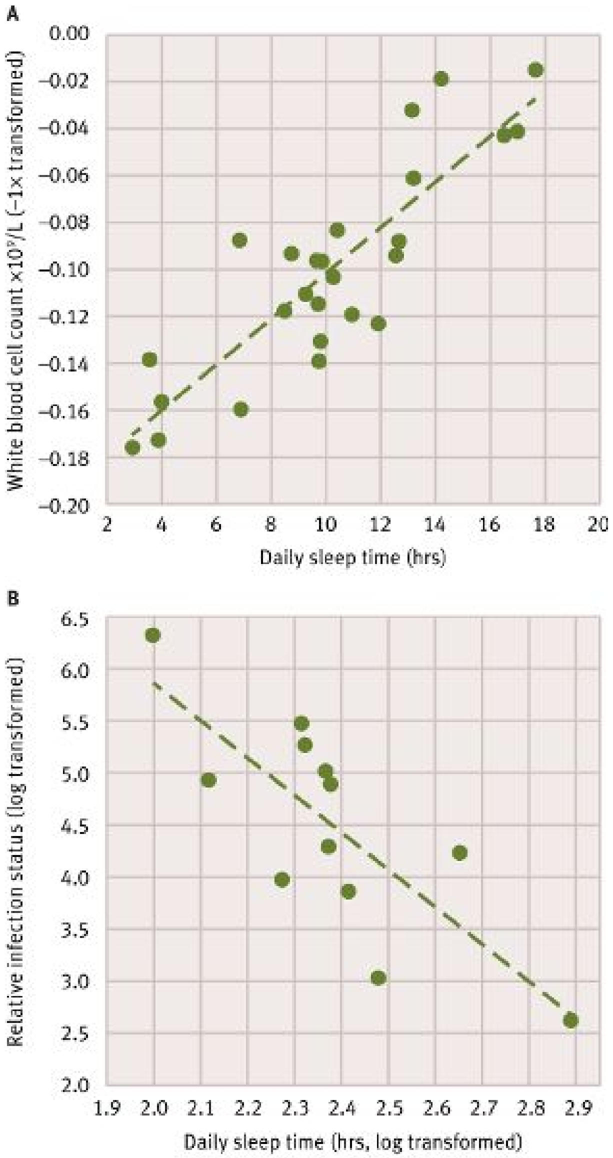

Figure 2.32. **Sleep, the immune system and parasites.** (A) A positive correlation was found between sleep duration and white blood cell count in 26 mammalian species. (B) A negative correlation was found between sleep duration and parasite load (in 12 mammalian species). *(From Preston et al., 2009)*

Nunn's team next addressed an even more specific hypothesis relating to sleep and immune system responses: that species that slept longer would have reduced parasite loads (via the direct and indirect effects of immune system responses). Their analyses, again accounting for shared phylogenetic history, found strong evidence for such a relationship (Preston et al., 2009) (Figure 2.32B).

PHYLOGENY AND PARENTAL CARE

Ethologists often use phylogenetic analysis to reconstruct the order in which a suite of behaviors has appeared over evolutionary time. For example, consider parental care behavior. At the most basic **level**, there are four “states” of parental care systems in animals: no parental care, maternal care, paternal care, and biparental (maternal and paternal) care. In what historical order, if any, do these forms of parental care most often appear? If we assume that no parental care is the primitive, or original, state in the taxa we are studying, do we most often see maternal care appear next? Paternal care? Biparental care?

Early theories on the order in which parental care systems evolve focused on fish and anuran frogs (Gross and Sargent, 1985). These analyses suggested a “stepping-stone” model in which parental care appeared in the following order: no parental care, paternal care, biparental care, and finally maternal care (as a consequence of male desertion). The sample size for these analyses, however, was relatively small, and subsequent studies in the same groups produced contradictory results (N. B. Goodwin et al., 1998; Summers et al., 1999).

Box 2.5. SCIENCE AT WORK

What is the research question? Why do we see so much variation in sleep duration across mammals?

Why is this an important question? We spend about one-third of our lives asleep. Chimps sleep a bit more. Armadillos spend more than 80% of their time sleeping. Explaining the variation in this sleep will shed light on how natural selection acts on a large chunk of how animals spend their time.

What approach was taken to address the research question? Large scale comparative analyses were made on sleep behavior and other variables on from 12 to 26 mammalian species. These comparisons took into account shared phylogenetic history and searched for what best explained the variation observed in sleep.

What was discovered? Some evidence was found that variation in size of the amygdala was positively correlated with variation in sleep duration, suggesting that sleep may help consolidate memory. Stronger evidence was uncovered that the sleep duration correlated positively with white blood cell count.

What do the results mean? Variation in size of the amygdala, which plays an important role in many cognitive functions, suggests that sleep may help consolidate memory. That variation in white cell count was positively correlated with sleep duration suggests that sleep boosts the strength of the immune system.

To better address the order in which parental care systems typically evolve—if such an order exists—we need to work with a large group of species. Ideally we would use a group in which we see each variety of parental care many times, and one in which we have good information on the phylogenetic relationship between species. One such group is the ray-finned fish (the *Actinopterygii*), which contains about 400 families of fish, made up of over 20,000 species (Figure 2.33). Ray-finned fish make up more than one-half of all known vertebrate species, and include the group most often studied by ethologists—the bony fish, or teleosts.

Figure 2.33. Parental care in fish. Different types of parental care (maternal care, paternal care, both maternal and paternal care, and so on) have been uncovered in ray-finned fish. Here we see a male clown anemonefish tending the eggs laid by its mate. This fish shows the bright coloration and paternal care often found in species with external fertilization. *(Photo credit: Fred Bavendam/Minden Pictures)*

To begin their phylogenetic study of parental care in ray-finned fish, Judith Mank and her colleagues first used already published morphological data and molecular genetic data to build a phylogenetic tree of 224 families of ray-finned fish, and then examined the evidence for parental care in these various families (Mank et al., 2005). That is, their phylogenetic tree was not built using data on parental care behavior—instead, inferences about the evolution of parental care were made based on the tree Mank and her colleagues built using morphological and molecular genetic data. They began by categorizing the species in their phylogenetic tree by using published data on parental care—no parental care, maternal care, paternal care, or biparental care—and then they examined the order in which these systems appeared over evolutionary time. Parental care was found in approximately 30 percent of the families of ray-finned fish analyzed by Mank and her colleagues. In external breeders, parental care was found in 25 percent of the families studied. For internally fertilizing fish, parental care was found in 90 percent of the families analyzed.

Mank and her colleagues found that in ray-finned fish paternal care evolved on twenty-two independent occasions—in other words, there were twenty-two independent occurrences of a shift from “no parental care” in an ancestral species to paternal care in a descendant species. Maternal care and biparental care also evolved independently numerous times within the ray-finned fish (Figure 2.34). No evidence, however, was found for the stepping-stone model described earlier. Indeed, aside from the fact that paternal care was the most likely evolutionary state to emerge from no parental care, no clear ordering of parental care systems was found. Instead, what phylogenetic analyses found was evidence for multiple origins of all parental care systems (particularly paternal care), as well as some fascinating evolutionary relationships between parental care, nesting behavior, mode of fertilization (external or internal), and male coloration pattern.

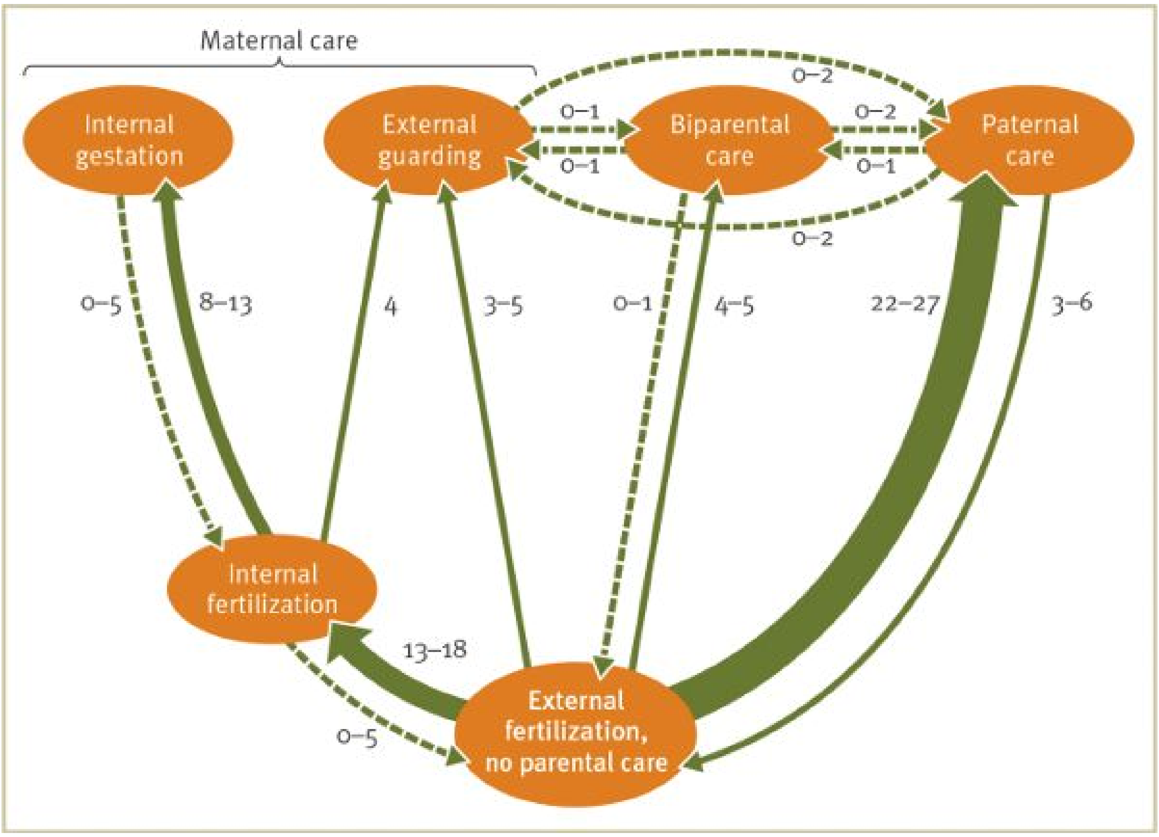

Figure 2.34. The evolution of parental care in ray-finned fish. Thickness of the arrows reflects relative numbers of evolutionary transitions (numerals near arrows indicate the estimated range of the number of transitions). Dashed arrows indicate cases in which transitions are unclear. *(From Mank et al., 2005)*

PHYLOGENY AND COURTSHIP BEHAVIOR

Though adaptationist and phylogenetic studies have historically been conducted by different groups of researchers, the two types of studies can complement each other, and together they provide a deep understanding of the evolution of behavior. Consider male mating behavior in the Poeciliidae, a family of fish composed of live bearers (females give birth to live young).

Males use two very different types of mating strategies. In some species, males have bright coloration (a type of sexual ornament) and display vigorously to females. If a female is receptive, the male and female mate, which involves the male inserting his gonopodium into a female and inseminating her. In other species, males tend to have drabber coloration and rely primarily on what is known as gonopodial thrusting, which involves a male approaching a female from behind and mating by inserting his gonopodium into the female.

From a phylogenetic perspective, which male strategy is the ancestral (primitive) mating strategy in Poeciliidae males, and which is the derived mating strategy? To address this question, Angelo Bisazza and his colleagues built a phylogeny of a part of the family Poeciliidae using sequences from a mitochondrial rRNA gene. They then mapped male mating strategy onto their phylogeny.

What they found was that in the groups they examined, gonadapodial thrusting was the ancestral (primitive) state in Poeciliidae, including the guppy. In Poeciliidae, courtship is derived from the primitive gonopodial thrusting state (Figure 2.35). Part of the power of this sort of phylogenetic analysis is that adaptationist methodology can then be employed to address what sort of selective pressures might have favored both courtship and sexual ornamentation in guppies. Much research has been done on this question, and in conjunction with the phylogenetic studies it is providing us with a rich and detailed picture of the evolution of mating in live-bearing fish (Houde, 1997; Magurran, 2005).

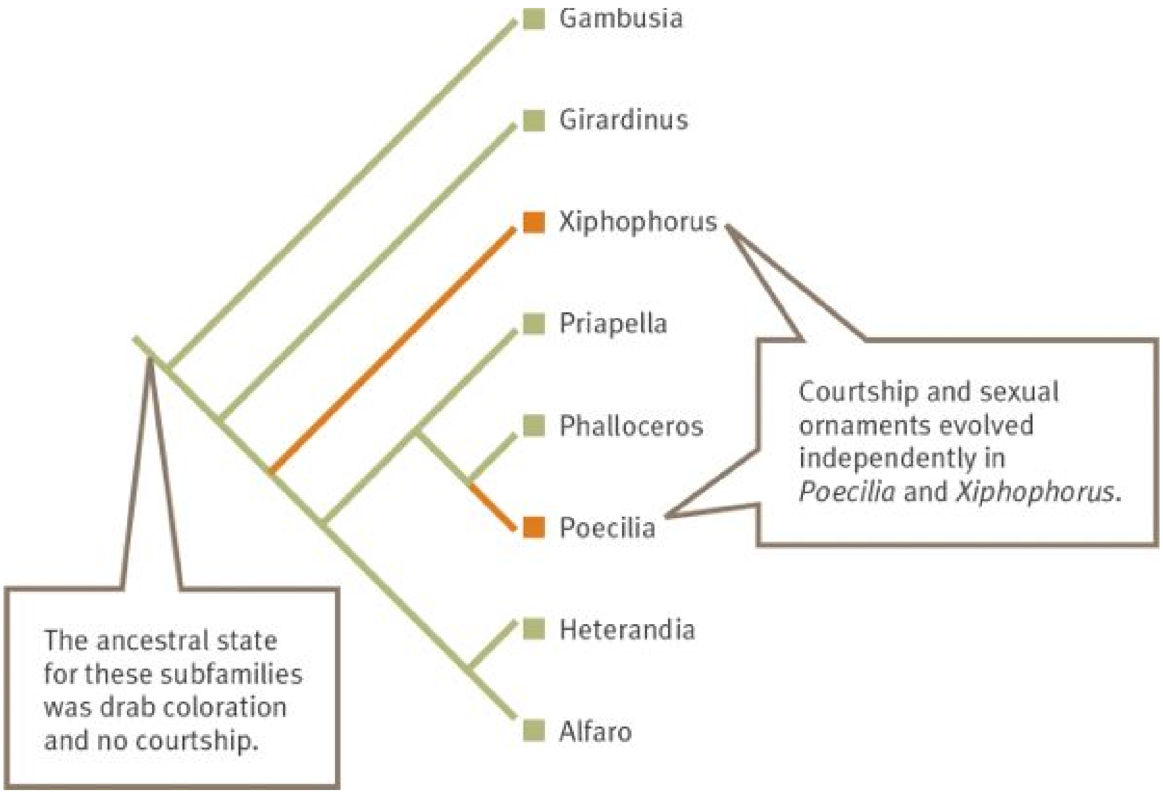

Figure 2.35. Phylogenetic history of male courting strategies. The evolutionary history of male mating fertilization strategies in *Poeciliinae* fish. Orange branches are species that use courtship and sexual ornaments, including color. Green branches lead to species that employ gonopodial thrusting and drab coloration. *(Adapted from Bisazza et al., 1997)*

This chapter has focused entirely on ultimate or “why” questions in animal behavior. Ultimate questions are often contrasted with proximate questions, which focus on immediate causes of behavior (release of a hormone, firing of a neuron, and so on). Chapters 3 and 4 are primer chapters that examine proximate factors. For the remainder of the book, both proximate and ultimate perspectives are integrated into each and every chapter.

Interview with Dr. Alan Grafen

If you had to explain natural selection to an alien who knew nothing of life on earth, how would you do it?

Richard Dawkins has convincingly argued that all adaptive complexity must arise through natural selection. It follows that an alien capable of communicating with me would themselves be the product of natural selection, and furthermore would be likely to come from a civilization that had understood how adaptive complexity arose. Thus, I would look forward to hearing what the alien had to tell me about natural selection.

Some have argued that the process of natural selection is a tautology—something that is circular, and true by definition. Where have they gone wrong?

They've almost certainly read the wrong explanation. You can't read Darwin's *Origin of Species*, or Dawkins's *The Selfish Gene*, and pay attention and come away thinking natural selection is a tautology. It is one of the features of natural selection that nearly everyone thinks they intuit the idea without being exposed to it! Indeed, Darwin's correspondence suggests he suspected that even Thomas Henry Huxley, who came to be known as “Darwin’s bulldog,” did not understand natural selection very well.

There are surely people who claim that special relativity is a tautology, or that Newtonian mechanics is fatally flawed, but they are a tiny green-inkish minority. The anti-intellectuals’ assault on natural selection is conducted on a broader front and, more worryingly, seems to be much more acceptable in respectable company.

The idea of natural selection needs to be treated with respect, so don’t waste your time arguing with someone who thinks he’s worked it all out for himself and claims to have discovered a mistake in it! Insist that he should have a proper explanation in front of him, make him point to the line where he doesn’t follow the argument, and do your honest best to help him over his obstacle.

Can it really be true that the same process—natural selection—operates on everything from viruses to humans?

That is what science is like. Gravity too operates on everything from viruses to humans and, just like natural selection, it operates in some ways just the same, and in other ways very differently, because of the different context.

Why is there such reluctance in the social science community to accept that natural selection has shaped much of our own behavior?

This is an interesting question, but there is another foot that may have a boot on. Might a social scientist not ask “Why is there such reluctance in the biological community to accept that human behavior has unique aspects and essentially cultural aspects for which biology provides no framework?”

It is a primary duty of an academic to respect other subjects, and the seriousness of their intellectual work, so we should not try to maneuver social scientists into giving up their lines of inquiry or their conceptual frameworks.

It is actually quite hard to understand another subject’s basic ideas, and this leads to trouble whenever subjects grow into new areas and acquire new neighbors. To have a dialogue with people absolutely requires mutual respect and a serious attempt at understanding each others’ positions.

One of my own papers, “Fertility and Labour Supply in *Femina economica*” was a consciously constructed attempt to build a model in which the same behavior could be understood biologically and economically. The resolution of the conflict between the points of view is all done formally and mathematically in that paper. There is no simple “one side is right, the other is wrong”—rather the explanatory forces are partly overlapping and partly intertwined.

It seems uncontroversial that at some level, biology will have something important to say about human behavior, and equally, that many of the patterns of behavior and explanations already discovered by social scientists will remain unaffected by biology. But in between these two easily accepted propositions lie many areas in which only detailed study and analysis can determine the role, if any, biology should play. Useful study of those areas can be done only by people with a good understanding both of the social sciences and of biology.

In what way has our fundamental understanding of the process of natural selection been changed by the revolution in molecular genetics?

Molecular biology has revolutionized the detailed facts we can discover about the organisms we’re studying. Do female birds have offspring by more than one male in the same nest? How long ago did humans and chimps diverge? The range of useful facts will no doubt grow and grow.

There is one, terribly important, aspect of natural selection that is completely unaffected by molecular biology, and it is in many ways the very core of Darwin’s argument: that the only known process capable of producing complex adaptations is natural selection. This argument was developed mathematically by the great biologist (and statistician and geneticist) R. A. Fisher, and Bill Hamilton wrote in his encomium on the variorum edition of Fisher’s *Genetical Theory of Natural Selection*: “And little modified even by molecular genetics, Fisher’s logic and ideas still underpin most of the ever broadening paths by which Darwinism continues its invasion of human thought.”

There is a tendency, particularly prevalent for obvious reasons among some practitioners, to believe that new technologies require a revisiting of all old knowledge. As if the discovery of the telescope might revise our view of how frequently the moon circles the earth. Read the *Origin of Species*, and be persuaded of the reality and biological significance of natural selection. Read G. C. Williams's *Natural Selection and Adaptation* (1966) and understand how to reason about natural selection. Read Dawkins's *The Selfish Gene* and see how Darwin's logic, rendered logically explicit, unifies the range of evolutionary theories biologists apply today. Biologists know a lot about natural selection, and molecular genetics will not make any substantial difference to their arguments.

Molecular genetics is nevertheless a hugely important scientific enterprise, both medically and intellectually. What *does* it have to offer to students of natural selection? For one thing, many more examples of Darwinian adaptations. To learn about the workings of the ribosomes, or DNA topoisomerases, or hundreds of other fabulous molecules, is to be filled with wonder at the achievements of natural selection, just as much as the sonar of bats or the workings of the vertebrate eye. In some ways the molecular examples are more impressive, because they reveal how life itself is possible at a very fundamental level.

The problem Darwin solved in 1859 has remained solved. While nothing in molecular genetics is likely to require the reopening of that case, molecular genetics *will* continue to supply further examples of adaptations and fuel further sophistications of our understanding of natural selection.

Dr. Alan Grafen is a professor at Oxford University, where he is a member of the Animal Behavior Research Group. He is the coauthor of *Modern Statistics for the Life Sciences* (Oxford University Press, 2002) and is one of the leading theoretical biologists in the area of evolution by natural selection.

SUMMARY

1. Artificial selection is the process of humans choosing certain trait varieties over others through implementing breeding programs that cause one or more selected varieties to increase in frequency. We have been shaping animals and plants by the process of artificial selection for at least 10,000 years.
2. Much of animal behavior work revolves around the notion that behavior, just as any trait, has evolved by the process of natural selection. The process of natural selection requires limited resources, variation, fitness differences, and heritability. If

individuals in a population display a number of different behavioral variants, and these variants translate into fitness differences and are heritable, then natural selection will act to increase the frequency of the variant associated with the greatest relative fitness.

3. Even a small selective advantage is sufficient for natural selection to dramatically change gene frequencies over evolutionary time.
4. Natural selection produces adaptations—traits with the highest relative fitness in a given environment.
5. To study common ancestry, evolutionary biologists construct phylogenetic trees that depict the evolutionary history of various species, genera, families, and so forth. These trees graphically depict the phylogeny, or history of common descent, between the groups of organisms under study.
6. Phylogenetic trees can be used in many ways by ethologists. In some cases, behavioral traits are used to construct phylogenies, but more often behavioral traits are mapped onto already existing phylogenetic trees to assess the order in which various traits appeared over evolutionary time.

DISCUSSION QUESTIONS

1. How was it possible for Darwin to come up with his theory of natural selection in the complete absence of a science of genetics? Many modern studies in ethology rely on genetics, particularly molecular genetics, as a critical tool. How did Darwin manage without this?
2. Francois Jacob and Jacques Monod have referred to natural selection as a tinkerer. Why is this a particularly appropriate analogy for how the process of natural selection operates?
3. When considering how much variation in a behavioral trait is genetic and how much is environmental, how does the “uterine environment,” in which a fetus matures, complicate matters?
4. Read Gould and Lewontin’s (1979) paper, “The Spandrels of San Marcos and the Paglossian Paradigm: A Critique of the Adaptationist Programme” in volume 205 (pp. 581–598) of the *Proceedings of the Royal Society of London, Series B*. List both the merits and flaws in Gould and Lewontin’s approach. Overall, do you think their critique is a fair one?
5. Maternal care behavior has been documented in such diverse groups as insects, fish, and mammals. Why would it probably be a mistake to use maternal care as a character in any analysis that examined the phylogenetic relationship between these very different groups? Cast your answer in terms of convergent evolution.

SUGGESTED READING

Buss, D. (2012). *Evolutionary psychology*. (4th ed.). Boston: Allyn & Bacon. A book on how “natural selection thinking” can shed light on the evolution of human behavior.

Darwin, C. (1859). *On the origin of species*. London: J. Murray. The starting point for both evolutionary biology and modern ethology and a joy to read.

Gardner, A. (2009). Adaptation as organism design. *Biology Letters*, *5*, 861–864. A discussion of recent work on the power of the adaptationist approach to studying behavior.

Klump, B. C., et al. (2015). Context-dependent “safekeeping” of foraging tools in New Caledonian crows. *Proceedings of the Royal Society B-Biological Sciences*, *282*, 1808.

An overview of some of the work on New Caledonian crow tool use we discussed in the Cognitive Cognition Box.

Williams, G. (1966). *Adaptation and natural selection*. Princeton, NJ: Princeton University Press. A critical approach to adopting the adaptationist perspective. A must read for those studying animal behavior.

3

Hormones and Neurobiology

Ethologists have studied both the costs and benefits that individuals in invasive species accrue when colonizing a new area.

The house sparrow (*Passer domesticus*) has one of the broadest distributions of all bird species, having invaded new habitats many times. One particularly well-studied house sparrow invasion has been occurring since the 1950s, when these birds were first introduced into Kenya, initially near the city of Mombasa. Over the last six decades, they have expanded north and (primarily) west (Figure 3.1).

Figure 3.1. Invading house sparrows. House sparrows were first introduced into Kenya near Mombasa (southeast corner of map). The Mombasa population and seven other populations within varying distances from Mombasa have been studied to look at how sparrows have adapted to colonizing new sites (Malindi, Voi, Nairobi, Nakuru, Nyeri, Isiolo, and Kakamega [blue squares]). *(From Liebl and Martin, 2012, by permission of the Royal Society)*

Lynn Martin and his colleagues have been studying this house sparrow expansion. Because glucocorticoid hormones such as corticosterone have been linked to stress responses (Wingfield et al., 1998), they hypothesized that birds on the edge of the expansion—furthest from Mombasa, and hence in the most novel environments—would show the strongest surge in corticosterone when exposed to a stressor. They collected birds from Mombasa and each of seven sites that varied in distance from Mombasa. Birds from each of the eight populations were placed in a stressful situation (a cloth sack for 30 minutes) and blood samples were obtained both before and after the stressor.

What the researchers found was that during the breeding season the change in corticosterone from before to after a stressor increased with increasing distance from Mombasa. As predicted, birds in a population on the leading edge of the expansion, where novelty was greatest, showed the strongest stress hormone response (Liebl and Martin, 2012; Martin and Liebl, 2014; Figure 3.2). Digging down even deeper using molecular genetic tools (messenger RNA [mRNA] expression), Martin and his team discovered that the distribution of stress hormone receptors—sites to which stress hormones bind—was also biased in such a way as to facilitate the strongest hormone response in leading edge populations (Liebl and Martin, 2013). Although explicit memory tests were not conducted, Martin et al.'s working hypothesis is that at the proximate level, increased corticosterone leads to better memory of stressors. From an ultimate perspective, the payoffs for better memory in environments with novel and unpredictable stressors should be greatest in leading edge populations during invasions.

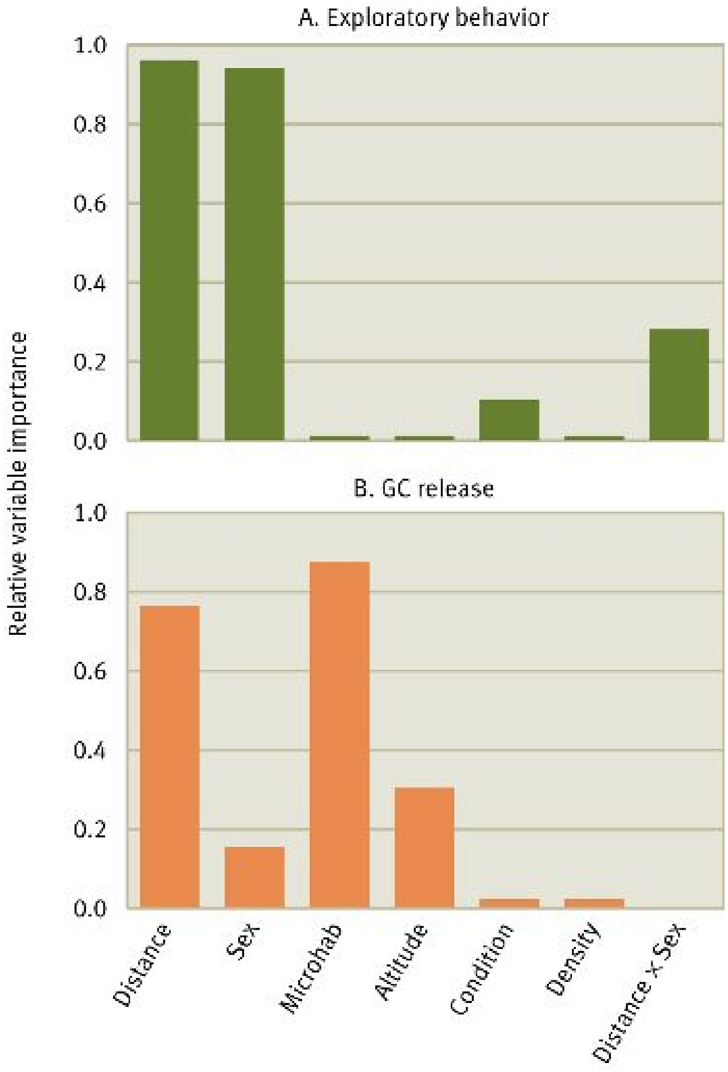

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Figure 3.2. **Stress hormones and invasion.** Stress responses in house sparrows increased as a function of distance from original introduction site. *(From Liebl and Martin, 2012, by permission of the Royal Society)*

* * *

Imagine that you are attending a roundtable discussion on visual acuity in birds. Sitting in the room with you are four scientists. The speaker on the podium is discussing visual acuity in robins, and on the screen in front of you are figures depicting the anatomy of a robin's eye, the neuronal underpinnings of robin vision, and the molecular genetics underlying visual acuity in robins.

When she has finished her presentation, the speaker asks everyone in the room to briefly explain visual acuity in robins. The first scientist explains how natural selection produced an increase in visual acuity over time. She outlines the process of natural selection on vision, and describes experiments that have found how better vision produces a robin that is a superior forager and more adept at avoiding predators. The next speaker stands up and explains how studying the curvature of the eye leads to a better understanding of why robins have better visual acuity than some other birds. The third scientist then describes the neural circuitry underlying vision and how that helps explain the increased visual acuity in robins. Finally, the fourth scientist proceeds to detail the changes associated with robin vision at the molecular genetic level, and how these changes are critical to understanding vision in robins.

They are all correct, but their explanations reflect different levels of analysis. The first scientist has provided an ultimate explanation—one based on evolutionary processes—whereas the last three scientists have provided answers at the proximate level. Ever since Tinbergen discussed the four sorts of questions ethologists ask (chapter 1), animal behaviorists have understood the importance of studying behavior from both an ultimate and a proximate perspective. One goal of ethologists is to integrate these different perspectives into a comprehensive view of animal behavior.

Ultimate and Proximate Perspectives

One common error is to confuse the level at which a behavior is being analyzed. For example, we can answer the question “Why do songbirds sing?” in terms of physiology, neurobiology, survival value, phylogenetic relationship to other species of birds, and so on (Sherman, 1988). Confusion arises when you ask a question about behavior at one level of analysis, and I answer your question at a different level. My answer to why songbirds sing might be based on the bird’s voice box (syrinx), its musculature, and the nervous system connecting the syrinx to the brain, when in fact you were looking for a reply that explains why natural selection seems to have favored birdsong in many species, or perhaps you were searching for an answer cast in terms of the role that phylogeny plays in explaining birdsong. When we talk past each other this way, it is because we are approaching the question from different perspectives—proximate vs. ultimate causation (Alcock and Sherman, 1994; Mayr, 1961; Reeve and Sherman, 1993; Sherman, 1988).

One way to think of the distinction between proximate and ultimate perspectives is that proximate questions tend to be of “How is it that . . . ?” and “What is it that . . . ?” form, while ultimate questions typically begin “Why is it that . . . ?” (Alcock, 2001, 2003). In that sense, proximate and ultimate explanations complement one another. Sometimes proximate causes are defined as those that are not evolutionary in nature. But this is probably not the most productive definition for two reasons. First, it can often be very useful to understand evolutionary (ultimate) forces when asking “how” and “what” questions, and that utility can be lost if proximate causation is defined as everything that isn’t evolutionary. Second, this definition intimates that the proximate level of analysis is less important than analysis at the ultimate level, but both levels are equally important to our understanding of animal behavior.

Conceptually, we need to think in different ways when working with proximate and ultimate questions. In a proximate analysis, we are working with factors that operate within the lifetime of an organism, in the here and now, rather than inferring (or testing) adaptationist or phylogenetic arguments as we do in an ultimate analysis about what evolutionary forces have operated in the past, how they are operating now, or how such evolutionary forces might operate in the future. But it is also important to recognize that there are fundamental links between proximate and ultimate analyses. Suppose we are undertaking a proximate analysis of some behavior—let’s say male aggressiveness. If we know something about the natural selection pressures that have acted on male aggression, that knowledge can help us design a better way to do our proximate analysis. For example, if we suspect that males direct aggression toward other males to gain access to food, we might focus on different proximate factors than if we suspect that males direct aggression toward other males during the breeding season to obtain mating opportunities with females. We would approach the question differently because the proximate underpinnings of foraging and mating behaviors are often not the same, and our understanding of natural selection might help provide focus for our proximate analysis.

Conversely, a proximate analysis might provide information that will help us better understand *how* natural selection has shaped male aggression. We might find that the hormones involved in male aggression also lower a male's resistance to disease, suggesting that we need to incorporate this disease effect into our natural selection model of male aggression. What's more, and just as important, a proximate analysis, by shedding light on neurobiology, endocrinology, molecular genetics, and so on, will help us understand the raw material that natural selection may operate on in the future. That is, proximate analysis will shed light on the variation available for natural selection to act on in the future.

Let's look at a more in-depth example of how animal behaviorists employ both proximate and ultimate perspectives to examine a trait—plumage or feather coloration—and how analysis from one perspective often leads to new questions being asked from *both* perspectives.

In the house finch (*Carpodacus mexicanus*), male plumage coloration is brighter than female plumage coloration. Geoff Hill was interested in understanding this difference in plumage coloration, so he designed experiments to study this trait at both a proximate and an ultimate level (Figure 3.3). He wanted to know *what* causes males and females to differ in plumage coloration (a proximate question) and *why* such color differences persist over evolutionary time (an ultimate question). To answer these questions, Hill examined foraging behavior, mate choice, parental care, and disease resistance, all of which play a part in understanding plumage coloration in male and female house finches. We begin by discussing his work on proximate causation, and then move on to his work on ultimate causation. But note that proximate studies do not necessarily precede ultimate studies—just as often the converse is true.

Figure 3.3. Natural variation. Natural variation exists in house finch coloration. *(Photo credit: Geoffrey E. Hill)*

To study the underlying proximate causes for plumage differences, Hill used within- and between-population comparisons and controlled feeding experiments. When he began this work, he already knew that plumage coloration in the male house finch was due to carotenoid color pigments (primarily red) that the birds ingested because house finches are unable to synthesize their own carotenoid pigments, and they rely completely on diet for this substance (A. Brush, 1990; A. Brush and Power, 1976; T. Goodwin, 1950; G. Hill, 1992, 1993a; G. Hill et al., 2002; Inouye et al., 2001). Hill's prior work and that of others had demonstrated that at the proximate level, differences in *male* plumage brightness within and between populations of finches were correlated with the amount of carotenoids in their diet. He next wanted to understand what was responsible for differences in plumage in females (A. Brush and Power, 1976; Butcher and Rohwer, 1989; G. Hill, 1993c).

To do that, Hill ran a series of controlled feeding experiments on two groups of female house finches that were fed a fixed diet while living in aviaries. Both groups were fed a commercially made finch food, and had their diets supplemented with water and apples. In one of these groups, however, the water and apples were treated with canthaxanthin—a red carotenoid pigment. Females in the canthaxanthin treatment developed much brighter plumage after their diet was supplemented, but females fed just apples and water maintained a drab plumage pattern.

From a proximate perspective, Hill could now address two questions: (1) What causes between-population differences in female coloration? and (2) What causes differences in plumage coloration between males and females? These sorts of "What causes . . . ?" questions are often where a proximate analysis begins. With respect to between-population differences, Hill found that female plumage coloration differed among females from Michigan, New York, and Hawaii (G. Hill, 1993a, 1993c). These differences appear to be a function of the amount of carotenoid-based food sources in these localities: The more such food is present in the environment, the brighter the average female is in a population. At the proximate level, the *differential availability* of carotenoid (primarily red) pigments in food across populations appears to explain the difference in plumage coloration among females across populations.

Differences in plumage coloration *between* males and females *within* a population seem to be due to differences in the way that males and females forage, rather than to the availability of carotenoid-based foods for males and females. Males actively search for and ingest carotenoid-based foods. Females eat cartenoid-based foods, but they do not actively search for such food. A proximate analysis focuses attention not solely on the amount of carotenoid-based food present in the environment, but on the differences in foraging strategies in males and females.

This proximate explanation for differences in male and female coloration led Hill to address an ultimate question: Why do males, but not females, actively search for carotenoid-based foods? Hill hypothesized that males receive significant benefits for having colorful plumage, but females do not. But what exactly were these benefits that males received for having bright plumage? To find out, he conducted a series of experiments using hair dyes to either brighten or lighten the plumage coloration of a group of wild eastern male house finches (G. Hill, 1990, 1991, 1993b; Figure 3.4).

Figure 3.4. Plumage manipulation. As part of the study on plumage coloration, researchers artificially brightened (top left photo to top right photo) or lightened (bottom left photo to bottom right photo) the plumage coloration of male house finches. *(Photo credit: Geoffrey E. Hill)*

Males that had their plumage color experimentally brightened were more likely to obtain a mate than males whose colors had been experimentally lightened (Table 3.1). From an ultimate perspective, then, one of the benefits that males obtain for searching for carotenoid-rich food is that females are attracted to males with bright plumage as potential mates. Next Hill examined an ultimate question regarding female mate choice—*why do* females prefer males with bright plumage?

Table 3.1. Plumage manipulation. Hill examined how brightening and lightening plumage coloration affected a suite of variables in male house finches. There were forty males in the brightened condition, twenty males in the sham control, and forty males in the lightened condition. *(From G. Hill, 1991)*

MALE CHARACTERISTICS	BRIGHTENED	SHAM CONTROL	LIGHTENED	STATISTICAL SIGNIFICANCE (P)
Original plumage score	140.7	139.9	141.00	0.95
Manipulated plumage score	161.6	139.9	129.40	0.0001
Proportion paired with a mate	1.0	0.6	0.27	0.0001
Time to pair (days)	12.1	20.2	27.80	0.07

When Hill and Farmer inoculated twenty-four male house finches with *Mycoplasma gallicepticum*, a bacterial pathogen, they found that males with more elaborate plumage coloration were able to rid themselves of this pathogen more quickly than drabber-colored males (Figure 3.5A). Follow-up work also found that colorful males that had been selected as mates had lower levels of bacteria that degrade the quality of feathers (Shawkey et al., 2009; Figure 3.5B). Such bacteria are not lethal in and of themselves, but degradation of feathers can lead to problems with thermoregulation and flight. From an ultimate perspective, by selecting more colorful males as mates, females expose themselves to fewer pathogens by selecting males that are more resistant to disease over males that are less resistant (we explore this benefit in more depth in chapter 7). And if such disease resistance is heritable, females that choose the more disease-resistant males as mates will produce offspring that are better able to stave off disease (Duckworth et al., 2001; G. Hill and Farmer, 2005).

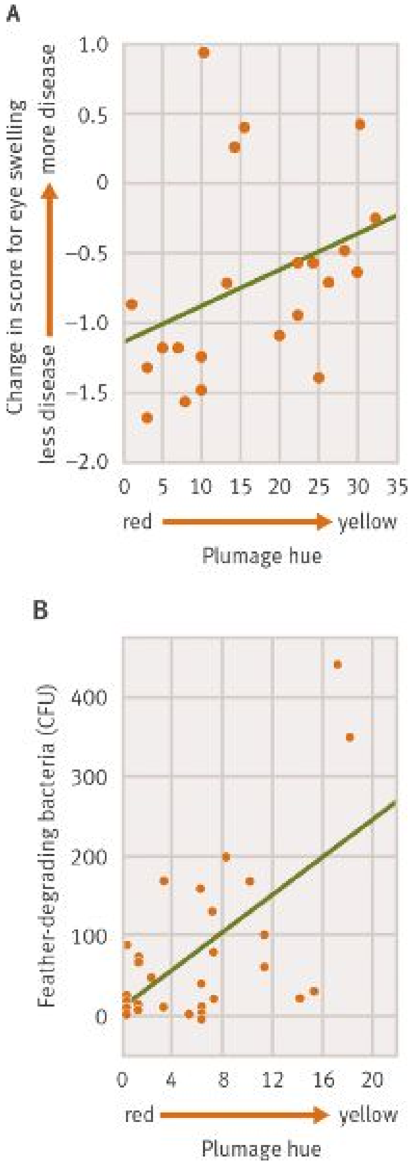
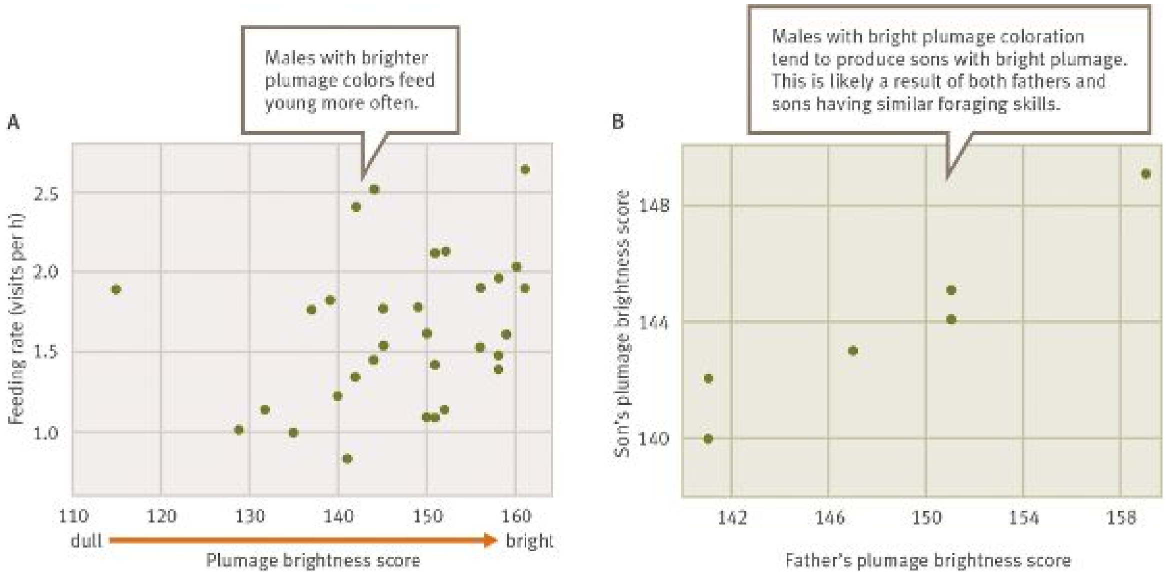


Figure 3.5. Plumage coloration and disease. (A) The rate at which birds recovered from *Mycoplasma gallicepticum*, which causes eye swelling, was linked with their plumage coloration. Birds with more red coloration recovered more quickly (in later phases of the experiment) than birds with more yellow coloration. (B) Individuals with redder plumage carried fewer feather-degrading bacteria. *(From G. Hill and Farmer, 2005; Shawkey et al., 2009)*

A second benefit that females may receive by choosing brighter-colored males over drabber-colored males centers on parental care and food provisioning. When examining the relationship between male color and male parental care in eastern populations of house finches, Hill found that the mean number of times a male fed a chick at his nest was positively correlated with the intensity of his plumage coloration: brighter males fed chicks more than twice as often as drabber males (G. Hill, 1991; Figure 3.6A). Females in this population likely prefer redder males because such males make good fathers with respect to feeding young. In other populations of house finches, however, more colorful males provide less parental care than drabber males, but females still prefer the more colorful males as mates (Badyaev and Hill, 2002; Duckworth et al., 2004; K. McGraw et al., 2001). Why such differences exist between populations remains an open question.



Males with brighter plumage colors feed young more often.

Males with bright plumage coloration tend to produce sons with bright plumage. This is likely a result of both fathers and sons having similar foraging skills.

Figure 3.6. Plumage, feeding, and between-generation correlation in house finches. (A) The relationship between male plumage and the rate of feeding offspring. (B) The relationship of father and son plumage brightness scores. *(From G. Hill, 1991)*

There is a third benefit that females may receive by choosing more colorful over less colorful males as mates. In eastern populations, brightly colored males appear to be better foragers (and not only with respect to feeding chicks at their nest), and hence they survive with a relatively high probability. If the traits responsible for this increased survival are passed on to offspring, then mating with colorful males may lead to the production of healthy, long-lived offspring. Hill found that males with more red plumage produced sons with colorful plumage (Figure 3.6B). But remember, red plumage coloration can't be inherited —such coloration is diet dependent. This suggests that males that are good foragers, and thus find and ingest the carotenoid-based foods needed to produce colorful plumage, produce sons that are also good foragers.

Hill’s work is an excellent example of how a combination of ultimate and proximate perspectives can provide an in-depth picture of animal behavior. Among other things, it shows how proximate explanations of what causes differences in coloration can also point the way to ultimate reasons for such differences.

In the remainder of this chapter, we examine the hormonal and neurobiological proximate factors affecting behavior. Chapter 4 tackles molecular genetic and developmental proximate factors. Of course, dividing proximate causation into four components—hormonal, neurobiological, molecular genetic, and developmental—is somewhat arbitrary. Neurobiological differences often underlie hormonal changes in behavior (and vice versa), and one could argue that all hormonal and neurobiological differences associated with behavior can be understood at the molecular genetic level. And hormonal differences can lead to behavioral differences that translate into animals having very different experiences during development. Developmental differences can also lead to different hormonal responses to some stressor in the environment, as well as affect various properties of neurons associated with behavioral responses. The justification for separating hormonal, neurobiological, molecular genetic, and developmental approaches here is that before we can understand the complicated *interactions* among these four types of causation, we need a basic understanding of how each one works.

Proximate Causation: Hormones

A bit of basic background will help set the stage for our discussion of proximate causation, hormones, and behavior. The **endocrine system** is a communication network that influences many aspects of animal behavior. This network is primarily composed of a group of ductless glands that secrete hormones (derived from the Greek word for “excite”) directly into the bloodstream (in vertebrates) or into fluid surrounding tissue (in invertebrates). In vertebrates, major glands producing hormones include the adrenal gland, pituitary gland, thyroid gland, pancreas, the gonads, and hypothalamus, but many other organs also produce hormones. Within these glands are endocrine cells, which synthesize and then secrete hormones (Figure 3.7). There is an exception to the rule that hormones are produced by ductless glands. Some hormones, called **neurohormones**, can be released into the blood via neurons (typically located in the brain) that secrete these hormones directly into the bloodstream (R. Nelson, 2011).

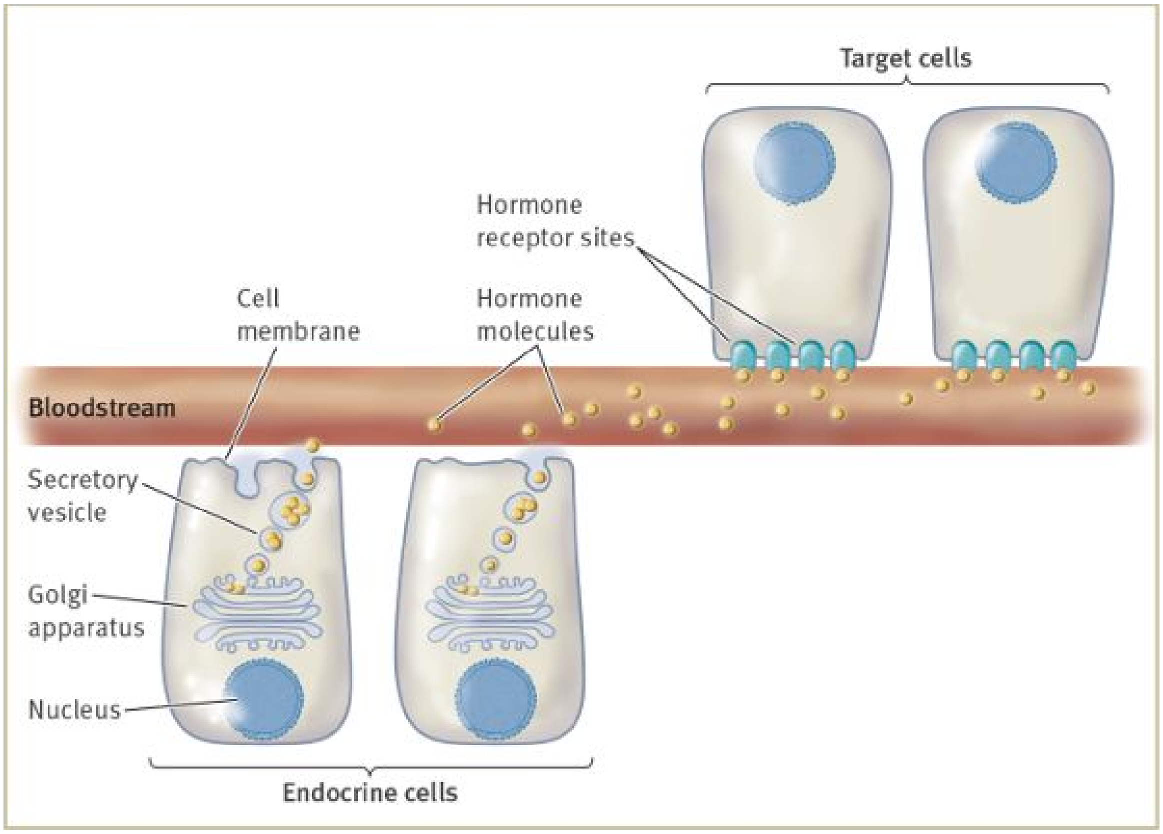


Figure 3.7. Endocrine cells and target cells. A schematic of how endocrine cells work and how hormones affect target cells. Enzymes in the Golgi apparatus process proteins into hormone molecules and package them inside secretory vesicles. These vesicles fuse with the cell membrane and release hormones into the bloodstream. The hormones travel through the bloodstream until they reach the receptor sites of the target cell, where they bond and initiate a series of interactions. Here we see the schematic for a membrane-bound receptor, which is often part of a peptide hormone system. Steroid hormones often pass right through a membrane to bind to receptors. *(Adapted from R. Nelson, 2005)*

Hormones act as chemical messengers, affecting target cells that reside some distance from the gland secreting the hormone. In **endocrinology**, hormones are classified in a number of different ways. Most vertebrate hormones are **protein hormones**, made up of strings of amino acids. When protein hormones are composed of only a small number of amino acids, they are called **peptide hormones** (for example, prolactin). Protein hormones can be stored in endocrine cells and do not have to be released immediately into the bloodstream. Protein hormones are soluble in water and blood (and therefore are referred to as hydrophilic, or “water-loving”) and do not require any other “carrier” chemicals to travel through blood. All other things being equal, the larger a protein hormone, the greater its half-life—that is, the longer it takes for half of the hormone to be removed from the blood.

Steroid hormones such as testosterone differ from protein hormones in number of ways. The lag time between when a stimulus is sensed and when a hormone is produced can be much longer for steroid hormones than for protein hormones. Steroid hormones cannot be stored in cells, so once they are produced by an endocrine gland such as the adrenal gland, they are immediately released into the bloodstream. Because they are fat soluble but not water soluble, steroid hormones are called hydrophobic (“water-hating”) and usually require a chemical “chaperone” (often a protein) to move them through the bloodstream to their target organ (R. Nelson, 2011).

Many glands can secrete more than one hormone, and the same hormone can have different effects on different target cells. Hormones affect many traits, including behavioral traits, both directly and indirectly through, for example, changes in cell metabolism or DNA expression. Hormones also affect intracellular processes that promote cell division, induce the ion channels leading to neuronal signal paths to open, cause muscle contractions, and lead to the production of other hormones. Malfunctioning of the endocrine system, either through diminished secretion (hyposecretion) or excessive secretion (hypersecretion), affects functions such as growth, metabolism, reactions to stress, aggression, and reproduction.

The endocrine system is not a disconnected amalgam of ductless glands. Hormones secreted by one endocrine gland can stimulate the production and secretion of hormones from another gland. These chains may have important behavioral consequences. One example is the activation of the **hypothalamic-pituitary-adrenal (HPA) axis**, which leads to changes in behavior. Let’s walk through this chain of events by focusing on hormonal cascades after a behaviorally subordinate animal interacts with a more dominant animal. In such a subordinate individual, in response to the production and secretion of one hormone called CRH (corticotropin-releasing hormone) from the hypothalamus, the anterior pituitary gland secretes another ACTH (adrenocorticotropic hormone), which in turn stimulates the adrenal glands to produce glucocorticoid hormones like cortisol (see also Box 3.1). These glucocorticoids play a critical role in behavior such as reduced aggression in the presence of dominant individuals.

Box 3.1. CONSERVATION CONNECTION

Community-Based Ecotourism: Using Hormones to Measure Effects on Animal Well-Being

Ecotourism has become an increasingly popular choice for environmentally conscious travelers. Ecotourism destinations typically involve a joint partnership between private enterprise and conservation biologists. Ecotourism is designed to draw tourists to ecologically beautiful and often ecologically imperiled areas of the world; to use the funds generated from this tourism to protect the wildlife in these areas; and to promote the local, often indigenous, human culture that lives around the ecotourism site.

Ethologists and conservation biologists seek to understand the effects of these programs on various aspects of animal behavior. One way that these have been measured is through the use of techniques developed in **field endocrinology**—measuring hormone levels in natural populations (B. Walker et al., 2005). For example, consisder the ethological implications of a large ecotourism program built around a colony of hundreds of thousands of Magellanic penguins in Punta Tombo, Argentina (B. Walker et al., 2005; Figure 3.9) At the turn of the twenty-first century, Punta Tombo was home to a large colony of breeding Magellanic penguins (*Spheniscus magellanicus*)—two hundred thousand breeding pairs of birds. In an ecotourism program designed to help sustain this population, several hundred penguin nests have been fenced off, and tourists can walk freely in this area. This program draws seventy thousand ecotourists per year. Observational work suggests that adult penguins exposed to tourists have habituated to their presence and show reduced defensive responses in the presence of humans compared with adult penguins from nests not exposed to tourists.

Figure 3.9. Magellanic penguins. Field endocrinology experiments on Magellanic penguin behavior have shed light on issues of conservation biology. *(Photo credit: © Frans Lanting/lanting.com)*

But has this habituation had a positive, negative, or neutral effect for the animals' well-being? At first glance, it appeared that ecotourism was not having adverse effects on the animals or causing them to display dangerous behavior. Indeed, when field endocrinologists measured corticosterone stress hormone levels in penguin adults, they found that those from areas with tourists showed lower stress responses to handling and release (Fowler, 1999).

More detailed follow-up work with chicks exposed to ecotourists, however, shows a different, more disconcerting picture (B. Walker et al., 2005, 2008; Villanueva et al., 2012). Within days of hatching, chicks from nests exposed to ecotourism showed very high levels of corticosterone compared with chicks from areas where ecotourists were excluded (Figure 3.10). Researchers are not certain what causes this rise in corticosterone levels, but they believe that it is linked to the altered behavioral responses of adults at the chicks' nests. In nests from unexposed areas, parents spend much of their time brooding on the nest. But in ecotourist areas, parents spend more time standing up and even walking among the tourists. This constant change in temperature for the chicks, in conjunction with the increased distance between parent and chick, may be the cause of the corticosterone stress response in the chicks from ecotourist areas. In many other species, including numerous Adele penguins, increased corticosterone during the chick stage has been shown to have detrimental effects on individuals when they mature (Bonier et al., 2009; Ninnes et al., 2011). Whether such detrimental effects will emerge in the Magellanic penguins remains to be tested, but the work to date from field endocrinology and ethology certainly flags these populations as at risk.

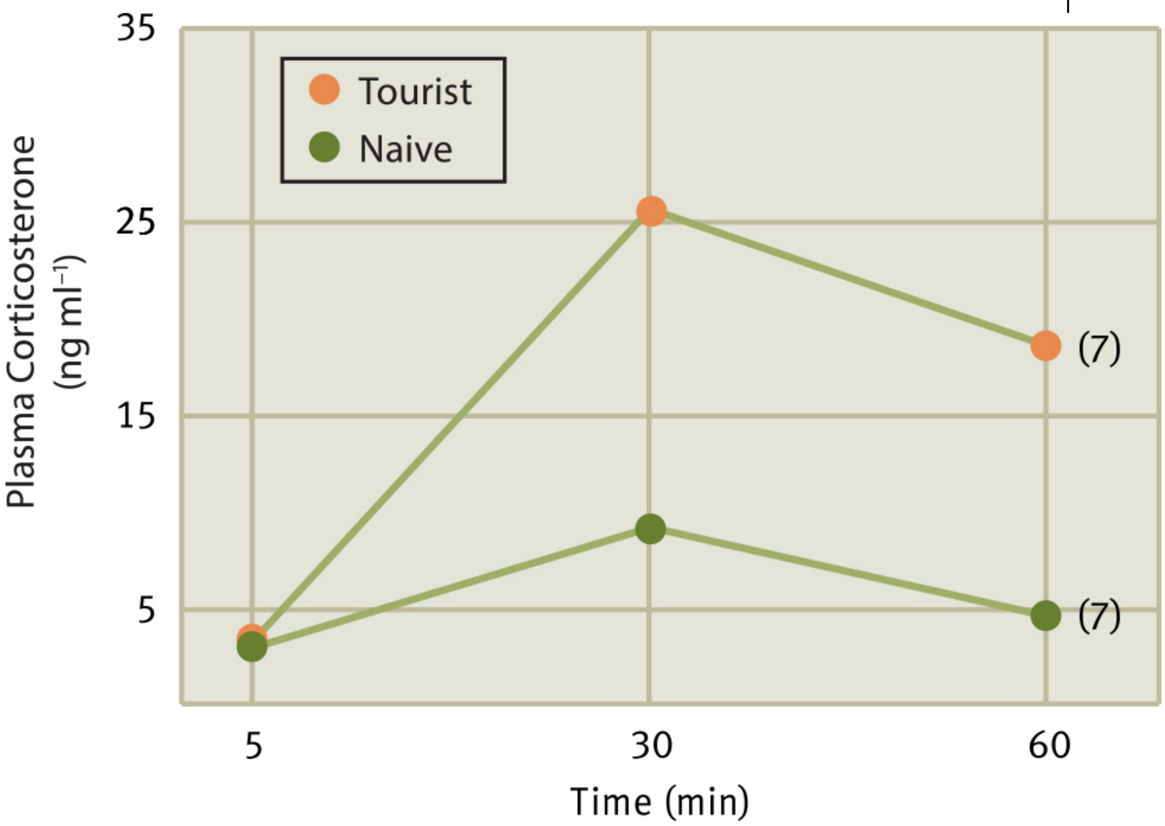


Figure 3.10. Stress and ecotourism. Very young Magellanic penguins exposed to humans from ecotourist groups showed much higher levels of stress hormones, such as plasma corticosterone, than did individuals from control groups. *(From B. Walker et al., 2005)*

Hormones are almost always transported through the bloodstream, and with one exception (the cells in the lens of the eye), all cells in the body have a direct blood supply. But a hormone will have an effect on a cell only if the cell has the proper receptor site for that hormone. Cells with the receptor site for a particular hormone are referred to as **target cells** for that hormone. The receptor site, which is often located on the surface of a cell, and the hormone itself act as a lock-and-key system that is known as the hormone receptor complex. A receptor (lock) is not activated until the correct hormone (key) reaches it, and a hormone has no effect on a cell unless the cell has the correct receptor. In this lock-and-key system, once a hormone reaches a cell and binds to the receptor site, a series of interactions occurs that affects the expression of genes and the synthesis of proteins. Precisely how these changes occur depends on the specific hormone, but changes in gene expression and protein synthesis can either directly or indirectly affect an animal's behavior.

The lock-and-key system is put into operation only when a hormone is released into the bloodstream. But what causes the release in the first place? The answer lies in the complex ways that animals respond to stimuli in their environment. To see this, let's look at one component of the endocrinology of reproductive behavior in birds.

Many birds breed during the spring and summer, when temperatures are warmer and food is more plentiful. Changes in day length are typically a reliable cue for seasonal change, and in many birds, levels of the hormones gonadotropin (which stimulates sperm production) and testosterone increase in males as day length increases. Some testosterone binds to receptor cells in the brain and is associated with a suite of behaviors related to mating and paternal care: males are more likely to be aggressive toward one another to gain access to females, guard their mates, build nests, and defend their brood when testosterone is high. Some testosterone is converted into estradiol or dihydrotestosterone, and this binds to receptors and leads to behaviors linked to mating and parental care (G. Ball, 1993; Dawson, 2002; Wingfield et al., 2001; Figure 3.8). When ethologists experimentally manipulated day length in the laboratory, they discovered that delaying the onset of increased day length can have profound effects. Because the cues for the onset of spring and summer breeding seasons were lacking, male testosterone levels remained low, and the testosterone-mediated behaviors just described were not set in motion. Similar experimental work has shown that manipulations of day length also affect hormone levels and the mating and breeding behavior of females as well as males.

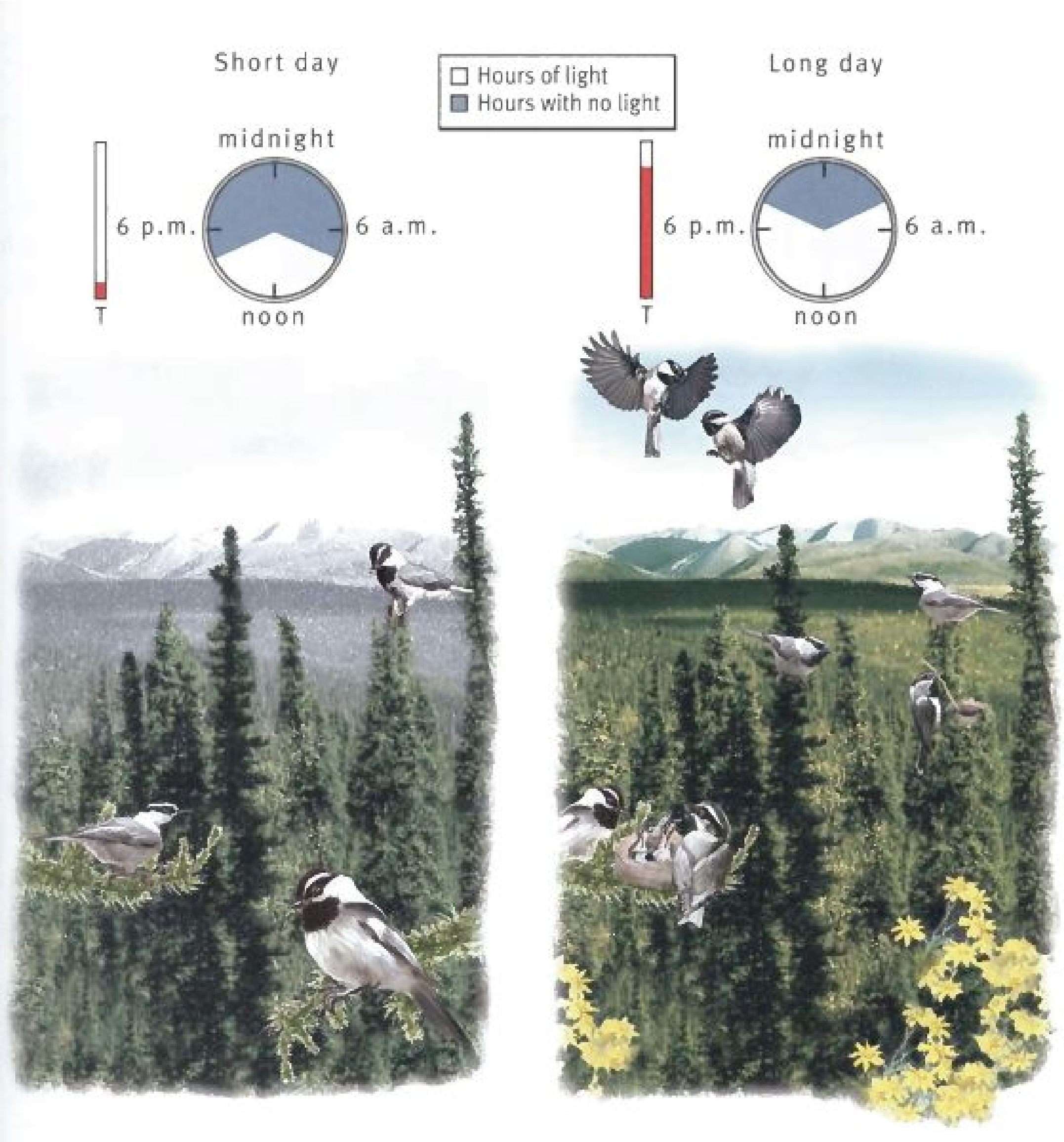


Figure 3.8. Day length, hormones, and behavior. Many bird species breed during the spring and summer, and changes in day length are an excellent cue for seasonal change. As day length changes, it triggers an increase in circulating levels of testosterone (T). Increases in T increase the probability that males are aggressive toward one another (to gain access to females), guard their mates, build nests, and defend their broods. *(From B. Walker et al., 2005)*

HOW THE ENDOCRINE SYSTEM INTEGRATES SENSORY INPUT AND OUTPUT

If we think of animals as an engineer might, we could describe them as possessing three interactive systems (Figure 3.11): (1) an input system made up of all the sensory systems (smell, sight, and so on), (2) a central processor made up of integrators that process and integrate the sensory information received, and (3) output systems—effectors such as muscles that move when stimulated (R. Nelson, 2005). What hormones do is change the probability that a specific sensory input leads to a specific output.

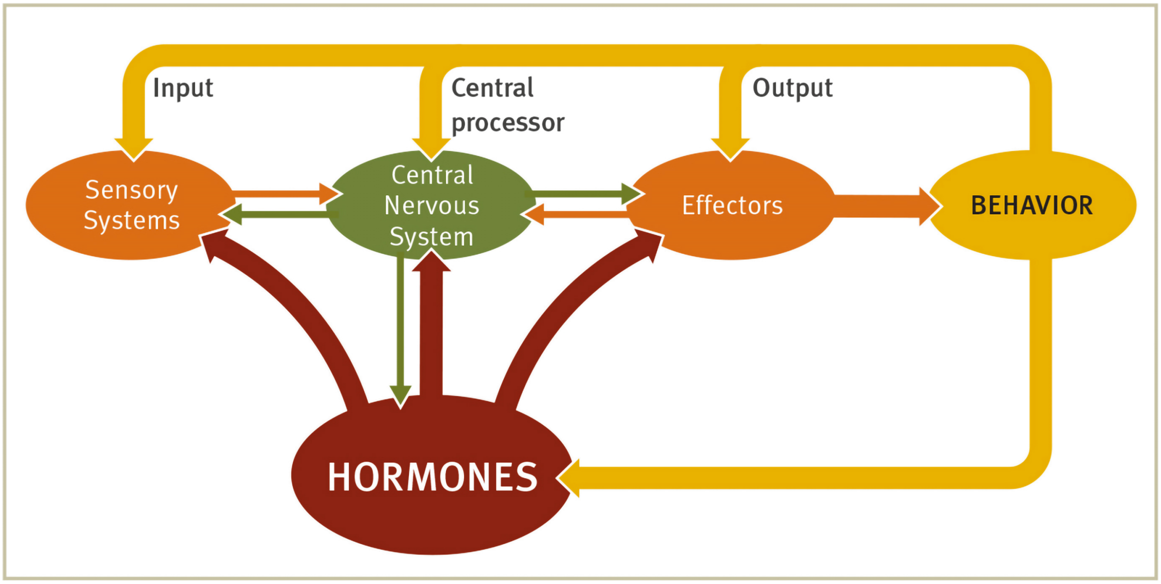


Figure 3.11. Complex effects of hormones. Hormones can affect input systems (sensory systems such as those for smell, sight, or hearing), central nervous system functions (processing), and output systems (for example, effectors such as muscles controlling movement). *(Adapted from R. Nelson, 2005)*

Hormones affect the probability that a specific sensory input leads to a specific behavioral response in many ways. Hormonal changes can *modify* some ongoing behavior by increasing or decreasing the frequency or duration of that behavior, or they can *trigger* the onset or end of a behavior or behavioral sequence. In addition, hormones can *prime* animals so that they are more or less likely to behave in a specific way in a specific environment. For example, when testosterone levels are high, males are more likely to engage in aggressive behavior than when testosterone levels are low—when baseline levels of testosterone are high, males are primed for aggressive behavior, in that they are more likely to display aggression when encountering another male than they are otherwise. With testosterone, as with many hormones, there is a hormonal-behavioral feedback loop in play. If an animal wins a fight, partly as a result of behaviors resulting from high baseline levels of testosterone, the act of winning may in turn increase the probability of winning future fights by further increasing testosterone levels or by lowering the level of stress hormones such as cortisol (Figure 3.12).

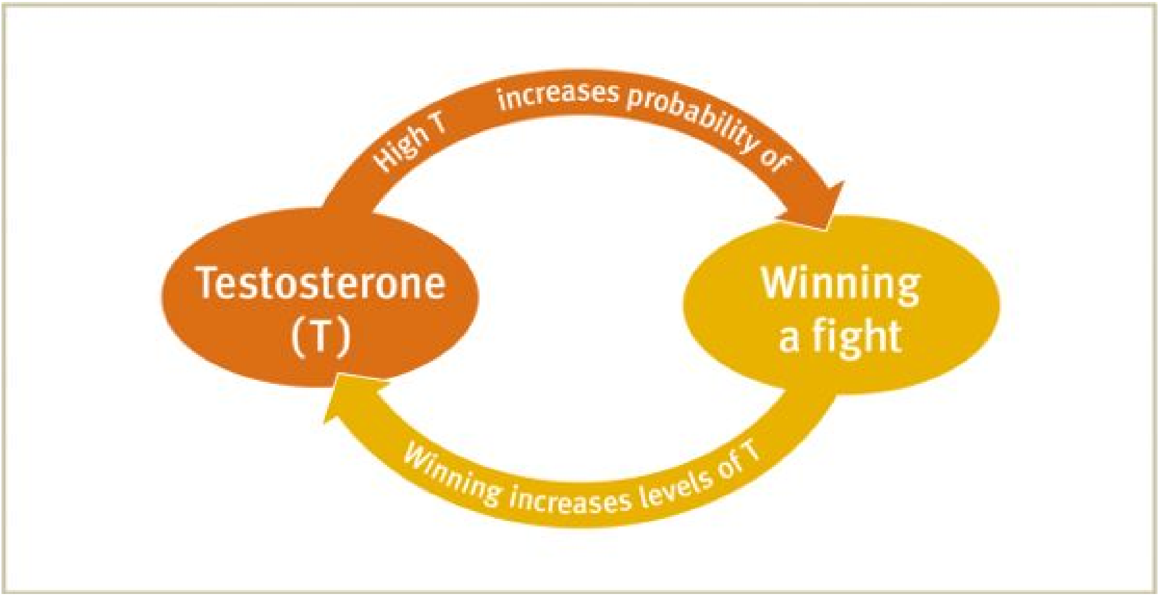


Figure 3.12. Testosterone (T) and aggression feedback loop. A positive feedback loop exists between levels of T and the probability of winning a fight. High levels of T increase the probability of winning, and winning further increases circulating levels of T.

Hormones also affect the *organization* of behavior systems during early development. For example, female mice gestate many fetuses simultaneously. If a developing male fetus is surrounded by females, it is often exposed to lower levels of circulating testosterone (Figure 3.13). When such males mature, they tend to be less aggressive and less sexually active than males that were surrounded by male fetuses in utero—the entire behavioral repertoire associated with aggressive interactions is fundamentally altered by hormonal effects early on in development. We delve into testosterone and in utero effects like this in more detail in the next section.

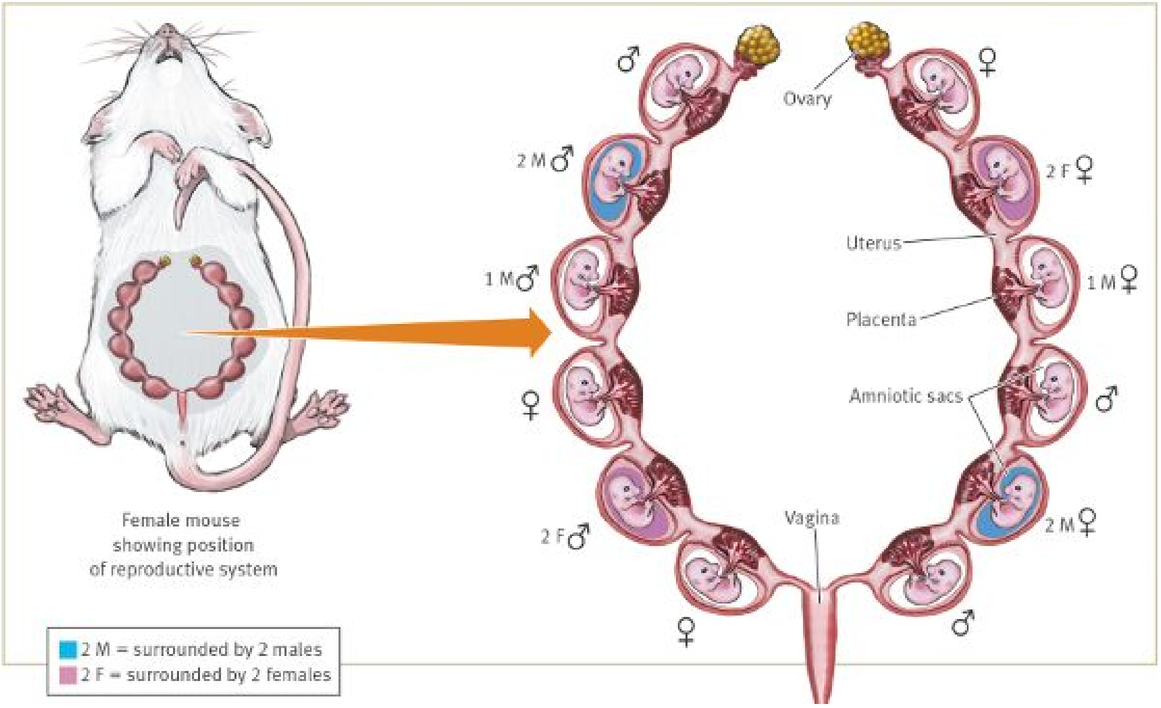


Figure 3.13. Intrauterine position. Males surrounded by two females in utero act relatively “feminized,” whereas females surrounded by two males act relatively “masculinized.” These behavioral differences are a result of differential exposure to hormones in utero. 1M = adjacent to one male; 2M = surrounded by two males; 2F = surrounded by two females. *(From vom Saal, 1989)*

Although the relationship between behavior and the endocrine system varies in different species, early work by Hans Selye found that the behavioral/endocrinological response to danger—sometimes called the “fight or flight” response—is similar across different types of stress. Subsequent work found this fight or flight response in many vertebrate species, including humans (R. Nelson, 2005; Selye, 1936; Stratakis and Chrousos, 1955). To understand the complex interaction between the endocrine system and behavior in a bit more detail, let’s examine some of the specifics of the fight or flight response.

When an individual senses a stressor—a predator, for example—the hypothalamus initiates a response, which works along two pathways. Along the first pathway, epinephrine (also known as adrenaline), which is secreted by both the adrenal glands and certain nerves in the central nervous system, binds to receptors on the smooth muscles around blood vessels and causes constriction or dilation, depending on which type of receptor is involved. Epinephrine also acts directly on receptors in the heart and lungs to increase cardiopulmonary activity. This burst of epinephrine (and norepinephrine) leads to a quick and large increase in blood sugar that, along with oxygen, is delivered quickly to vital organs. In particular, the brain, skeletal muscles, and heart receive both increased blood sugar and oxygen. As a result of the increased sugar and oxygen, circulation increases and "nonessential" systems—for example, the digestive and reproductive systems—are shut down. All of these effects allow for an appropriate behavioral response to the stressor. The increase in sugar and oxygen might, for example, enable an animal to quickly flee from a predator or perhaps to fight off this danger.

Along a second pathway, another reaction chain is put into motion when a stressor is sensed. Here corticotropin-releasing hormone (CRH), growth hormone-releasing hormone (GHRH), and thyrotropin-releasing hormone (TRH) are secreted by the hypothalamus. CRH stimulates the anterior pituitary gland to increase the production of ACTH, which then stimulates the adrenal gland to secrete cortisol. This hormonal cascade converts noncarbohydrates into sugars—energy that can be used to handle the stressor in question by, for example, fleeing quickly from danger or standing put and fighting. The adrenal gland also increases its production of aldosterone, which increases water retention and reduces bleeding if the stressor causes injury. These two parallel hormonal/behavioral responses to stressors illustrate the intricate and complex ways that organisms respond to dangers in their environment. It is only when stress is chronic that the endocrine system fails to respond in the appropriate manner.

With this brief overview of the endocrine system and behavior complete, let's examine a few case studies from the animal behavior literature.

THE LONG-TERM EFFECTS OF IN UTERO EXPOSURE TO HORMONES

Let's revisit the long-term behavioral effects of in utero exposure to testosterone. In a number of species of rodents, the sex of the siblings immediately surrounding an individual in utero can have dramatic effects on testosterone level and an individual's behavior after birth (B. Ryan and Vandenbergh, 2002; vom Saal, 1989). Males that are surrounded by two other males in utero (2M males) are more aggressive than males that were surrounded by two females (2F males). In addition, 2M males mark their territories by scent and mount more females than 2F males (Drickamer, 1996; B. Ryan and Vandenbergh, 2002; vom Saal and Bronson, 1978). To better understand the behavioral endocrinology of testosterone and intrauterine position, we begin by examining mating and parental care in male gerbils (*Meriones unguiculatus*; Figure 3.14).

Figure 3.14. Helping in male Mongolian gerbils. Male helping behavior as a function of prior intrauterine position has been examined in Mongolian gerbils. *(Photo credit: Julian Barker)*

In 1991, Mertice Clark and her colleagues measured in utero testosterone levels of 2M and 2F male gerbils (M. Clark et al., 1991). They found that testosterone levels in 2M males were significantly higher than in 2F males (Figure 3.15). It is still not clear exactly what causes this difference, but it is likely, in part, a result of 2M males being exposed to higher levels of testosterone in their amniotic sacs because they are surrounded by two other males (Clemens et al., 1978). These in utero differences between 2M and 2F males have long-term consequences—adult 2M males have twice the level of circulating testosterone levels as adult 2F males (M. Clark et al., 1991, 1992a; Even et al., 1992; vom Saal, 1989). Clark and her colleagues hypothesized that testosterone differences that had been initiated in utero and continued through life would affect male reproductive behavior, both with respect to obtaining mates and dispensing parental care (M. Clark and Galef, 2000; Clark et al., 1992b, 1998).

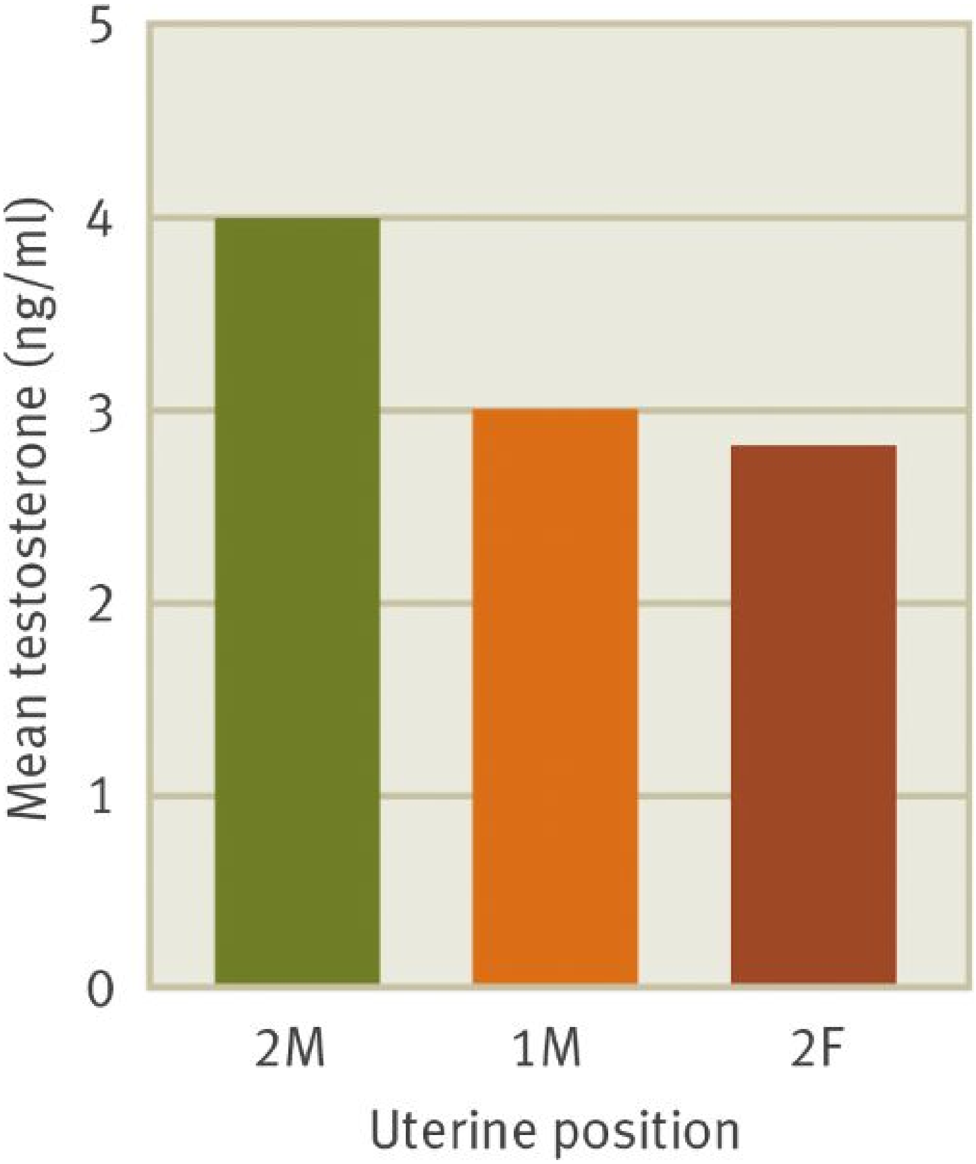


Figure 3.15. Testosterone measurements. Circulating testosterone levels for Mongolian gerbil males that were adjacent to two (2M), one (1M), or zero (2F) other males in utero. *(Adapted from M. Clark et al., 1991)*

They began their comparison of the mating behavior of 2M and 2F males by housing a single male (either 2M or 2F) and a single female together in a cage. They measured how long it took before the male sexually mounted the female, and the time it took between mounting the female and ejaculation. 2M males mounted females more quickly, and they ejaculated sooner (similar results have been obtained in comparisons of 2M and 2F mice; vom Saal, 1989; vom Saal et al., 1983). Follow-up experiments indicated that 2M males also sired more offspring after being paired with a female than did 2F males.

Clark also hypothesized that as a result of high testosterone levels 2M males would provide less parental care (M. Clark and Galef, 1999; M. Clark et al., 1998). To test this hypothesis, twenty-three 2F males and twenty-one 2M males were each housed individually with a female, until the female was pregnant and gave birth. After a female had given birth, the behavior of males toward pups was examined. Both when their mates were present and when their mates were absent, 2M males spent significantly less time in contact with pups than 2F males did (Figure 3.16). In a follow-up experiment, Clark and Galef castrated adolescent males to experimentally reduce testosterone levels. Such castrated males increased the time they spent caring for pups. When castrated males had their testosterone levels brought back to normal, through silicon implants, their parental behavior decreased, suggesting a causal link between testosterone and parental care (M. Clark and Galef, 1999; M. Clark et al., 2004; Figure 3.17; Box 3.2).

Figure 3.16. In utero position and subsequent parental behavior. Mongolian gerbil males that were surrounded by two males in utero (2M males) provided less parental care when they matured than did males that were surrounded by two females in utero (2F males). *(From M. Clark et al., 1998)*

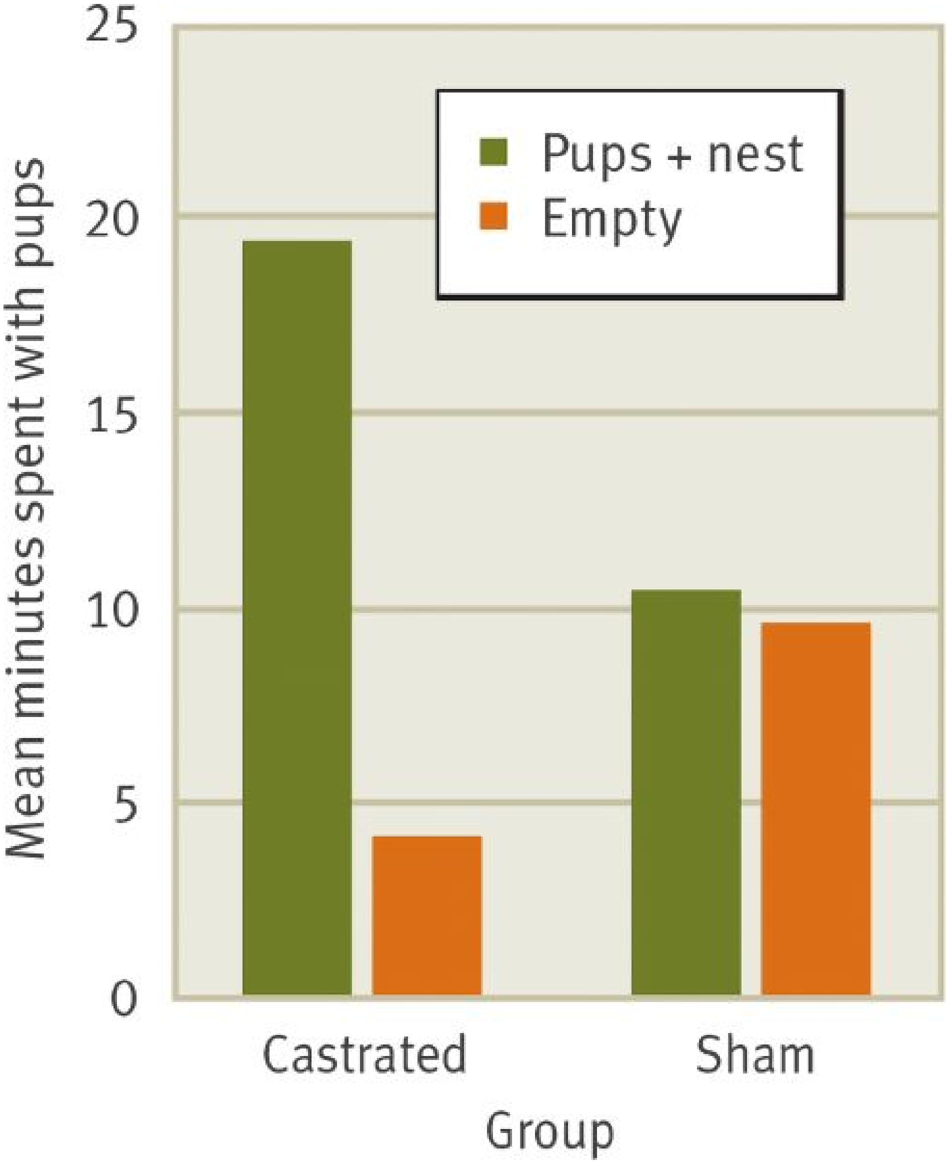


Figure 3.17. Testosterone and male parental care. When male Mongolian gerbils were castrated, they spent more time with pups than did "sham" castrated males that had undergone a similar operation but were not castrated. *(From M. Clark et al., 2004)*

Box 3.2. SCIENCE AT WORK

What is the research question? Does in utero exposure to hormones affect sexual behavior later in life?

Why is this an important question? In many species, placement along the uterine horn during development exposes individuals to a hormone “cocktail” that might affect their behavior as adults.

What approach was taken to address the research question? Many approaches were used. In one, researchers measured in utero testosterone levels in (2M) males that had been surrounded by two other males in utero versus (2F) males that had been surrounded by two females in utero.

What was discovered? 2M males had higher levels of circulating testosterone than 2F males. Subsequent behavioral experiments found that 2M males mounted females sooner and ejaculated sooner after mounting females than did 2F males.

What do the results mean? Adult sexual behavior is the product of a complex web of direct and indirect effects, including in utero position and exposure to hormones.

In gerbils, the in utero position of *females* also affects the level of testosterone to which they are exposed. When 2M females (females surrounded by two males) mature, they have relatively high levels of circulating testosterone and lower levels of circulating estradiol. These 2M females are less often preferred as mates, in part because they are more aggressive than other females. They also have fewer litters and begin reproducing later than other females.

Researchers have a good understanding of how exposure to testosterone produces the behavioral variation between 2M females and other females. The key seems to be how in utero exposure to testosterone affects metabolic activity in certain brain areas of 2M females. In gerbils, the preoptic area of the hypothalamus portion of the brain controls copulatory behavior, and this area of the brain is sexually dimorphic, meaning that males and females show different activity patterns in the preoptic area; 2M females have preoptic metabolic activity that resembles that of males more than that of 2F females. More specifically, 2M females have 20 percent greater metabolic activity in the preoptic area of the hypothalamus than do 2F females (D. Jones et al., 1997). One long-term effect of in utero exposure to high levels of testosterone in gerbils is to “masculinize” the preoptic area of the brain of 2M females. This relationship between in utero testosterone exposure and subsequent effects on brain activity sheds light on the tight connection between the hormonal and neurobiological underpinnings of behavior.

VASOPRESSIN AND SOCIALITY IN VOLES

Vasopressin and oxytocin, neurohormones produced in the hypothalamus and then transported to various brain regions or projected to the pituitary gland for release, play important roles in reproduction and parental care in mammals. Homologs of vasopressin and oxytocin—that is, hormones that share the same evolutionary history—originated about 700 million years ago and are found in a diverse array of animals (Figure 3.18). Vasopressin and oxytocin themselves appear to have arisen from a gene duplication that occurred before the emergence of vertebrates. Just as these neurohormones are produced and often expressed in the hypothalamus of vertebrates, the homologous hormones in worms are produced and expressed in the neurosecretory brain regions (Donaldson and Young, 2008).

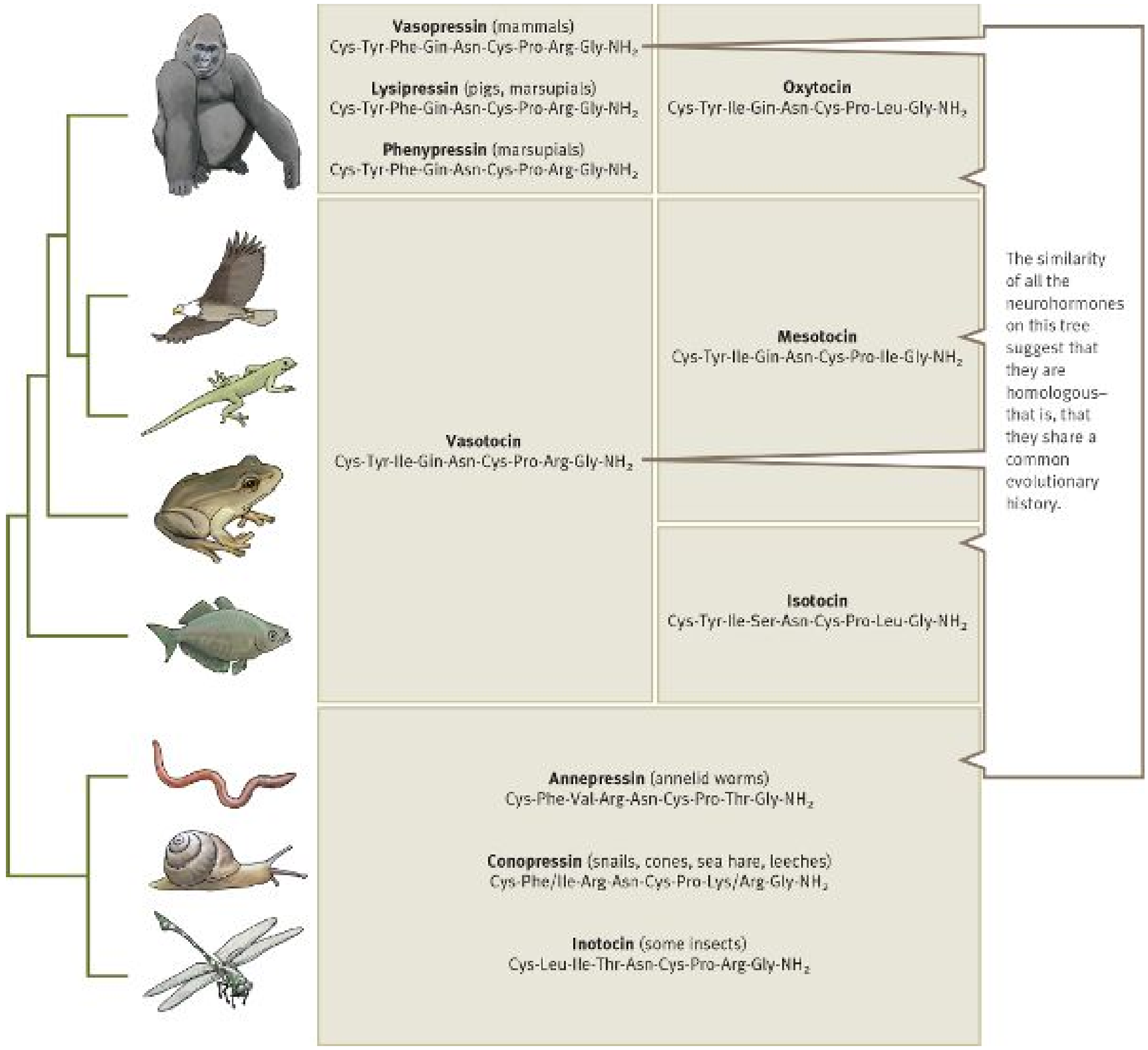


Figure 3.18. Evolutionary history of vasopressin and oxytocin. Note the similarity in amino acid structure between all the neurohormones on this phylogenetic tree. *(From Donaldson and Young, 2008).*

Vasopressin and oxytocin have been studied extensively in the context of parental care in two vole species: the prairie vole (*Microtus ochrogaster*) and the meadow vole (*Microtus pennsylvanicus*). Here, we focus on studies of vasopressin: in chapter 4, we will examine the role that oxytocin plays in these vole systems by discussing molecular genetic work centering on oxytocin in these species.

Prairie voles are monogamous—both males and females have a single mate each breeding season (chapter 8)—and males often display parental care and guard their mates. Meadow voles have a polygynous mating system, in which males mate with multiple females during a breeding season; in addition males display very little, if any, parental care or prosocial behavior toward their mates (McGuire and Novak, 1984; Oliveras and Novak, 1986). One of the major differences in male behavior toward their young and their mate centers on the vasopressin system in these two species.

In prairie voles, individuals have many more vasopressin receptors in the ventral pallidium area of their brains than meadow voles do (Figure 3.19). A number of lines of evidence suggest that this difference in the number of vasopressin receptors in the brain is responsible for the difference in male social behavior in prairie versus meadow voles. If vasopressin is experimentally administered to male prairie voles, it stimulates mate guarding and parental care. Such an experimental increase in vasopressin does not produce mate guarding and parental care in polygamous meadow voles, who lack the receptors to bind the extra vasopressin (Cho et al., 1999; Wang et al., 1994). If, however, molecular genetic techniques are used to experimentally increase the number of vasopressin *receptors* in the typically polygamous meadow vole, males display behaviors toward their mating partners that are similar to those seen in the monogamous prairie vole (Lim et al., 2004; Barrett et al., 2013; Donaldson and Young, 2013; Freeman and Young, 2016; Box 3.3).

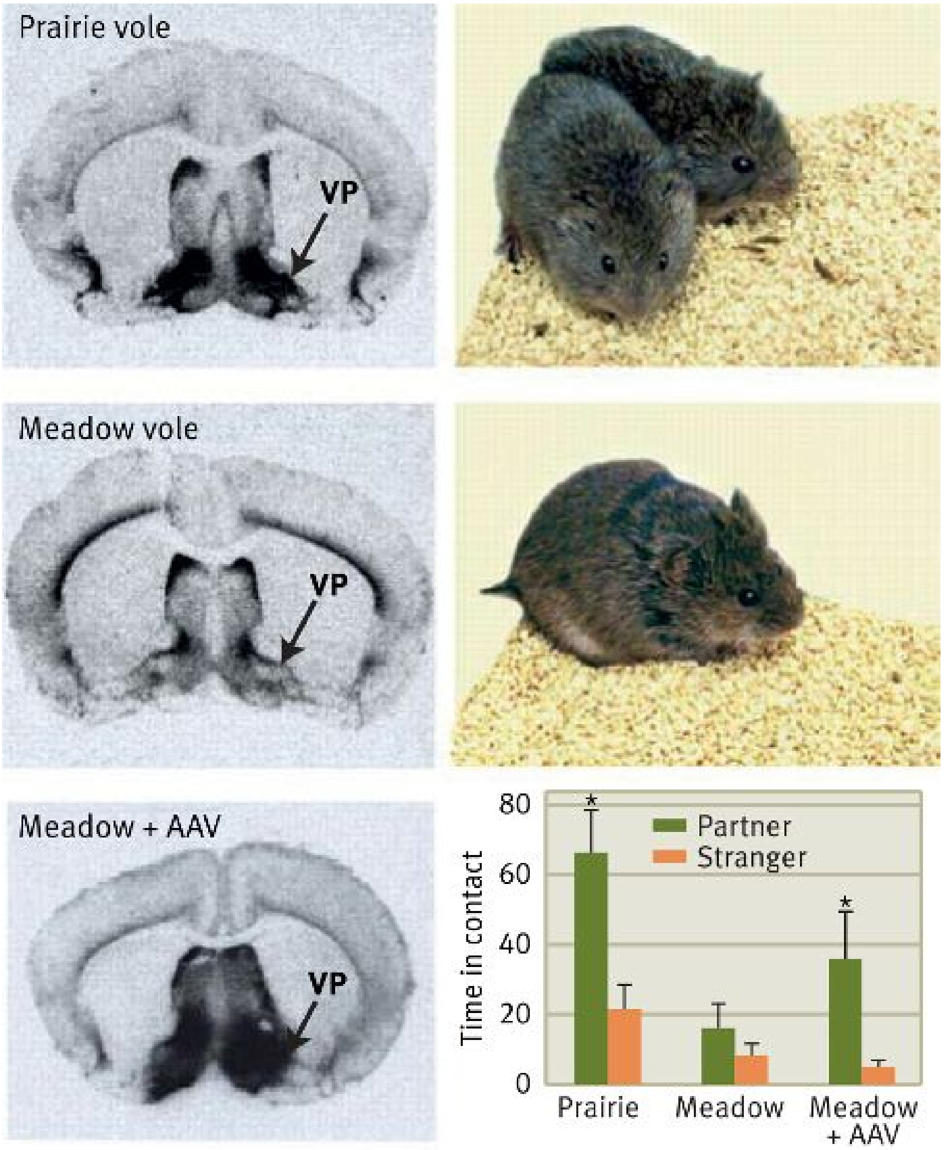


Figure 3.19. Vasopressin receptors in prairie and meadow voles. Vasopressin receptors in both species are concentrated in the ventral pallidum (VP) area of the brain. *(From Donaldson and Young, 2008, reprinted with permission from AAAS)*

Box 3.3. SCIENCE AT WORK

What is the research question? What role does vasopressin play in parental care in two closely related species of voles?

Why is this an important question? Parental care is critical both to offspring and to the reproductive success of parents, and vasopressin is thought to play an important role in parental care.

What approach was taken to address the research question? Many approaches were employed. In one, vasopressin receptors were examined in prairie voles, a monogamous species that exhibits parental care, and in meadow voles, a closely related polygamous species, in which parental care is greatly reduced.

What was discovered? Prairie voles have significantly more vasopressin receptors in certain areas of the brain. When vasopressin was experimentally increased in prairie voles, their parental care behaviors increased in frequency, but when vasopressin was administered to meadow voles, who lack the necessary receptors to bind the extra vasopressin, levels of parental care did not increase.

What do the results mean? Vasopressin plays a key role in social behaviors such as monogamy and parental care in prairie voles and sheds light on the differences between prairie voles and meadow voles in their parental care behaviors.

HORMONES AND HONEYBEE FORAGING

This chapter and chapter 4 use honeybee foraging behavior as a case study of an integrated proximate approach toward animal behavior, examining the effects of hormones, neural structures, genes, and development on honeybee foraging behavior. We begin with hormones and honeybee foraging (Figure 3.20).

Figure 3.20. Honeybee foraging. The proximate underpinnings of foraging behavior in honeybees have been studied in depth. *(Photo credit: Juniors Bildarchiv GmbH / Alamy Stock Photo)*

After emerging from their pupal cells individuals play many roles within a honeybee hive. Depending on the specific needs of a colony, during the first three weeks of life, young bees may clean the hive, feed larvae, produce wax, process honey, guard a hive, or fan the hive for thermoregulation. At approximately twenty-one days of age, some bees become foragers that leave the nest, search for pollen and nectar, and return to the nest with what they find. The shift to forager is associated with an increase in levels of juvenile hormone III (JH III), which is produced in a gland called the corpus allatum (Hagenguth and Rembold, 1978; Wyatt and Davey, 1996). Gene Robinson and his colleagues hypothesized that an increase in JH III was not only *correlated* with the shift to the forager stage but that changes in levels of JH III *caused* changes to the rate at which bees curtailed within-hive activities, like cleaning and hive thermoregulation, and became foragers. To test their hypothesis, Joseph Sullivan, Robinson, and their team surgically removed the corpus allatum (in a procedure known as allatectomy) in bees from four colonies (J. Sullivan et al., 2000, 2003;

Figure 3.21). The behavior of bees in the allatectomized group was then compared with that of two control groups, one in which the bees went through a similar surgical procedure but did not have their corpus allatum removed, and the other in which the bees were only anesthetized.

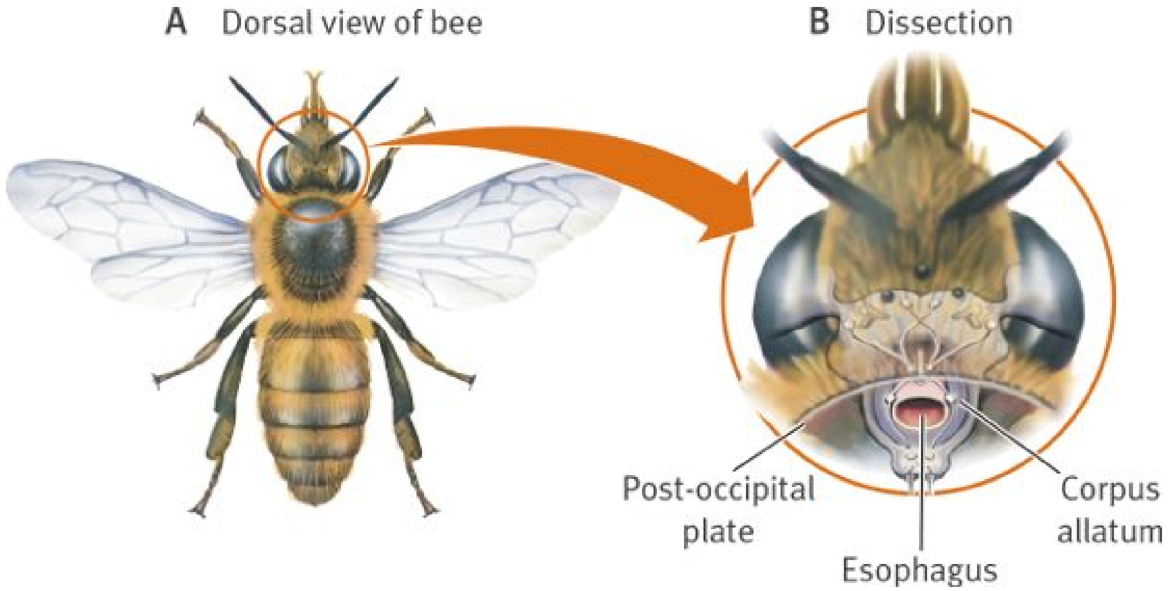
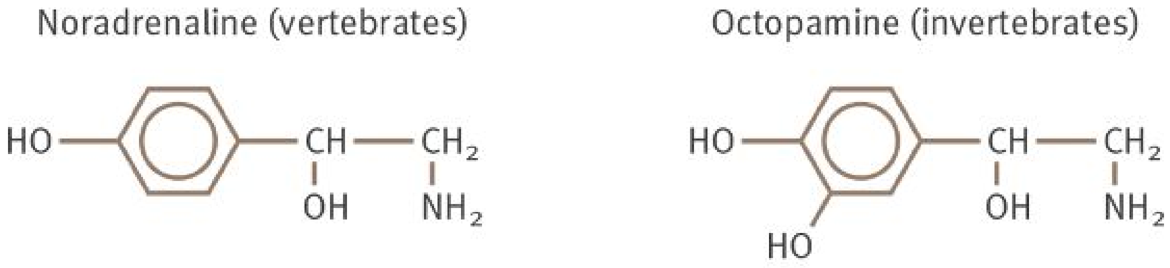


Figure 3.21. Removal of corpus allatum. To examine the effect of juvenile hormone (JH III) in honeybee foraging, researchers removed the corpus allatum—the gland that produces this hormone. The inset shows a view through the incision. *(Adapted from J. Sullivan et al., 2000)*

Sullivan and his colleagues found that although both allatectomized bees and control bees eventually became foragers, in three of the four colonies observed, bees that had been allatectomized (and thus had no JH III) began foraging significantly later than did bees in the control groups. When allatectomized bees eventually did become foragers, they returned to the nest much less often than did bees in the control treatments, and some work suggests that allatectomized bees are poor navigators in their environments. Sullivan and his team uncovered additional support for the link between JH III and the shift to foraging when they found that no other major behavioral changes resulted from removing the corpus allatum—just changes related to foraging (J. Sullivan et al., 2000, 2003).

The researchers hypothesized that if increased JH III levels were causing increased foraging behavior, experimentally increasing the JH III levels in allatectomized bees would result in a return to normal foraging behavior by the bees. Experiments designed to test this idea have found that when allatectomized bees are given a dose of a chemical called methoprene—a chemical that is similar to JH III—they show no differences in age-related foraging when compared with control bees, providing strong evidence for a causal role of JH III in foraging behavior in honeybees (G. Robinson, 1985, 1987; G. Robinson et al., 1989).

The neurohormone octopamine has also been linked to increased foraging activity in honeybees. Octopamine is found in invertebrates and is homologous with noradrenaline found in vertebrates (Farooqui, 2007; Roeder, 1999; Verlinden et al., 2010; Figure 3.22). Early work had shown that octopamine modulates learning and memory in honeybees and also affects their visual, olfactory, and gustatory senses (Erber et al., 1993; Hammer and Menzel, 1998; Scheiner et al., 2002). Forager bees have higher concentrations of octopamine in their brains than do nurse bees that stay at the hive, and octopamine reaches its highest concentration when a bee switches from nest-bound activities to foraging activities, including foraging-related flight behavior (Schulz et al., 2003; Wagener-Hulme et al., 1999; Liang et al., 2012). But does an increase in octopamine affect other activities in newly foraging bees, or does it just target flight activities related to foraging? How specific are the effects?



Both noradrenaline and octopamine:
Are stress hormones
Prepare animal for energy-demanding situations (“fight or flight”)
Stimulate sugar production
Regulate arousal in the nervous system

Figure 3.22. Comparing vertebrate and invertebrate systems. A comparison of the vertebrate adrenal system with the invertebrate octopamine system. *(Adapted from Roeder, 1999)*

Barron and Robinson found two lines of evidence that the effects of octopamine were specific to foraging activities (Barron and Robinson, 2005): (1) Although experimental treatment with octopamine increased flight activity related to foraging, it did not increase a second flight-related behavior—the removal of corpses from the colony; and (2) When bees treated with octopamine were exposed to other hormones associated with the production of a new brood of offspring, they increased their foraging behavior (to feed a now-larger hive), but they did not increase other activities associated with caring for the new brood.

Controlled experimental work on octopamine, along with JH III, illustrates the ways in which a proximate perspective of the honeybee endocrine system can shed light on a fundamentally important behavior in the life of a bee—foraging.

HORMONES AND VOCALIZATIONS IN PLAINFIN MIDSHIPMAN FISH

The endocrine system not only is a within-body communication network, but also is integrally involved in communication between individuals. To see this, let's examine work that Andrew Bass and his colleagues have done on communication and reproduction in the plainfin midshipman fish (*Porichthys notatus*). Bass and his colleagues have found two different types of males—type I and type II—in plainfin midshipman (Bass, 1998; Bass and Grober, 2009; Bass and Zakon, 2005; Forlano et al., 2015; Figure 3.23). Type I males build nests, are four times larger than type II males, have a higher gonad-to-body size ratio, and produce sounds in a number of behavioral contexts (Table 3.2). These males generate short-duration grunts when engaged in aggressive contests with other males and generate long-duration "hums" when courting females (Bass and McKibben, 2003; Bass and Zakon, 2005; Brantley and Bass, 1994). If selected as a mate, a type I male remains on the nest after a female lays her eggs there. In contrast, type II males are small and have low gonad-to-body size ratios. They are often referred to as "sneakers" because they do not build nests, but rather stay around the nests of type I males, where they dart in and shed sperm in an attempt to fertilize the nesting female (see chapter 7 for more on this behavioral strategy in bluegill sunfish). Unlike type I males, type II males do *not* hum to attract females, and they only occasionally produce grunt sounds.

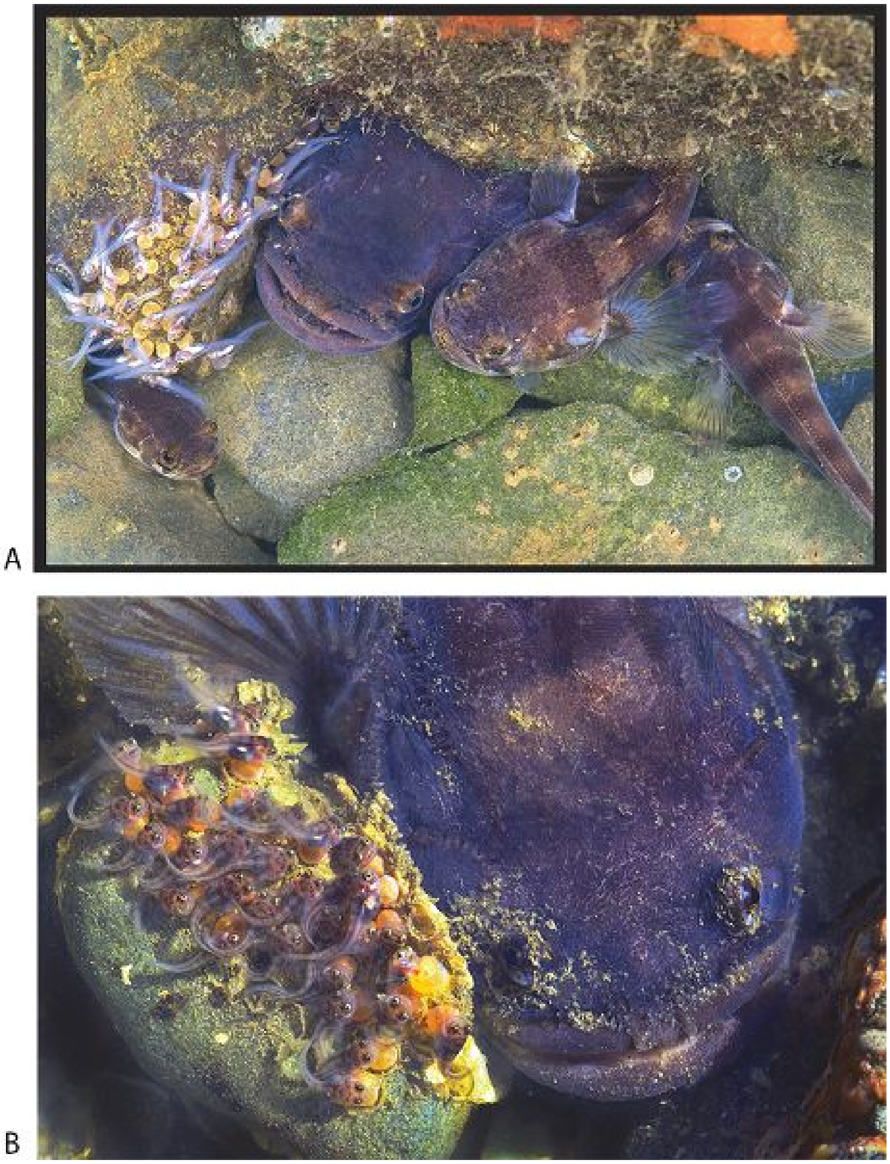


Figure 3.23. Vocalizations in plainfin midshipman. In plainfin midshipman, some male types produce vocalizations while others do not. (A) The two smaller fish on the ends are type II sneaker males (that do not sing), whereas the fish that is second from the left is a “singing” type I parental male. (B) A type I male in his nest with his brood attached to the rocks. *(Photo credits: © Margaret Marchaterre)*

Table 3.2. Traits of type I and type II males. A summary of the differences between type I and type II plainfin midshipman, and a comparison with plainfin midshipman females.

SEXUALLY POLYMORPHIC TRAITS	TYPE I MALE	TYPE II MALE	FEMALE
Nest building	yes	no	no
Egg guarding	yes	no	no
Body size	large	small	intermediate
Gonad-size/body-size ratio	small	large	large (gravid), small (spent)*
Ventral coloration	olive-gray	mottled yellow	bronze (gravid), mottled (spent)*
Circulating steroids	testosterone, 11-Ketotestosterone	testosterone	testosterone, estradiol
Vocal behavior	hums, grunt trains	isolated grunts	isolated grunts
Vocal muscles	large	small	small
Vocal neurons	large	small	small
Vocal discharge frequency	high	low	low

*Gravid connotes pregnant; spent connotes postpregnant.

Bass and his team discovered that a number of hormones, including melatonin, 11-Ketotestosterone (11 Kt; a form of testosterone), and cortisol are linked to differences in the sounds produced by type I and type II males (Forlano et al., 2015, Feng and Bass, 2014, Genova et al., 2012). Here we focus on the studies on 11 Kt and cortisol. Prior work on vocalizations in fish, as well as in birds and amphibians, had found that high levels of androgens such as testosterone and low levels of glucocorticoids like cortisol are associated with increased male sound production during the reproductive season. As such, Bass and his colleagues expected differences in the balance between androgens and glucocorticoids in plainfin midshipman males: more specifically, they hypothesized that they would find higher levels of circulating 11 Kt and lower levels of circulating cortisol in type I than type II males during periods of reproduction. Their results are in line with these predictions: type I males had higher levels of 11 Kt in plasma samples and higher KT levels in their testes than type II males, while Type II males had higher plasma cortisol levels.

Later in the chapter we will also examine the neurobiological differences between type I and type II males.

Neurobiological Underpinnings of Behavior

The endocrinological system is based on chemical communication. But chemical communication takes *time*—on the order of minutes to hours. A second communication network—the nervous system—relies on electrical impulses that allow for *much quicker* responses, including behavioral responses. This section of the chapter will serve as a primer on the nervous system and behavior, providing an overview of the neurobiological underpinnings of behavior. This field of work is often called **neuroethology**.

Animals possess specialized nerve cells, called neurons, which share certain similarities regardless of what message they conduct. Each neuron has a cell body that contains a nucleus and one or more nerve fibers. These nerve fibers, called **axons**, transmit electrical information from one cell to another. Axons can range in size from less than a millimeter to over a meter long. Axons also differ in terms of diameter. This variation is important because the speed of the nervous impulse affects the speed at which animals respond behaviorally, and the thicker the diameter of an axon, the faster the nervous impulse travels along it.

Each neuron has only a single axon. The first section is called the axon hillock, and the last section consists of the axon terminals (sometimes called synaptic terminals). There may be many branches of axon terminals, and it is from these branches that information leaves a neuron as it passes along the nervous system (Figure 3.24). Neurons receive impulses from other cells via fibers called **dendrites**. A neuron may have thousands of dendrites, forming a dendritic tree. In addition, in certain types of neurons, each “branch” on this dendritic tree may have many *dendritic spines* that receive input from other neurons.

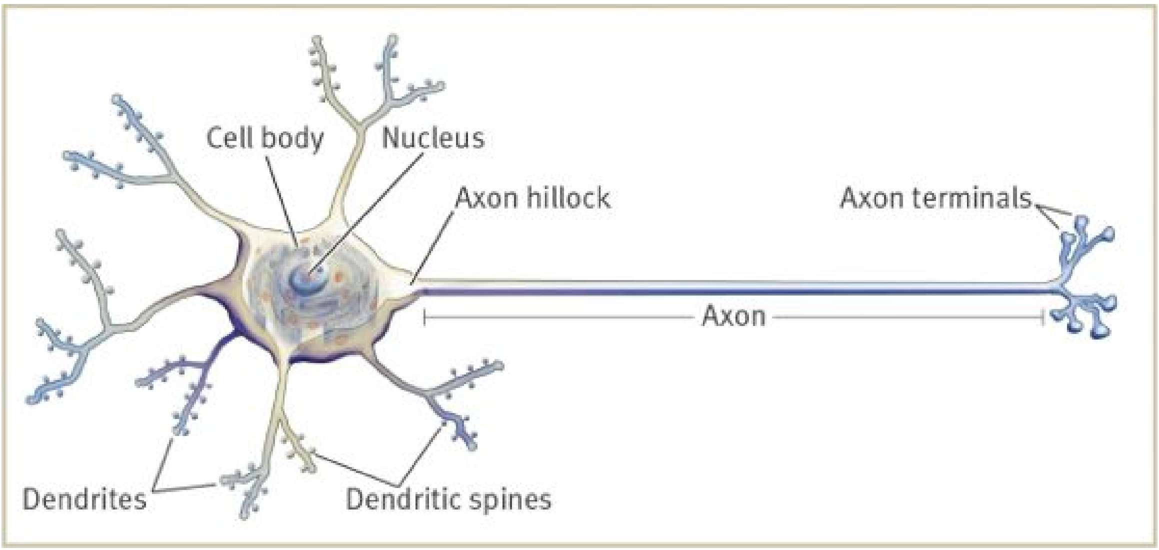


Figure 3.24. Nerve cell. Information is collected by dendrites, which often have dendritic spines projecting off their surfaces, conducted along an axon, and transmitted from the axon terminals across the synaptic gap to the dendrites of neighboring cells.

THE NERVOUS IMPULSE

Let's trace what happens from the point at which the nervous system of an animal responds to something in the environment to the point at which some sort of behavioral response can be measured. Suppose the external stimulus is tactile—the animal touches or is touched by something. In response to this stimulus, a wave of electrical activity sweeps down along the axons of sensory nerve cells that are in contact with the skin. Not all stimuli produce such a response. For this process to begin, the stimulus—the external touch in our example—must exceed the nerve cell's "threshold." Technically, the threshold is a function of the amount of change in the voltage across a neuron's membrane, but what is most important is that stimuli that don't meet this threshold fail to cause the nerve cell to fire, and stimuli above the threshold always cause the nerve cell to fire.

To use an analogy from electrical engineering, nerve cell thresholds are the equivalent of on-off switches, rather than a dimmer switch. Any stimulus greater than the threshold, regardless of how much greater, causes the nerve cell to fire. The nerve cell fires in exactly the same manner whether the stimulus is 1 percent greater than the threshold or 1,000 percent greater. But even though the nerve cell fires the same way each time its threshold is reached, organisms are still able to use their nervous systems to gauge the strength of a stimulus in at least two ways: (1) the number of times a neuron fires increases with the strength of the stimulus, and (2) the number of neurons that fire in response to a stimulus also increases as a function of stimulus strength.

Once an impulse has reached the end of an axon, it is transmitted to other neurons. This transmission may involve an electrical impulse jumping across the synaptic gap between neurons or, more commonly, the release of a neurotransmitter—for example, acetylcholine—from thousands of synaptic vesicles located on the tips of the branches at the end of the axon terminals. Once neurotransmitters migrate across the synaptic gap, they are absorbed by the membrane of the next neuron, or they bind to receptors that open an ion channel and/or initiate intracellular signaling cascades. Neurotransmitters add a chemical component to the nervous system—that is, some nervous impulses require both electrical and chemical transmission.

If the next neuron’s threshold has been met, it will fire. This process continues over and over as the nerve impulse migrates along its neural path. The neural pathway that was initiated by an animal being touched may end when the terminal neurons in the pathway *innervate* (stimulate) some *effector*, such as a muscle, to take action; in this case, terminal neurons might stimulate foraging behavior by opening or closing the jaw muscle if the animal has encountered potential prey or initiate flight behavior by innervating muscles associated with such flight, if the touch was that of an aggressive, dominant group member. In other instances, depending on the stimulus, nerve pathways might end with the secretion of a chemical that causes an endocrine gland to secrete a hormone. This cause-and-effect relationship between the terminal neurons and the secretion of hormones that affect behavior demonstrates that the neural and endocrinological communication systems are not independent of one another but are part of a complex communication web that provides an organism with information about its external and internal environments.

This communication web can work in many ways. Our example involving the neuroethological response to touch focused on a stimulus that causes an excitatory response along the nervous system, eventually translating into an animal taking some behavioral action (for example, foraging, fleeing). But some stimuli cause inhibitory effects, whereby a neuron sends a signal that does not meet the threshold of the cell that receives the signal, eventually resulting in the inhibition of behavior. Such inhibitory responses might be lifesaving—as a result of this process an animal might, for example, freeze in the presence of predators that hone in on the motion of prey.

At a very general level, nervous systems across many animals show some consistent evolutionary trends: Nerve cells that served specific functions—including functions linked to behavior—became clustered. Over evolutionary time, nervous systems became centralized, and longitudinal nerve cords became the major highways across which nervous impulses traveled. The front end of the longitudinal nerve cord became dominant, leading to the evolution of the brain.

Many new technologies are now in place that allow neuroscientists to scan activity in the brains of animals, providing researchers with a better understanding of the way that the nervous system shapes the immediate, as well as the long-term, behavioral responses of animals to stimuli in their environment. For example, functional magnetic resonance imaging (fMRI) allows scientists to measure neuronal activity across large sections of animals' brains, and to do so with high resolution. This procedure allows ethologists to address important questions related to behavior: Do different salient stimuli—a potential mate, a competitor, a predator, a food item—translate into different neural activity at the brain level, and if so, how (Ferris et al., 2008)? Do we see similar patterns in closely related species? Do we see similar patterns in distantly related species? Does the same general behavioral pattern—for example, aggressive behavior—involve different brain activity patterns in different contexts? At the brain level, does aggression toward a potential predator look similar to aggression toward a conspecific? If so, why? Do behaviors associated with a positive reward—food, access to mates, and so on—generally look similar at the level of the brain? Why or why not? Though researchers are still trying to understand exactly how to interpret patterns across large areas of the brain, early work in whole-brain neuroimaging is already providing useful insight into the ways that important stimuli in the environment "map" onto brain activity (Figure 3.25).

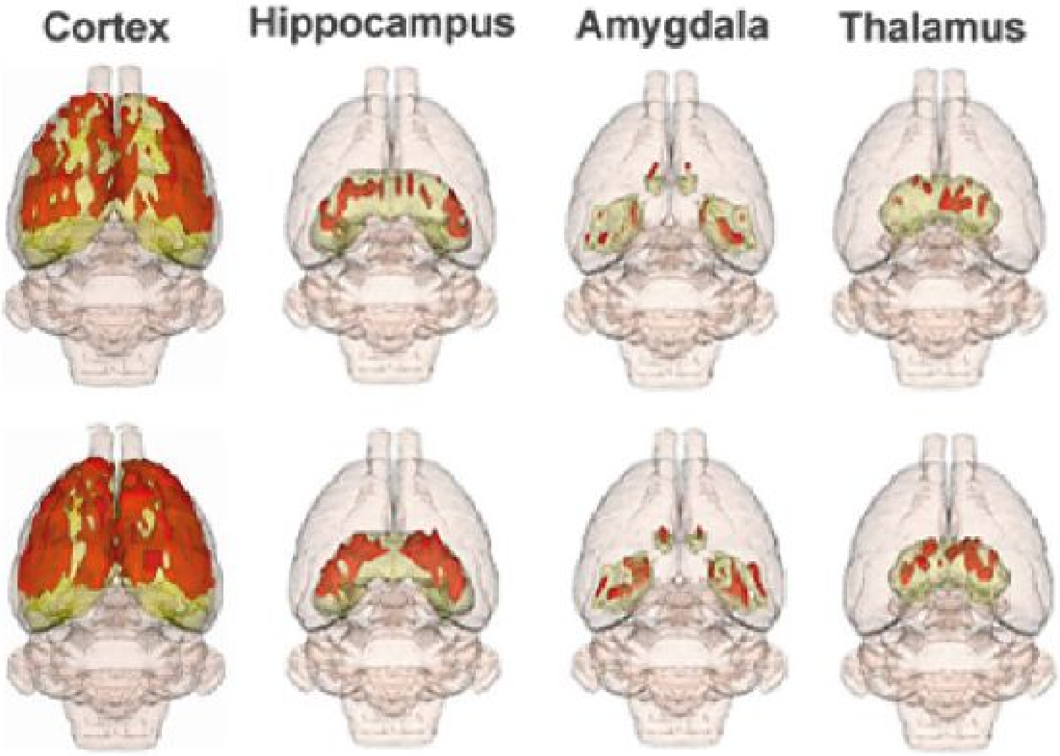


Figure 3.25. Brain scans in rats. Ten male rats were presented with either their female cage mate or their female cage mate and a male intruder. Different activity patterns in different parts of the brain were detected (red indicates activity). *(From Ferris et al., 2008, courtesy of BioMed Central)*

With this brief review of the animal nervous system in hand, we can now move on to examine how animal behaviorists might address proximate questions using a neuroethological approach.

MUSHROOM BODIES AND HONEYBEE FORAGING

We now return to the proximate analysis of foraging behavior in bees that we earlier discussed, but here we approach this topic from the standpoint of neuroethology. Honeybee foragers must navigate outside their hives in search of food. In vertebrates this spatial navigation is often associated with the hippocampus, but in invertebrates, it is most often linked with a cluster of small neurons located at the front of the brain. This cluster, known technically as the *corpora pedunculata*, is often referred to as the **mushroom bodies** (Capaldi et al., 1999; Fahrbach, 2006; Aso et al. 2014; Figure 3.26).

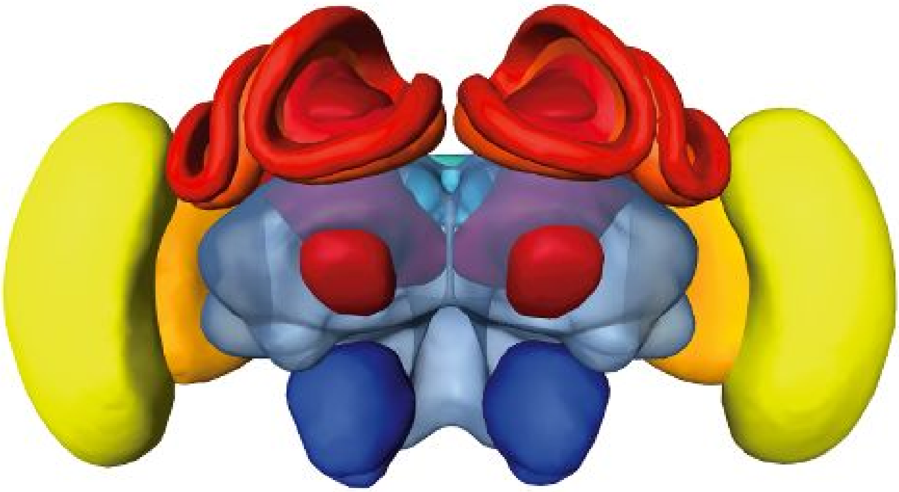


Figure 3.26. Mushroom bodies. The mushroom bodies—shown in light blue—are clusters of neurons located at the front of the bee brain and are involved in spatial learning. The yellow denotes the optic lobes of the bee brain. *(Photo credit: Amira Software)*

As discussed earlier in the chapter, younger bees usually stay within the hive and later switch to foraging outside the hive (G. Robinson, 1992). Foragers—who sometimes travel many kilometers in search of food—use both visual and olfactory cues in their search for food, and mushroom bodies play a key role in this process.

Rather than immediately beginning a search for food in the nearby environment, would-be foragers often turn back toward the nest and hover up and down for several minutes, in what is referred to as an "orientation flight," orienting the foragers to the relative position of their nest in the environment (Willmer and Stone, 2004). Bees often begin these orientation flights when they are about one week old, though they don't actually start foraging until they are about three weeks of age. Ginger Withers, Susan Fahrbach, and Gene Robinson examined bees of different ages and castes within a colony (foraging versus caring for the larvae in the hive) to see whether the relative size of their mushroom bodies differed as a function of task allocation. They found that mushroom bodies of foragers were 14.8 percent larger than those of the other groups that they measured, suggesting a link between mushroom bodies and foraging (Withers et al., 1993; Figure 3.27). The volume of other nerve clusters *relative* to total brain size in the honeybee brains did not differ as a function of task allocation; only the mushroom bodies increased in relative size. But there is a confound here: The exact age of the foragers was unknown, and the age of the “nurse” bees from the hive was also unknown. The relationship between mushroom body size and foraging might be the result of age differences, rather than differences in task.

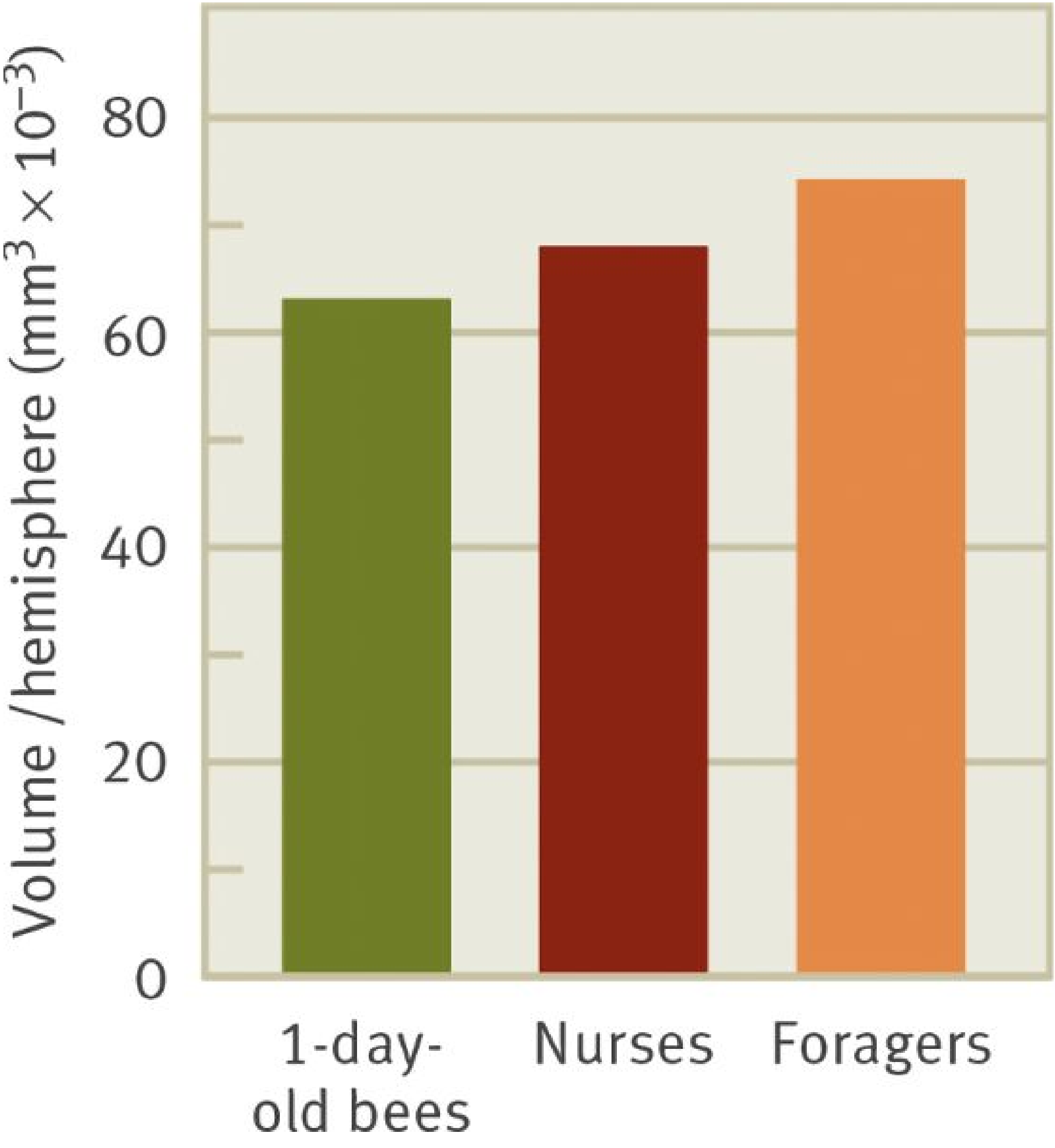
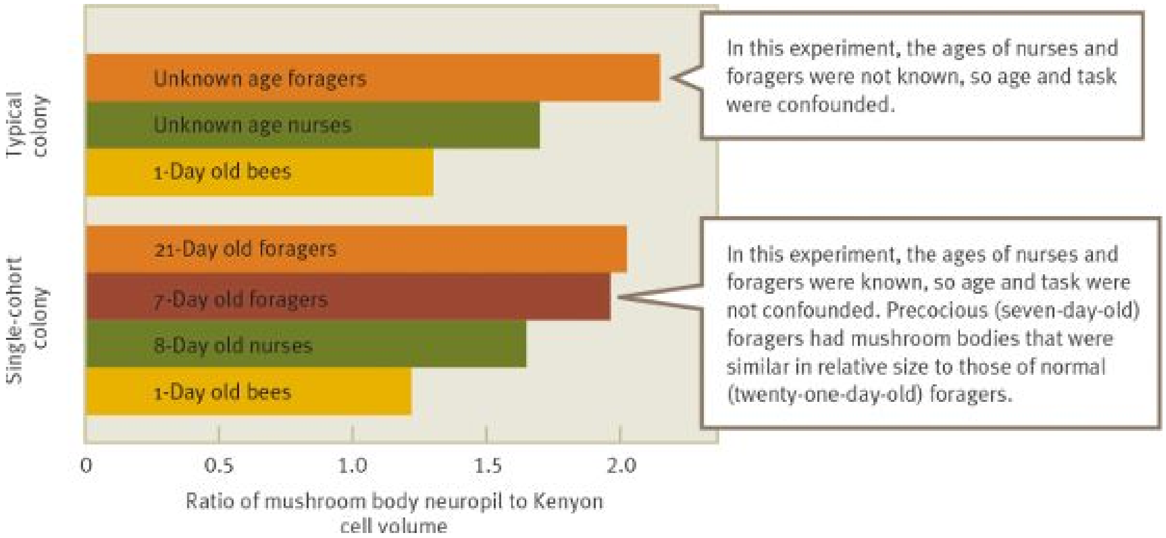


Figure 3.27. Mushroom bodies and foraging. Mushroom bodies were larger in foragers than in honeybees that remained in a colony (one-day-old bees and nurses who care for the larvae in the hive). *(From Withers et al., 1993)*

To separate the effect of age and task on mushroom body size, Withers and her team gathered together one-day-old bees from numerous groups and formed a colony composed only of one-day-old bees. Creating a colony of young, same-aged individuals induces early foraging behavior—bees in the experimental treatment began foraging at around four to seven days of age. The configuration of the mushroom bodies in these precocious foragers resembled that of normal-aged foragers, suggesting that activities related to foraging trigger a series of neural-based changes in mushroom body volume, illustrating yet another instance of neural plasticity (Sigg et al., 1997; Withers et al., 1993; Figure 3.28). In the next chapter, we will examine the molecular genetic underpinnings of mushroom body growth and neural plasticity (Lutz et al., 2012).



In this experiment, the ages of nurses and foragers were not known, so age and task were confounded.

In this experiment, the ages of nurses and foragers were known, so age and task were not confounded. Precocious (seven-day-old) foragers had mushroom bodies that were similar in relative size to those of normal (twenty-one-day-old) foragers.

Figure 3.28. Disentangling age and task in the division of labor. Researchers could disentangle age and task in relation to honeybee foraging. They found that the relative size of mushroom bodies of precocious foragers was about equal to that of normal foragers. *(From Withers et al., 1993)*

NEUROBIOLOGY AND VOCALIZATIONS IN PLAINFIN MIDSHIPMAN FISH

Returning to the work on reproduction in midshipmen that we discussed earlier in the chapter, let’s now examine the neurobiological underpinnings of the difference in the way that type I and II males communicate.

The vocal organ of the midshipman is a set of paired sonic muscles attached to its swim bladders (Figure 3.32). *Both* type I and type II males have such sonic muscles, so the presence of the vocal organ per se does not explain the different ways that type I and II males produce sounds. But type I males have larger sonic muscles with more muscle fibers, and this difference in size affects sound production (Bass, 1992; Bass and Marchaterre, 1989). This difference in size of the sonic muscles is only part of the reason that type I and II males produce such different vocalizations. Each of the sonic muscles receives nervous impulses from a sonic motor nucleus that runs from the hindbrain of the fish down along the spine to the sonic muscles. The two sonic motor nuclei themselves are innervated by "pacemaker" neurons that generate impulses in a regular cyclic, rhythmic pattern. Bass and his colleagues have mapped out much of this pathway and have found differences in the rate at which pacemaker neurons generate impulses. The pacemaker neurons in type I males fire at a rate that is 15 to 20 percent higher than that of type II males, helping explain the differences in the vocalizations of type I and II males, and therefore the differences relating to reproductive behavior and aggression.

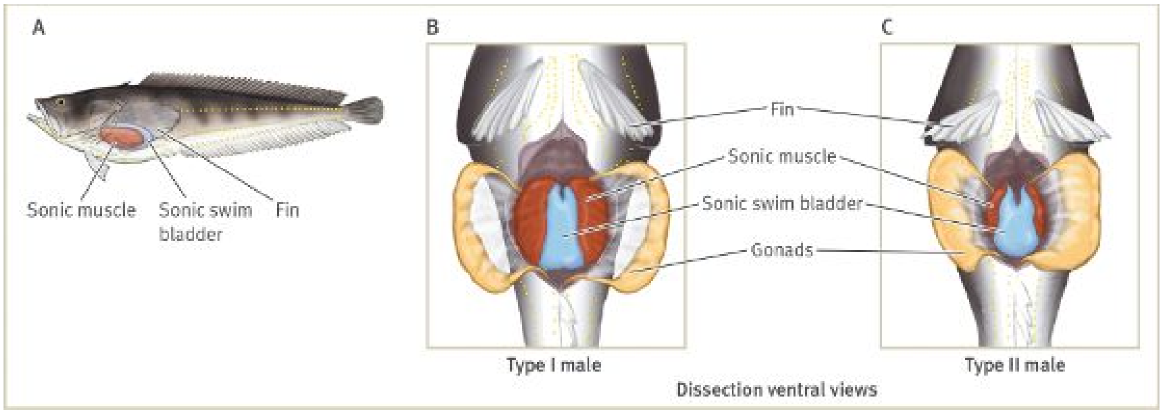


Figure 3.32. Sonic muscles and vocalization. (A) The vocal organ of the plainfin midshipman is made up of a pair of sonic muscles attached to the walls of the swim bladder. (B) Sonic muscles of type I males are well developed in comparison with muscles from type II males (in C). *(From Bass, 1996, p. 357)*

Box 3.4. COGNITIVE CONNECTION

Brain Size and Problem Solving

Brain size in mammals varies from less than 1/1000 of a gram in some ant species to 9 kilograms in sperm whales, with some species having larger than expected brain sizes for their body mass (for example, the dusky dolphin, *Lagenorhynchus obscurus*), and others smaller than expected (for example, the common hippo, *Hippopotamus amphibius*). Yet how, indeed whether, brain size per se affects social behavior has a long and somewhat controversial history in ethology. Rather than delve into that history here, we will instead examine recent cutting edge modern work that looks at whether brain size is correlated with problem solving. In particular, we will test the hypothesis that mammalian carnivores with brain sizes that are relatively large for their body mass are better at solving foraging-related problems.

Kay Holekamp and her colleagues ran an experiment in which they used a standardized “puzzle box” paradigm to examine problem solving in 140 individuals in thirty species of mammalian carnivores housed at nine zoos in North America (Benson-Amram et al., 2016; Figure 3.29). The puzzle box was a steel-meshed locked box with a food item placed in it; the size of the box and the food item were tailored to the size and diet of the species tested. All animals were tested alone and after they had been deprived of food for 24 hours.

Figure 3.29. **The puzzle box paradigm.** Individuals from 39 species of mammals were tested on their ability to open a locked puzzle box to get access to food. (A) Amur tiger (*Panthera tigris*) with a larger puzzle box, (B) red panda (*Ailurus fulgens*), and (C) white-nosed coati (*Nasua narica)* with smaller puzzle boxes. *(From supplemental material in Benson-Amram et al., 2016)*

Forty-nine of the 140 individuals (35%) tested solved the puzzle box problem and retrieved the food (Figure 3.30). Somewhat surprisingly, individuals from group living species were no better at solving the puzzle box problem than those from social living species, and how quickly individuals approached the puzzle box also did not affect their proclivity to solve the problem.

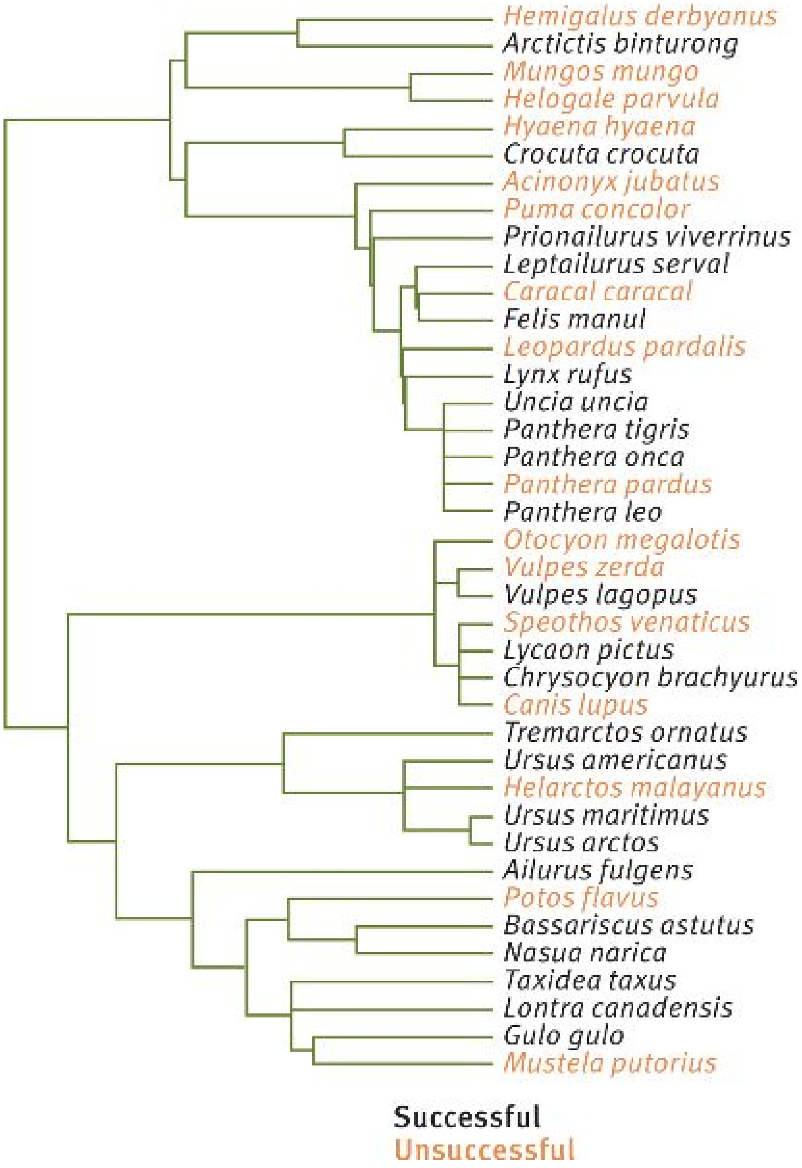


Figure 3.30. **Solving the puzzle box.** The phylogenetic relationship among the species that were tested in the puzzle box paradigm. Successful = at least one individual solved the puzzle box problem. *(From Benson-Amram et al., 2016)*

The results, corrected for shared phylogenetic history, show that absolute brain size and brain size scaled to body size both are positively correlated with an increased ability to solve the puzzle box problem, but the relationship is only significant for brain size scaled to body size (Figure 3.31). Indeed, larger-bodied animals tended to fare worse than smaller-bodied individuals, leading the researchers to conclude “it truly does seem that a larger brain size relative to body size is an important determinant of performance on this task, and it is not the case that larger animals are more successful simply because their brains are larger than those of smaller species” (Benson-Amram et al., 2016).

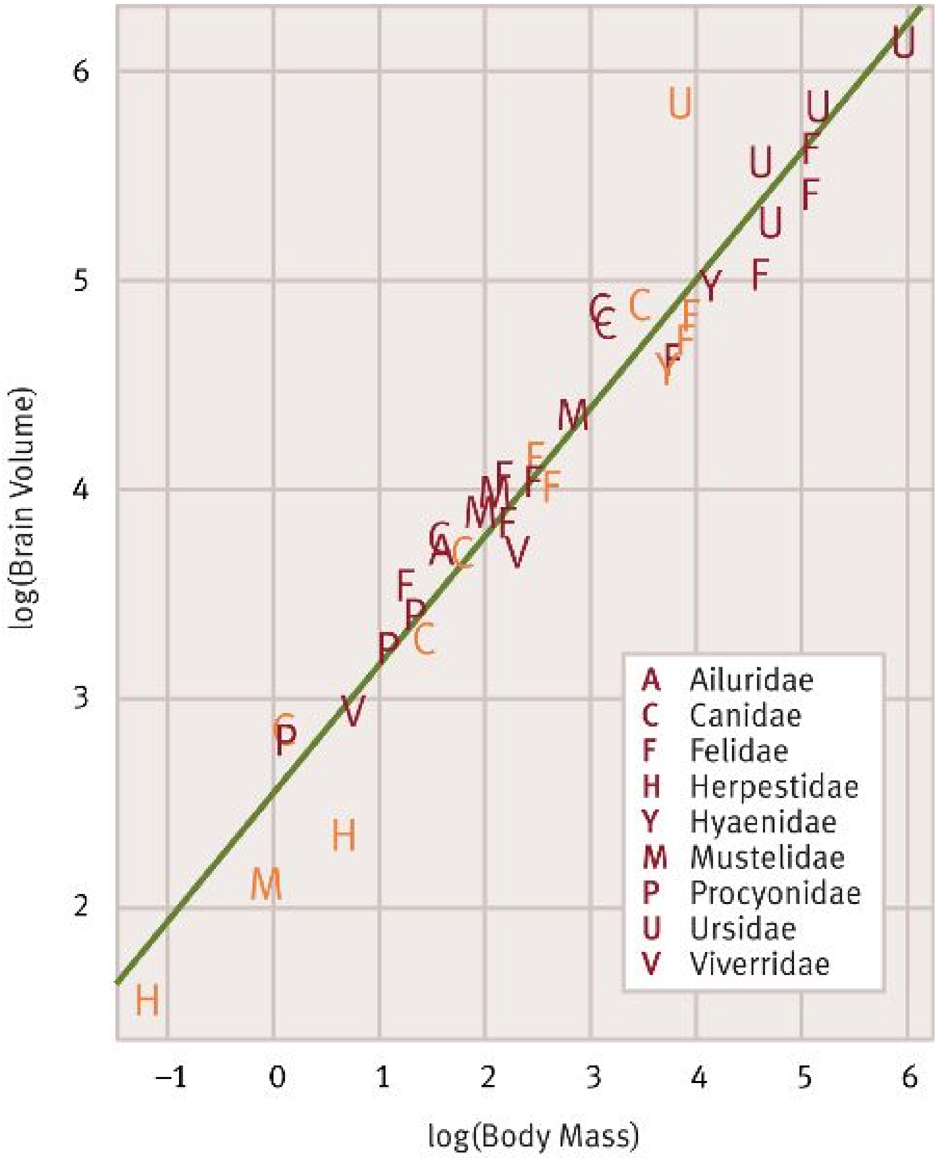


Figure 3.31. **Relative brain size and the puzzle box problem.** Individuals from species with relatively large brain size for their body mass were more likely to solve the puzzle box problem. *(From Benson-Amram et al., 2016)*

Bass and his team have demonstrated a tight linkage between neurobiological and endocrinological approaches to sound production in type I and type II males (Bass and Zakon, 2005; Remage-Healey and Bass, 2007; McIver et al., 2014). Arginine vasotocin (AVT) inhibits activity in the neurobiological circuitry associated with the production of sounds in type I males, but AVT does not affect vocal motor activity and sound production in type II males. Isotocin (IT) has the exact opposite effect, inhibiting activity in the neurobiological circuitry associated with sound production in type II males, but having no effect on sound production in type I males (Bass and Baker, 1990, 1991). The areas of the brain involved in sound production in the midshipman—more specifically, the preoptic and anterior hypothalamus—are similar to brain sections involved in sound production in numerous other species. The linkage among hormones, neurobiology, and sound production in the midshipman thus may have some important general applications for other vertebrate groups. In that sense, midshipman fish are a “model species” for examining the interplay of the neuronal and endocrinological systems involved in the production of sound. Work on plainfin midshipman also shows how *internal* communication systems—endocrinological and neuronal—help us understand an *external* communication system, namely, sound production (Goodson and Bass, 2001).

SLEEP AND PREDATION IN MALLARD DUCKS

Ethologists have studied sleep behavior from both a proximate and an ultimate perspective (Capellini, 2008; Lesku et al., 2008, 2011; Rattenborg et al., 2011, 2012; Roth et al., 2010). Sleep is necessary for normal functioning in animals, but poses a problem; sleeping individuals are more susceptible to being attacked by predators. Here we will look at the proximate underpinnings of a remarkable antipredator behavior seen in a number of creatures—sleeping with one eye open and one eye shut. This type of sleep was first recorded in chickens (Spooner, 1964), but here we focus on John Rattenborg and Steve Lima’s studies of sleep and antipredator behavior in mallard ducks (*Anas platyrhynchos*; Lima et al., 2005; Rattenborg et al., 1999a, 1999b, 2000; Beckers and Rattenborg 2015).

Mallards are able to sleep with one eye open and one hemisphere of the brain awake: they sleep with half their brain awake and half their brain asleep, in what is referred to as unihemispheric sleep (N. Ball et al., 1988). Rattenborg and Lima examined unihemispheric sleep in mallards and found that not only could they sleep with one eye open, but mallards on the periphery of a group, where they are more susceptible to predation, relied on unihemispheric sleep more than birds in the center of the group (Figure 3.33). Indeed, birds on the periphery of the group slept with the open eye outward, away from their group and toward areas of potential predation (Figure 3.34).

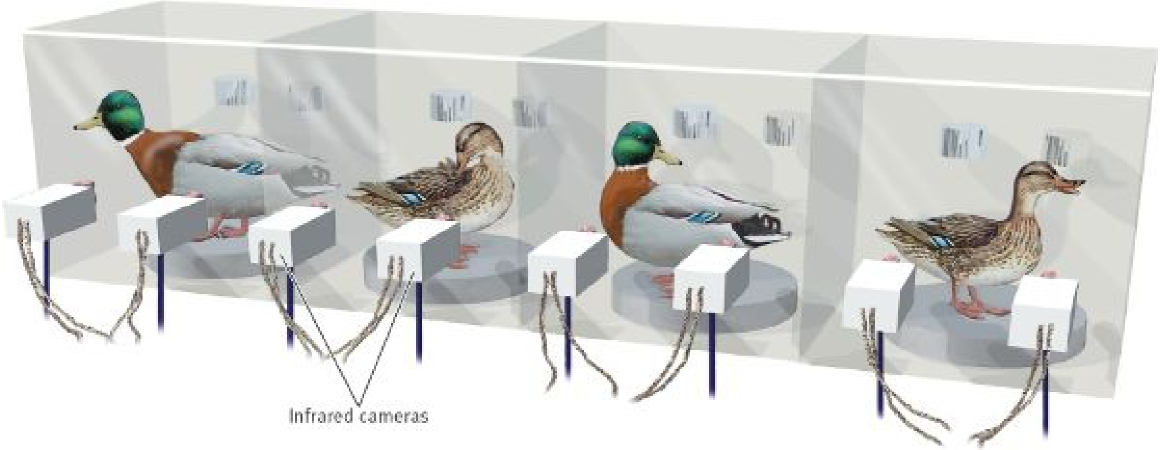


Figure 3.33. Sleeping apparatus. This experimental housing unit was employed to record eye state and electrophysiology of four mallard ducks. Eight infrared cameras were used to allow the movement of each eye of each mallard to be recorded. Birds on the extreme left and right were considered to be on the edges of the group. *(From Rattenborg et al., 1999a)*

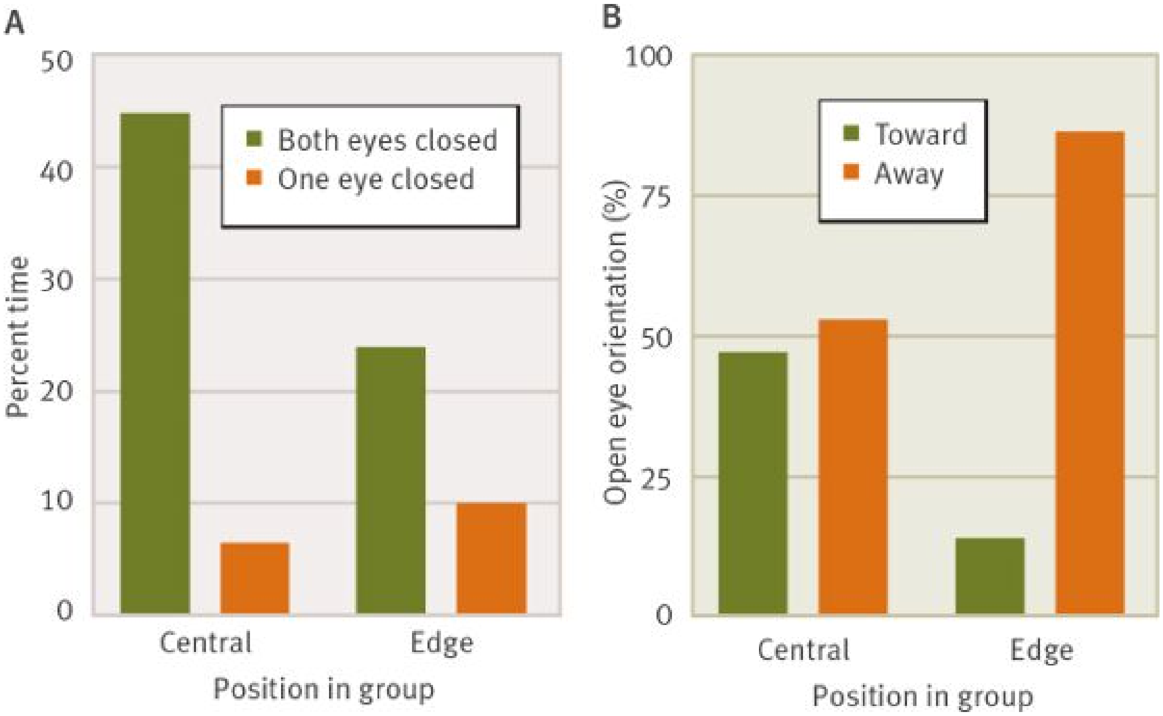
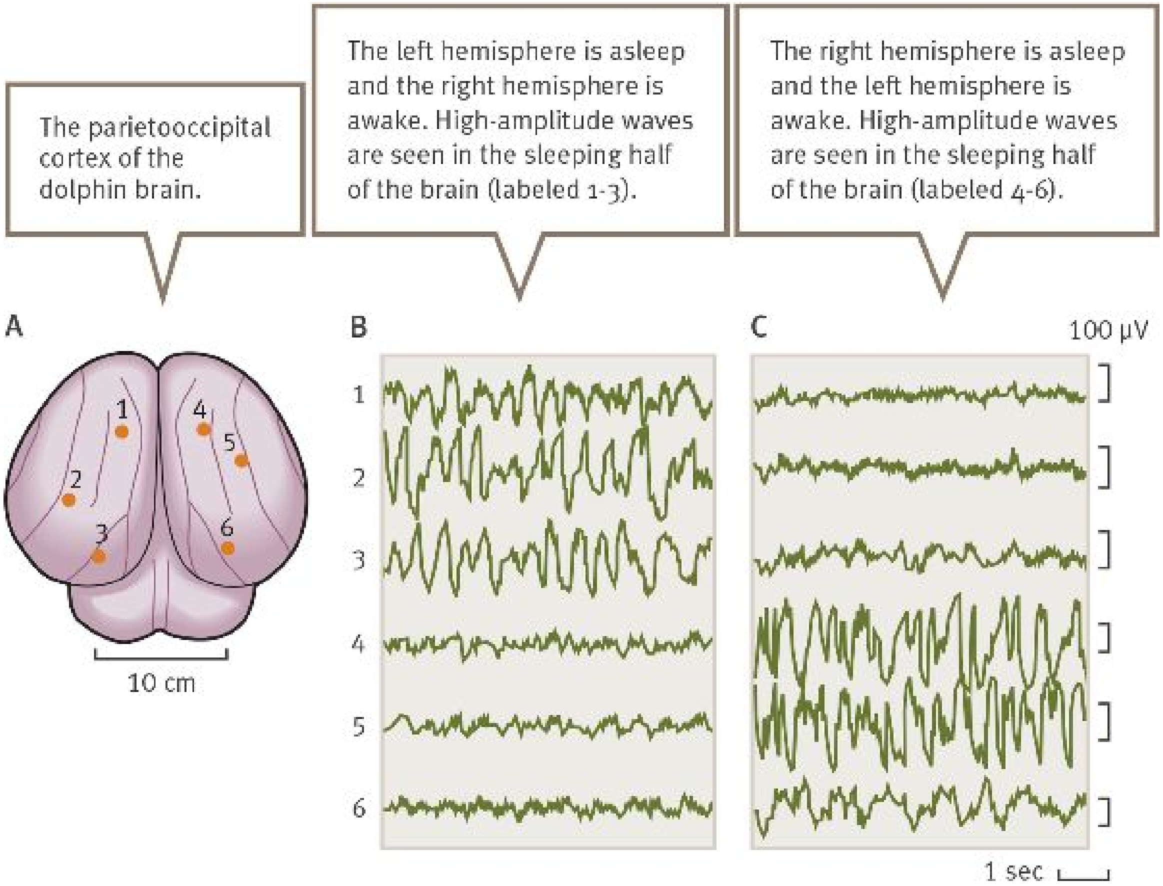


Figure 3.34. Unihemispheric sleep. (A) Percentage of time ducks spent with one eye closed or both eyes closed as a function of position in the group (at the group's center or on its edge). (B) When ducks were at the edge of a group and had one eye open, they spent much more time looking away from the group's center than when they had one eye open and were at the center of the group. Elsevier © 2000. *(From Rattenborg et al., 1999a)*

How do mallards manage this split-brained sleep? It seems that they are capable of putting one hemisphere of the brain—the hemisphere active during sleep—into what is called slow-wave sleep (Rattenborg et al., 1999a, 1999b). Slow-wave sleep in birds has a signature (in terms of wave frequency and amplitude) that is quite different from other states of sleep or wakefulness. This slow-wave state allows quick responses to predators, but it does not interfere with the sleeping half of the bird's brain until danger is present. EEG recordings indicate that the part of the brain controlling the open eye during unihemispheric sleep showed the low-frequency range characteristic of slow-wave sleep, while the other half of the mallard's brain showed EEG patterns that were similar to those of true sleep.

Much of the work on unihemispheric sleep has been undertaken in birds, but they are not the only group in which this form of sleep has been studied. Although most mammals sleep with both halves of the brain asleep (bihemispherically), aquatic mammals are an exception. In aquatic mammals like dolphins, whales, fur seals, and sea lions, unihemispheric sleep is thought to allow individuals to swim to the surface and breathe during sleep (Lyamin and Chetyrbok, 1992; Mukhametov et al., 1988; Figure 3.35). Various techniques have been used across these studies to measure activity in the two sides of the brain, including brain temperature measurements, in which temperature was found to be higher in the "awake" side of an animal's brain than in the "sleeping" side (R. Berger and Phillips, 1995; Kovalzan and Mukhametov, 1982; Box 3.5).



The parietooccipital cortex of the dolphin brain.

The left hemisphere is asleep and the right hemisphere is awake. High-amplitude waves are seen in the sleeping half of the brain (labeled 1-3).

The right hemisphere is asleep and the left hemisphere is awake. High-amplitude waves are seen in the sleeping half of the brain (labeled 4-6).

Figure 3.35. Sleeping in dolphins. EEG activity was measured in dolphins during unihemispheric sleep *(From Mukhametov et al., 1988)*

Box 3.5. SCIENCE AT WORK

What is the research question? How do mallards sleep with one eye open and one eye closed?

Why is this an important question? Sleeping with one eye open is a fascinating antipredator adaptation, and studying the proximate underpinnings will help us better understand this behavior.

What approach was taken to address the research question? Brain wave patterns from mallards sleeping with one eye open, and one eye closed, were recorded.

What was discovered? The side of the brain that controls the eye that remained open during sleep was put into what is called slow-wave sleep, which allowed a quick response to threats of predation.

What do the results mean? Sleep makes up a large portion of the lives of many animals. Differential patterns of brain activity allow mallards to employ an antipredator behavior that protects them during sleep.

Interview with Dr. Geoffrey Hill

Why do you think so few ethologists design experiments to test both proximate and ultimate questions? Why do researchers tend to specialize in one or the other?

Increasing specialization has been a trend in Western culture for hundreds of years, and specialization in all endeavors is accelerating in the twenty-first century. Science is a reflection of society at large, and in modern science all researchers are specialists. Consider a scientist during the time of Darwin or Newton. Scientific meetings in the nineteenth century included researchers from all branches of science and every scientist was conversant and up to date on the latest discoveries in all fields of science. Part of the inspiration for Darwin’s theory of natural selection was a book that he read that presented a new theory for geological processes. Today, scientists cannot realistically stay abreast of discoveries even within a single discipline like biology or chemistry. With the explosion of knowledge in past decades, a scientist has to spend all of his or her time just keeping up with the latest research in a very narrow subdiscipline like behavioral ecology. So, it is not surprising that many researchers who are focused on ultimate questions related to the function and evolution of behaviors do not engage in parallel lines of research investigating the proximate neural or hormonal mechanisms underlying the behaviors that they study. The techniques for one scientific approach are essentially unknown to individuals trained in another scientific approach.

A trend in modern science that helps to counteract the move toward increasing specialization is collaboration. Collaborative, multidisciplinary studies are drawing in more top scientists, and many funding agencies are actively encouraging multidisciplinary studies by providing special funding for such projects. Collaborative projects allow a topic to be studied from both ultimate and proximate perspectives by combining the skills and knowledge of scientists with different training. Such collaborative efforts can lead to breakthroughs in our understanding of behavioral processes.

What drew you to focus your research program on bird behavior?

Since I was a preteen I’ve been a bird nut. I got my first pair of binoculars when I was eleven and I’ve been chasing birds ever since. I’m very fortunate in being able to turn my hobby into my profession. I never seriously considered studying anything but bird behavior. As much as I enjoyed finding and identifying different species of birds as a young bird-watcher, my greatest exhilaration came when I captured birds, put bands on their legs, and followed and chronicled their individual successes and failures. There is really nothing like walking onto a university campus where every individual house finch is wearing colored bands that I placed on their legs and slowly gaining an understanding of why the birds behave as they do.

Early on in my career, I made the conscious decision to give up some travel opportunities and focus on common local bird species that are logistically easy to study. At times I envy my colleagues who get to travel to exotic locations for their studies of bird behavior, but the exhilaration of having a tractable population of birds where I can conduct convincing tests of key behavioral hypotheses is more than compensation for travel opportunities lost.

Generally speaking, how do you think proximate and ultimate perspectives interact in helping us to better understand animal behavior?

I think we clearly need both ultimate and proximate explanations of all behavioral phenomena if we want to really understand them. The two levels of explanation do not work in opposition to each other—they reinforce one another. Evolution of behaviors can only proceed within the constraints of the underlying proximate mechanisms. Proximate mechanisms are shaped by evolution. An understanding of proximate control of behavioral traits inevitably leads to new insights about how they function and why they evolved. Conversely, an evolutionary prospective can guide studies about proximate mechanisms and make such mechanisms more comprehensible.

As an example of how ultimate and proximate studies reinforce each other, consider studies of red coloration in fish and birds. Explaining such red coloration was a focus of both physiologists and ethologists in the mid-twentieth century, but through several decades these two groups of scientists paid little attention to each other's work. During this period, ethologists showed that red coloration often functioned in mate attraction, and physiologists determined that red coloration of both birds and fish was commonly created by deposition of carotenoid pigments. Moreover, physiologists discovered that carotenoid pigments could not be synthesized by birds or fish but had to be ingested as macromolecules. Coming out of this era, scientists had both a proximate and ultimate understanding of red coloration, but a comprehensive understanding of red coloration eluded both groups.

A breakthrough in the understanding of red coloration (and ornamental traits in general) occurred when pigment physiology was united with observations of mating preferences and sexual selection theory. Observations and bits of information that seemed disconnected and inexplicable suddenly made perfect sense. Carotenoid pigmentation was a useful criterion in mate choice because carotenoid pigments cannot be synthesized. These pigments have to be ingested, and acquisition and utilization of carotenoid pigments could be interrupted by environmental conditions. Red pigmentation was a signal of success in dealing with environmental challenges. This conclusion could only have been reached by working from and uniting the foundations laid by initial proximate and ultimate studies.

Suppose, for the sake of argument, that a hypothetical "house finch genome project" was now complete. How would this sort of information affect the way you studied behavior in this species?

A finch genome would lead to breakthroughs in our understanding of many aspects of the behavioral ecology of house finches, such as the genetic basis for behaviors, the co-evolution of display traits and preferences for such traits, and the link between genetically based immunity and ornamentation. There is no house finch genome project in the works, but the genome of the domestic chicken has already been sequenced, and the first songbird genome—from the zebra finch—is currently in the works. The chicken genome is already very useful for interpreting genetic data from house finches, and a zebra finch genome will be even more useful, even though zebra finches are in a different songbird family than house finches.

Even without a house finch genome, my colleagues and I have seen great opportunities for testing behavioral hypotheses with new genetic tools, and I've been increasingly involved in genetic work with house finches. I do not ever actually get into the lab and do DNA work. My genetic studies are a great example of the sort of collaborative research that I mention above. I provide data sets on behavior and reproductive history and blood samples as a source of DNA from my field studies, and my collaborators sequence the DNA and interpret the genetic information.

Over the next five years, what sort of advances in the proximate study of behavior do you envision?

We live in an exciting age of discovery. Breakthroughs in DNA sequencing and gene expression will revolutionize our understanding of the genetic control of many traits, including behavioral traits. In addition, equipment for all sorts of analytical analyses—from hormone assays to action potentials along individual neurons—will allow behaviorists to gain a firmer understanding of the mechanistic basis of behaviors. Truly exciting, but perhaps more than five years away, is the delivery of specific doses of hormones or neurotransmitters to specific tissues of the body or the instantaneous measurement of circulating hormones or the release of neurotransmitters. Such ability to manipulate the chemistry of the body or to measure short-term changes in body chemistry will rapidly advance our understanding of the proximate bases for behaviors.

As great a tool as these new analytical methods present, it will always be the creative application of technology by insightful researchers that leads to breakthroughs in our understanding of how nature works.

Dr. Geoffrey Hill is a professor at Auburn University. His work on the house finch is a classic example of employing both proximate and ultimate perspectives when studying animal behavior. This work is summarized in his wonderful book *A Red Bird in a Brown Bag: The Function and Evolution of Colorful Plumage in the House Finch* (Oxford University Press, 2002).

SUMMARY

1. One way to distinguish between proximate and ultimate perspectives is to remember that the former tends to address “How is it that . . . ?” and “What is it that . . . ?” questions, while the latter addresses “Why is it that . . . ?” questions.
2. Proximate and ultimate approaches complement one another and together provide a comprehensive picture of the ethological trait under study.
3. The endocrine system, a powerful communication system that strongly influences many aspects of animal behavior, is composed of a group of ductless glands that secrete chemical messengers, in the form of hormones, directly into an animal’s bloodstream. Correct functioning of the endocrine system is of fundamental importance to behavioral functions and to the modification of rates and directions of various cellular functions.
4. The nervous system provides an electrical impulse designed for instantaneous communication. Animals possess specialized nerve cells called neurons that share certain similarities, regardless of what message(s) they conduct. Understanding how neurobiology affects behavior is an important component of proximate analyses of behavior.

DISCUSSION QUESTIONS

1. Go back and reexamine one of the behaviors discussed in chapter 2, on ultimate causation. Suggest how you might go about studying this behavior from a

proximate perspective, and how the ultimate and proximate perspectives together provide a richer understanding of whatever behavior you have chosen.

2. Find the 1998 special issue of *American Zoologist* (vol. 38), which was devoted to proximate and ultimate causation. Choose two papers in this issue, and compare and contrast how they try to integrate proximate and ultimate causation.
3. If you could design some behavioral endocrinology experiments to add to the integrative work on plumage and carotenoid food in finches discussed in this chapter, what sort of experiments would you design? How would these experiments complement what is already known?
4. How does the work on the neuroethology of learning in voles illustrate the way that proximate studies can use between-population and between-sex comparisons to help us better understand animal behavior?
5. Box 3.1 describes how an endocrinological approach to animal behavior might inform questions in conservation biology. What might be an equivalent example regarding neuroethology and conservation biology?

SUGGESTED READING

Adkins-Regan, E. (1998). Hormonal control of mate choice. *American Zoologist*, *38*, 166–178. A review of the endocrinology of mate choice.

Alcock, J., & Sherman, P. (1994). The utility of the proximate-ultimate dichotomy in ethology. *Ethology*, *96*, 58–62. A short defense of the proximate/ultimate classification.

Bass, A. H., & McKibben, J. R. (2003). Neural mechanisms and behaviors for acoustic communication in teleost fish. *Progress in Neurobiology*, *69*, 1–26. A nice illustration of how animal nervous systems play a critical role in behavioral decision making.

Satterlie, R. A. (2013). Toward an organismal neurobiology: Integrative neuroethology. *Integrative and Comparative Biology*, *53*, 183–191. A review of the neuroethology, focusing on the swimming behavior of *Clione limacine*.

Donaldson, Z. R., & Young, L. J. (2008). Oxytocin, vasopressin, and the neurogenetics of sociality. *Science*, *322*, 900–904. An overview of the neuroendocrinology of social behavior, with an emphasis on the meadow and prairie vole systems.

4

Molecular Genetics and Development

Of the estimated 1–10 million species of insects, about 10,000 feed on blood, and only about 100 (between 0.01% and 0.001%) show a preference for human hosts for those blood meals. But those that do prefer humans for their blood meals can be problematic. In Africa, for example, the mosquito *Aedes aegypt* is the vector for spreading yellow fever, and the dengue virus, infecting up to 400 million people a year.

A. aegypti originated in sub-Saharan Africa, and there are two subspecies, only one of which is dangerous to humans. One subspecies, *A.e. formosus*, is still native to sub-Saharan Africa where it tends to be found in forests. This forest subspecies, which has black body coloration, gets its blood meals primarily from nonhumans. The other subspecies, *A.e. aegypti*, arose outside of Africa, has browner body coloration, primarily gets its blood meals from humans, and is sometimes called the “domestic” subspecies.

The different foraging preferences of the forest and domestic subspecies—nonhuman vs. human blood meals—have important implications for human health. Researchers comparing these subspecies have asked, at the proximate level, what explains why the forest subspecies prefer blood from nonhumans and the domestic species prefer human blood. Some promising work addressing this question focuses on the aftermath of an accidental introduction of the domestic form into Kenya in the early 1950s. Unlike the forest subspecies, these mosquitos entered people’s houses and preferred to lay their eggs in water containers kept inside homes (Lumsden, 1955; Figure 4.1).

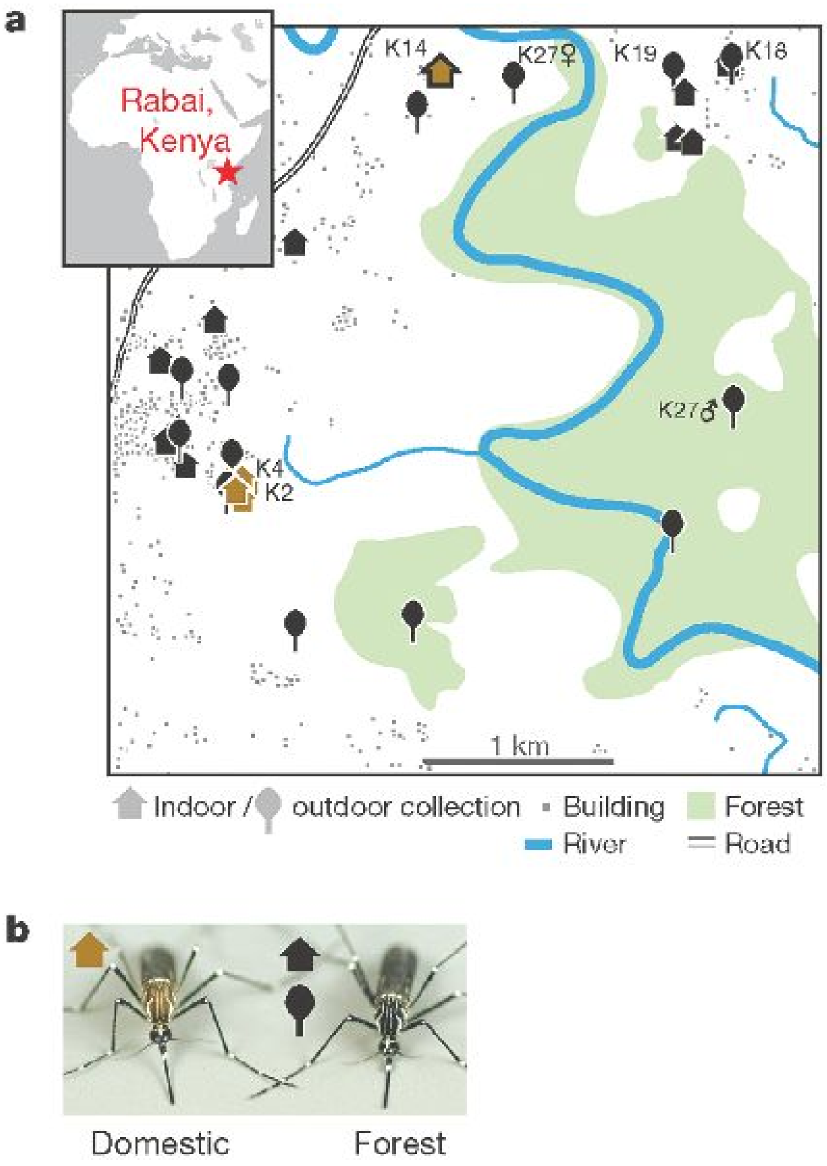


Figure 4.1. **Domestic and forest subspecies of mosquitos.** (A) A map of collection sites in Rabai, Kenya (brown indicates domestic subspecies, black indicates forest subspecies). (B) Photos of domestic and forest subspecies of *Aedes aegypt*. Reprinted by permission from Macmillan Publishers Ltd. © 2014. *(From McBride et al., 2014)*

One clue to the different foraging preferences came when researchers found that not only do individuals from the Kenyan forest subspecies prefer to feed on nonhuman blood and the Kenyan domestic subspecies prefer human blood, but the two subspecies are differentially attracted to the odors of nonhumans and humans, respectively (McBride et al., 2014; Figure 4.2).

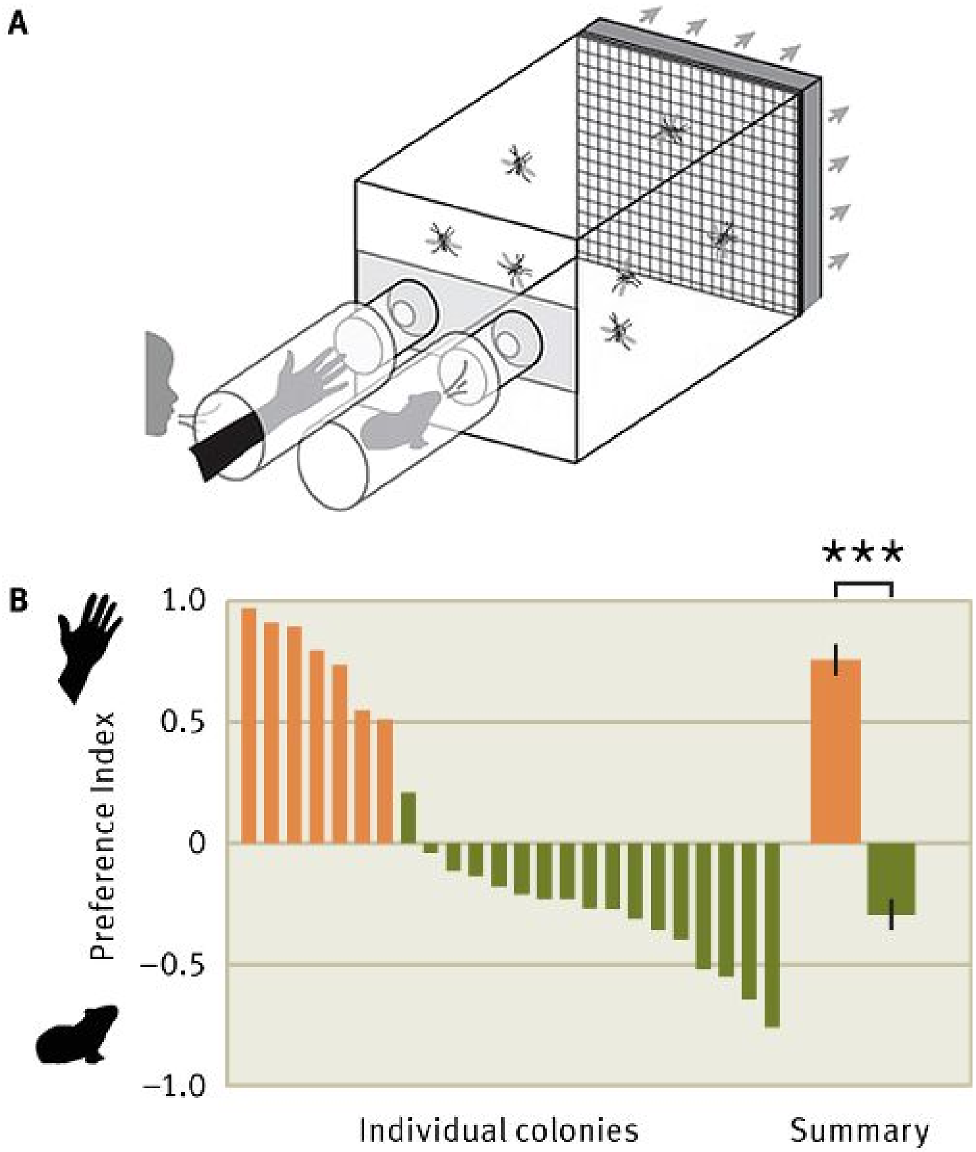


Figure 4.2. **Odor preference for humans in domestic subspecies of mosquitos.** (A) The device used to test for odor preferences. *Aedes aegypt* mosquitos on the right and a human hand and a guinea pig on the left, with odor being circulated through the device. (B) Domestic subspecies prefer human odor, while forest subspecies prefer nonhuman odor. Reprinted by permission from Macmillan Publishers Ltd. © 2014. *(From McBride et al., 2014)*

The key question then became whether the difference in odor preference was due to genetic differences between the subspecies. While populations of the two species often live just hundreds of meters apart in nature, they typically don’t breed with one another, but they do produce viable offspring when crossed with one another in the lab. This allowed researchers to develop a breeding protocol to examine the possible genetic underpinnings of the differences in foraging (blood meal) preferences.

A two-generation breeding experiment found strong evidence for genetic differences in scent preference associated with a family of chemosensory receptors known as the odorant receptors (OR). What researchers found was that there were genetic differences associated with how ORs responded to sulcatone, a chemical found in relatively large quantities in human odorants, but at much lower levels in nonhumans. Genetic variants of OR genes in the domestic subspecies were much more sensitive to the presence of sulcatone than was the case for the forest subspecies. These OR genetic variants were also overexpressed—that is, they produced more functional products—in the domestic versus forest subspecies. Together these results suggest that differences in the foraging preferences for human vs. nonhuman blood in the forest and domestic subspecies are, at the genetic level, due in part to differences in both the sensitivity and the expression of OR variants in the forest versus domesticate subspecies (McBride et al., 2014).

* * *

In chapter 3, we examined proximate analyses of animal behavior by focusing on endocrinology and neuroethology. In this chapter, we extend our examination of the proximate causes of behavior (though on occasion we touch on ultimate causation as well in the chapter) and discuss the ways that molecular genetics and development shed light on ethological questions. Studying genes from a proximate perspective, as in our discussion of foraging preferences above, may seem strange. Why are such studies on molecular genetics considered proximate analyses? After all, most of the primer chapter on evolutionary approaches to behavior (chapter 2) was devoted to discussing how natural selection favors one behavioral *genetic* variant over another. Genes, however, can also be used in the proximate explanation of a trait. If, rather than expounding on what *selective* forces are involved in changing allele frequencies, we study which specific allele or set of alleles is responsible for a trait, then genes serve as a proximate causative factor. If we find that allele 1 is associated with a variant of behavior Y, and allele 2 with another variant of the behavior, we are studying genes from a proximate, rather than an ultimate, perspective.

The two foci of this chapter—developmental and molecular genetic proximate approaches to the study of animal behavior—can be tightly linked. To see this, let's examine some work on termite sociality. In most colonies of social insect species—bees, ants, wasps, and termites—the queen or queens in the colony produce virtually all the offspring in that colony. Some of these colonies can have thousands, even millions, of workers that do not produce offspring even though they are physiologically capable of doing so. Why? What causes such a division of labor (Smith et al., 2008)? We can address that question from both a proximate and an ultimate perspective. From the ultimate perspective, the question is why natural selection would ever favor this sort of reproductive caste system. We return to that question in chapter 9. For our purposes in this chapter, the question is "What is the *molecular genetic*, proximate basis for workers that, during *development*, do not even attempt to reproduce when they are capable of doing so (Korb et al., 2009; Weil et al., 2007)?"

One clue to answering this question comes from what happens when the queen in a termite colony dies. Upon the queen's death, some workers become aggressive, butting one another often. After a series of such aggressive interactions, one of the workers becomes queen. Judith Korb and her team hypothesized that termite workers not reproducing was the product of queen-worker *chemical signaling* (Korb et al., 2009). When this signaling ceases, the butting behavior among the workers begins. Because a gene homologous with the termite gene *Neofem2* is known to be involved in queen-worker communication in other insect species (Cornette et al., 2003; Weil et al., 2007), Korb and her colleagues focused their proximate analysis on this gene.

They used sophisticated molecular genetic techniques involving RNAi (RNA interference) to silence the expression of the *Neofem2* gene in queens. Silencing this gene had no effect on the behavior of the queens themselves—they behaved like their counterparts in control colonies in which *Neofem2* was not silenced in queens. But silencing the expression of this gene in the queen, and therefore suppressing the chemical signals it codes for, did dramatically affect the behavior of workers, increasing their butting behavior toward one another (Figure 4.3). In addition, when the queen in a colony failed to produce the pheromones coded by the *Neofem2* gene, workers began a series of aggressive interactions that, in nature, would eventually lead to one of them reproducing. These results suggested that the suppression of worker reproduction by the queen was directly related to the pheromones associated with the *Neofem2* gene.

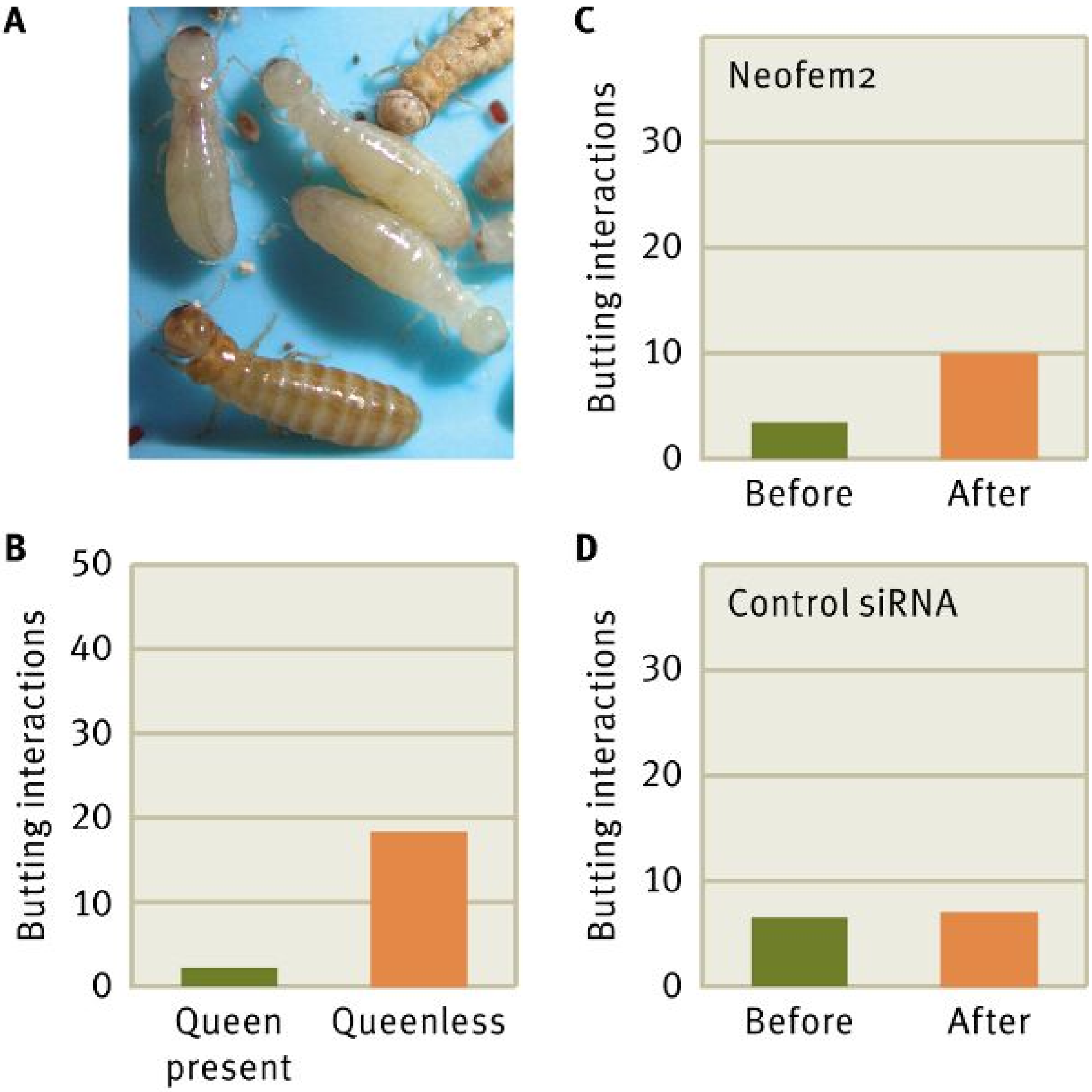


Figure 4.3. **Genes, termite workers, and queens.** (A) Queen *Cryptotermes secundus* (bottom left) with male (top right) and workers. (B) Butting among workers in colonies with queen and without queens. (C) and (D) Butting before and after treatment of the queen with *Neofem2* small interfering RNA (siRNA) and control siRNA. Reprinted with permission from AAAS. *(From Korb et al., 2009)*

Molecular Genetics and Animal Behavior

Behavioral geneticists have examined the molecular genetic underpinnings of traits associated with foraging, mate choice, aggression, division of labor, and so on. We have already looked at one aspect of **behavioral genetics** in the heritability analyses discussed in chapter 2. Here we will look at two other important ways that behavioral genetics contributes to the study of ethology:

- Using Mendel's laws of genetics to predict the distribution of behavioral phenotypes.
- Using quantitative trait loci (QTL) analysis to map the location of clusters of genes linked to behavioral traits.

MENDEL'S LAWS

As a consequence of Gregor Mendel's simple but brilliant experiments on inheritance in pea plants, behavioral geneticists have formulated what are known as **Mendel's laws**. Mendel's first law—the principle of segregation—states that individuals have two copies of each gene (or "factor," as Mendel called them), that such genes remain distinct entities, and that these genes segregate (that is, they are distributed) fairly during the formation of eggs or sperm. Mendel's second law—the law of independent assortment—states that whichever allele is passed down to the next generation at one locus is independent of which allele is passed down at other loci. Today, we know this second law is true only for what are called unlinked loci.

With respect to Mendel's first law, alleles can be **dominant**, meaning that a single copy of the allele is all that is necessary for a trait to be expressed, or they can be **recessive**, in which case two copies of an allele are necessary for the expression of a trait. To understand behavioral genetics and dominant and recessive alleles as they apply to animal behavior, let's look at the mating behavior of male ruff birds (*Philomachus pugnax*).

In ruffs, males display one of two behavioral strategies during the mating season. "Independent males," which make up the majority of individuals in most populations, guard small mating territories. "Satellite males," in contrast, do not defend their own territories but instead temporarily share an independent male's mating arena and form a kind of alliance with independents, in which both individuals court simultaneously to attract the attention of females. Independent and satellite males differ not only in mating strategies but also in coloration and body mass; satellites are smaller and have lighter plumage than independents (Bachman and Widemo, 1999; Hogan-Warburg, 1966; Lank et al., 1995; Figure 4.4).

Figure 4.4. **Satellite and independent ruff males.** Some of the differences in the mating behavior of (A) satellite males and (B) independent males are controlled by a single gene with two alleles denoted S and s. *(Photo credits: FLPA / Alamy Stock Photo; blickwinkel / Alamy Stock Photo)*

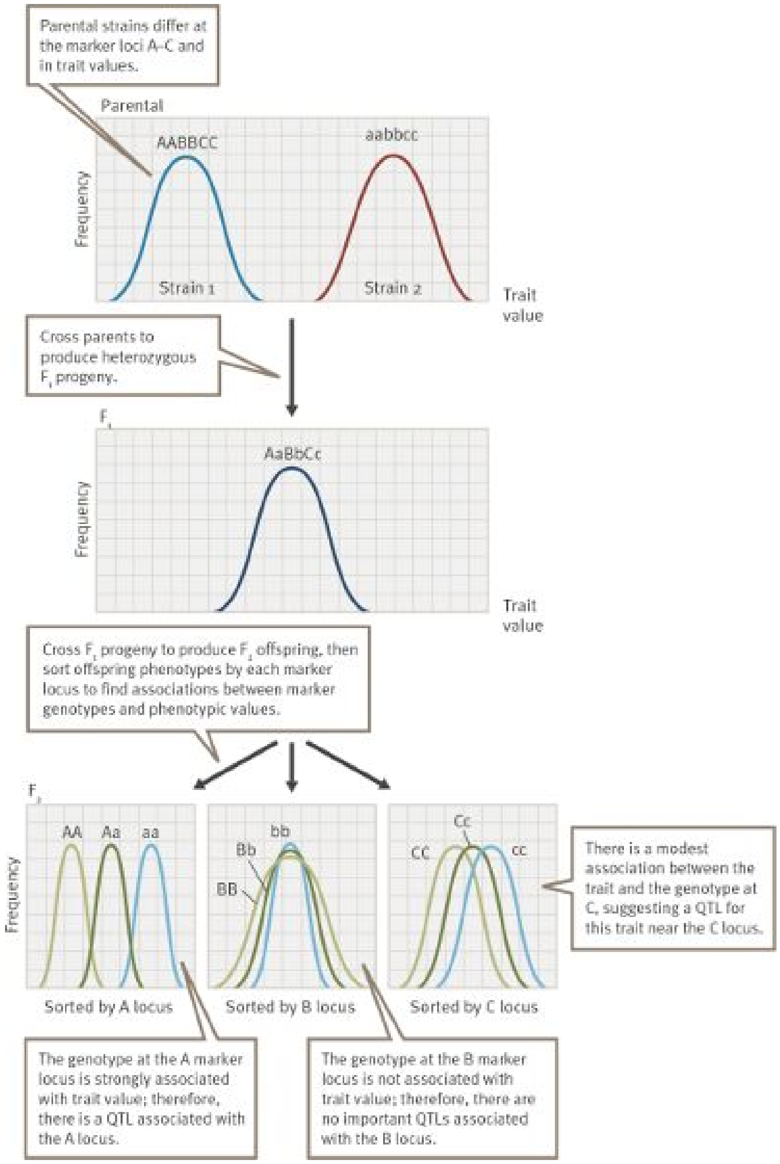
David Lank found that these two alternative mating types—independent and satellite—are primarily controlled by a single gene with two alleles labeled S and s (there is a third male strategy—“female mimic”—but less than 1% of males use this strategy: Kupper et al., 2016). The S allele is dominant and codes for satellite male behavior, whereas the s allele is recessive, and two copies of this allele are necessary for the development of an independent male. As such, SS and Ss males are satellites, and ss males are independents. If we take the knowledge that mating behaviors in ruffs are coded by one gene with two alleles, and we combine that with a natural history–based understanding of mating preferences (which males with which genotypes are preferred as mates), we can make predictions about the distribution of SS, Ss, and ss genotypes over time. But keep in mind that the relationship between genotype and behavioral phenotype is often not nearly as simple as that seen in the case of ruff mating behavior. Many, if not most, behaviors have a much more complex underlying genetic structure.

LOCATING GENES FOR POLYGENIC TRAITS

Using a number of experimental and quantitative techniques, behavioral genetics can shed light on the basis of **polygenic** behavioral traits—traits associated with variation at more than one locus. For polygenic behavioral traits, behavioral geneticists often search for a *set* of genes, each of which contributes a small amount to the expression of the trait of interest. When researchers conduct such searches, they are looking for what are called **quantitative trait loci** (**QTLs**; Flint and Mackey, 2009).

First, let’s walk through an overview of how QTL experiments are designed.

QTL mapping is a powerful way of finding the general region of the genome in which quantitative trait loci reside. The idea is that we can use *marker loci* that are easily assayed, but causally unrelated to the trait in question, in order to identify the approximate locations of the unknown alleles that affect the behavioral trait of interest. Figure 4.5 illustrates the basic concept behind the QTL mapping procedure.



Parental strains differ at the marker loci A–C and in trait values.

Cross parents to produce heterozygous F_1 progeny.

Cross F_1 progeny to produce F_2 offspring, then sort offspring phenotypes by each marker locus to find associations between marker genotypes and phenotypic values.

There is a modest association between the trait and the genotype at C, suggesting a QTL for this trait near the C locus.

The genotype at the A marker locus is strongly associated with trait value; therefore, there is a QTL associated with the A locus.

The genotype at the B marker locus is not associated with trait value; therefore, there are no important QTLs associated with the B locus.

Figure 4.5. Quantitative Trait Loci mapping. Quantitative Trait Loci (QTL) mapping allows researchers to find the general region of the genome in which quantitative trait loci reside by using *marker loci* that are easily assayed, but unrelated to the trait in question, in order to identify the approximate locations of the unknown alleles that do affect the trait of interest. *(From Bergstrom and Dugatkin, 2016)*

Step 1. Select two parental strains that (1) differ considerably in their values of the quantitative trait and (2) differ at a set of marker alleles. Parental strain 1 has a lower distribution of trait values than does strain 2; strain 1 is homozygous for the *A*, *B*, and *C* marker alleles, while strain 2 is homozygous for the *a*, *b*, and *c* marker alleles.

Step 2. Cross these two strains to produce a set of progeny, referred to as the F_1 generation. If the parents are homozygous at the marker loci, these F_1 progeny will be heterozygous at each marker locus, and typically they will manifest intermediate values of the quantitative trait.

Step 3. Mate F_1 individuals to produce an F_2 generation. For the F_2 individuals, measure (1) the genotypes at the marker loci, and (2) the value of the quantitative trait. From this information, we can infer which marker loci are most closely associated with QTLs for the behavioral trait in question. The F_2 generation in Figure 4.5 illustrates the basic logic behind this inference. In each frame, the quantitative trait values are plotted with the genotypes sorted according to one of the marker loci.

In Figure 4.5, we see a large difference in the quantitative trait values associated with the *AA*, *Aa*, and *aa* genotypes in the F_2 generation. This does not mean that the *A* marker locus is itself influencing the quantitative trait value, but it does imply that this locus is linked to an important quantitative trait locus.

To better understand how QTL mapping works with respect to behavior, let's examine the work of Jonathan Flint and his colleagues on QTLs and fear/fearlessness in mice (Flint and Mackay, 2009; Flint and Mott, 2008; Flint et al., 1995; Solberg et al., 2006; Talbot et al., 1999; Yalcin et al., 2004). Flint's group first studied fear and anxiety by recording open-field behavior in mice. Open-field behavior measures fear when animals are placed in large, open, well-lit environments. Flint's group used two genetic lines of mice that had been bred under artificial selection for many generations: one line of mice had been selected for high open-field activity, and the other for low open-field activity. The behavior of mice from both lines was measured in open-field tests, and their fear/anxiety response was measured when they were placed in two different types of mazes. Fear was measured in a number of ways, including measuring the mice's activity level and the rates at which they defecated, because low activity and high defecation rates are associated with fear in rodents.

After all the behavioral tests were complete and the more fearful mice were identified, Flint and his colleagues collected DNA from the animals' spleens. Using a more complicated, and slightly different, version of the QTL analyses discussed above, Flint and his colleagues were able to identify QTLs for fear on six mouse chromosomes—chromosomes 1, 4, 12, 15, 17, and 18. QTLs for fear during open-field trials were found on these six chromosomes, while QTLs for fear displayed in mazes were found on only a subset of these chromosomes (1, 12, and 15). In follow-up studies, Flint's group studied 1,636 laboratory-bred mice and examined the fear response shown by mice in five different laboratory environments (open field, mazes, mirrored chambers, and so on). Across these five behavioral measures, researchers found evidence of QTLs associated with fear on fourteen chromosomes (Turri et al., 2004). More recent work has found QTLs linked to "emotionality," including fear and anxiety, on twenty chromosomes in mice (Willis-Owen and Flint, 2006; Figure 4.6). These sorts of analyses give us a much more detailed and in-depth picture of how molecular genetic variation effects behavioral variation (Flint, 2011).

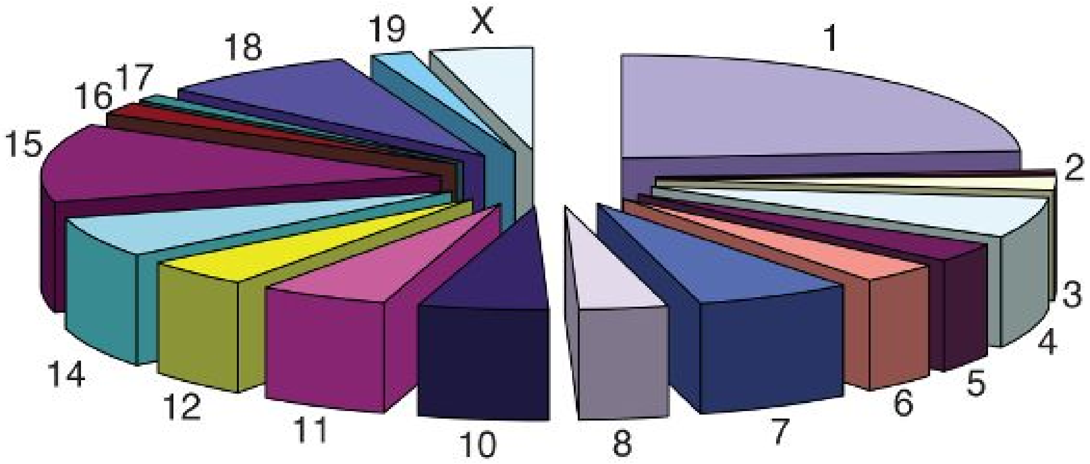


Figure 4.6. QTLs for mouse behavior. Chromosomal distribution of QTLs linked to anxiety in mice. © 2006, rights managed by Nature Publishing Group. *(From Wills-Owen and Flint, 2006)*

GENES, mRNA, AND HONEYBEE FORAGING

Let's return to the proximate factors associated with foraging in honeybee colonies that we discussed in chapter 3. To examine the molecular genetic underpinnings of the developmental shift from working in the hive by younger bees to foraging outside the hive by older bees, Alberto Toma and his colleagues built on earlier studies indicating that the *period* (*per*) gene influences circadian rhythms and development time in fruit flies (Konopka and Benzer, 1971; Kyriacou et al., 1990). They examined how levels of *per* messenger RNA (mRNA)—a single-stranded RNA that is critical for protein synthesis—might influence the developmental changes associated with the transition to forager (Toma et al., 2000).

Toma and his colleagues measured mRNA levels in the brains of three groups of laboratory-raised honeybees—four- to six-day-old bees, seven- to nine-day-old bees, and twenty- to twenty-two-day-old bees. Individuals in a group of one-day-old bees were also marked and added to a natural colony of bees in the field. They recaptured marked bees at day 7 and day 24 of their experiment, and measured *per* mRNA levels. In both laboratory and natural populations, *per* mRNA was significantly greater in older individuals that foraged for food and brought such food to their colony, when compared with younger bees that remained at the hive (Figure 4.7).

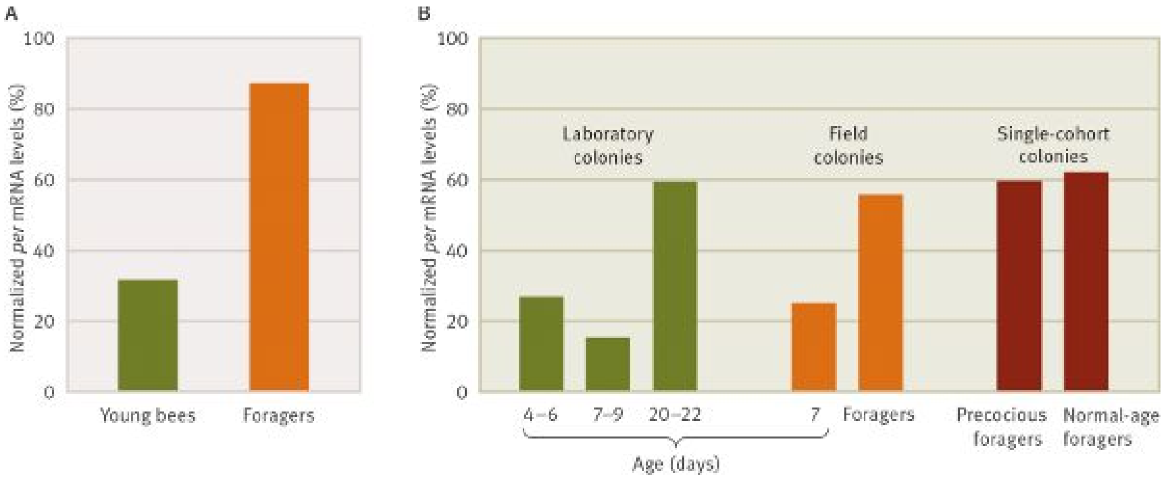


Figure 4.7. Foraging, age, and mRNA. (A) Foraging honeybees have significantly higher levels of *per* mRNA than younger, nonforaging bees. This difference could be due to age, behavior caste (forager versus nonforager), or both. (B) Some individual bees developed into precocious foragers that began searching for food much earlier than usual. When ten-day-old precocious foragers were compared with normal foragers (twenty-two-day-old foragers), no statistical differences in *per* mRNA levels were found. *(From Toma et al., 2000)*

It is possible that increased *per* mRNA levels could be due to age differences alone, rather than to the age-related *shift* to forager. As in the Withers experiment examined in chapter 3, Toma studied “precocious” foragers who begin searching for food outside of the nest at about seven days old. These foragers provided Toma and his colleagues with the chance to remove age effects from the *per* mRNA/foraging connection. Precocious foragers had *per* mRNA levels that did not differ from those of typical (older) foragers, suggesting a link between *per* mRNA and foraging, rather a more general connection between *per* mRNA and development. We still do not know the direction of the causality here: time will tell whether increased *per* mRNA level is a cause or a result of increased foraging.

Over the last few years, with the explosion of molecular genetic technology, a much more detailed picture of genes, mRNA abundance in the brain, and foraging in honeybees has emerged. In a large-scale study of 5,500 genes, Charles Whitfield, Anne-Maire Cziko, and Gene Robinson found that changes in mRNA levels associated with 39 percent of these genes were involved in the transition from hive work to foraging behavior in honeybees (Whitfield et al., 2003, 2006; Elsik et al., 2014). In addition, QTL analysis has been used to localize genes associated with age at first foraging on chromosomes 4 and 5 (Rueppell, 2009, 2014; Page et al., 2012).

These sorts of large-scale genomic approaches to animal behavior will become common as the genomes of more species are sequenced (G. Robinson et al., 2005; S. Sumner, 2006). The challenge will be figuring out how to go from the massive amount of data gathered when a genome is sequenced to understanding specific behaviors. Although the field of genomics and behavior is growing quickly, at present we can't examine each of the thousands of genes and mRNA products associated with the transition to honeybee forager. Nor would we want to, as little is known about exactly how these genes and their mRNA products operate in the transition to honeybee forager. In some instances, however, we can study specific genes associated with the transition to foraging in honeybees to give us a finer understanding of the proximate underpinnings of social insect foraging. To see how, let's examine the work of Yehuda Ben-Shahar, Nichole Dudek, and Gene Robinson, who examined the effect of the gene *malvolio* (*mvl*) on manganese transport to the honeybee brain, and its implications for foraging in this species (Ben-Shahar et al., 2004). The gene *mvl* is an excellent "candidate" gene for this sort of work, as earlier experiments have shown that it affects the way fruit flies respond to sucrose, an important component of honeybee food and drink.

In honeybees, foragers that specialize in collecting pollen have a higher responsiveness to sucrose than those that specialize in nectar foraging, and both types of foragers have a stronger response to sucrose than younger "nurse" bees (that feed the larvae) in the hive. Ben-Shahar and his colleagues examined whether such differences were linked to differences in *mvl* transport of manganese to the honeybee brain. They found that both the amount of manganese in the head of a honeybee and the amount of *mvl* mRNA in the honeybee brain were high in pollen foragers and nectar foragers, and low in nurses.

On a finer scale, when Ben-Shahar and his team looked at pollen foragers versus nectar foragers, they found even more evidence suggesting a link between *mvl* and foraging. Recall that pollen foragers show a stronger response to sucrose than do nectar foragers. If *mvl* plays an important role in foraging, we would expect to see more manganese in the heads of pollen foragers versus nectar foragers, and the evidence suggests that this is the case (Figure 4.8, Box 4.1).

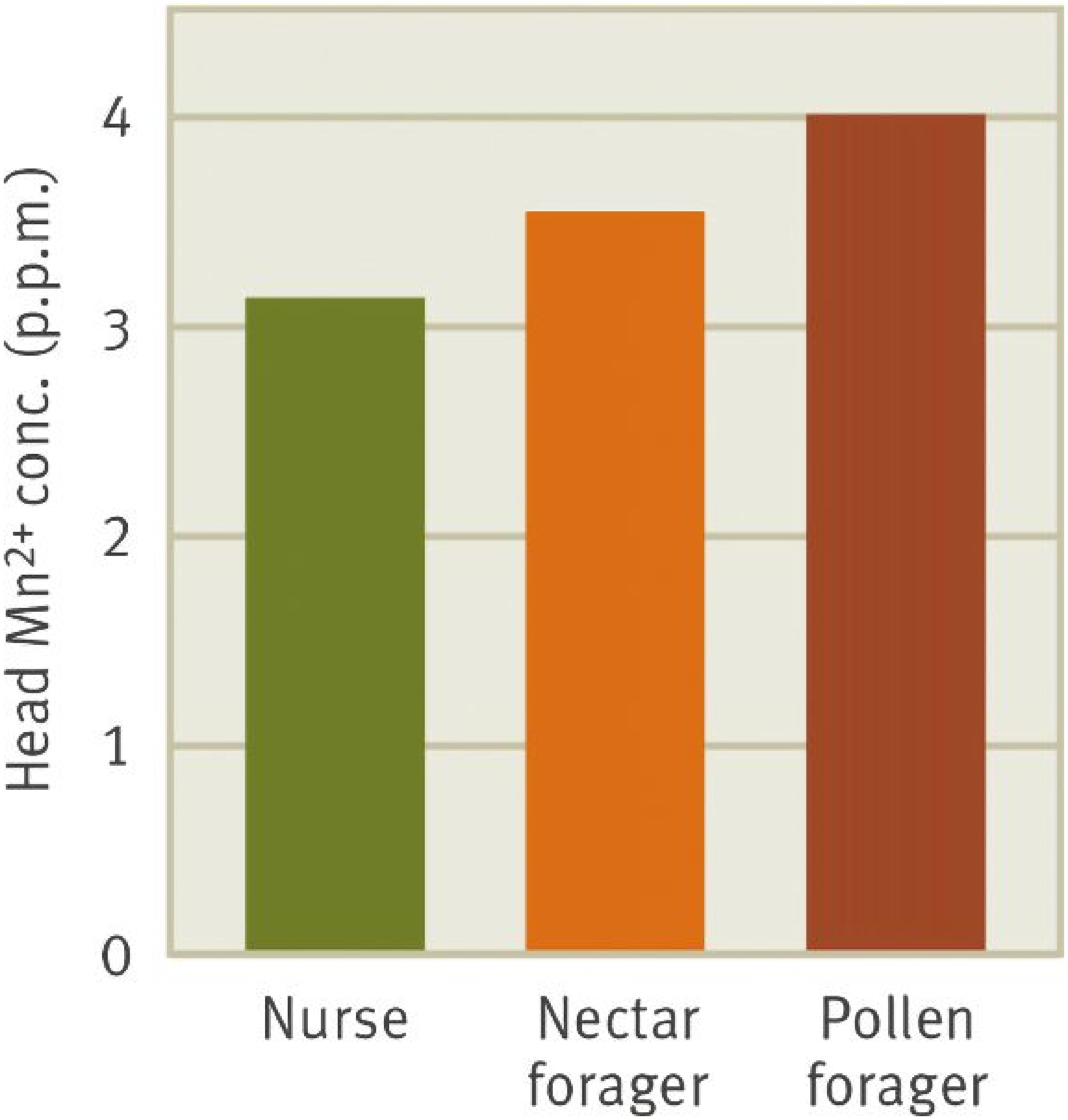


Figure 4.8. Pollen foragers, nectar foragers, and manganese. Pollen foragers in honeybees have more manganese in their heads than both nectar foragers and nurses. *(From Ben-Shahar et al., 2004)*

Box 4.1 SCIENCE AT WORK

What is the research question? What molecular genetic mechanisms underlie the behavioral shift to forager in honeybees?

Why is this an important question? The complex division of labor that exists in social insect colonies has remained a subject of interest to animal behaviorists from the time that Darwin first wrote about it in *On The Origin of Species*.

What approach was taken to address the research question? mRNA levels were measured in lab-raised, marked, honeybees at different stages in the transition to forager mode.

What was discovered? mRNA levels were higher in foragers than same aged individuals that were not acting as foragers. The arrows of causality here are still not clear—high mRNA levels may lead to switching to forager mode, vice versa, or the relationship might be two-way.

What do the results mean? Complex behavioral changes in highly structured social groups such as social insect colonies can be studied at the proximate level using molecular genetic tools paired with behavioral tests.

SONG ACQUISITION IN BIRDS

Songbirds use songs in many contexts, including attracting potential mates and fending off intruders from their territory. A molecular genetic approach to birdsong highlights the role of gene expression and gene regulation in behavior. For example, researchers have found that the expression of the *FOXP2* gene in certain brain regions is associated with both song perception in birds and language acquisition in humans (Enard et al., 2002; Haesler et al., 2004; Teramitsu et al., 2004; Nudel and Newbury, 2013; Ayub et al., 2013). Experimental work in young zebra finches has found that when the *FOXP2* gene is “knocked out”—deactivated—their ability to copy the song of adults is severely impaired (Haesler et al., 2007; Figure 4.9).

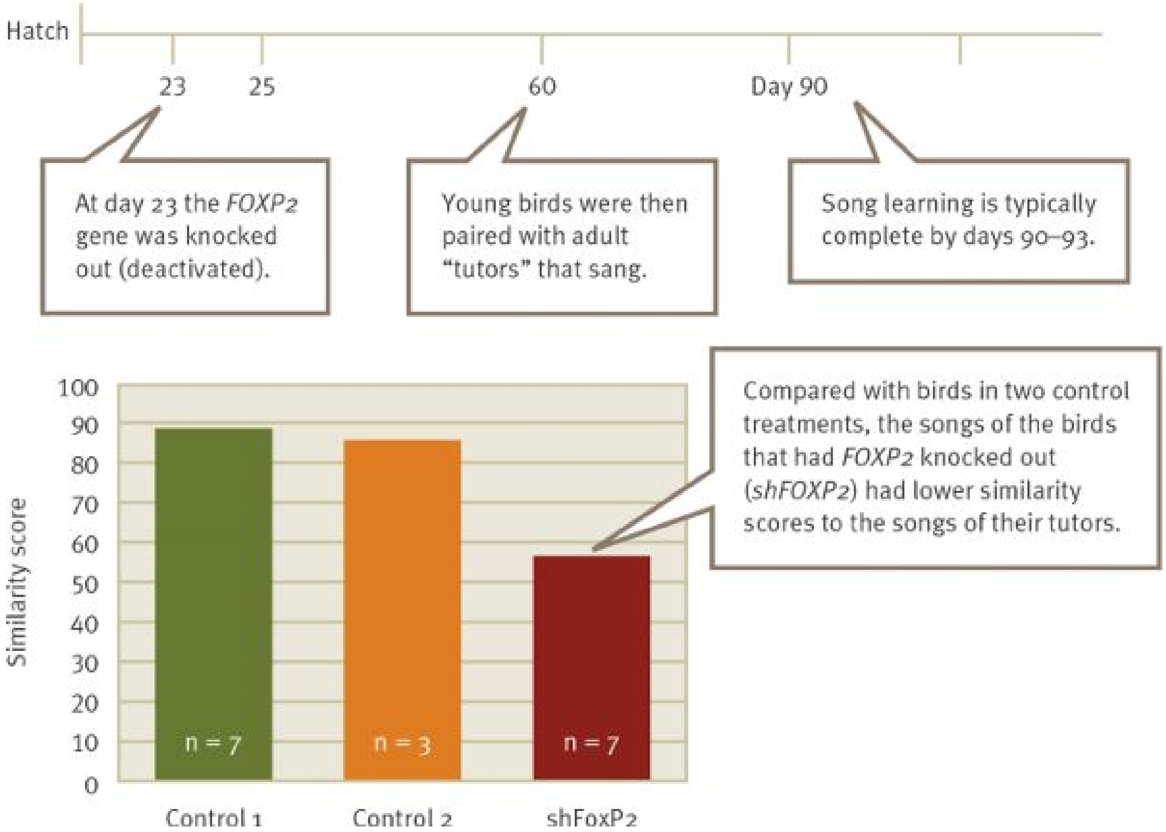


Figure 4.9. FOXP2 and song learning. When the *FOXP2* gene was knocked out in young zebra finches, their ability to learn other finches' songs was diminished. *(From Haesler et al., 2007)*

The zebra finch (*Taeniopygia guttata*) has become a model system for studying the relationship between gene expression and birdsong. Early work in this species by David Clayton, Claudio Mello, and their colleagues involved exposing zebra finches to birdsong, and then measuring mRNA levels in the brains of these birds (Mello et al., 1992). Clayton and his colleagues focused on mRNA levels in the neostriatum section of the forebrain because this area is associated with song pattern recognition, song discrimination, and the processing of auditory cues in birds. They found that mRNA levels associated with the *zenk* gene increased after the birds heard zebra finch songs, and that increase was associated with an increase in the number of neurons in the neostriatum (Figure 4.10). Other research also suggests a role for *zenk* in zebra finch birdsong: (1) zebra finches exposed to the song of another species (the canary) showed a much-reduced *zenk* mRNA response to the other species' birdsong compared with their responses to a conspecific's song, and (2) no increase in *zenk* expression was discovered either after the birds were placed in a “no song” experimental treatment, or when they heard “tone bursts” that did not correspond with the song of any bird species.

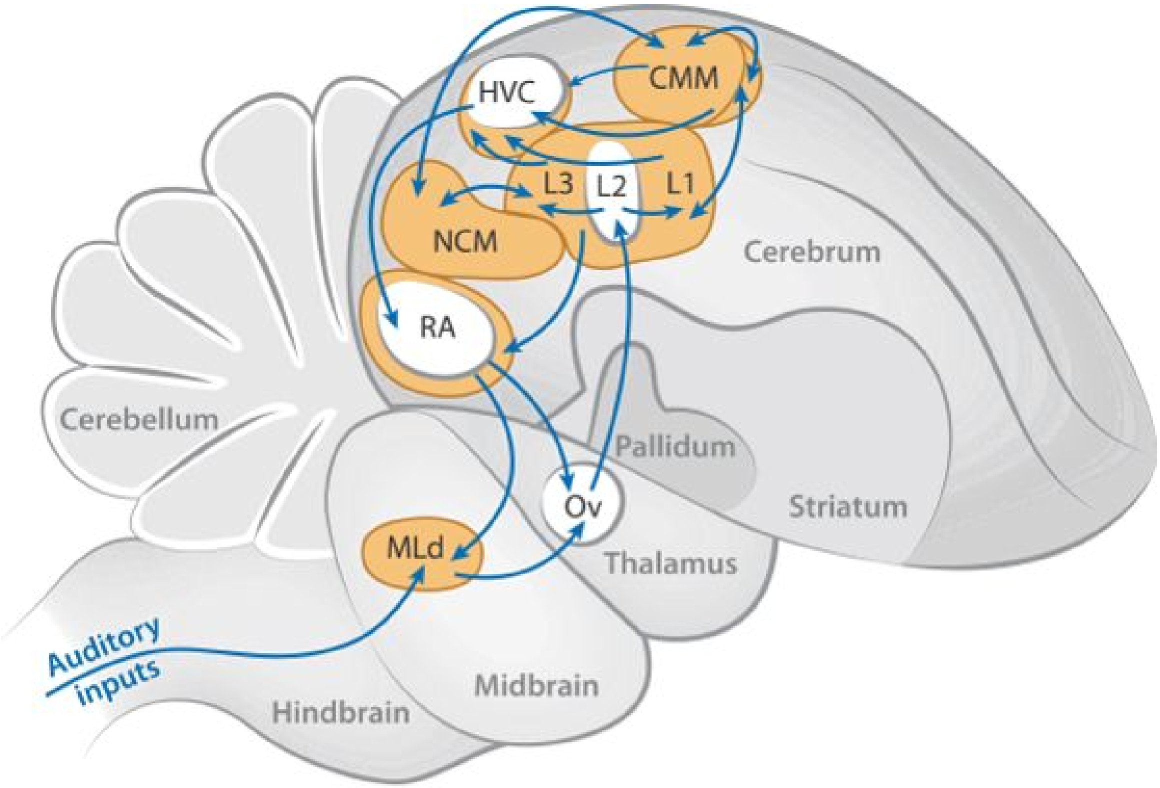
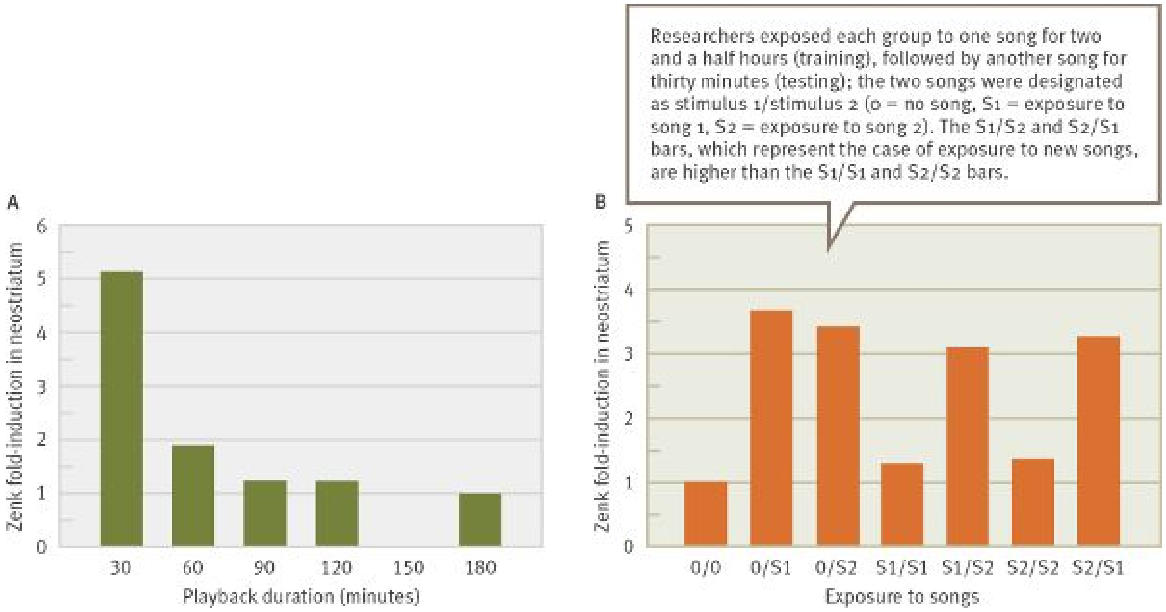


Figure 4.10. Zenk and exposure to song. A schematic representation of the brain of a songbird. After a song is heard mRNA levels of ZENK change in the areas shown in orange. Reproduced with permission of Annual Review of Genomics and Human Genetics, http://www.annualreviews.org. *(From Clayton, 2013)*

If a zebra finch is exposed to the same conspecific song repeatedly, all of the responses described above begin to decrease and slowly return to their baseline levels (Figure 4.11A). This sort of **habituation** occurs when an animal is exposed to the same stimulus over and over. Clayton and his team examined the interaction between expression of the *zenk* gene and habituation of zebra finches to familiar song. They first exposed a zebra finch to the song of a conspecific and found the same increase in *zenk* mRNA and the number of neurons in the forebrain discussed earlier (Mello et al., 1995). Once a bird had habituated to a familiar song, the song of a new zebra finch was played, and an increase in *zenk* mRNA and neural recruitment to the forebrain was again recorded. These results suggest that after repeated exposure, a song is categorized by a bird as “familiar,” and it no longer elicits the molecular genetic and neural changes associated with increased *zenk* expression (Figure 4.11B), but a new song will generate new molecular genetic and neural changes.



Researchers exposed each group to one song for two and a half hours (training), followed by another song for thirty minutes (testing); the two songs were designated as stimulus 1/stimulus 2 (0 = no song, S1 = exposure to song 1, S2 = exposure to song 2). The S1/S2 and S2/S1 bars, which represent the case of exposure to new songs, are higher than the S1/S1 and S2/S2 bars.

Figure 4.11. Zenk levels and habituation. (A) Induced *zenk* mRNA levels decreased with increased exposure to the same song in male zebra finches. (B) Induced *zenk* mRNA levels increased when a male zebra finch was exposed to a new song. *(Adapted from Mello et al., 1992)*

It is still not clear precisely how the increased *zenk* mRNA levels and neuron development associated with *zenk* expression are tied to song learning. The protein produced by the *zenk* mRNA may affect the auditory neurons, which are connected to song recognition. More generally, there is some evidence that *zenk* may be part of a complex genetic pathway leading to the neural plasticity that is critical to song learning in birds (Mello et al., 2004). Indeed, the entire genome of the zebra finch has been sequenced, and researchers have discovered changes in gene expression in at least 807 genes in the zebra finch brain when males sing (Warren et al., 2010; Gunaratne et al., 2011; Figure 4.12).

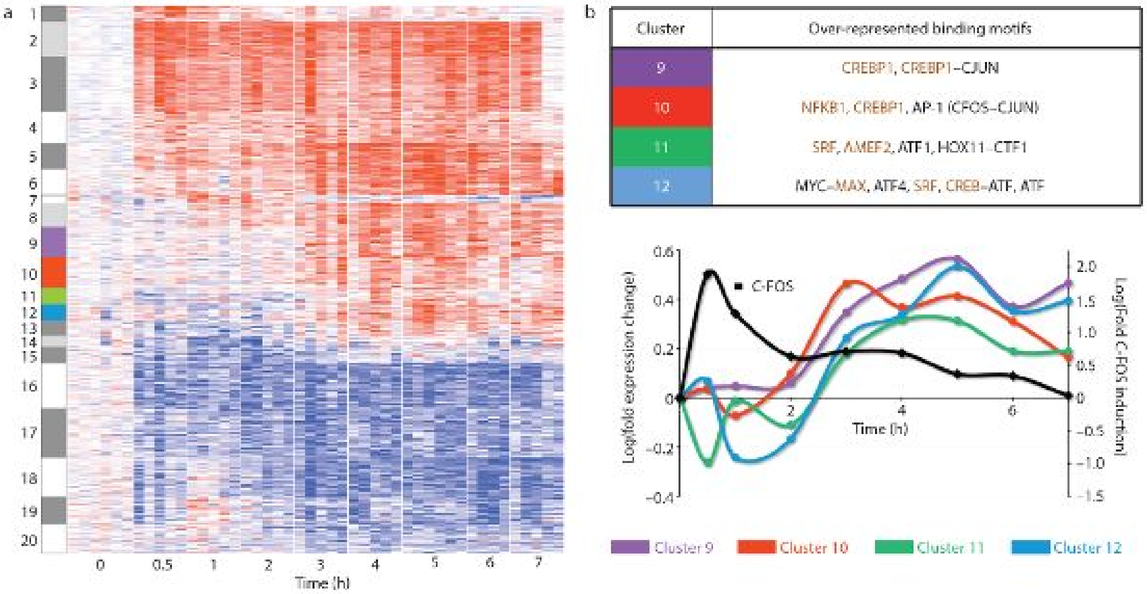


Figure 4.12. Gene expression levels change as songbirds sing. Expression of some genes increases as zebra finches sing, while expression of others decreases. Red indicates increased gene expression. Blue indicates decreased gene expression. *Reprinted by permission from Macmillan Publishers Ltd. © 2010,* rights managed by Nature Publishing Group. *(From Warren et al., 2010)*

avpr1a, VASOPRESSIN, AND SOCIALITY IN VOLES

In the last chapter we looked at the critical role that the hormone vasopressin plays in prairie voles (*M. ochrogaster*), where males often display parental care and guard their mates, and meadow voles (*M. pennsylvanicus*), in which males display very little, if any, parental care or prosocial behavior toward their mates. Here, we return to this system but focus on *within*-species variation in prairie voles. Though they display much more parental care than meadow voles, there is still variation in these prosocial behaviors among prairie voles (Hammock and Young, 2002; R. Roberts et al., 1998).

At the molecular genetic level, vasopressin receptors are controlled by the *avpr1a* gene (Insel et al., 1994; Lim et al., 2004; Hammock, 2015). Two alleles of this gene—the long-version allele and the short-version allele—have been the subject of much research. Early work, both within prairie voles and between prairie and meadow voles, suggested that the long version of the *avpr1a* allele was more strongly associated with prosocial behaviors like parental care and affiliative interactions with mates (Phelps and Young, 2003). To examine this connection in more detail, Elizabeth Hammock and Larry Young bred two lines of prairie voles—one line was homozygous for the long version of the *avpr1a* allele, and one line was homozygous for the short version of the *avpr1a* allele (Hammock and Young, 2005).

Box 4.2. COGNITIVE CONNECTION

Genomic Approaches

Experimental and observational studies have found that great tits (*Parus major*) employ cognitively sophisticated strategies with respect to foraging and mate choice (Alpine et al., 2015; Cole et al., 2012; Firth et al., 2015). As a result, great tits have become a model system for behavioral ecologists interested in the evolution of cognition. Recently the entire genome of this songbird (as well other songbirds) has been sequenced, allowing researchers the opportunity to better understand the genetics of cognition from both proximate and ultimate perspectives (Clayton, 2013; Zhang et al., 2014; Laine et al., 2016).

Veronika Laine and her colleagues collected genomic data on thirty great tits from populations scattered across Europe (Figure 4.13). From a proximate perspective, this work provides important information about which genes, and clusters of genes, play a role in great tit behavior. This data, in conjunction with genomic work on zebra finches and chickens, also allowed the researchers to use population genetic algorithms and statistics that estimate natural selection pressure on genes and clusters of genes to look for evidence of natural selection pressure.

Figure 4.13. **Genomics of cognition in great tits.** (A) Great tits (*Parus major*). *(Photo credit: © Victor Tyakht / Shutterstock)* (B) The sites from which great tits were captured and genomic data was obtained. *(From Laine et al., 2016)*

These techniques can get very complicated, but most operate like this: in chapter 2, we discussed that mutations can be categorized by the way that they affect fitness. Synonymous mutations do not change amino acid sequence and so have no effect on fitness. Nonsynonymous mutations do change the amino acid sequence, and we predict that such changes will often have fitness consequences. The difference between synonymous and nonsynonymous mutations allows us to measure the strength of natural selection at a locus. This can be done in many ways, but almost all of them calculate the ratio of nonsynonymous to synonymous substitutions (a substitution here means a mutation that has gone to fixation). The higher that ratio, the stronger the evidence that positive natural selection has occurred.

Laine and her colleagues scanned the great tit genome and searched for evidence for natural selection acting on clusters of genes on great tit chromosomes. Identifying and locating these clusters of genes on various chromosomes provides us with data relevant to proximate cause. From an ultimate perspective, what the researchers found was that many genes linked to cognition were overrepresented in areas of the genome that showed evidence for positive natural selection. For example, Lane et al. found positive selection on the early-growth-response protein gene (*EGR1*), a gene linked to general memory and learning abilities, and one that is critical to song learning in song birds (Hara et al., 2007; Dragunow, 1996; Clayton, 2013). Selection was also strong on the *FOXP2* gene that we discussed in the context of zebra finch song learning in the text. Together with other findings, Laine et al.'s genomic analysis provides general information on the location of gene clusters associated with cognitive functions and it suggests that natural selection has favored a suite of genes associated with cognitive functions linked to survival and reproduction in great tits.

If the *avpr1a* allele was primarily responsible for male behaviors toward mates and offspring, then males from these two lines should display different suites of social behaviors. That is in fact what Hammock and Young found. Males homozygous for the longer version of *avpr1a* displayed more pup licking and grooming of pups, and responded more positively toward familiar females than males that were homozygous for the shorter version of *avpr1a* (Figure 4.14). These studies complement those discussed in chapter 3 and provide another piece to the puzzle regarding what proximate factors are responsible for key behavioral aspects of sociality in voles.

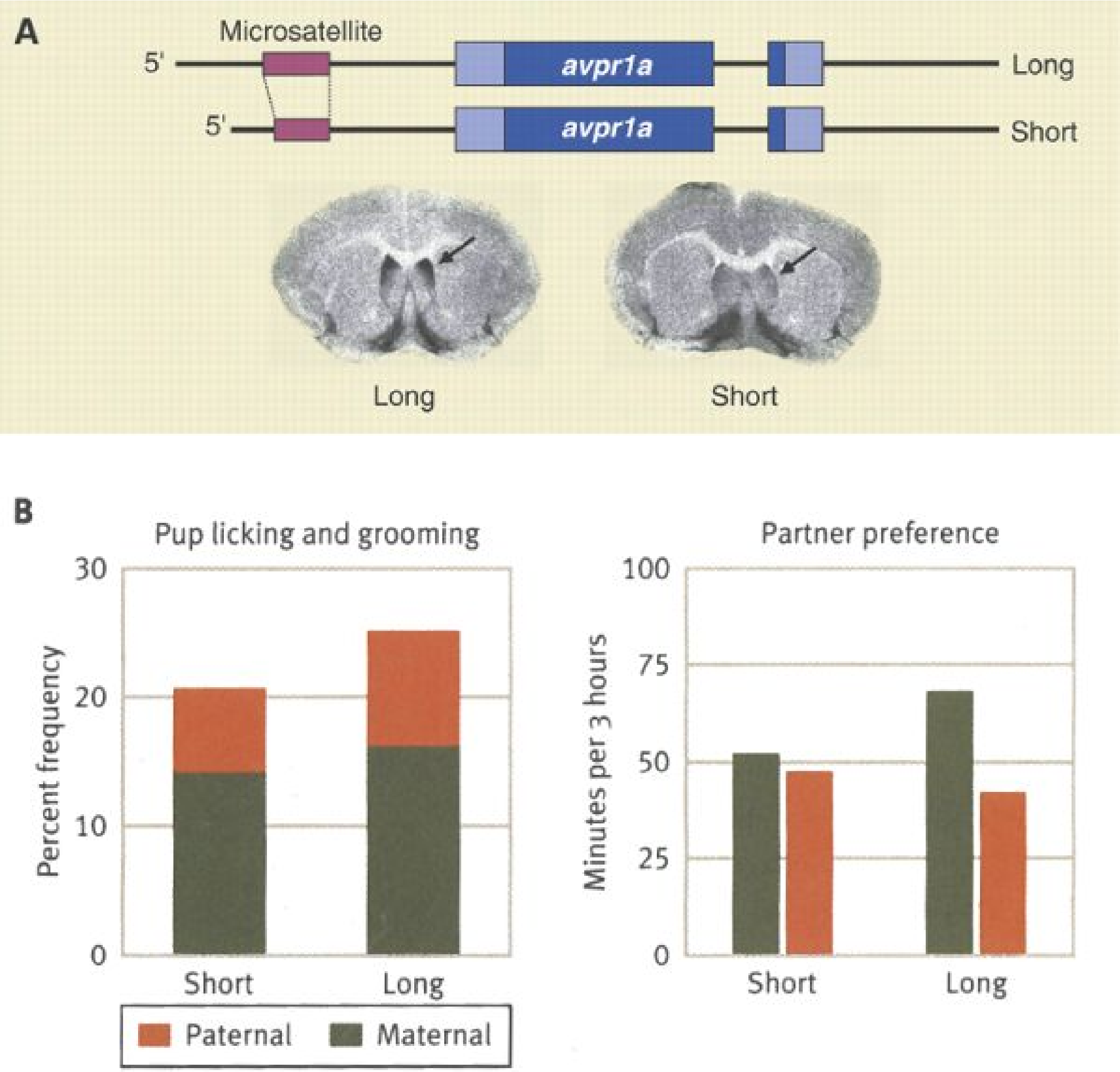


Figure 4.14. ***Avpr1a*** **length and behavior.** (A) A schematic of the long and short *avpr1a* alleles and the expression of vasopressin receptors in the brain of prairie voles (differences in expression can be seen at the two arrows). *Reprinted with permission from AAAS. (From Donaldson and Young, 2008)* (B) Both male care of offspring and the strength of partner preference were greater in males who were homozygous for the longer *avpr1a* allele. *(From Hammock and Young, 2005)*

GENETIC TOOLKITS, TRANSCRIPTION FACTORS, AND TERRITORIALITY

Some suites of behaviors, such as those associated with territoriality, are seen in similar form in species that are only distantly related from a phylogenetic perspective. Why? Is this due to convergent evolution or instead to a group of conserved genes—sometimes called a “genetic toolkit”—shared by these distant phylogenetic relatives? Clare Rittschoff and her team investigated this question by examining the molecular genetics of territoriality in three model species—the house mouse (*Mus musculus*), three-spined sticklebacks (*Gasterosteus aculeatus*), and the honeybee (*Apis mellifera*) (Figure 4.15).

Figure 4.15. **Molecular genetics of territoriality.** The molecular genetics of territoriality was examined in the house mouse (*Mus musculus*), three-spined stickleback (*Gasterosteus aculeatus*), and honeybee (*Apis mellifera*). *(Credits: Lubomir Hlasek; © Daniel Prude / Shutterstock)*

For each species, they exposed individuals to either a territorial intruder or a neutral object that served as a control. They then sequenced mRNA from the brains of individuals. In the case of the honeybee, they did whole brain sequencing, and for sticklebacks and mice they focused on areas of the brain that prior work had shown were associated with territoriality. While there were certainly many unique molecular genetic *responses* seen in each species, a number of patterns emerged. Responses to territorial intrusion in all three species involved a “toolkit” of what are called G-protein-coupled receptors (GPCR). GPCRs are known to be involved in hormonal and neurobiological processes associated with behavior and so likely played a role in response to territorial intrusions in these species (Rosenbaum et al., 2009). In addition to the presence of such conserved suites of genes associated with territoriality, similarities across these three species were found in the expression patterns of many genes linked to territoriality.

To understand gene expression patterns, think about this: multicellular creatures, including humans, *develop* from a single cell, but, with the exception of eggs and sperm, every cell contains the same set of genes. Some develop into skin cells, others into hair cells, and on and on, but, remarkably, these cells have the same genes. Very early on in development, cells (except sperms and eggs) in an embryo are *totipotent*; they could, in principle, develop into any cell types. Which of these they become depends on the complex manner in which genes are regulated and expressed within the environment of a cell (Bergstrom and Dugatkin, 2016).

One key to this process is that genetic bits called transcription factor proteins guide development by binding to stretches of DNA known as regulatory enhancers. A regulatory enhancer of a gene is a section of DNA that lies outside of that gene but is involved in regulating the timing and level of that gene’s expression—the amount of product (primarily proteins) produced by a gene and when it is produced. Regulatory enhancers are stretches of DNA that do not code for protein sequences, but instead control the spatial and temporal expression of nearby genes (Figure 4.16). These noncoding regions of DNA explain, in part, why every cell in the body of a multicellular creature (except for sperm and eggs) contains the same set of genes, but cells do such very different things. Regulatory enhancers act as switches that turn genes on and off, and they affect their expression. A single gene can have numerous regulatory enhancers associated with it, and these regulators can operate independently of one another on that gene.

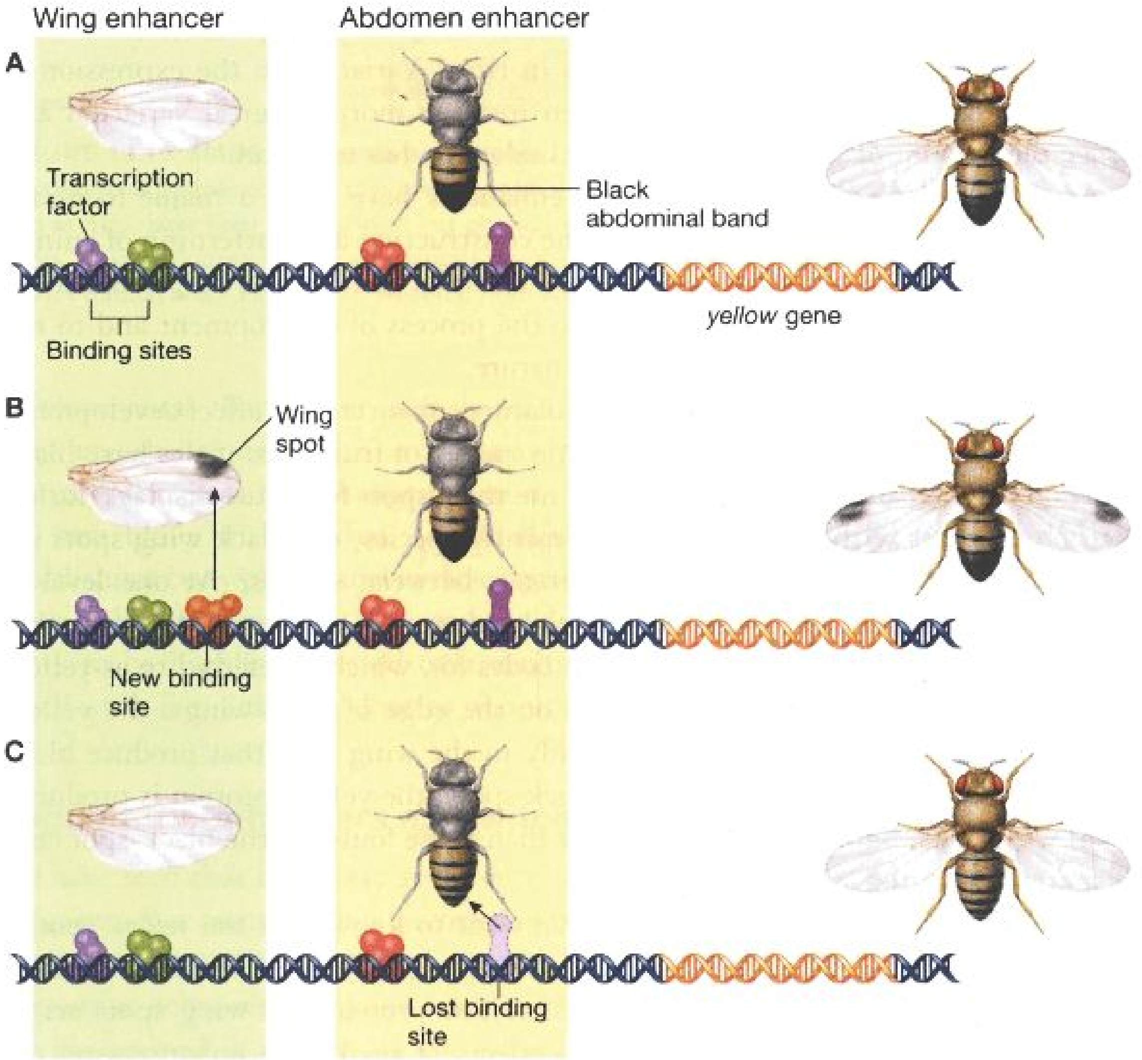


Figure 4.16. **Gene expression.** Gene expression and regulatory enhancer sequences in DNA. Transcription factor proteins bind to the regulatory enhancer, and like a switch being turned on, they trigger RNA polymerase to start transcribing an RNA copy of the gene. *(Adapted from Carroll et al. 2008 and Bergstrom and Dugatkin 2016)*

In the case of gene expression of mice, sticklebacks, and honeybees, the researchers found a number of genes linked to synapsis formation, dendrite growth, and nerve cell differentiation in the brain that showed similar expression patterns in response to territorial expression. In addition, they found seven homologous transcription factors across these species that appear to be part of the molecular genetic toolkit associated with responses to territorial intrusions (Box 4.3).

Box 4.3. SCIENCE AT WORK

What is the research question? Are there shared “genetic toolkits” employed in similar suites of behavior seen in widely divergent species?

Why is this an important question? Some suites of behaviors are seen in species that are only distantly related. Studying genetic toolkits will help us understand when this is due to convergent evolution or, instead, due to deeply conserved genetic mechanisms.

What approach was taken to address the research question? Researchers examined the behavioral response to territory intrusion in house mice, three-spined sticklebacks, and honeybees. They also sequenced mRNA from the brains of individuals tested.

What was discovered? House mice, three-spined sticklebacks, and honeybees share a genetic toolkit that includes G-protein-coupled receptors linked to territoriality. In addition, these species show similar patterns of gene expression with respect to a number of genes likely important in territoriality.

What do the results mean? Deeply conserved clusters of genes, and deeply conserved gene expression patterns, may help explain similar behavior in phylogenetically distant species.

Development and Animal Behavior

In “On the Aims and Methods of Ethology,” Niko Tinbergen emphasized the importance of developmental factors in shaping an animal’s behavior (N. Tinbergen, 1963) (Burkhardt, 2014; Stamp-Dawkins, 2014, chapter 1). Tinbergen and those who followed in his footsteps were using the term *development* in a broad sense to encompass everything from the in utero effects to the specific effects that environmental factors might have throughout an individual’s life (Stamps, 2003; M. West et al., 2003). Environmental factors relevant to development and behavior encompass both abiotic (nonliving) and biotic (living) factors.

Throughout this book, we will explore myriad ways that development affects behavior. Here, we focus on four case studies, examining (1) development, temperature, and ovipositing behavior in wasps; (2)

family structure and the development of vole social behavior; (3) development of cichlid fish in the nest; and (4) early development and its effect on parental behavior in the oldfield mouse.

DEVELOPMENT, TEMPERATURE, AND OVIPOSITING BEHAVIOR IN WASPS

One abiotic factor that often has important developmental consequences is temperature. Animals that are native to colder climates often show developmental differences when raised in warmer environments, and vice versa. Temperature, for example, is known to have strong effects on olfactory senses in insects (Herard et al., 1988), and because olfaction is a primary way in which insects interact with both abiotic and biotic factors in their environment, developmental differences caused by temperature likely have important fitness effects (Moiroux et al., 2016; see Box 4.4 for more).

Box 4.4. CONSERVATION CONNECTION

Development, Dispersal, and Climate Change

Individuals employ numerous dispersal strategies in which they use environmental cues they experience during development to choose which dispersal strategy to adopt (Ronce, 2007). Two dispersal strategies seen in spiders are rappeling and ballooning behavior. The spider *Erigone atra* uses silk threads for both rappeling and ballooning dispersal behavior. In ballooning behavior, the spiders rely on the silk threads to sail long distances, often hundreds of yards. When rappeling, spiders use silk thread to create a bridge that they can move along for short dispersals (Figure 4.18).

Figure 4.18. Dispersal strategies in *Erigone* altra. These spiders use temperature as a development cue for when to use risky (ballooning) versus less risky (rappeling) dispersal strategies. *(Photo credit: blickwinkel / Alamy stock Photo)*

The life cycle of *E. atra* involves colonizing and breeding in crop fields to which they migrate in the early spring. While silk production is costly (Bonte et al., 2016), dispersal in the spring is not especially risky, in the sense that crop habitats are often large with many available areas for breeding. In the fall, these spiders migrate to noncrop areas, where they may breed again and then spend the winter (Toft, 1995). Mortality risks are higher during cooler fall migrations to noncrop areas (Bonte et al., 2003, 2006, 2011).

Bonte and his colleagues predicted that spiders would use short-distance rappeling behaviors more often during the spring migrations, when potential territories are abundant, and then switch to ballooning dispersal—a riskier strategy, in which spiders have little control where they land—during the cooler fall migration when fewer suitable spider habitats are available. During the fall migration, the chances of getting a suitable habitat close by others is small enough that ballooning to distances far away may be worth the costs of having little control where a landing will occur. Bonte and his colleagues further hypothesized that spiders would employ temperature as the environmental cue they used during development to decide which strategy to employ. When examining the dispersal choices of spiders raised under controlled temperature conditions, they found that, as predicted, spiders that were raised at higher temperatures (similar to those they would experience in the spring) were most likely to rappel; spiders that were raised at lower temperatures (similar to those they would experience in the fall) were most likely to balloon (Bonte et al., 2008).

If the choice of dispersal strategy can differ depending on various temperature cues during development, think for a moment how spiders' dispersals might be affected by climate change. If animals use temperature as reliable cues for selecting how to disperse in both the spring and the fall, then climate change induced by humans—change that is unlikely to reflect other natural environmental changes—might induce the wrong dispersal choice (during either fall, spring, or both), in the sense of leading an individual to disperse using a strategy that is not beneficial in that environment. On a larger scale, Bonte and colleagues argue that if enough animals made such choices, population sizes might decline, potentially causing species-level extinction.

Joan van Baaren and her colleagues examined temperature-related developmental changes in the parasitoid wasp, *Anaphes victus*. Parasitoids usually lay their eggs inside a host species, and adult females learn to avoid hosts that have already been parasitized (Papaj and Lewis, 1993; Papaj et al., 1989). Van Baaren and her colleagues tested whether the temperature that female larvae were exposed to during development would affect their ability to learn how to find suitable hosts when they themselves were ready to lay eggs (van Baaren et al., 2005).

To examine the effect of temperature on learning and host choice behavior, they raised larvae at 4°C in two experimental treatments—one of which lasted three weeks and one of which lasted twelve weeks. In addition, they ran a control treatment in which larvae were not exposed to a temperature of 4°C. Afterward, female larvae were raised at a more typical temperature for this species (24°C). Wasps' ability to find suitable hosts was examined when these females were ovipositing (laying) their own eggs (Figure 4.17). When tested, females were presented with three different patches, which differed in the number of good hosts (unparasitized) and “bad” hosts (already parasitized). Van Baaren and her colleagues then measured the number of eggs the females laid and the females’ ability to learn to avoid already parasitized hosts.

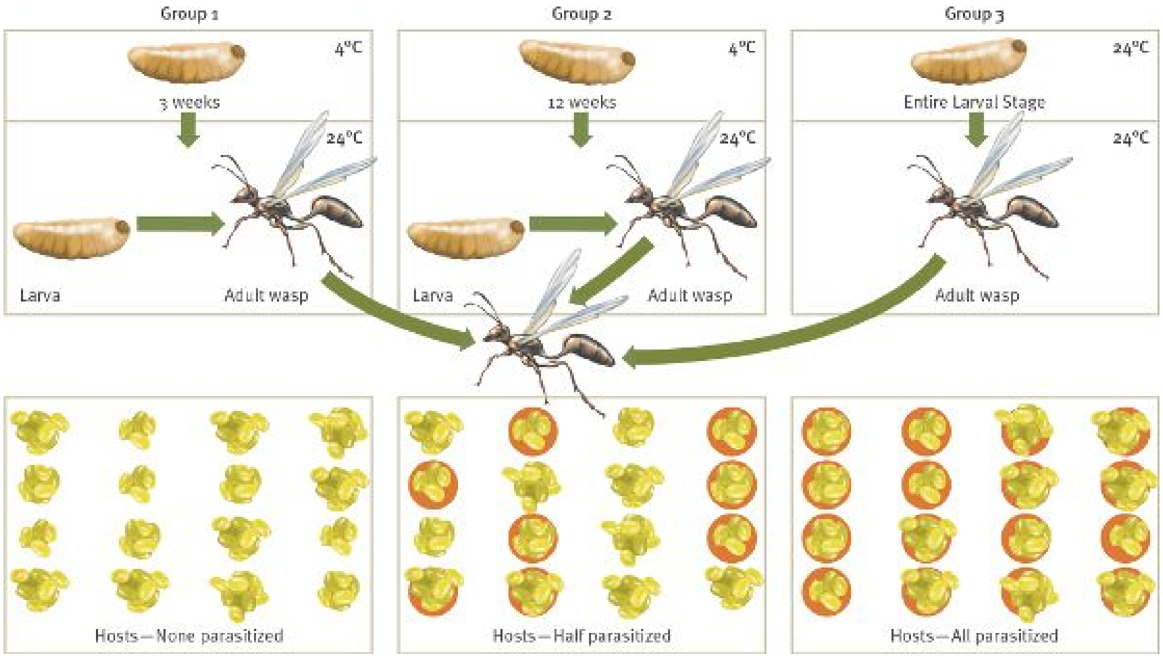


Figure 4.17. Temperature, learning, and egg laying. Exposure to cold temperature (4° C for three weeks for larvae in group 1, 4° C for twelve weeks for larvae in group 2) during development had significant effects on a female wasp’s ability as an adult to discriminate between hosts of different quality. Larvae in group 3, which were continuously raised at normal temperatures of 24° C, did not experience these effects. Exposure to cold temperature also had a strong negative effect on the speed at which females learned to avoid already parasitized hosts, when they had to choose to lay their eggs in patches in which none of the hosts had been parasitized (left), half had been parasitized (center), or all had been parasitized (right). Orange circles indicate a parasitized host. *(Based on van Baaren et al., 2005)*

Their results indicated that exposure to cold temperature during development had significant effects on (1) the number of eggs a female laid inside a host and (2) the female’s ability to discriminate among hosts of different quality. Equally interesting, exposure to cold temperature had a strong negative effect on the speed at which females *learned* to avoid already parasitized hosts. Females from low-temperature regimes would usually reject parasitized hosts after injecting their ovipositor into such hosts, but compared with females raised at higher temperatures, they fared more poorly at discriminating hosts through use of the external cues on the host after it had been parasitized. Such external cues were learned more quickly by females raised at higher temperatures (Box 4.5).

Box 4.5. SCIENCE AT WORK

What is the research question? Do environmental cues during development trigger dispersal behavior?

Why is this an important question? Dispersal plays a critical role in life history, and the role of developmental plasticity in dispersal strategy is not well understood.

What approach was taken to address the research question? Controlled laboratory experiments were undertaken, in which spiders were exposed to different temperature regimes to examine how that affected dispersal behavior.

What was discovered? In the spider *Erigone altra*, individuals use riskier “ballooning” dispersal strategies when temperatures are cooler, and less risky “rappelling” dispersal strategies when temperatures are warmer.

What do the results mean? Cooler temperatures are associated with fewer available habitats to colonize in *Erigone altra*, while warmer temperatures are associated with more habitats available to colonize. Spiders change their dispersal strategy—riskier or less risky dispersal—in response to temperature. In addition to informing us about complex decision-making behavior in invertebrates, this study has implications for how dispersal patterns may change as a result of anthropogenic climate change.

FAMILY STRUCTURE, DEVELOPMENT, AND BEHAVIOR IN PRAIRIE VOLES

One of the most salient features of an animal’s development is the family social environment in which it is raised. In particular, the type of parental care received and the frequency with which it is obtained can have important consequences later in life (Taborsky, 2016). Here we look at two case studies that center on development and interactions (or lack of interactions) between young and their parents and other adults. We first examine this aspect of development in prairie voles, and then in cichlid fish.

Within prairie voles there is significant variation in family structure. Getz and Carter (1996) found that about one-third of pups were raised by only their mother, one-third were raised by their mother and father, and one-third were raised in communal nests where they received care from their mother, their father, and other adult nest mates. Ahern and colleagues wanted to understand how this variation in parental care affected the behavioral development of voles (Ahern and Young, 2009; Ahern et al., 2011). In particular, they examined the amount of care a pup received when raised by a mother alone (labeled SM for single mother) versus when raised by a mother and father (labeled BP for biparental), and tracked whether the care an individual received affected its own parental behavior later in life.

Pups raised in the SM group were left in their nest alone (no parent present) more often than pups in the BP care group, and BP pups received significantly more grooming and licking behavior than SM pups (Figure 4.19A). The amount of grooming and licking provided by mothers in the SM group was approximately the same as that provided by mothers in the BP group; group differences were due to the absence of a male and any licking or grooming he might have provided. When pups from the SM and BP groups matured, Ahern and Young found differences in their social behaviors. SM females licked and groomed their pups less than BP individuals (Figure 4.19B). Both males and females from the SM group took longer to find a mate and bond with that individual than did males and females from the BP group. Differences in early development—being raised by one parent or by two parents—had long-term effects on the ontogeny of vole social behavior.

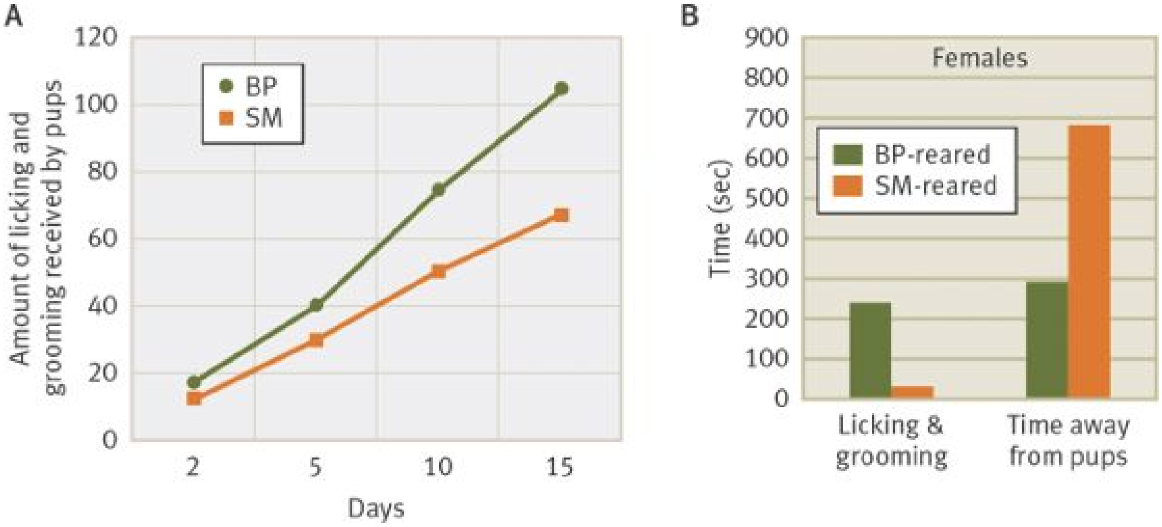


Figure 4.19. Amount of licking and grooming differed in one- versus two-parent nests. (A) In prairie voles, pups in the biparental (BP) treatment received more licking and grooming than pups in the single-mother (SM) treatment. (B) After they matured, females that were raised by a male and female (BP-reared) displayed more licking/grooming and pup care than females raised by only a female (SM-reared). These females also spent less time away from their pups than females raised by only their mother. *(From Ahern and Young, 2009)*

EARLY NEST DEVELOPMENT AND BEHAVIOR IN CICHLID FISH

Cornelia Arnold, Barbara Taborsky, and their colleagues studied early nest environment and its long-term behavioral effects in the cooperatively breeding cichlid, *Neolamprologus pulcher* (C. Arnold and Taborsky, 2010; Taborsky et al., 2012). In this species, the young in nests are raised not only by adults but also by older siblings that act as “helpers-at-the-nest,” aiding adults in rearing the latest clutch of offspring (chapter 9). Adults and helpers defend the nest against predators and remove parasites from eggs and developing fry. Arnold and Taborsky hypothesized that the presence of parents and helpers-at-the-nest may provide younger individuals with behavioral skills that are beneficial in a species that lives in complex social groups, by (1) freeing up time for developing offspring to interact with others, rather than to be vigilant for predators; and/or (2) serving as role models for the developing offspring, which could copy their actions.

To test their hypothesis, they raised newly born fish in groups together. In one treatment, no adults were present, in a second treatment an adult male and female were present, and in a third treatment an adult male and an adult female plus helpers-at-the-nest were present. In all cases, when the subjects matured, individuals from different treatments were tested in a series of competition experiments with one another. For example, an individual might be given time to establish a territory and then have ownership of that territory challenged by another fish. What Arnold and Taborsky (2010) found was that fish raised with either adults or adults and helpers displayed behaviors that were less costly in terms of energy but were still very effective in defending their territories compared with fish that were raised in the absence of adults or adults and helpers. It remains unclear whether this difference was due to young copying the behavior of older individuals at the nest or simply having more time to interact socially with one another when there were adults present, but in either case it is clear that the early environment experienced by these fish had important consequences for behavioral decisions later in life.

EARLY DEVELOPMENT AND ITS EFFECT ON PARENTAL BEHAVIOR IN THE OLDFIELD MOUSE

Animals often become better parents as they raise more and more offspring. Direct experience as a parent, however, is only one way to learn how to become a successful mother or father. Developmental factors early in life can also potentially affect future parental behavior. For example, in many species of birds and mammals, some individuals remain in their natal group even after they are capable of reproduction, and they often help their parents raise additional broods of offspring (as in the cichlid example above). Is it possible that such developmental experience may affect subsequent parenting success in helpers that eventually leave their natal territory? Susan Margulis and her colleagues examined this possibility in oldfield mice (*Peromyscus polionotus*).

Data on helping behavior among oldfield mice in natural settings are difficult to gather, but indirect evidence suggests that some females remain at the nest and help their mothers raise the next litter of young. For example, natural history data suggest that a mother can be both pregnant and nursing a brood of mice, while an older litter still remains at the nest, providing ample opportunity for potential helpers to aid in rearing their younger siblings (Foltz, 1981). Margulis tested whether experienced females—females that remained at their parents' nests during the rearing of a litter of their younger siblings—were better mothers to their own offspring than inexperienced females that did not remain at the nest while a younger litter of siblings was being reared (Margulis et al., 2005).

Margulis and her colleagues experimentally created inexperienced and experienced females by removing (or not removing) females from their natal nests. They began their work using a large colony of oldfield mice housed at the Brookfield (Illinois) Zoo, and they used mice that were ten to fifteen generations removed from wild-caught individuals. Margulis and her team formed a series of male-female mating pairs. Quickly thereafter, mating occurred, and pups were born. In the "inexperienced female" (IF) treatment, IF females were removed from the nest at twenty days of age, and were raised in all-female groups until the experiment began. In the "experienced female" (EF) treatment, when EF females were twenty days old, they were *not* removed from the nest but rather remained at the nest with their pregnant mother until she gave birth again, and nursed and weaned a second brood. At that point, EF females were removed from the nest and reared in an all-female group until the experiment began.

IF and EF females were mated with inexperienced males and produced offspring, and the females' parental activities and offspring survival were recorded. The results suggested that all females—both EF and IF—became better parents as they produced more and more litters over time, but the key comparison was between inexperienced and experienced females at any given point in time. Here, Margulis and her colleagues found that the litters of experienced females had a higher probability of survival than those of inexperienced females, in part because of the superior nest-building behavior displayed by experienced females (Figure 4.20). The results indicate that the developmental experience of being present when one's mother raises a subsequent clutch of offspring has long-term consequences for parenting abilities (see Harding and Lonstein, 2016; Wu et al., 2013 for similar results in other rodents).

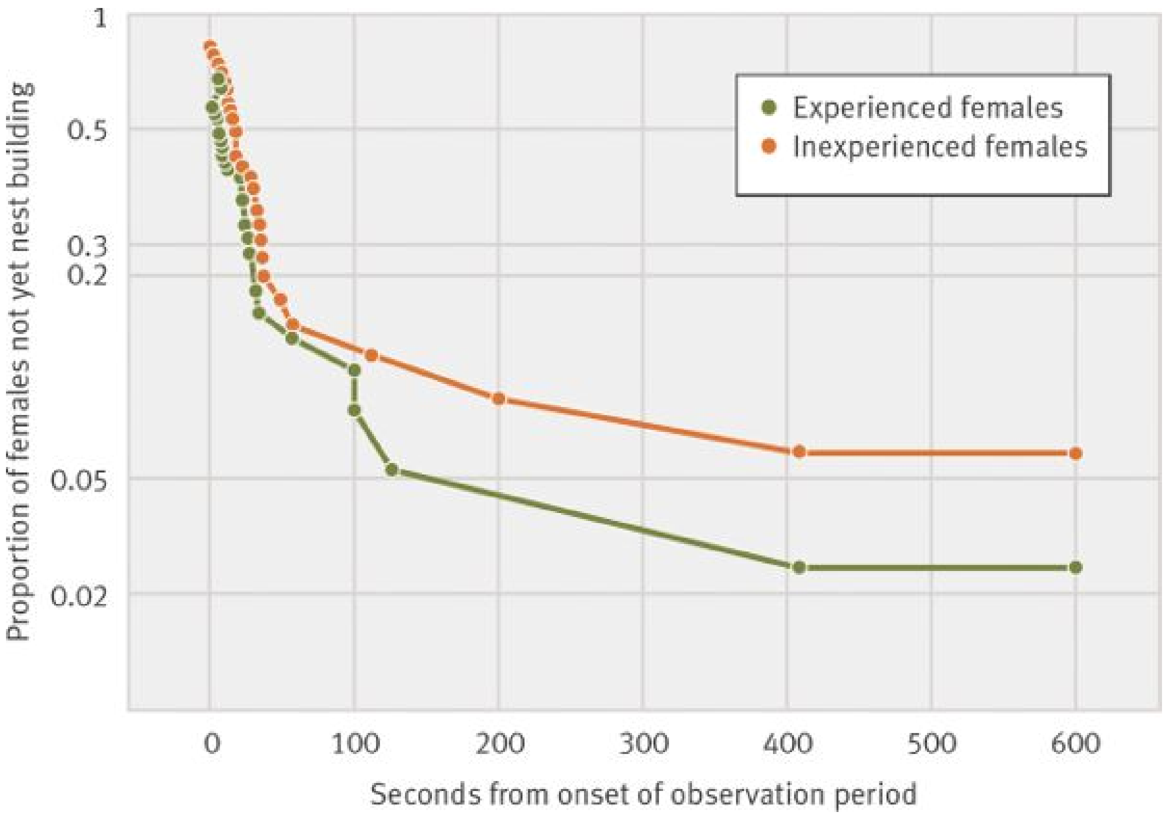


Figure 4.20. Nest building and experience in oldfield mice. The proportion of females that did not start building nests was lower in experienced females (green) versus inexperienced females (orange). Experienced females began to build nests sooner than inexperienced females and built superior nests. *(From Margulis et al., 2005)*

Interview with Dr. Gene Robinson

Why did you decide to work on honeybees?

I first became fascinated with honeybees at the age of eighteen, when I took time off from college to work on a kibbutz in Israel. One day I was asked to help the kibbutz beekeeper with the bees, and from that very first day I was struck by the combination of order and chaos in their behavior. Because of that experience, I decided to major in biology, with a focus in entomology. After college, I worked as an apiary inspector, a queen breeder, and a bee-keeping trainer overseas. It was in the course of my doctoral research that I started to study the division of labor in the hive, first from an endocrinological perspective and then, as a postdoc, from a genetic perspective. Since then, one of the main goals of my research has been to determine the various mechanisms that control the highly ordered yet highly plastic division of labor among honeybees.

Why sequence the genome of the honeybee?

Honeybees have proved to be an ideal model system for studying complex animal society. The honeybee system is at once both organized and flexible, depending on the needs of the colony. Research has already shown how the division of labor is influenced by various factors including hormones, pheromones, and environmental changes. It is also clear from my research that bees of different genotypes have different behavioral tendencies, and this also contributes to the structuring of the division of labor.

To further these studies, I decided in 1998 to begin laying the groundwork to sequence the honeybee genome. A sequenced genome provides many forms of knowledge to help in mechanistic and evolutionary analyses of social behavior. We have used several, including transcriptomic analyses of all the genes active in the brain during the performance of specific behaviors. For example, genetic research has allowed us to discover that hive bees and foragers differ in approximately 40 percent of their brain gene expression and that these differences arise from hereditary, environmental, and physiological effects. We also have partially sequenced the genomes of ten other species of bees, some social and some with more solitary lifestyles, and employed molecular evolution analyses. We found a particularly strong signature of selection for genes related to metabolism. In other words, genes involved in regulating basic metabolic processes appear to have been shaped by natural selection during the evolution of complex social life in the bees.

What is the most difficult part of taking what you learn at the genomic level and applying it to the study of behavior?

There are many levels of biological organization in the brain that stand between the genome and behavior. Understanding how changes at the genomic level give rise to changes in the brain that ultimately cause changes in behavior is a key challenge.

What has been your basic strategy when trying to understand the complex developmental pathways we see in honeybees?

There are two key elements to our strategy. On the behavioral side, our strategy has been to start with the behavior as it occurs naturally in the field and then use robust assays to capture the natural behavior in such a way that it is amenable to genomic analysis. On the genomic side, we have generally applied the candidate gene approach to either developing hypotheses about individual genes or interpreting results from large-scale transcriptomic analyses. That is, we have used knowledge of gene function from other species or knowledge of bee physiology to guide our study of genes. However, we also maintain an open mind and are occasionally surprised by results that implicate a family of genes or a biological process that we had not previously targeted. For example, we have implicated changes in brain metabolism, especially a down-regulation of genes in the oxidative phosphorylation pathway, as being critical to increases in arousal and aggression, and we would not have predicted that.

What is the next big question you and your lab are going to tackle?

We are trying to understand the transcriptional architecture underlying socially regulated gene expression in the brain and how it has evolved from the architecture underlying solitary behavior.

Dr. Gene Robinson is a professor at the University of Illinois at Urbana-Champaign and a member of the National Academy of Sciences. He is one of the world's foremost experts on the honeybee.

SUMMARY

1. Molecular genetics can be a powerful tool in proximate analyses of behavior. Researchers can use genes in the proximate explanation of a trait by studying which specific gene or set of genes codes for a trait. Studies of animal behavior and molecular genetics, often identifying (and sometimes sequencing) the genes behind behavioral traits, are large-scale endeavors going on in many labs around the world today.
2. Gene expression and gene regulation—whether, when, and to what extent a gene is switched on—are also the subject of more and more ethological work focusing on proximate causation.
3. Development in a broad sense encompasses everything from in utero effects to the specific effects that environmental factors might have after birth on the behavior of a developing organism. Environmental factors relevant to development and

behavior include both abiotic (nonliving) and biotic (living) components of the environment.
4. Developmental pathways affect dispersal strategies and can be influenced by temperature change. More and more evidence suggests that animals choose which dispersal strategy to adopt as a function of the temperature they experience during development.
5. Two examples—honeybee foraging behavior and comparative social behavior in two closely related species of voles—have run through chapter 3 and this chapter on proximate approaches to behavior. These examples allow us to bring together numerous approaches to the proximate study of behavior—molecular genetic, hormonal, developmental, and neurobiological approaches—in a single system, and provide us with a comprehensive understanding of the proximate underpinnings of behavior.

DISCUSSION QUESTIONS

1. The entire genome of many animals is now being sequenced. How might these studies affect work on molecular genetics and behavior? Are there any pitfalls you can imagine to having such a large genetic database available to behavioral researchers?
2. How are genes used to address different types of questions in proximate versus ultimate analyses?
3. Medical school curricula tend to be dominated by courses dealing with proximate analyses. How might physicians benefit from understanding the relationship between proximate and ultimate causation?
4. In addition to the developmental factors discussed in this chapter, can you name one other biotic and one other abiotic developmental factor that might be important in shaping behavior? Provide a one-paragraph explanation for each of these.
5. Make a detailed argument that no matter which of the four proximate approaches you employ, you can always complement your study with one or more of the other approaches. You may use the honeybee foraging and/or sociality in voles examples discussed in this chapter as a fulcrum for your discussion.

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5

Learning

Molecular Genetics and Endocrinology of Learning

- Molecular Genetics of Learning in Rats
- Endocrinology of Learning in Rats

Interview with Dr. Sara Shettleworth

In chapter 3 we learned that male meadow voles are polygynous. Males also have larger territories than females, outperform females on spatial memory tasks, and have a larger hippocampus region, an area strongly linked to spatial learning. Presumably the superior spatial memory found in males is the result of selection acting more strongly on males than females, because keeping track of resources on larger territories is a more difficult problem than on smaller territories. More generally, animal behaviorists hypothesize that when males and females consistently face spatial learning tasks that differ in their degree of difficulty, we expect selection to act differently on the sexes.

Cowbirds (*Molothrus alter*) allow for a strong test of this spatial learning hypothesis. In cowbirds, it is females that face the more challenging spatial learning tasks, and females who have a larger hippocampus than males. Cowbirds are obligate nest parasites, meaning that females always lay their eggs in the nests of other species (Figure 5.1). Females spend time and energy locating nests where they will lay their eggs. They search for potential host nests by monitoring their environment from the canopy, observing nest building in other species, checking such nests and returning to them numerous times, attempting to flush out the resident female early in the morning, laying their own eggs in the nest, and then sometimes returning again to remove host species' eggs (Norman and Robertson, 1975; Rothstein et al., 1987). This whole process is demanding in terms of spatial memory. Males face no comparable problems. As such, ethologists predict that in cowbirds, selection should have favored better spatial memory abilities in females.

Figure 5.1. **Spatial learning in cowbirds.** Spatial learning has been studied in parasitic cowbirds, *Molothrus alter*. *(Photo credit: S & D & K Maslowski/ FLPA / Minden Pictures)*

Melanie Guigueno and her colleagues tested cowbirds on a memory task. Birds were presented 25 open cups. One randomly selected cup had millet seed in it. A cowbird was allowed to search and find the cup with the food reward and to feed at that cup for 2 minutes. Then the bird was removed from experimental area. It was returned again later, to the same grid with 25 cups. The same cup that had seed in it before, again had seed placed in it, but this time all 25 cups were covered with a lid so the bird could not see which cup had food (Figure 5.2). In addition, prior to this second round of the test, all cups had millet seed placed in them, and then the millet seed was shaken and removed, so that odor cues were minimized. In one treatment, birds were returned to the arena one hour after the first test, and in a second treatment, they were returned 24 hours after the first test. The success rate of males and females was recorded.

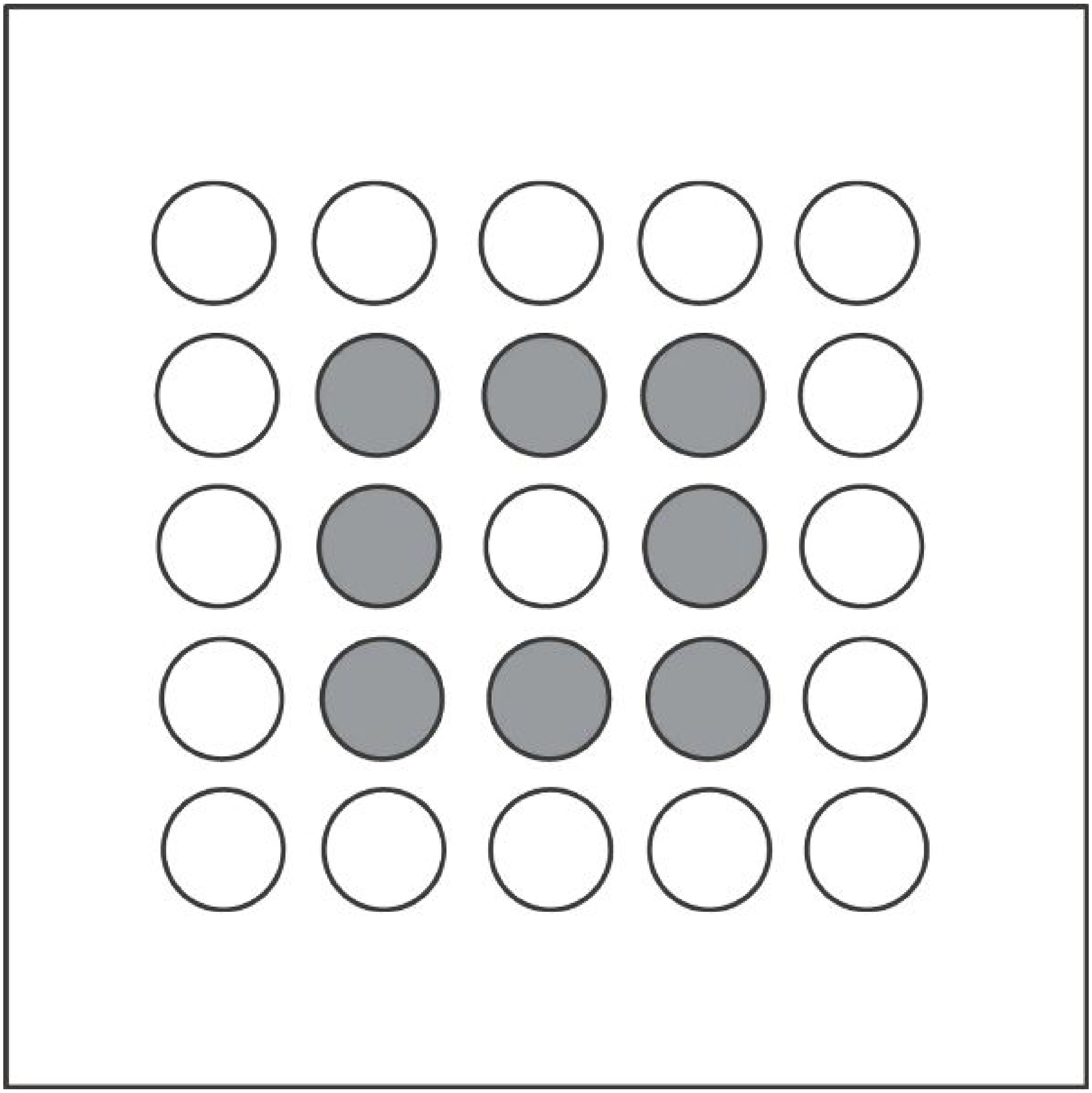


Figure 5.2. **Cowbird memory test.** The spatial grid used in the cowbird memory test. Only one of the center cups (shaded in gray here but not in the experiment itself) had food in it. By permission of the Royal Society. *(From Guigueno et al., 2014)*

What the researchers found was that while males and females spent approximately the same amount of time searching in the second test—suggesting their motivation levels were equal—as predicted by the spatial memory hypothesis, females made fewer errors before finding the correct cup in the second test. This effect was uncovered in both the breeding and nonbreeding season (Figure 5.3, new). As with the meadow voles, evidence suggests that natural selection has favored spatial memory more strongly in the sex that consistently faced more difficult spatial memory tasks (males in voles, females in cowbirds; Box 5.1).

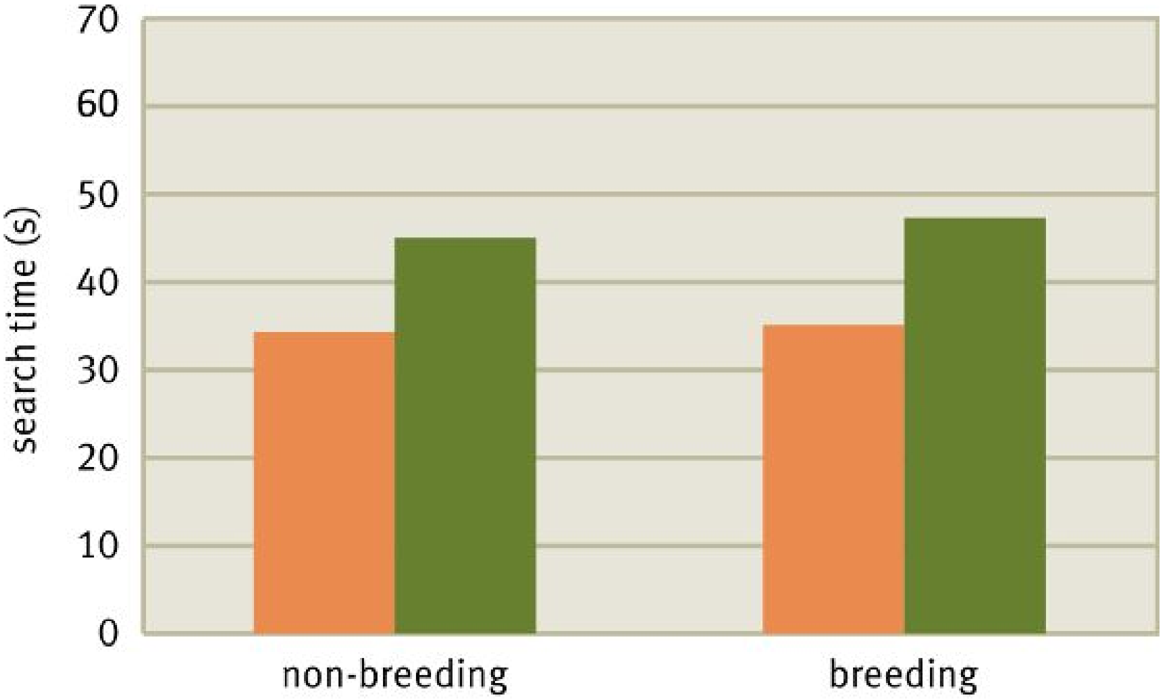


Figure 5.3. **Female cowbirds have better spatial memory.** Females made fewer errors than males finding the cup with food in it. Data here are from when first and second trials were separated by 24 hrs. Light gray bars = females and dark gray bars = males. By permission of the Royal Society. *(From Guigueno et al., 2014)*

Box 5.1. SCIENCE AT WORK

What is the research question? Do female cowbirds show better spatial memory skills than males?

Why is this an important question? Theory predicts that individuals from the sex that has more difficult memory tasks in nature will have better spatial memory abilities. This has been tested previously in species where males have more difficult spatial memory tasks, but not where females do.

What approach was taken to address the research question? Male and female cowbirds were given a spatial memory task associated with foraging.

What was discovered? Female cowbirds performed better than males on the spatial memory task.

What do the results mean? In conjunction with other studies, these results suggest that natural selection favors superior spatial memory in individuals from the sex with the more difficult spatial memory tasks.

* * *

What Is Individual Learning?

This chapter examines the role that **individual learning** plays in animal behavior. The role of social learning—learning from other individuals—is the subject of chapter 6. In our analysis of individual learning—which we will refer to as learning in the rest of this chapter—we start by addressing three related questions: How do animals learn? Why do animals learn? What do animals learn?

Before tackling these broad questions, it is important to address a few more basic issues, first and foremost among them being: What do we mean when we speak of learning? This is a complicated question, but the definition of learning we adopt here is straightforward, and fairly widely accepted within psychology. *Learning* refers to a relatively permanent change in behavior as a result of experience (Shettleworth, 1998). This definition does have a downside, in that it is not clear how long a time period is encompassed by the words *relatively permanent*. That being said, this is a working definition, already adopted implicitly by most ethologists, and it will serve our purposes here.

It is interesting to note that the phrase *relatively permanent* was added to an older definition of learning, which was something like "a change in behavior as a result of experience." The insertion of *relatively permanent* was meant to address a particularly difficult problem regarding the definition of learning. Sara Shettleworth describes the problem as follows: A rat that experiences no food for twenty-four hours is more likely to eat than a rat that has just been fed. Most people would say that hunger per se, not any learning by the rat, explains its increased proclivity to forage, even though the experience of *not being fed* did affect the rat's behavior when it was presented with food (Shettleworth, 1998). Insertion of the phrase "relatively permanent" into the definition of learning eliminates this problem.

Our definition of learning—"a relatively permanent change in behavior as a result of experience"—suggests an interesting relationship between learning and what evolutionary ecologists refer to as "phenotypic plasticity" (Gianoli and Valladores, 2012; Harvell, 1994; Levins, 1968; Pfennig et al., 2010; West-Eberhard, 1989, 2003). A

phenotype is typically defined as the observable characteristics of an organism (P. Walker, 1989), and **phenotypic plasticity** is broadly defined as the ability of an organism to *produce different phenotypes* depending on environmental conditions. For example, many invertebrates, such as the bryozoan *Membranipora membranacea*, live in colonies (Harvell, 1998). When living in such colonies, individuals typically lack the spines that are used as an antipredator defense in related species. These spines are simply not grown when a *Membranipora membranacea* colony develops in the absence of predators. Yet individuals grow spines relatively quickly when exposed to predatory cues (Harvell, 1991, 1994; Tollrian and Harvell, 1998; Figure 5.4). The resultant change, from spineless to spined, constitutes a case of phenotypic plasticity. The phenotype of this bryozoan shifts dramatically as a result of environmental changes—in this case, the addition of a predator—and hence is thought of as “plastic” (Figure 5.5).

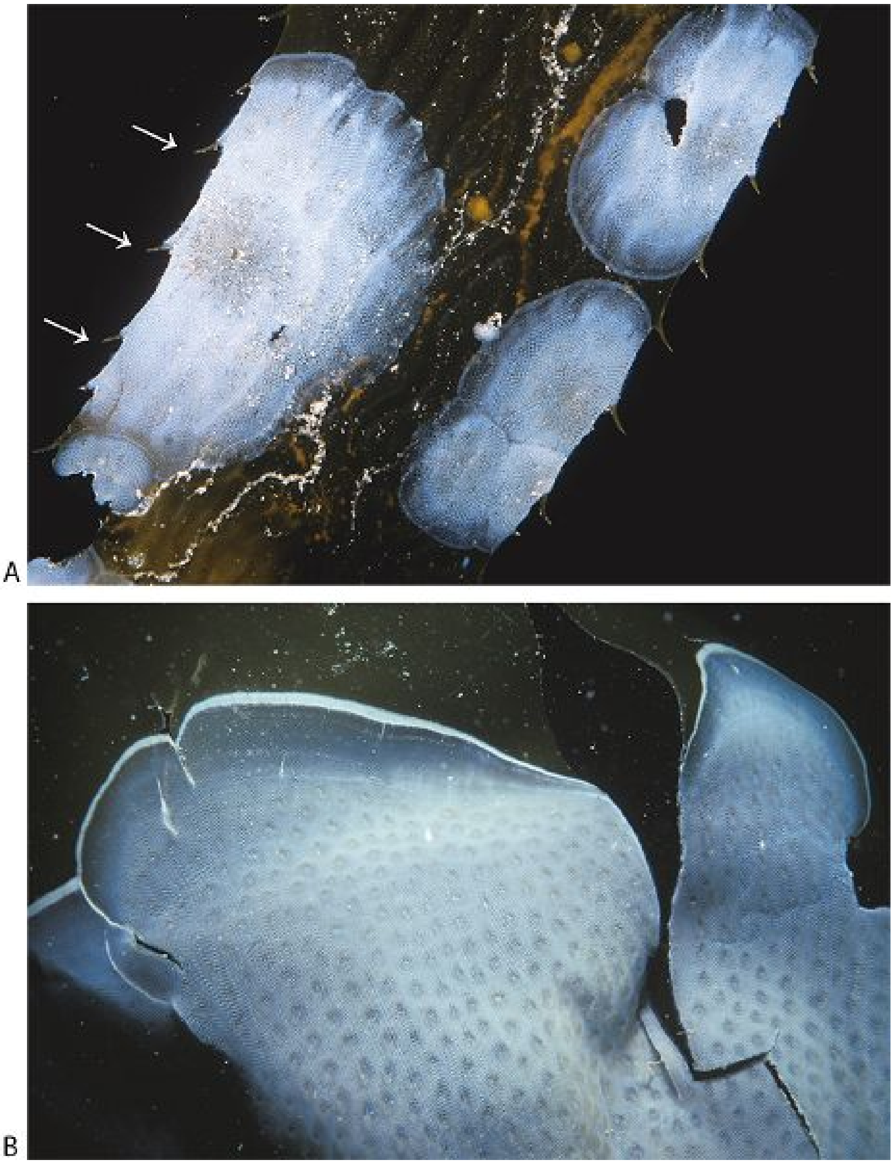


Figure 5.4. Inducible defenses. In some bryozoans, like *Membranipora membranacea*, colonies produce spines when predators are present. (A) Spines are shown protruding from a colony as a defense against predators (arrows point to spines), and (B) a colony of *Membranipora membranacea*. *(Photo credits: © Ken Lucas/Visuals Unlimited; © Sue Daly/naturepl.com)*

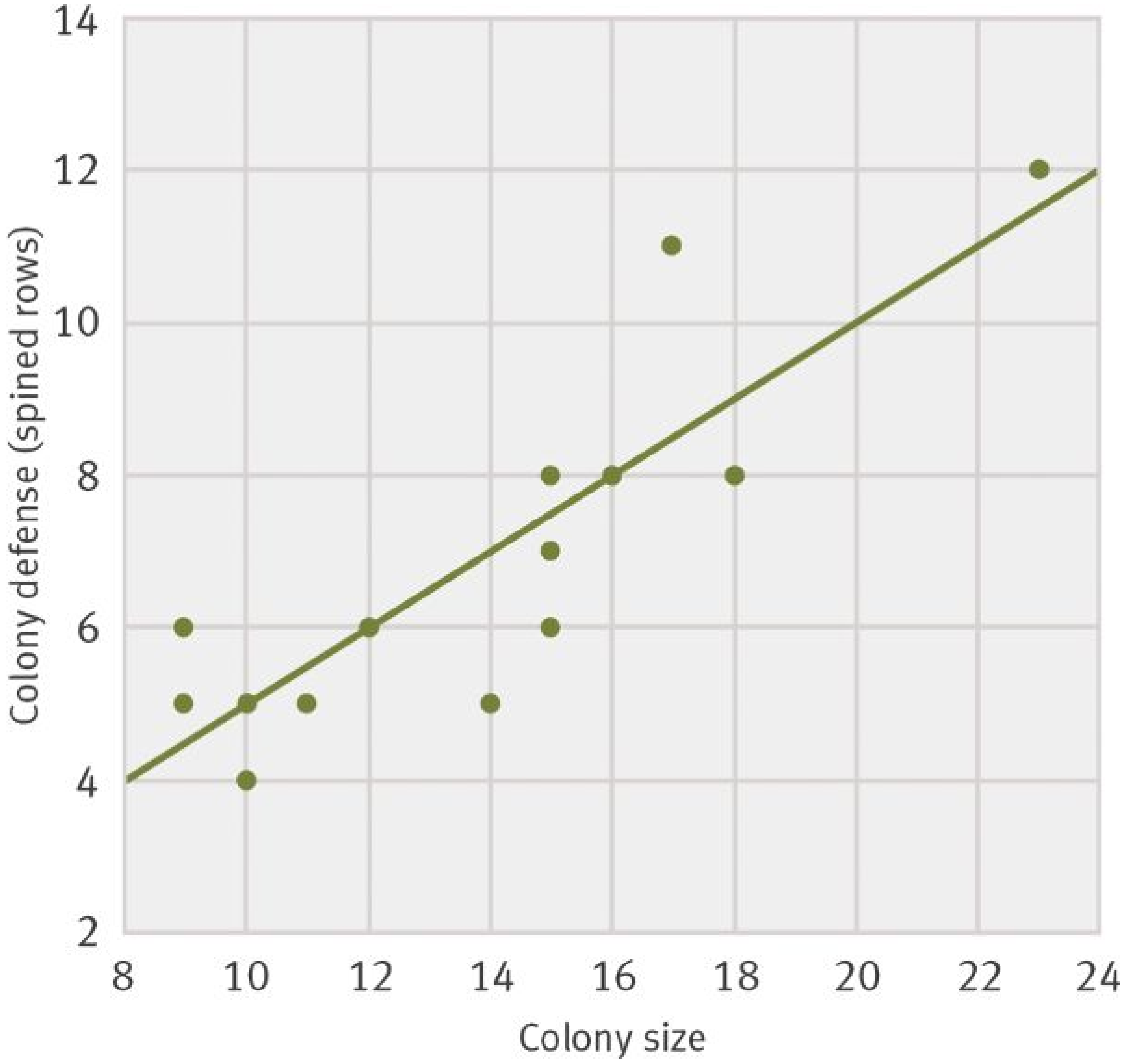


Figure 5.5. Phenotypic plasticity. When colonies of the bryozoan *Membranipora membranacea* are exposed to chemical stimuli from a predator, individuals in these colonies grow spines. This graph shows the response to a single "dose" of water conditioned with bryozoan predators. Large colonies produce more spines. *(From Harvell, 1991, p. 4)*

If learning is "a relatively permanent change in behavior as a result of experience," it then becomes one type of phenotypic plasticity because behavior is part of a phenotype (Dukas, 1998a). That is, if we replace *behavior* with *phenotype* in our definition of learning, phenotypic plasticity becomes the broader category under which learning is subsumed. So all learning is a type of phenotypic plasticity, but not all phenotypic plasticity involves learning. To see why, consider the "flushing" behavior often seen in foraging birds. While searching for food, some birds may move their tails and wings in a way that flushes insects out from cover—insects that the bird then eats. In the painted redstart (*Myioborus pictus*), for example, when individuals are under branches, they increase their wing and feather motion and flush insects from the overhanging branches. One hypothesis to explain this flushing behavior is that the birds learn that when they are under branches and flap their wings, they will get food. However, this response could be based on a relatively fixed genetic response rather than learned.

Piotr Jablonski and his colleagues designed an experiment to distinguish between these two hypotheses. What they found is that, while it is true that birds in nature increase their wing-flapping behavior when they are under branches, the same increase in wing flapping also occurs in the laboratory, even when the birds are not rewarded for such behavior: when Jablonski's team put naive birds under branches, they started flapping more as well, even when they got no food for doing so (Jablonski et al., 2006). These results suggest that flushing insects under branches does represent a case of phenotypic plasticity—the ability of an organism to *produce different phenotypes* depending on environmental conditions (whether the birds are under trees or not)—but it is not a case of learning.

How Animals Learn

In this section, we delve into *how* animals learn what they learn. There is a large psychological literature on this, both theoretical and empirical, but here we will just review some very basic ideas on how animals learn, or what psychologists often refer to as the processes underlying learning. This discussion of how animals learn follows an outline developed by Cecilia Heyes, both because of its conciseness and its attempt to tie *how* animals learn to *why* they learn (Heyes, 1994). Heyes notes that there are three commonly recognized types of experience that can lead to learning—namely, single stimulus, stimulus-stimulus, and response-reinforcer—each of which facilitates certain forms of learning.

LEARNING FROM A SINGLE-STIMULUS EXPERIENCE

The simplest experience that can lead to learning involves a single stimulus—a stimulus that can take almost any form. For example, let's imagine that we are interested in studying learning in rats and that numerous times throughout the day we place an arbitrary cue—a blue-colored stick—in a rat's cage (Figure 5.6). Rats will often take note of such a disturbance and turn their heads in the direction of the blue stick. If, *over time*, the rats become more likely to turn their heads in the direction of the blue stick—that is, if they become more sensitive to the stimulus with time, **sensitization** has occurred. Conversely, if, over time, the animals become less likely to turn their head, **habituation** is said to have taken place. Sensitization and habituation are two simple single-stimulus forms of learning.

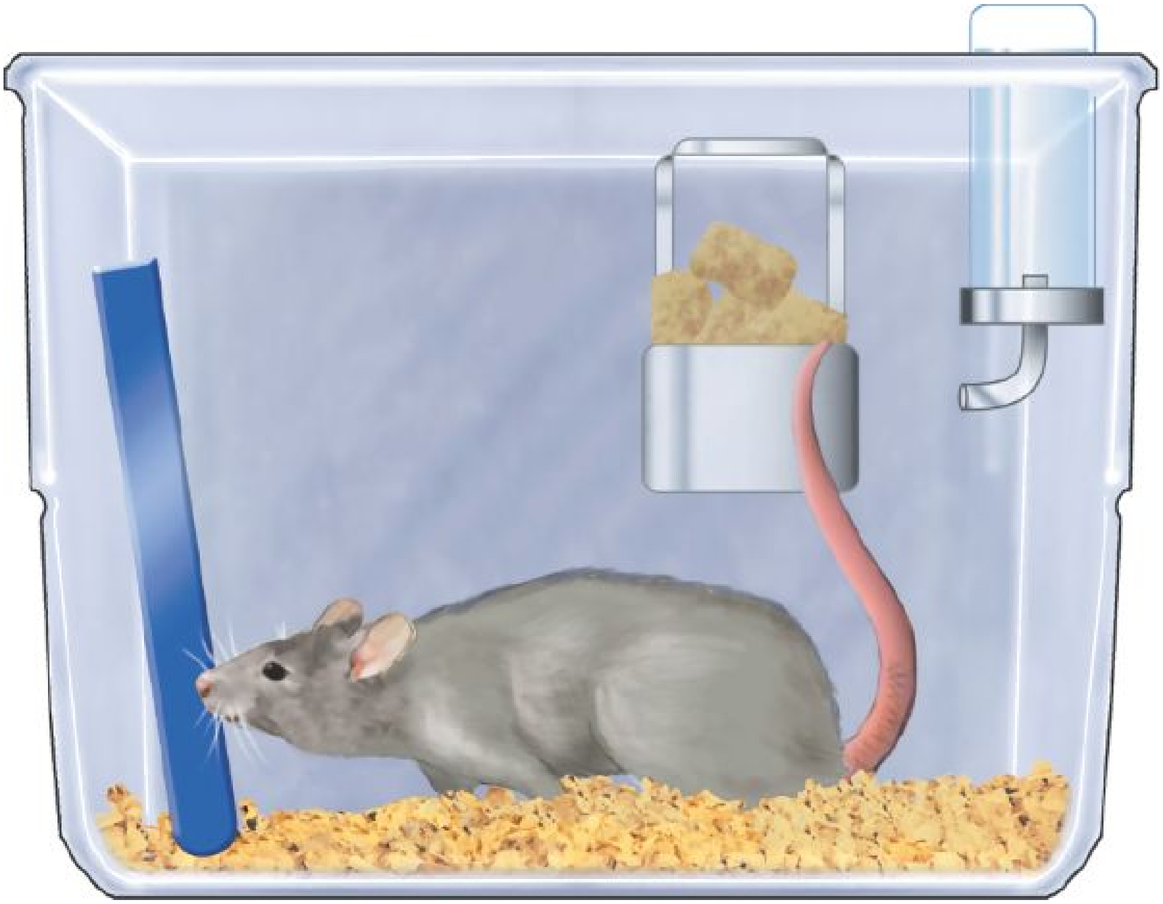
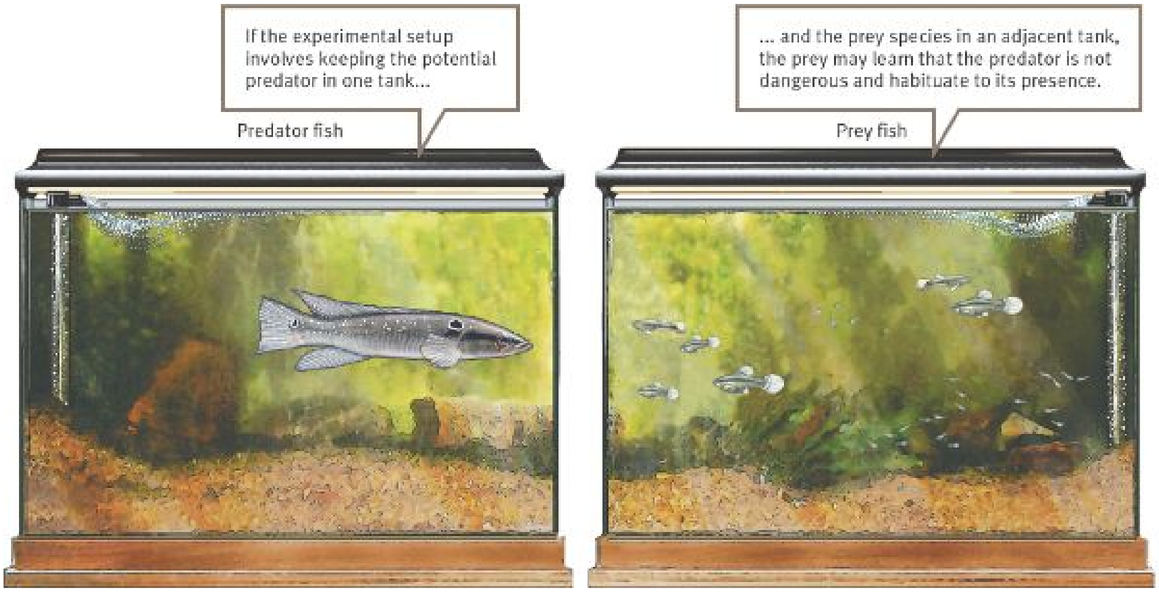


Figure 5.6. Habituation and sensitization. Numerous times each day, a blue stick is placed in a rat's cage. If, over time, the rat takes less and less notice of the stick, habituation has occurred. If the rat pays more attention to the blue stick over time, sensitization has taken place.

The process of habituation can be problematic when it comes to designing an ethological experiment, because it can be difficult to examine behavior if animals habituate quickly to stimuli. For example, in many experiments involving antipredator behavior, predators may be housed such that visual interactions between predator and prey are possible, but the predator can't actually harm the prey (Figure 5.7). This ethical compromise spares the life of the potential prey, but it also creates a scenario in which the prey may now habituate to the predator, having learned that the predator cannot in fact move close enough to present any real danger (Huntingford, 1984). Because of these sorts of issues, ethologists often need to go to great lengths to be certain that habituation has *not* occurred in their study system (Rowland and Sevenster, 1985).



If the experimental setup involves keeping the potential predator in one tank...

... and the prey species in an adjacent tank, the prey may learn that the predator is not dangerous and habituate to its presence.

Figure 5.7. Habituation as a problem. In controlled laboratory experiments, prey may habituate to the presence of a predator over time.

Conservation biologists also worry about habituation in animals that may be trained in captivity and then released into the wild. In the safety of the lab, animals may habituate to certain stimuli that might prove very dangerous upon the animals' release into the wild (Bauer, 2005; Higham and Shelton, 2011). Animal trainers, however, particularly those working with economically valuable animals such as horses, often try to habituate the animals they work with to various stimuli, so that the animals become less frightened by stimuli that elicit innate fear responses (Christensen et al., 2006; Christensen, 2013; Brubaker and Udell, 2016).

An animal's habituation to a stimulus may interfere with later attempts to get the animal to associate that stimulus with some other cue. For example, if rats habituate to the blue stick, it might prove more difficult for them to subsequently learn that the blue stick signals the arrival of food. In contrast, if sensitization to a single cue has occurred, it may facilitate the association of the sensitized stimulus with other cues.

PAVLOVIAN (CLASSICAL) CONDITIONING

Suppose that rather than giving a rat a single stimulus like the blue stick, from the start we *pair* this stimulus with a second stimulus, let’s say the odor of a cat—an odor that rats fear, even when they are exposed to it for the first time. Let’s imagine that five seconds after the blue stick is in place, we spray the odor of a cat into one corner of the cage (Figure 5.8). If the rat subsequently learns to pair stimulus 1 (blue stick) with stimulus 2 (cat odor) and responds to the blue stick by climbing under the chip shavings (a safer location) in its cage as soon as it appears, but *before* the odor is sprayed in, we have designed an experiment in **Pavlovian** or **classical conditioning** (Kim and Jung, 2006).

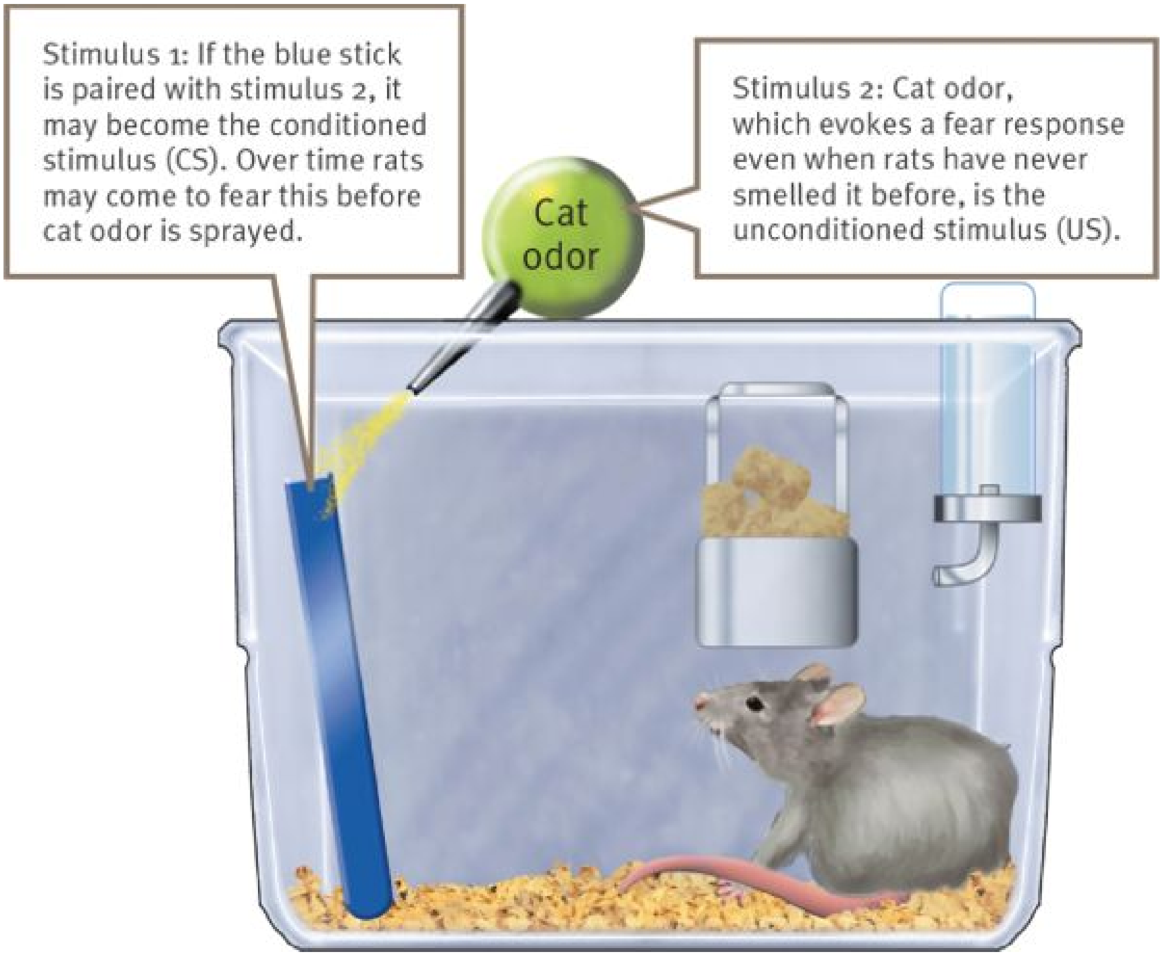


Figure 5.8. Paired stimuli. Five seconds after a blue stick (stimulus 1) is placed in a rat's cage, the odor of a cat (stimulus 2) is sprayed in. The question then becomes: Will the rat pair the blue stick with danger (cat odor)?

This form of conditioned learning was first developed by Ivan Pavlov in the late 1800s (Pavlov, 1927; Figure 5.9). Pavlovian conditioning experiments involve two stimuli—the conditioned stimulus and the unconditioned stimulus (Domjan, 2005, 2006). A **conditioned stimulus (CS)** is defined as a stimulus that initially fails to elicit a particular response but comes to do so when it becomes associated with a second (unconditioned) stimulus. In our rat example, the blue stick is the conditioned stimulus, as initially the rat will have no inherent fear of it. The **unconditioned stimulus (US)** is a stimulus that elicits a vigorous response in the absence of training. In our rat example, the US would be the cat odor, which inherently causes a fear response in rats. Once the rat has learned to hide after the blue stick (CS) alone is in place, we can speak of its hiding as being a **conditioned response (CR)** to the presence of the blue stick (Figure 5.10).

Figure 5.9. Ivan Pavlov and classical conditioning. Pavlov watches a classical conditioning experiment as it is being conducted in his laboratory. In the experiment, a device to measure salivation has been attached to the dog’s cheek, the unconditioned stimulus is a dish containing meat powder, and the conditioned stimulus is a light. *(Photo credit: Sovfoto/Eastfoto)*

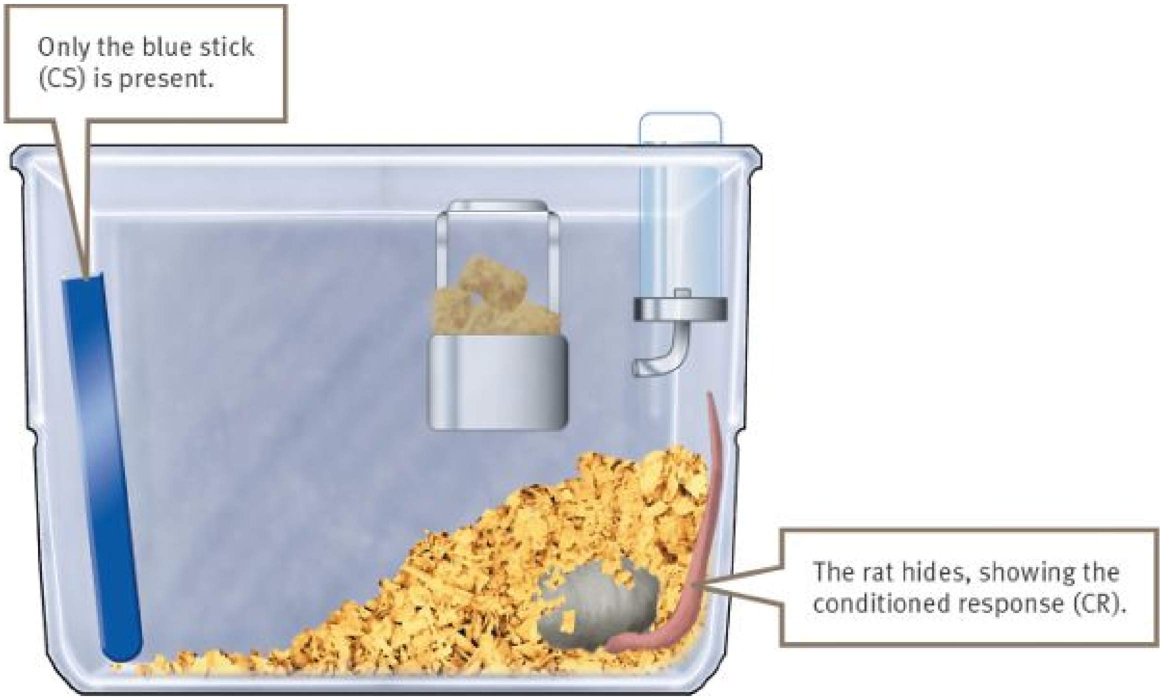


Figure 5.10. Conditioned response. If the rat pairs the blue stick (CS) and the cat odor (US), it will hide under the chips when the blue stick alone is presented. Such hiding represents a conditioned response (CR).

To examine Pavlovian conditioning in a bit more detail, we need to define a few more terms. In the learning literature, any stimulus that is considered positive, pleasant, or rewarding is referred to as an **appetitive stimulus**. Appetitive stimuli include food, the presence of a potential mate, a safe habitat, and so on. Conversely, any stimulus that is unpleasant—shock, noxious odors, and so forth—is labeled an **aversive stimulus**. Another important distinction made in the learning literature is between positive and negative relationships. When the first event (placement of the blue stick) in a conditioning experiment predicts the occurrence of the second event (cat odor), there is a positive relationship between events. Conversely, if the first event predicts that the second event will *not* occur—imagine that a blue stick is always followed by *not* feeding an animal at its normal feeding time—there is a negative relationship. Positive relationships—for example, blue stick predicts cat odor—produce **excitatory conditioning.** Negative relationships—for example, blue stick leads to no food at a time when food is usually presented—produce **inhibitory conditioning**.

Pavlovian conditioning experiments can become complicated when second-order conditioning is added on (Figure 5.11). In **second-order conditioning,** once a conditioned response (CR) has been learned by pairing US and CS1, a new stimulus is presented *before* the CS1, and if the new stimulus itself eventually elicits the conditioned response, then the new stimulus has become a conditioned stimulus (CS2). In our case, any rat that has learned to pair the blue stick (CS1) with danger might now see a yellow light (CS2) preceding the appearance of the blue stick. Once the rat has learned to pair the yellow light (US) with the danger associated with cat odor, second-order Pavlovian conditioning has occurred.

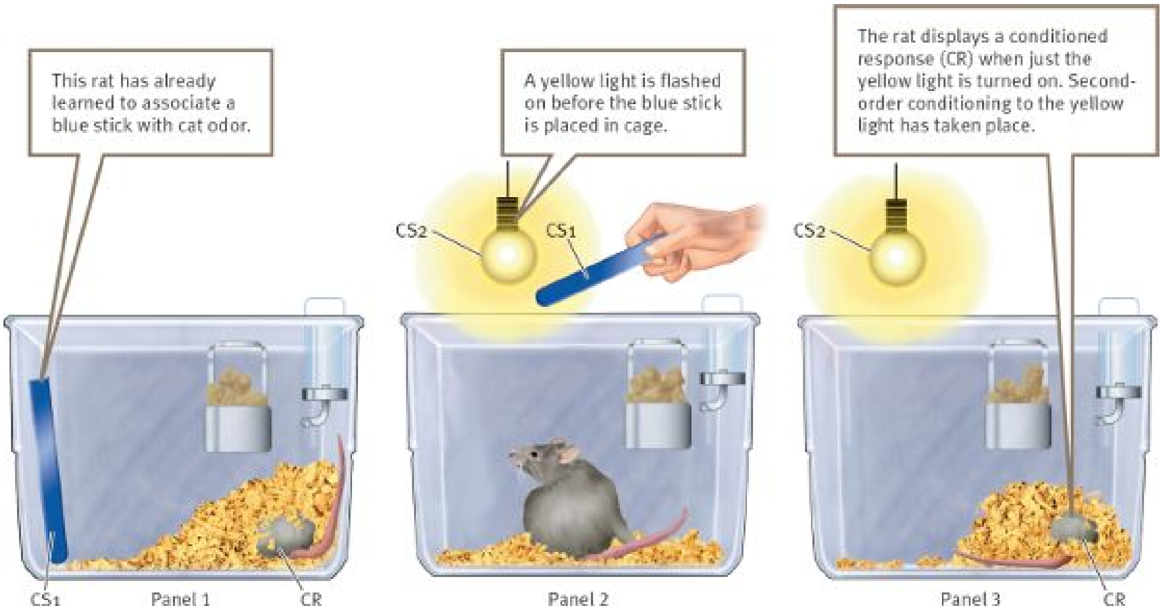
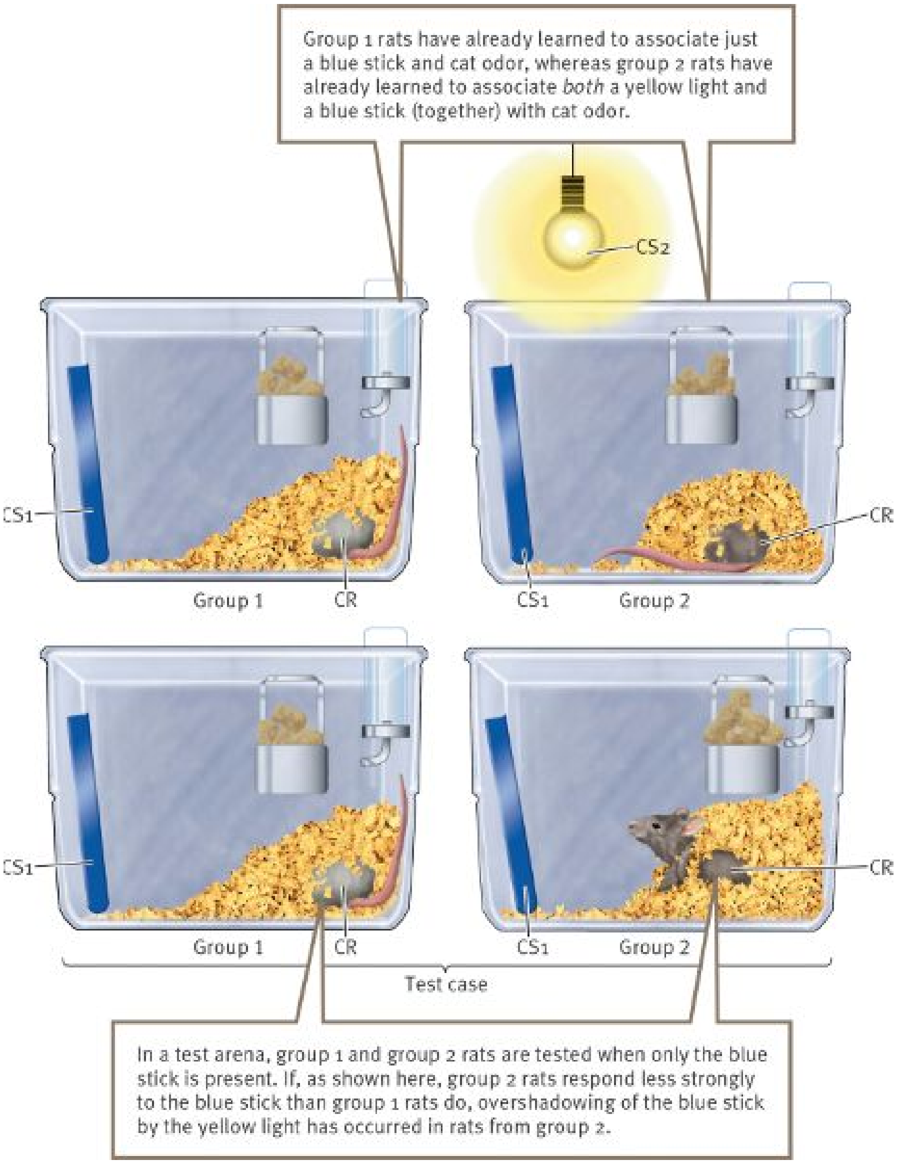


Figure 5.11. Second-order conditioning. The rat learns to respond to a second CS—the yellow light—with the conditioned response.

Overshadowing, Blocking, and Latent Inhibition

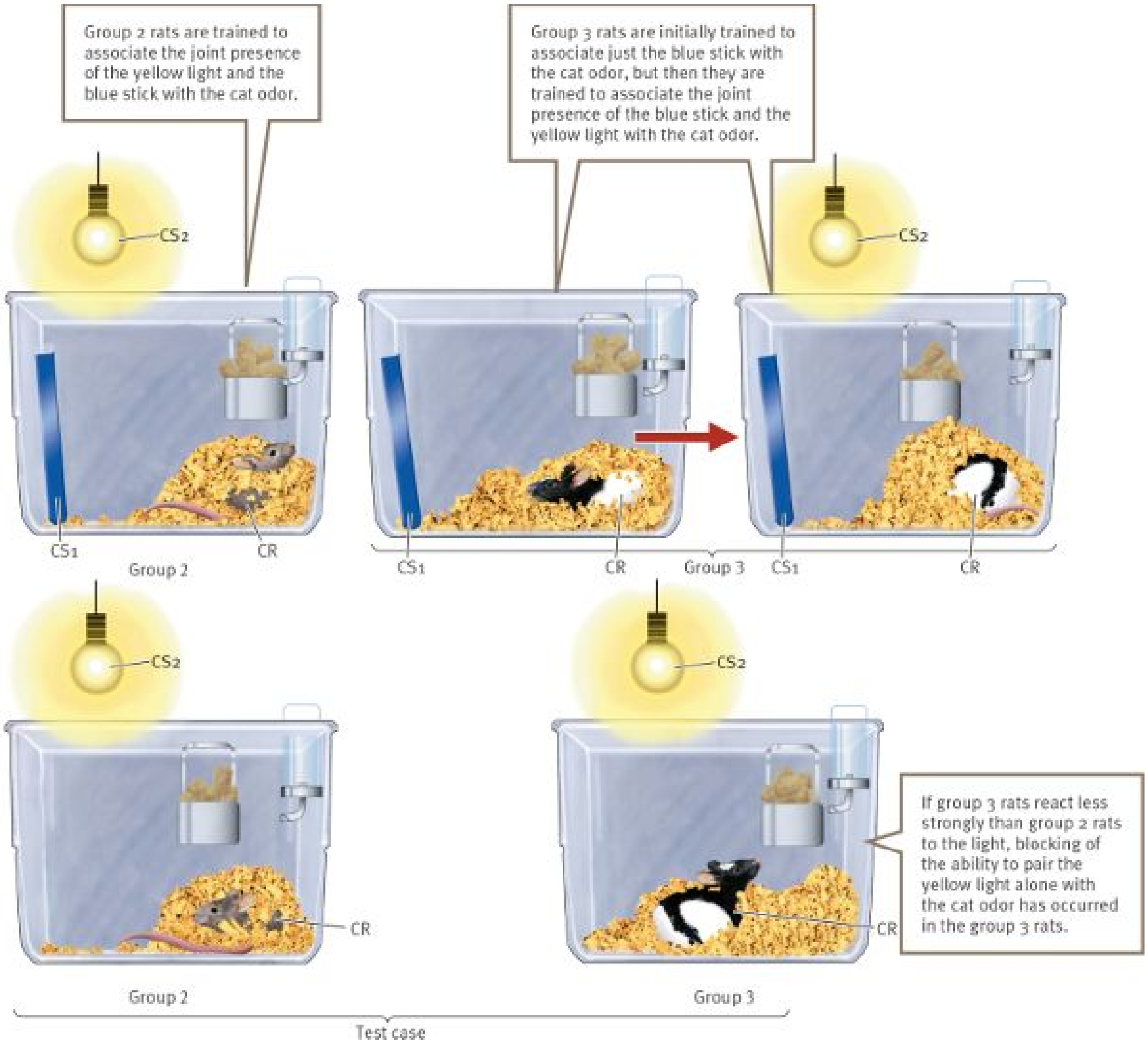
Pavlovian conditioning affects not only behavior per se but also what is referred to as *learnability*, that is, the ability to learn under certain conditions. We will explore three types of learnability: overshadowing, blocking, and latent inhibition. Consider an experiment with four groups of rats. Suppose that group 1 individuals undergo a standard Pavlovian paradigm with two stimuli: the blue stick (CS1) and a cat odor (US). In group 2, a second conditioned stimulus (CS2), a yellow light, is always presented *simultaneously* with the blue stick, just before the cat odor is sprayed (Figure 5.12). Subjects from both groups are then tested in response to the blue stick alone. If the yellow light is **overshadowing** the blue stick, rats in group 2 will respond less strongly to the blue stick (when it is presented alone) than will rats in group 1. The CS2—the yellow light—has made it more difficult for the rats to pair the blue stick and the cat odor.


Group 1 rats have already learned to associate just a blue stick and cat odor, whereas group 2 rats have already learned to associate *both* a yellow light and a blue stick (together) with cat odor.

In a test arena, group 1 and group 2 rats are tested when only the blue stick is present. If, as shown here, group 2 rats respond less strongly to the blue stick than group 1 rats do, overshadowing of the blue stick by the yellow light has occurred in rats from group 2.

Figure 5.12. Overshadowing. The process of overshadowing is shown in two groups of rats.

In group 3 of our rats, individuals are first trained to associate the blue stick with the cat odor, but after this training, the yellow light is presented at the same time as the blue stick, and this compound stimulus is paired with the cat odor. Recall that in group 2, the blue stick and the yellow light were always presented together. Rats in group 3 differ from those in group 2 in that they first learned to associate the blue stick and cat odor before any yellow light is added to the protocol. Now, after the animals are trained, let us compare the reaction of rats in groups 2 and 3 when they are presented with the stimulus of a yellow light. **Blocking** occurs when those in group 3 respond less strongly to the yellow light (when it is presented alone) than individuals in group 2 do (Kamin, 1968, 1969). It is as if initially learning to associate the blue stick alone with the cat smell *blocked* group 3 subjects' ability to pair the yellow light with the cat odor (Figure 5.13).



Group 2 rats are trained to associate the joint presence of the yellow light and the blue stick with the cat odor.

Group 3 rats are initially trained to associate just the blue stick with the cat odor, but then they are trained to associate the joint presence of the blue stick and the yellow light with the cat odor.

If group 3 rats react less strongly than group 2 rats to the light, blocking of the ability to pair the yellow light alone with the cat odor has occurred in the group 3 rats.

Figure 5.13. Blocking. The rate of learning can be slowed depending on prior association or lack of association between stimuli.

A fourth group of rats is initially exposed to a blue stick, but no cat odor, for a long period of time. We then attempt to pair the blue stick with cat odor at some subsequent point in time. If we find that the rats in group 4 have more difficulty learning than the rats in group 1 (where standard Pavlovian pairing has occurred), then we would say that rats in groups are displaying **latent inhibition**.

INSTRUMENTAL (OPERANT) CONDITIONING

Instrumental conditioning, also known as **operant** or **goal-directed learning**, occurs when the response that is made by an animal is reinforced (increased) by the presentation of a reward or the termination of an aversive stimulus, or when the response is suppressed (decreased) by the presentation of aversive stimulus or the termination of a reward. One of the most fundamental differences between Pavlovian and instrumental learning is that, in instrumental learning, the animal must undertake some *action or response* in order for the conditioning process to produce learning. The classic example of instrumental learning is a rat pressing some sort of lever (that is, taking an action) to get food to drop into its cage. Rats associate pressing on the lever (response) with some probability of getting food (outcome) and learn this task.

The earliest work on instrumental learning was that of Edward Thorndike and involved testing how quickly cats could learn to escape from “puzzle boxes” that Thorndike had constructed (Thorndike, 1898, 1911). When Thorndike placed a cat in a locked box, the cat initially tried all sorts of things to get out of its confined space. Some of these behaviors, by chance, led to a successful escape from the box. Thorndike hypothesized that the cat began to pair certain behaviors that it undertook in the box with a positive effect—escape—and it was then more likely to use such behaviors when confined in the puzzle box. His data suggested they did. Combining the findings from his puzzle box experiment with other results he had obtained, Thorndike postulated the **law of effect**, which states that if a response in the presence of a stimulus is followed by a positive event, the association between the stimulus and the response will be strengthened. Conversely, if the response is followed by an aversive event, the association will be weakened.

Work in instrumental learning was revolutionized by B. F. Skinner, who devised what is now known as a Skinner box (Skinner, 1938). His idea was to create a continuous measure of behavior that could somehow be divided into meaningful units. When a rat pushes down on a lever, it is making an **operant response** because the action changes the rat's environment by adding food to it (Figure 5.14). Because "lever pushing" is a relatively unambiguous event that is easily measurable, and because it occurs in an environment over which the rat has control, the Skinner box has facilitated the work of psychologists doing research within the instrumental learning paradigm.

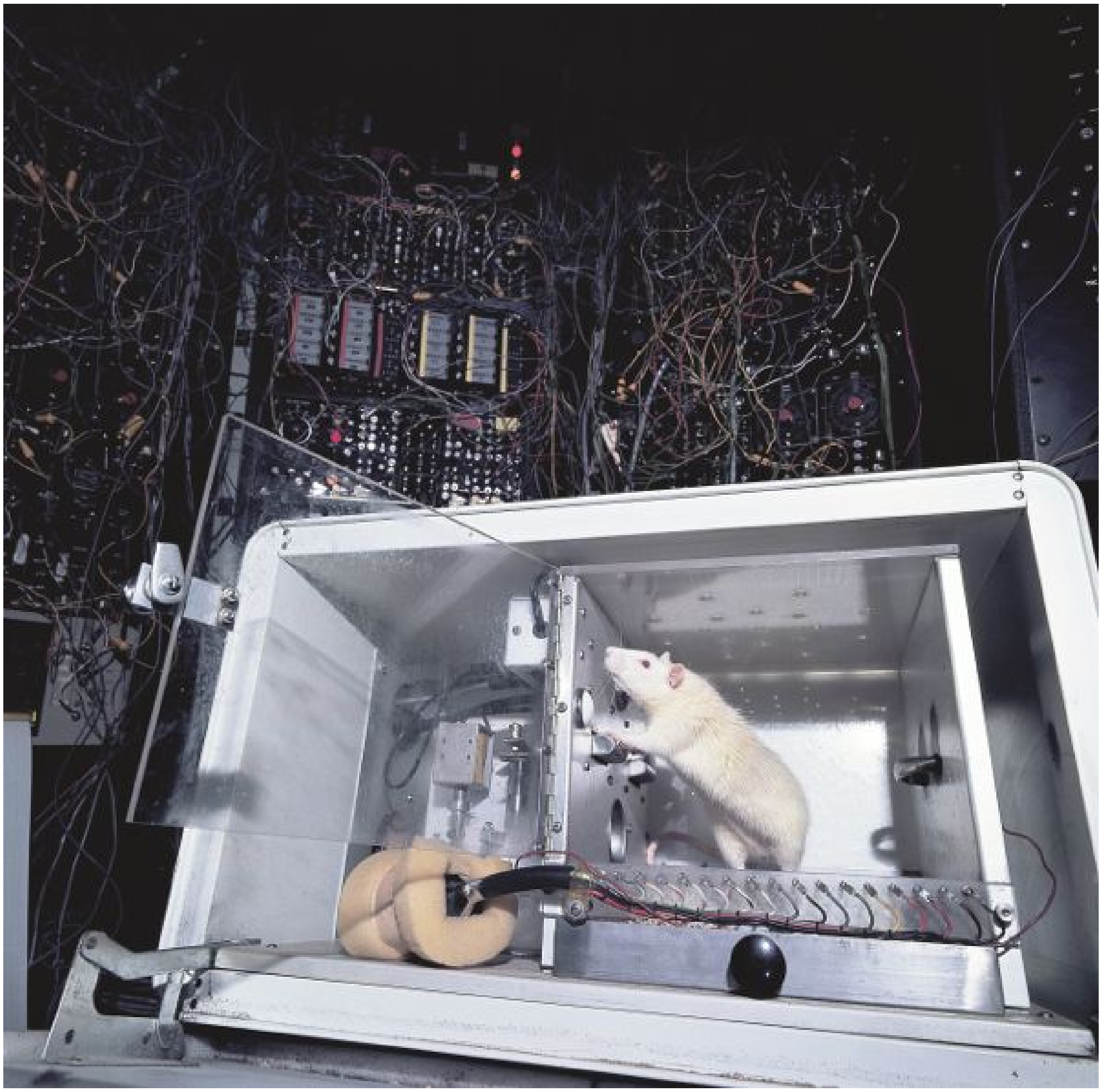


Figure 5.14. Rats in a Skinner box. To test various theories of animal learning, rats are often placed in “Skinner boxes,” where they have to take an action (here, pressing a button) to get a reward of food or water. *(Photo credit: Walter Dawn/Getty Images)*

Why Animals Learn

With an understanding of *how* animals learn, we can now take a more explicitly evolutionary perspective and ask *why* animals learn. Given mounting evidence that cognitive traits are heritable (Croston et al., 2015), we can ask whether learning is favored by natural selection, and if so, under what circumstances. In so doing, we will address three related questions: (1) How can within-species studies help us understand natural selection and learning? (2) How can population comparisons be used to shed light on the evolution of learning? and (3) What theories examine how learning evolves in different environments?

WITHIN-SPECIES STUDIES AND THE EVOLUTION OF LEARNING

Both Edward Thorndike and Ivan Pavlov argued that, aside from the details, the qualitative features of learning are the same in all animals, including human beings—that is, all animals learn in a fundamentally similar fashion (Bitterman, 1975; Pavlov, 1927; Thorndike, 1911). This view became widely accepted, and was promoted by such psychologists as Skinner and Harry Harlow (Harlow, 1959; Skinner, 1959). If Thorndike and Pavlov were correct that the particular environment an organism evolved in has no effect on learning, the same sort of learning should be seen in all creatures that learn, regardless of the sort of learning tasks with which they are presented.

Could it really be the case that natural selection on learning does not lead to differences in learning across populations and in different species? It seems unlikely. The ability to learn should be under strong selection pressure, such that individuals that learn appropriate cues that are useful in their particular environment should be strongly favored by natural selection. This is the “ecological learning” or “cognitve ecology” model, and its influence is getting stronger as our knowledge about evolution and learning increases (Dukas, 1998a; Johnston, 1985; Shettleworth, 1998; Mettke-Hofmann, 2014). Such ecological learning was first brought to the attention of many researchers with the work of Garcia and his colleagues.

Garcia’s Rats

In the mid-1960s, Garcia and his team ran a series of experiments that made many researchers in both psychology and biology rethink their approach to the study of learning (Garcia et al., 1972; Seligman and Hager, 1972). What is striking about Garcia’s work on rats is that in many ways the protocol he used was very similar to that already being used in psychology learning experiments. In essence, Garcia tried to get rats to form an association between a series of cues (Garcia and Koelling, 1966). The “bright-noisy” water treatment had water associated with a noise and an incandescent light and the “tasty” water had water paired with a particular taste, a gustatory cue. He then paired the bright-noisy water or the tasty water with one of the following negative stimuli: radiation, a toxin, immediate shock, or delayed shock. The radiation and the toxin made the rats physically ill, while the shocks were painful. For example, in the bright-noisy water/radiation treatment, bright-noisy water would be presented and the rats that were being trained to this cue were exposed to radiation after drinking the water.

Garcia and Koelling found that X-ray and toxin treatments, each of which made the rat physically ill, were easily paired with tasty water (gustatory) cues, but not with bright-noisy (audiovisual) cues. Rats quickly learned that tasty water was to be avoided after this cue was paired with X-rays or toxins, but they did not learn to avoid bright-noisy water after it was paired with X-rays or toxins. In contrast, when Garcia and Koelling examined the rats that were given shock treatments, they found that shock was easily paired with bright-noisy water (audiovisual cue), but not tasty water (gustatory cue).

Garcia and Koelling explained their results in terms of adaptation—something quite unusual for psychologists of the 1960s. They argued that, on the one hand, natural selection would favor the ability to pair gustatory cues (tasty water) with internal discomfort (getting ill). After all, many instances of internal discomfort in nature are likely to be caused by what an animal has consumed, and rarely are food cues associated with audiovisual cues (as in the bright-noisy water treatment). On the other hand, peripheral pain, like that caused by a shock, might be more commonly associated with some audiovisual cue like hearing or seeing a conspecific or a predator, so again natural selection should favor the ability to pair these cues together.

In another apparent blow to orthodoxy in psychological learning circles of the period, Garcia found that learning in their rats occurred without immediate reinforcement (Garcia et al., 1966). Most psychologists believed that delays in reinforcement on the order of seconds can stifle animal learning, yet Garcia found that learning occurred even after delays of seventy-five minutes, when injections of noxious substances were paired with drinking saccharin-flavored water. From an adaptationist perspective, one would expect a delay between the time that a rat consumed a substance and any subsequent negative effect of such consumption. As such, natural selection would have favored rats that were able to associate what they ate with becoming ill, even if the events were separated by significant time intervals.

Box 5.2. COGNITIVE CONNECTION

Natural Selection and Associative Learning

Garcia’s experiments suggest that knowledge of the selection pressures that animals face in nature will help us better understand the nature of learning. If researchers were to experimentally manipulate selection pressures on the reliability of the cues used during associative learning, then we should be able to predict patterns of learning. Aimee Dunlap and David Stephens designed such a study by examining a form of associative learning called prepared learning in fruit flies (*Drosophila melanogaster*; Dunlap and Stephens, 2014).

In their experiment, female fruit flies chose between different locations for laying their eggs. In part 1 of the study, one of the locations had quinine added to it—a chemical the flies are averse to. The quinine location had two cues associated with it—a color cue (aqua or blue) and an odor cue (amyl acetate or benzaldehyde). In part 2 of the study, when females were ready to lay eggs, they were exposed to the two locations again, the quinine was removed, but both color and odor cues were still present.

Dunlap and Stephens had four treatment groups, but here we will focus on only two of these treatment groups. In treatment 1, the color cue in part 2 was a reliable indicator of quinine in part 1 (color always indicated the “correct” location to lay eggs in), but odor was an unreliable cue. In treatment 2, the odor cue in part 2 was a reliable indicator of where to lay eggs, but color was not. The experiment went on for forty generations—in each generation, only eggs laid in the location with the reliable cue were selected.

At generation 40, when the researchers tested the response of flies in treatment 1, they found more individuals learned to pair color and quinine than to pair odor with quinine. Flies from treatment 2 showed the opposite pattern with more flies learning to pair odor and quinine (Figure 5.15). Taken together, these results suggest that selection pressures can indeed change the nature of associative learning.

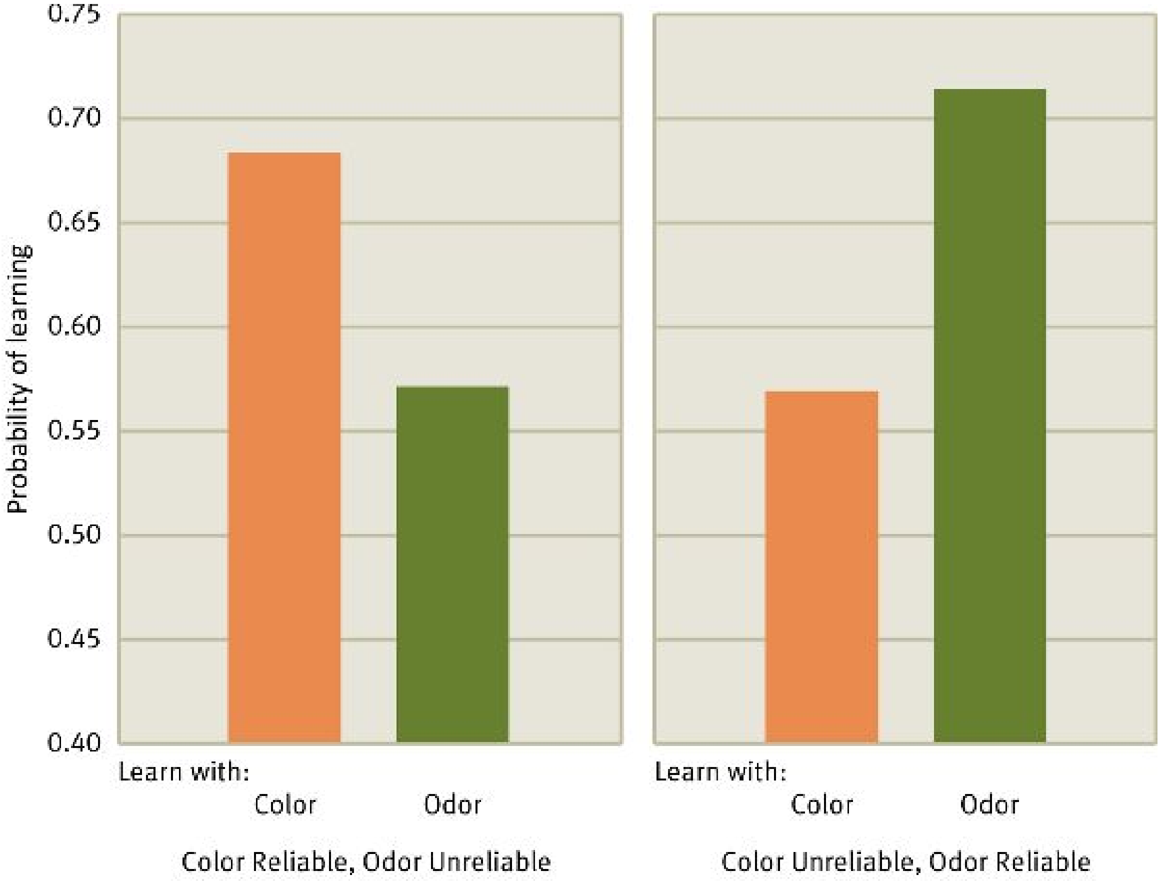


Figure 5.15. **Prepared learning.** Left panel: when tested on color alone or odor alone, flies from a forty-generation experiment in which color was a reliable indicator of quinine, but odor was an unreliable cue, show prepared learning for color and quinine. Right panel: when odor was a reliable indicator of quinine but color was not, prepared learning for odor and quinine was seen in generation 40. *(From Dunlap and Stephens, 2014)*

POPULATION COMPARISONS AND THE EVOLUTION OF LEARNING

In chapter 2 we learned that one technique that ethologists use to study the evolution of behavior is to compare behavior across different populations of the same species. This approach compares behavior in individuals in two or more populations in an attempt to understand how natural selection has shaped behavior in each (Balda et al., 1998; Bitterman, 1975; Dukas, 1998a; Roth et al., 2010; Shettleworth, 1998).

Here we will use this approach to study learning in doves and sticklebacks.

Learning, Foraging, and Group Living in Doves

Animals in groups often find food faster and have more time available for foraging than solitary foragers (Krebs and Davies, 1993). Carlier and Lefebvre predicted that individuals that live in groups, and who must compete with groupmates for resources, should learn more quickly than territorial (isolated) individuals (Carlier and Lefebvre, 1996). Ideally, one would like to test this hypothesis in a single species, where natural selection has favored group living in some populations but solitary living in others. Zenaida dove populations from Barbados (*Zenaida aurita*; Figure 5.16) allow for such a comparison. Carlier and Lefebvre studied learning in a solitary living (territorial) population and a population, just nine miles away, where group living is the norm. Because these populations are geographically close, differences in other environmental variables, above and beyond those associated with territoriality, are likely minimal.

Figure 5.16. Zenaida doves. Zenaida doves from populations where individuals live in groups are better at learning foraging tasks than individuals from populations where doves are solitary and territorial. *(Photo credit: © GlenroyBlanchette / Shutterstock)*

Sixteen doves from each of the group-living and territorial populations were brought into the laboratory. All subjects were presented with the challenge of learning how to operate an experimental apparatus that required the birds to pull on a metal ring, which in turn opened a drawer containing food. Carlier and Lefebvre found evidence that group-living doves learned this task more quickly than did birds from the territorial population (Figure 5.17; see also Sasvari, 1985). They also found that the more difficult the learning task the birds had to solve, the more pronounced the between-population differences.

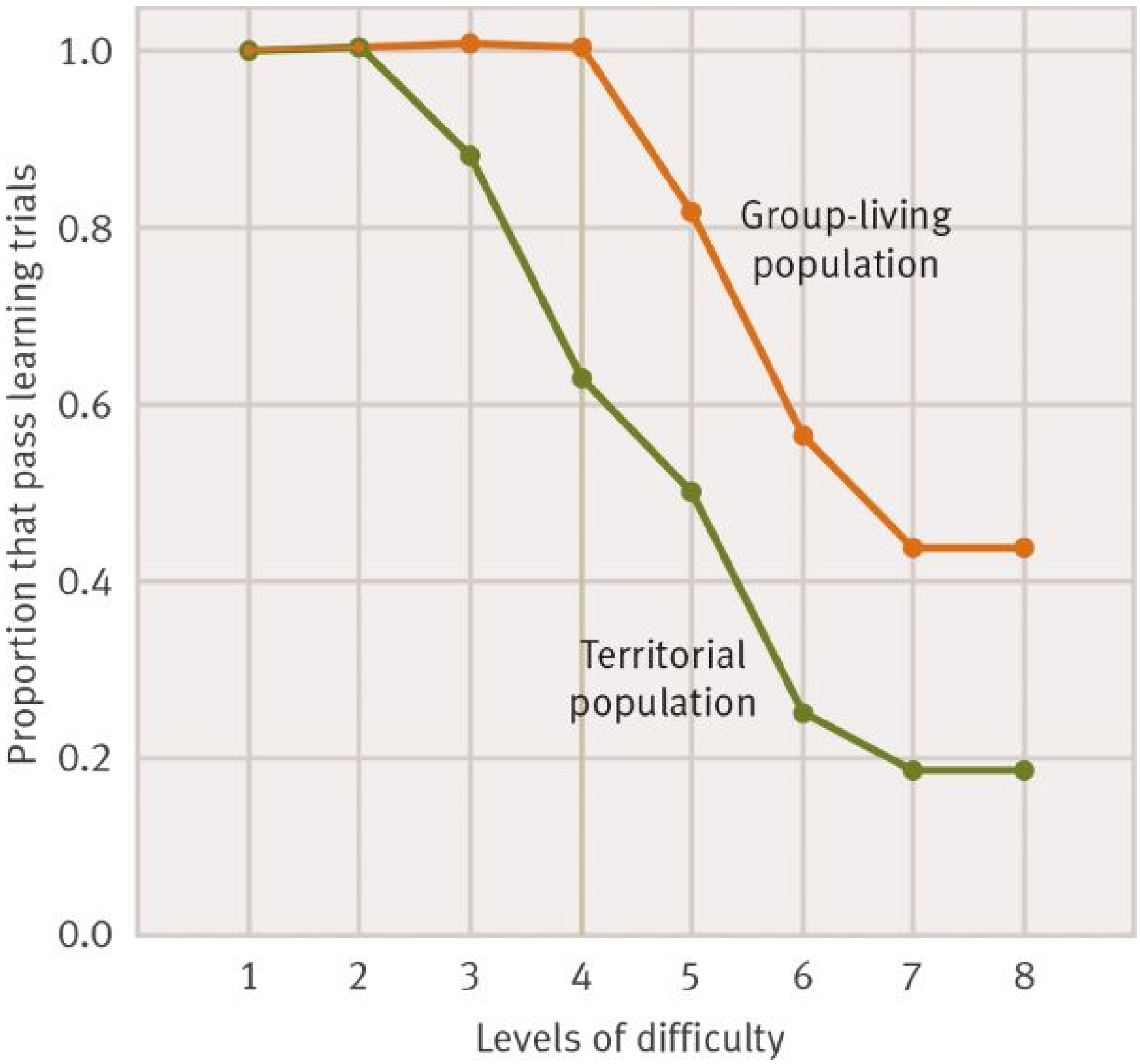


Figure 5.17. Group living and learning. More birds from the group-living population met the learning criteria for foraging tasks than did birds that had lived alone (territorial population). *(From Carlier and Lefebvre, 1996, p. 1203)*

There are at least two explanations for these differences (Carlier and Lefebvre, 1996). First, the animals may have already differed in foraging experience before the experiment, and hence some of the differences the researchers uncovered may have been due to what individuals had experienced, and potentially learned, prior to being brought into the laboratory. Second, *above and beyond* what experiences any given set of birds took into Carlier and Lefebvre's experiment, natural selection may have operated on learning ability across these populations. To test this second possibility, the researchers would need to raise both territorial and group-living doves in the laboratory under controlled conditions, and test whether differences in learning still remained: if they did, this would suggest that natural selection had favored learning more strongly in the group-living population of doves (Box 5.3).

Box 5.3. SCIENCE AT WORK

What is the research question? Do individuals that live in groups have better learning skills than individuals that are more solitary?

Why is this an important question? Theory predicts that the competition inherent in group-living strongly favors learning.

What approach was taken to address the research question? Two populations of Zenaida doves were tested on their ability to learn about a food source. Individuals in one population lived in groups, while individuals in the second, geographically close, population were more territorial and tended not to live in groups.

What was discovered? Doves from the population where individuals lived in groups outperformed individuals from a more solitary-living population on a learning-related foraging task.

What do the results mean? Because doves were taken from two different wild populations, and not raised from birth in a controlled environment, these results could be due to different experiences the doves had in the wild and/or due to stronger selection pressures with respect to learning in the group-living doves.

Learning and Antipredator Behavior in Sticklebacks

One way to partially circumvent the confounding effects of learning per se (in real time) versus natural selection acting on the ability to learn is through the use of controlled laboratory experiments, where it is possible to raise individuals from two very different populations in a similar environment, and in so doing minimize differences associated with experience. Huntingford and Wright used this approach to study avoidance learning in two populations of three-spined sticklebacks (*Gasterosteus aculeatus*; Huntingford and Wright, 1992). Some sticklebacks live in locales that contain many predators, and some live in populations in lakes with virtually no predators; and differences in predation pressures across locales have been in place for long periods of evolutionary time.

Huntingford and Wright raised individuals derived from predator-rich and predator-free streams in the laboratory, and during their development individuals had no interactions with predators. If natural selection has acted more strongly on antipredator strategies—including learning about danger—in the sticklebacks descended from predator-rich populations, then we should see such differences in learning abilities across sticklebacks descended from the different populations even in the absence of experience with predators.

The researchers began by training eight sticklebacks from each of their population groups to associate one side of their home tank with food. They found no differences in learning across populations in the context of foraging alone—individuals from both populations were equally adept at learning that food would come to one side of their tank. Then, after a stickleback had learned that one side of its tank was associated with food, fish were subjected to a simulated attack from a heron predator on the side of the tank that contained food. Huntingford and Wright then examined whether between-population differences emerged in terms of how long it took the fish to learn to avoid the side of the tank associated with heron predation (and food; Figure 5.18).

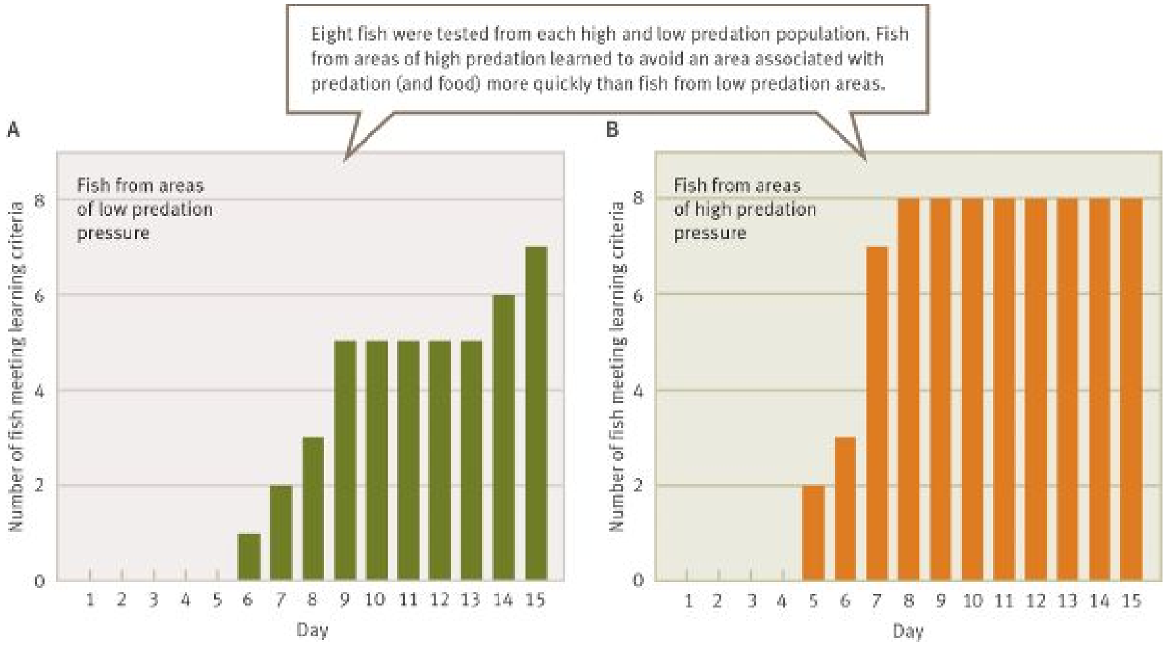


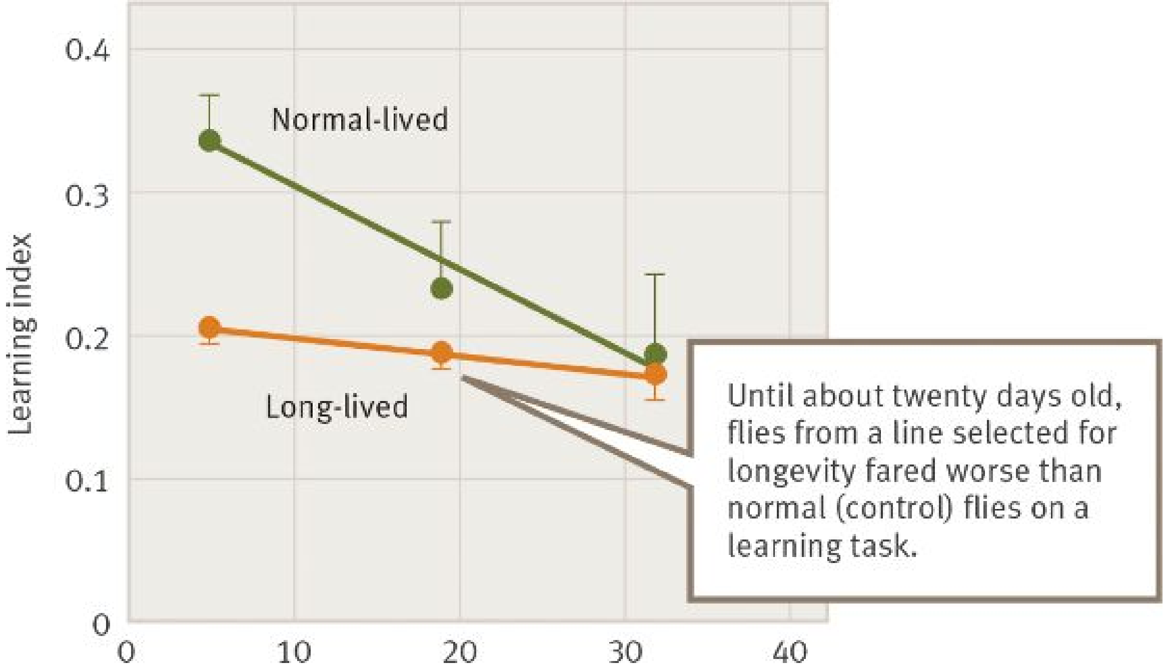
Figure 5.18. Learning differences across populations. The number of sticklebacks that learned to avoid areas associated with predation. (A) Fish descended from individuals from low-predation sites. (B) Fish descended from individuals from high-predation sites. *(From Huntingford and Wright, 1992)*

While all but one fish from both high and low predation populations eventually learned to avoid the dangerous end of their tank, fish from high-predation areas learned this task more quickly than did fish from predator-free populations. Two lines of evidence support the hypothesis that natural selection has operated on learning and antipredator behavior in these populations of sticklebacks. First, the laboratory protocol used minimized the probability that individual experiences differed across the populations they examined. Second, Huntingford and Wright did *not* find between-population differences in all learning contexts. When the task was a simple association of food and place, interpopulational differences with respect to learning were absent; such differences were found only when the learning task was to avoid feeding in areas associated with danger.

A MODEL OF THE EVOLUTION OF LEARNING

Many cost-benefit models have been developed to examine when natural selection might favor the ability to learn (Bergman and Feldman, 1995; Borenstein et al., 2008; Boyd and Richerson, 1985; Irwin and Price, 1999; Nakahashi, 2010; Odling-Smee et al., 2003; Stephens, 1991, 1993). Imagine a behavioral scenario in which the options are to respond to some stimuli with a fixed genetically programmed response, or to respond to stimuli based on prior experience—that is, by learning. Are the net benefits associated with learning greater or less than the net benefits that might be associated with a fixed genetic response to some stimuli?

Ethologists, behavioral ecologists, and psychologists have argued that natural selection should favor the ability to learn over the genetic transmission of a fixed trait when the environment an animal lives in changes often, but not too often, because most of these models assume (1) that there is some cost to learning, even if it is only a very small cost; and (2) that the ability to learn has an underlying genetic basis. Though difficult to measure, evidence for both these assumptions has been found in fruit flies and butterflies (Burger et al., 2008; Burns et al., 2011; Kawecki, 2010; Figure 5.19).



Until about twenty days old, flies from a line selected for longevity fared worse than normal (control) flies on a learning task.

Figure 5.19. A trade-off between learning and life span. “Learning index scores” for normal (control) fruit flies and fruit flies from a line selected for artificially prolonged life spans. The difference between these groups suggests a trade-off between long life and the ability to learn. *(From Burger et al., 2008)*

The cost to learning can take different forms. In one experiment using a line of *Drosophila melanogaster* fruit flies that had been selected for better learning skills for more than 50 generations, Mery and Kawecki subjected flies to a learning test in which they were trained to associate an odor with a mechanical shock (Mery and Kawecki, 2002, 2005). The learning protocol involved five trials to pair odor and shock. After that the flies were deprived of food and water, and the researchers noted how long it was before they died.

Female flies in the learning treatment died about 9 hours sooner than females flies from the same line that had been selected for better learning abilities, but that had not been exposed to the learning trials or shocked. That difference could have been due to a cost of learning, the exposure to shock, or both. Evidence for a cost to learning per se was seen when comparing the flies in the learning treatment to a control that did not involve learning, but did have flies experience the shock that was used in the learning trials. Flies in the learning treatment died 4–5 hours sooner than those who had just suffered the shock alone (Figure 5.20).

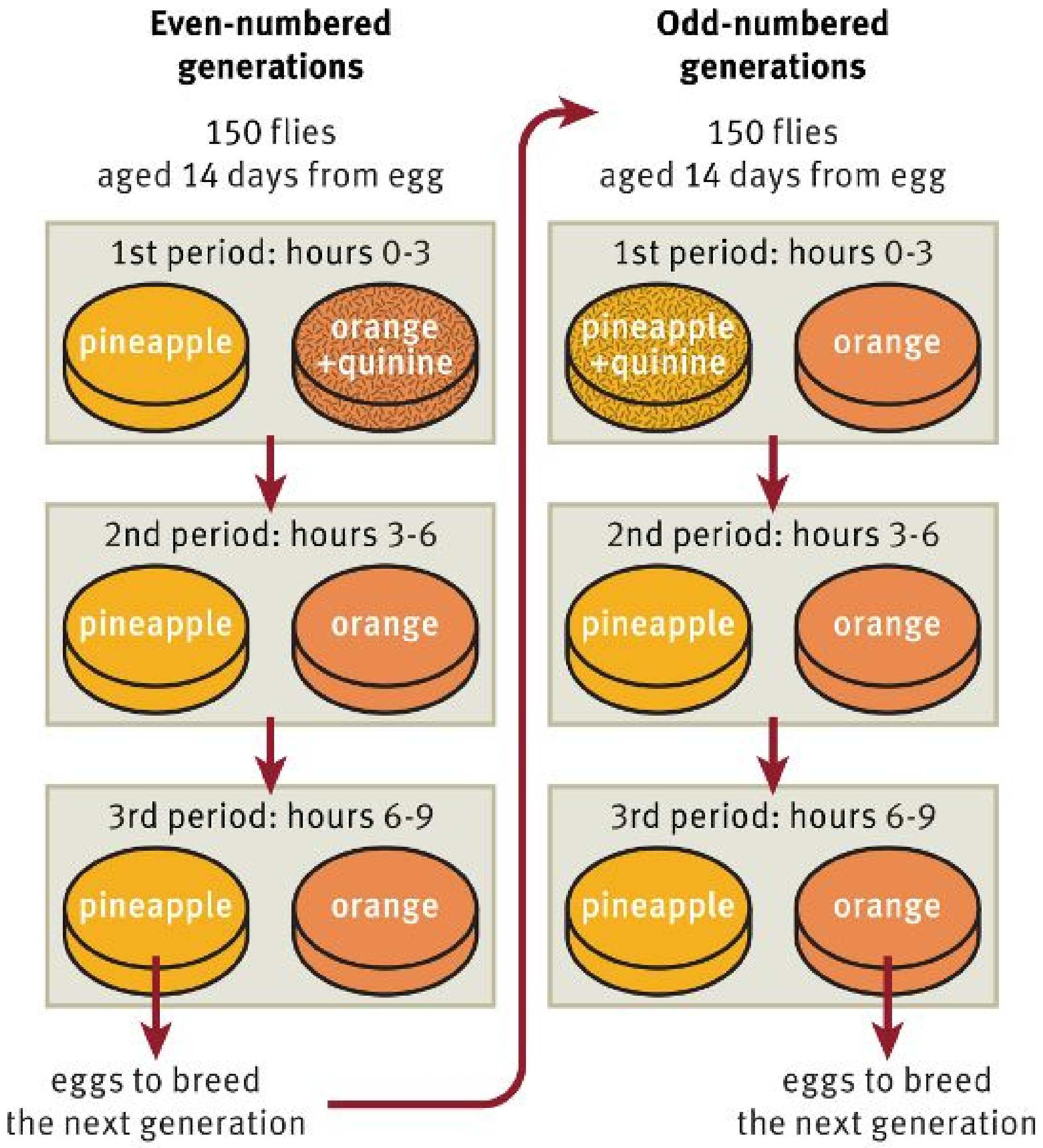


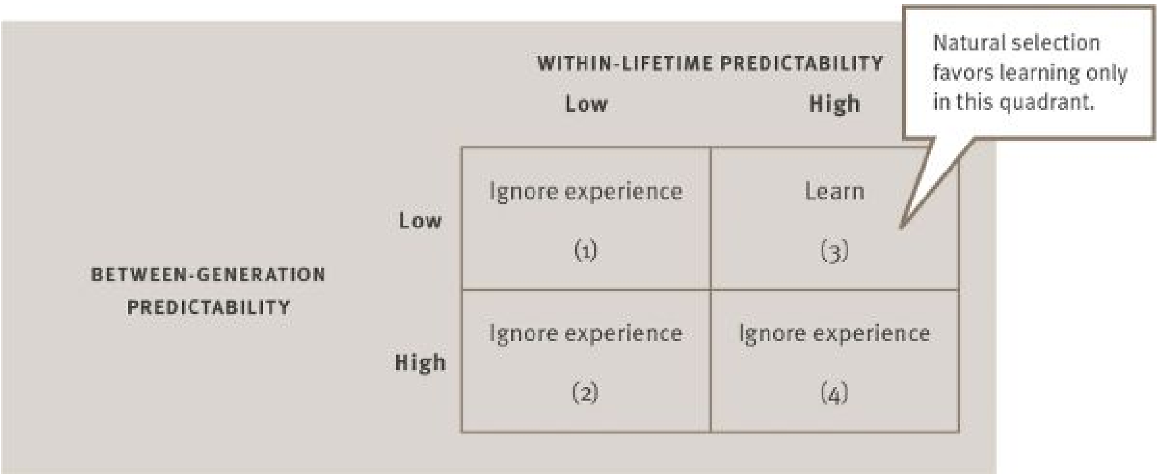
Figure 5.20. **Mortality cost of learning.** All females tested were part of a line of fruit flies that had been selected for better learning abilities. When deprived of food and water, females that had learned to pair odor and shock died earlier than females who did not take part in learning trials and were not shocked, as well as females who did not take part in learning trials but were shocked. *(From Mery and Kawecki, 2005)*

Reduced survival is not the only cost to learning. Emilie Snell-Rood and her colleagues have found a fecundity cost of learning in the cabbage white butterfly (*Pierus rapae*) (Snell-Rood et al., 2011). This work allows us to distinguish between two different types of costs to learning, “constitutive costs” and “induced costs.” Constitutive costs are paid by good learners, regardless of whether they learn some task, while inducted costs are paid only when learning has occurred. Both costs were examined in the cabbage white butterfly system.

Cabbage white butterflies lay their eggs (oviposit) on green plants, and show an innate preference for searching for green items, but there is genetic variation in the extent to which individual butterflies can be trained to search for red items. When Snell-Rood and her colleagues measured reproductive success, they found that females from families with individuals who best learned to forage for red items produced fewer and less well developed eggs, *even when given no learning tasks* (Snell-Rood, 2011). This constitutive cost of learning is likely related to the investment in the larger brains of individuals seen in individuals in these families (Snell-Rood et al., 2009). On top of this constitutive cost was an induced cost to learning: butterflies in the families selected for the ability to learn to forage on red items, showed an greater decrease in reproductive success after being part of learning trials involving red items.

Returning to our discussion of a model for the evolution of learning, when the environment *rarely changes*—and hence the environment that offspring encounter is similar to that of their parents—information is best passed on by a fixed genetic rule, since such a means of transmission avoids the costs of learning. On the other end of the spectrum, if the environment is *constantly changing*, there is little worth learning because what is learned is completely irrelevant in the next situation. When the environment is constantly changing, acting on past experience is worthless, as past experience has no predictive value and so genetic transmission of a fixed response, rather than a costly learned response, is again favored. Somewhere in the middle, in between an environment that never changes and one that always changes, learning is favored over the genetic transmission of a fixed response and it is worth paying the cost of learning. The environment is stable enough to favor learning, but not so stable as to favor genetic transmission.

Because many models confuse two types of stability, David Stephens reformulated the way that environmental stability is represented in models (Stephens, 1991, 1993). The model that Stephens developed breaks environmental predictability into two types: (1) predictability within the lifetime of an individual, and (2) predictability between the environment of parents and offspring. These two types of predictability can be very different, and conflating them may hinder our understanding of the evolution of learning (Figure 5.21). For example, consider a case in which early in life the offspring A move to environments that are far removed from those of their parents, and the environment to which they migrate is stable over the course of their lifetime. Here, between-generation environmental predictability is quite low, while within-lifetime environmental predictability is much higher. This distinction is lost when models lump together within- and between-generation environmental predictability.



		WITHIN-LIFETIME PREDICTABILITY	
		Low	High
BETWEEN-GENERATION PREDICTABILITY	Low	Ignore experience (1)	Learn (3)
	High	Ignore experience (2)	Ignore experience (4)

Natural selection favors learning only in this quadrant.

Figure 5.21. **Model for the evolution of learning.** The key variables in this model are within-lifetime environmental predictability and between-generation environmental predictability.

Stephens found that learning is favored when predictability within the lifetime of an individual is high, but environmental predictability between generations is low. To see why, let's step through each of the possible scenarios in Figure 5.21. In boxes 1 and 2, predictability within generations is low, so neither strategy does particularly well. But since learning has a cost associated with it, genetic transmission of a fixed response is favored. Fixed genetic transmission is again favored in box 4, because with high predictability at all levels, the cost of learning is never worth the investment. Only in box 3, with high within-generation predictability but low between-generation predictability, is learning favored. Learning is favored here because once an organism learns what to do, it can repeat the appropriate behaviors during its lifetime. But isn't this the sort of predictability that usually favors a fixed genetic transmission? Yes, but now the environment changes so much between generations that fixed genetic transmission, per se, would be less advantageous than learning.

What Animals Learn

In this section we examine learning in the context of predation, mating, familial relationships, and aggression. Box 5.4 discusses learning with respect to habitat and conservation biology. Learning about food sources is covered in chapter 11.

Box 5.4. CONSERVATION CONNECTION

Learning, Alarm Chemicals, and Reintroduction Programs

One way in which conservation biologists try to protect threatened or endangered species is through **reintroduction programs** (Batson et al., 2015; Ewen et al., 2012; Kemp et al., 2015; Abbott and Richardson, 2015). These programs often involve managers raising individuals of a threatened or endangered species in captivity and then releasing them into an area that the species formerly occupied. Reintroduction programs have had mixed success. One problem is that reintroduced individuals are often especially susceptible to predation, in part because they experience no threats while being raised in captivity. A similar issue arises in translocation programs, when individuals are moved from one natural habitat to another, and in fisheries, when fish are released into the wild (Olson et al., 2012).

Conservation biologists understand this very well, and many programs now try to present individual animals with the opportunity to learn something about one aspect or another relative to the environment into which they will be released or transferred, *before* the release or introduction occurs. For example, hellbenders (*Cryptobrancus alleganeinsis*), large aquatic salamanders whose natural range has declined dramatically, have an innate fear response when exposed to an alarm chemical—a white mucus—that is produced by other hellbenders. To better understand how to design reintroduction programs for hellbenders, Crane and Mathis used a classic conditioning protocol in which one group of hellbenders was given the opportunity to pair the alarm chemical with the scent of brown trout—a predator of hellbenders. For a second (control) group, the alarm chemical was paired with water (Crane and Mathis, 2011, 2013). The hellbenders that were given the chance to pair the trout odor and the alarm chemical showed more fine-tuned antipredator behaviors in response to trout than the hellbenders in the control group (Figure 5.22). These classical conditioning protocols could be used in reintroduction programs for hellbenders. Individuals trained to show fear responses when exposed to real predator cues would be more likely to take action to avoid the danger and therefore survive when encountering predators in nature for the first time.

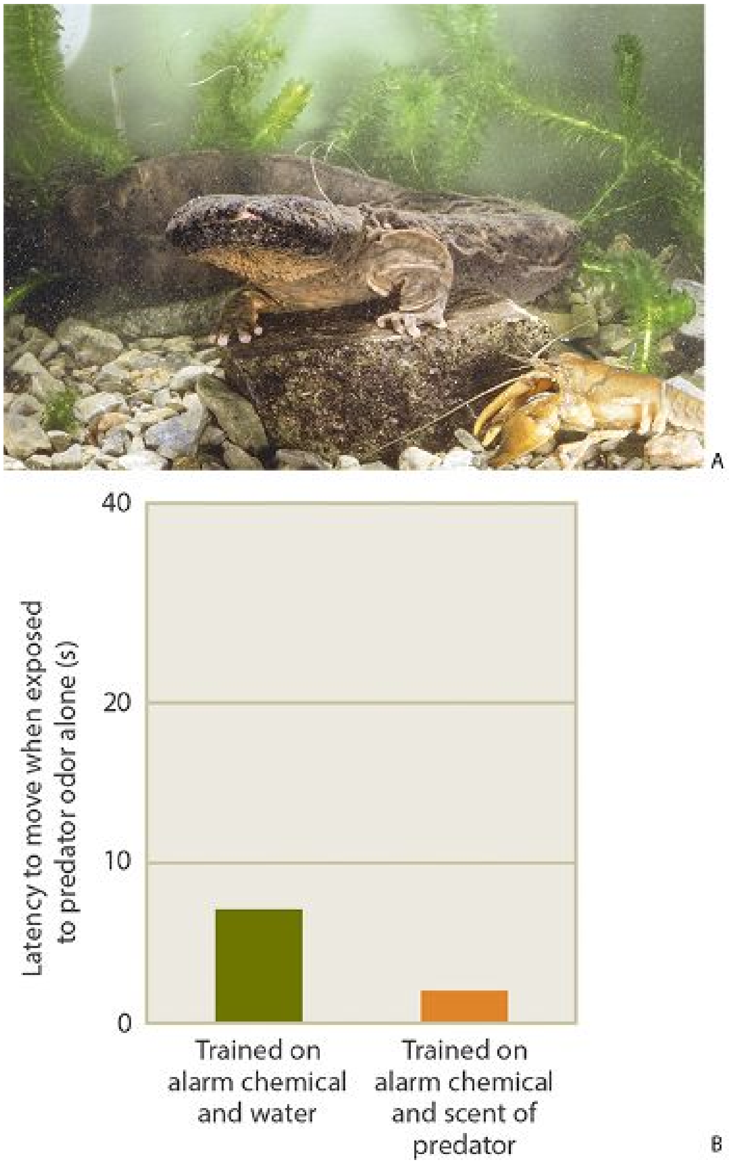


Figure 5.22. Learning and response to predators. (A) A hellbender salamander. *(Photo credit: Paul Zahl/Photo Researchers)* (B) Hellbenders that were given the opportunity to pair an alarm secretion and the odor of a predator moved quickly when exposed to the odor of the predator alone.

LEARNING ABOUT PREDATORS

Prey often live in areas that contain both predatory and nonpredatory species, and learning which species is which has fitness consequences. Even encounters with the same predator are not always the same, as at any given time some individuals are in hunting mode while others are not actively hunting prey (Chivers et al., 1996). If prey can learn to distinguish between dangerous and benign encounters with potential predators, they may free up time for other activities: learning about possible predation pressure may allow animals to handle the trade-offs they constantly face.

If the food that a potential predator eats produces a chemical cue that is recognizable to its prey, then that cue may provide an opportunity for such prey to learn what is dangerous and what isn’t (Howe and Harris, 1978; Mathis and Smith, 1993a, 1993b; D. J. Wilson and Lefcort, 1993; Mitchell et al., 2015). Douglas Chivers and his colleagues examined chemical cues and the role of learning in the antipredator behavior of damselfly larvae (*Enallagma spp*; Chivers et al., 1996; Figure 5.23).

Figure 5.23. Damselfly. Larval damselflies (*Enallagma* spp) learn about predation threat through chemical cues. An adult damselfly is shown here. *(Photo credit: © alslutsky / Shutterstock)*

Damselfly larvae are found in ponds with minnows, and both species are often attacked and eaten by pike (*Esox lucius*). Chivers and his colleagues hypothesized that damselfly larvae might learn about the potential dangers associated with pike encounters by using chemical cues. To test this hypothesis, the researchers fed pike predators either minnows, damselflies, or mealworms; mealworms served as a control as they are not eaten by pike. After four days on one of these three diets, a pike was removed from its tank, and damselflies that had never before had any contact with a pike were exposed to the water from the pike's tank.

When damselfly larvae were exposed to the water containing chemical cues from a pike that had eaten damselflies or a pike that had eaten minnows, Chivers and his colleagues found that the damselfies had significantly reduced their foraging behavior. But the damselfly larvae did not reduce their foraging behavior when they were exposed to the water treated with pike that had eaten mealworms (Figure 5.24). Because damselflies are found in the same ponds as minnows, but the damselflies tested by Chivers had never before experienced a pike, these results strongly suggest that damselflies innately associate the scent of pike plus damselfly or pike plus minnow with danger, but they make no such association between pike, mealworm, and danger. The damselflies here hadn't learned anything; they simply were predisposed to respond to the smell of pike and prey (minnows and damselflies) as dangerous.

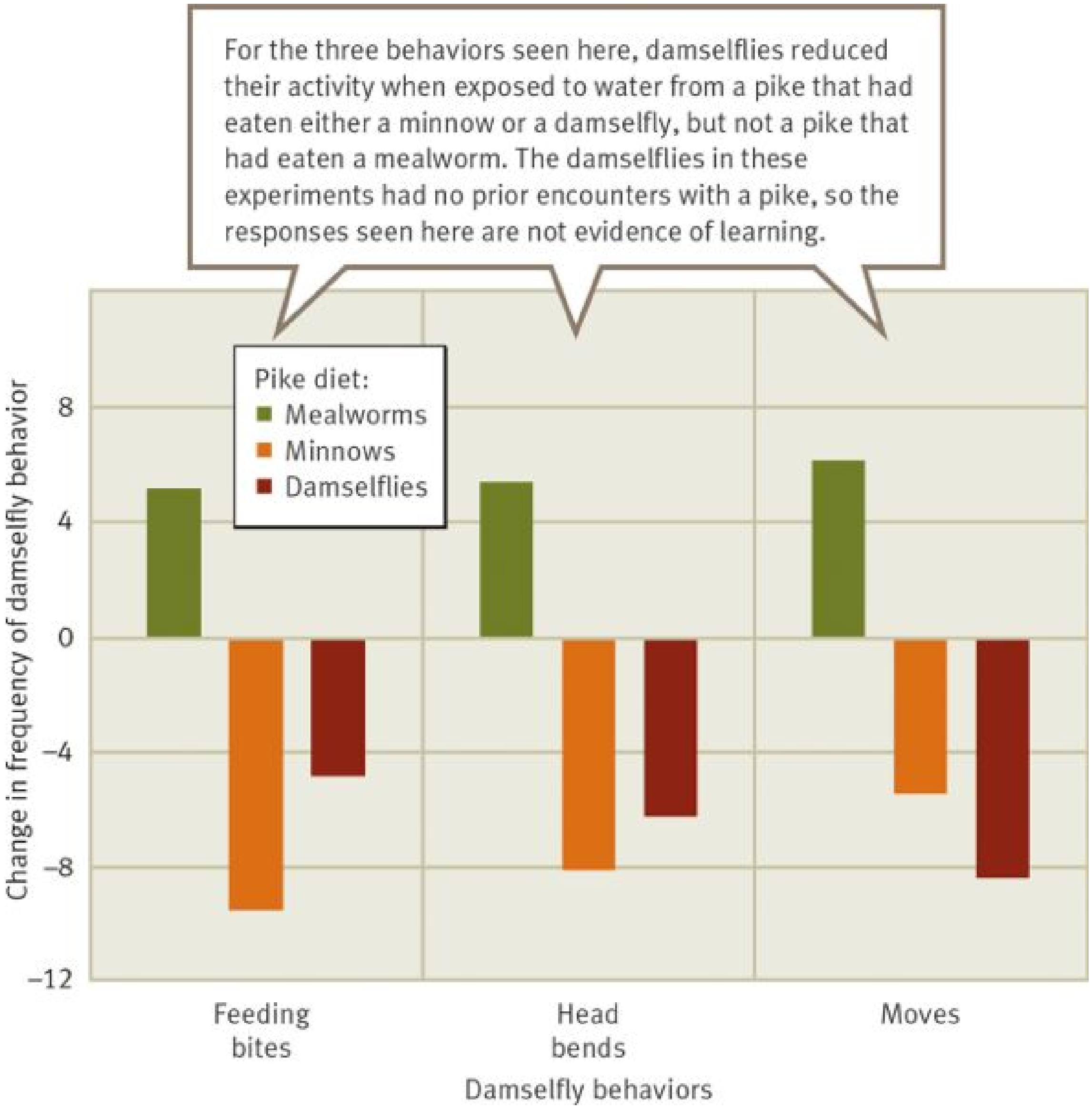


Figure 5.24. Chemically mediated changes. Numerous aspects of damselfly (*Enallagma* spp) behavior, including the frequency of feeding bites, head bends, and moves, changed as a function of whether the damselflies were exposed to chemical stimuli from a pike predator that had eaten mealworms, minnows, or damselflies. *(From Chivers et al., 1996)*

Chivers's team followed up this experiment by examining the role of learning in the antipredator behavior of damselflies. Here they took the damselflies that had been exposed to the three treatments above (water from pike plus damselfly, water from pike plus minnow, and water from pike plus mealworm) and isolated them for two days. Then each damselfly was exposed to water from a pike that had been fed mealworms. With respect to learning and antipredator behavior, there were three groups of damselflies; group 1: damselflies that were initially exposed to water from pike plus damselfly, but that were subsequently exposed to pike plus mealworm water; group 2: damselflies that were initially exposed to water from pike plus minnow, but that were subsequently exposed to pike plus mealworm water; and group 3: damselflies exposed to water from pike plus mealworms twice. Damselflies from groups 1 and 2 had responded with antipredator behaviors in the first experiments, but damselflies in group 3 had not.

Damselflies in groups 1 and 2 responded to the scent of pike plus mealworm by decreasing their foraging activities. Damselflies in group 3 did not decrease their foraging. Recall that in the first experiment, damselflies did *not* curtail feeding when they encountered the smell of pike plus mealworm for the first time, but they did curtail feeding in this second experiment. These results suggest that, based on their earlier experience in the first experiment, damselflies in groups 1 and 2 in the second experiment had learned to associate pike plus *the scent of any potential prey* with danger, and this association translated into a reduced foraging rate even when they encountered the scent of pike and mealworm.

LEARNING ABOUT THEIR MATE

Michael Domjan and his colleagues have studied the role of Pavlovian conditioning in mate choice in the Mongolian gerbil (*Meriones unguiculatus*), a species of desert rodent that relies on chemical communication during the formation of pair bonds (Ågren, 1984; Thiessen and Yahr, 1977; Domjan et al., 2000). Villarreal and Domjan first allowed pair bonds to form between a male and a female Mongolian gerbil. They presented one group of males with an olfactory cue (mint or lemon) and then gave them access to their partners, and exposed males in another (control) group to the odor, but did not provide them with access to females following this presentation. Males that experienced the pairing of an odor and subsequent access to a pairmate learned relatively quickly to approach an area where access to the female was signaled by an odor, while males in the control group formed no such association (Villarreal and Domjan, 1998).

Villarreal and Domjan next tested whether females learned to associate an odor with the presence of their pairmates, and whether any male/female differences emerged. Females did learn to pair odor and access to their pairmates—conditioned females responded to odor cues by approaching the area associated with this cue, and differences between males and females disappeared over time.

While no sex differences were found in the Mongolian gerbils, Domjan and Karen Hollis have hypothesized that in species where differences between males and females in their learning abilities when selecting mates do exist, this should be linked with differences in male and female parental investment (Domjan and Hollis, 1988). The more equally parental investment is shared, the more the sexes should be similar in terms of learning the location of partners. One way to think about Domjan and Hollis's hypothesis is in terms of how much each sex is willing to invest in future offspring (Trivers, 1974). If both males and females provide resources for offspring, selection pressure for learning ability about partners should be strong on both sexes. In such a case we expect males and females to have the ability to learn where their mate—the co-provider of resources for their offspring—is at any given time.

In many species, only females provide resources for offspring. There are many reasons that females are more likely to take this role (see chapters 7 and 8), but for the purposes of Domjan and Hollis's hypothesis, what this translates into is that males in such systems should be better at learning about the location of mates than females. In terms of parental care for subsequent offspring, females are a valuable resource for males, as they alone provide food for offspring. From a parental care perspective, males are much less valuable a resource to females. Males then are under strong selection pressure to find receptive females, while females can almost always find males that are willing to mate. In such mating systems, selection for learning locations associated with potential mates should be stronger in males than in females. More experimental work needs to be done in this area, but some support for this hypothesis has been found. First, in both Mongolian gerbils and gourami fish, parental investment is shared, and differences in learning about mates between the sexes is small. Second, in contrast to Mongolian gerbils and gourami fish, in Japanese quail, where there is no parental investment on the part of males, males show greater learning abilities than do females, though the extent of differences in learning between males and females may be specific to certain mating contexts (Gutierrez and Domjan, 1996, 2011; Hollis et al., 1989; Villarreal and Domjan, 1998; Figure 5.25).

Figure 5.25. Parental investment and learning ability. (A) Parental investment is shared in blue gourami, and difference in learning about pairmates between the sexes is small. (B) In Japanese quail, the females care for the young, as shown by this female at the nest with her eggs, and there is no parental investment by males. In this species, males show greater learning about mates' abilities than females. *(Photo credits: Arco Images GmbH / Alamy Stock Photo; © Mark Valencia/Self Sufficient Me)*

LEARNING ABOUT FAMILIAL RELATIONSHIPS

If individuals can learn how they are related to others around them, as well as how different individuals in their group are related to one another, natural selection might favor altruistic and cooperative behavior being preferentially allocated to close genetic kin (chapter 9). Here we examine learning and kin recognition in the context of helpers-at-the-nest.

As we have seen, in some birds and mammals, individuals forgo direct reproduction and instead help their relatives raise their offspring (Brown, 1987; Solomon and French, 1996; Stacey and Koenig, 1990). Sometimes these offspring remain at their natal nest and help their parents raise a subsequent brood (the helper’s siblings). But this is only one way in which helping may emerge. For example, young, reproductively active long-tailed tits (*Aegithalos caudatus*) breed independently as soon as they can, but many nests fail because of predation on the young (Figure 5.26). When that happens, breeders often become helpers at the nests of their close genetic relatives, and such helpers accrue indirect fitness benefits by helping raise their kin (Hatchwell and Sharp, 2006; Hatchwell et al., 2004, 2014). How do the birds know who are kin? Do they learn who is kin, and who isn’t, and if so, how?

Figure 5.26. Learning who is kin. Young long-tailed tits (*Aegithalos caudatus*) often become helpers at the nests of their close genetic relatives, building nests and foraging for food to feed the chicks. As helpers, they accrue indirect fitness benefits by contributing to the survival of their close genetic kin. *(Photo credit: Lubomír Hlásek)*

To address these questions, Stuart Sharp and his colleagues ran a series of experiments that focused on the “churr” call made by long-tailed tits. This call develops before young birds fledge and leave the nest, and it remains consistent throughout the lifetime of an individual (Sharp and Hatchwell, 2005). Churrs are given by males and females in the context of short-range communications, such as those regarding nest-building and aggression (Gaston, 1973; Hatchwell et al., 2001; Sharp and Hatchwell, 2005).

Sharp and his team set up a “playback” experiment, in which an individual heard the taped call of either a close genetic relative or a nonrelative, and the long-tailed tits showed a preference for the calls given by their kin (Figure 5.27). Following the playback trials, the researchers designed an experiment to assess whether the birds learned the churr calls of their relatives, or whether their preference was based on genetic predispositions for certain churr calls. To do this, they ran a cross-fostering experiment (see chapter 2), in which chicks either were raised with their biological parents or were switched to another nest and raised by foster parents.

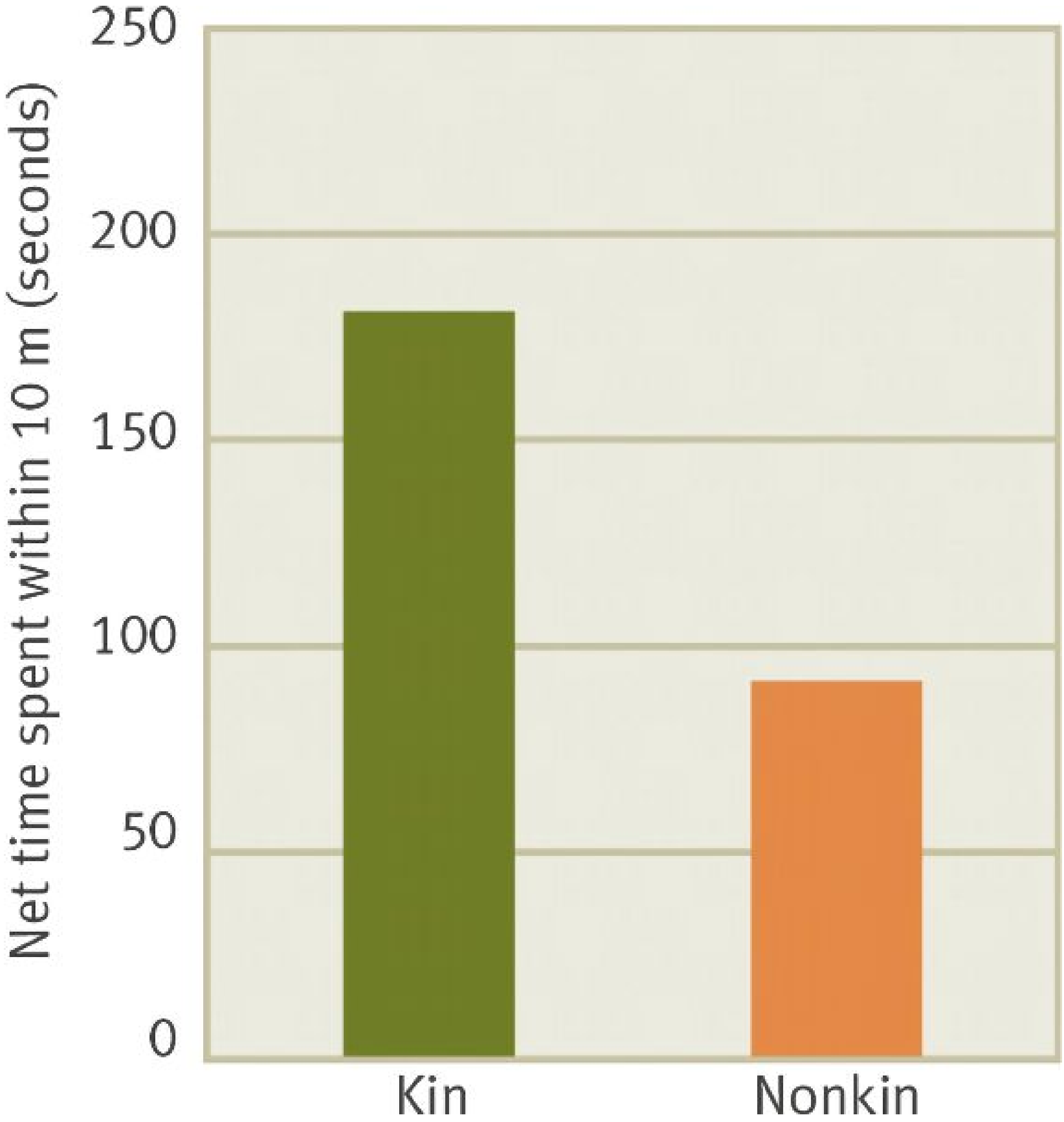


Figure 5.27. Playback calls and kin. Individual long-tailed tits showed a strong preference for the calls given by their close genetic kin, staying for a longer time near the speakers that gave off the calls of their kin. *(From Sharp and Hatchwell, 2005)*

A number of lines of evidence suggest that the churr call is learned: (1) The calls of foster siblings raised together were as similar as the calls of biological siblings raised together; (2) the calls of biological siblings raised apart were as dissimilar as the calls of unrelated individuals in nature; (3) the songs of foster parents and their foster offspring were similar, whereas the songs of biological parents and their offspring were different when those offspring were raised by foster parents. These results all suggest an important role for learning in the development of churr calls that are subsequently used to distinguish kin from nonkin.

LEARNING ABOUT AGGRESSION

Paper wasps (*Polistes fuscatus*) live in colonies in which individuals are constantly interacting with one another. Reproduction in paper wasp colonies is tightly linked to the position a wasp holds in a dominance hierarchy, so knowing who is who in such a hierarchy has important consequences for reproductive success. Prior work has shown that paper wasps recognize their hive mates, but how do they do so? Because these wasps have facial marks that might allow for such recognition, researchers have examined whether *facial learning* occurs in the species. This type of specialized learning, which is especially prominent in humans, has been demonstrated in other mammals, but until Michael Sheehan and Elizabeth Tibbets's work on paper wasps, had not been found in invertebrates (Sheehan and Tibbetts, 2011; Sheehan et al., 2014a,b).

To test for facial learning, Sheehan and Tibbets took wasps and exposed them to the facial images of two other (stimulus) wasps. One of the pictures was paired with an electric shock, the other was not. They tested whether the wasps learned to avoid the facial image associated with the electric shock, and how quickly they learned. Results indicated that wasps were able to pair a specific facial image with the electric shock (recently candidate genes associated with this ability have been identified: Berens et al., 2016). One clue that the wasps were truly exhibiting facial learning, and not some general ability to learn, was that when the pictures of the stimulus wasps lacked antennae, or the faces on these pictures had been artificially rearranged, wasps were not capable of pairing one image with an electric shock—only intact faces produced learning. What's more, wasps were not capable of pairing basic geometric patterns with an electric shock, again strongly suggesting facial learning (Figure 5.28).

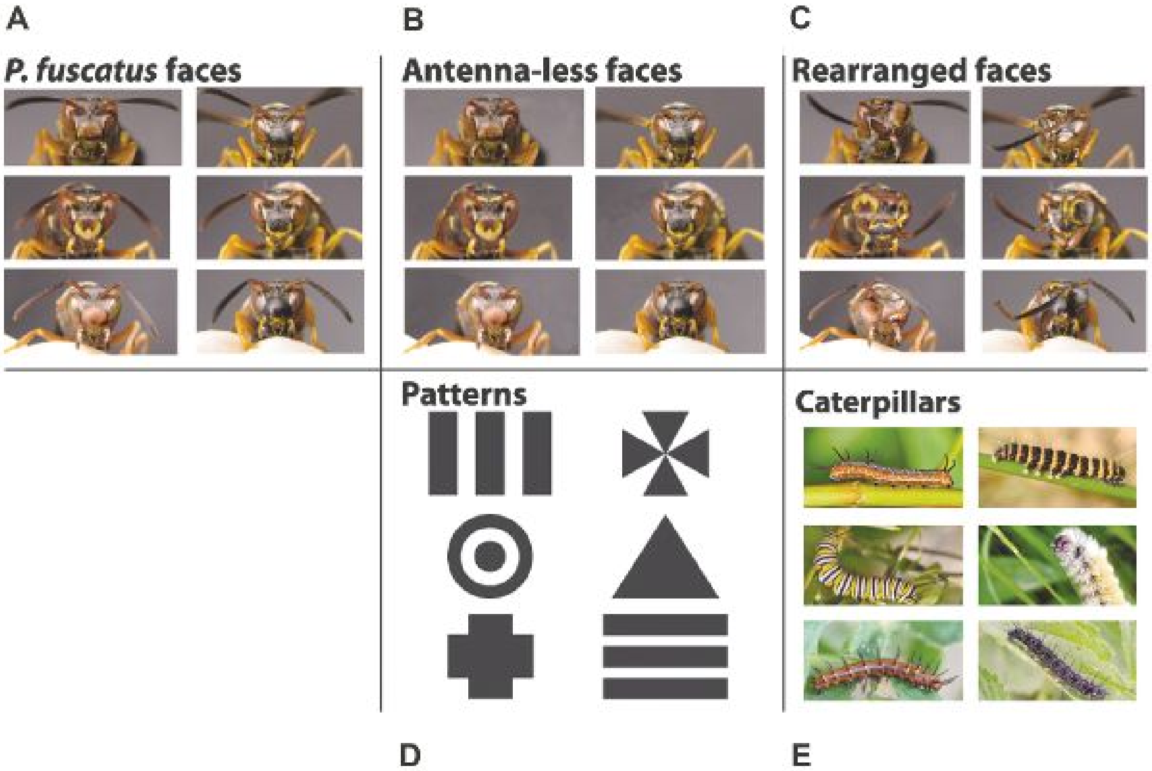


Figure 5.28. Facial learning in wasps. Set of images used for learning trials in wasps. To see how trials were run, look at panel A (*P. fuscatus* faces). A wasp paired one of the images in each row of panel A with a shock, and was then tested to see how quickly it learned to select the image that was not paired with the shock. A similar approach was used for all treatments. Wasps learned the facial images in panel A, but did not learn to pair an image with shock in panels B, C, or D. The “caterpillar treatment” (E) found that wasps did not learn to avoid the caterpillar image associated with a negative stimulus, further suggesting that the learning was specific to conspecific facial learning. *Reprinted with permission from AAAS*. © 2011. *(From Sheehan and Tibbetts, 2011)*

Sheehan and Tibbets wanted to understand the selective forces that might have shaped facial learning in these wasps. They hypothesized that if this sort of facial learning had been selected in paper wasps because it allows them to recognize individuals in their colony, and if such recognition has effects on reproduction, then in other wasp species that live a more solitary lifestyle and lack specific markings on their face, facial recognition may be absent. To test this idea, Sheehan and Tibbets ran experiments like those described above, but this time using *Polistes metricus*, a species in which individuals typically nest alone, and in which individuals have much less facial pattern variability. No facial learning was observed in this species. While a two-species comparison is far from definitive in terms of what it suggests about how natural selection has operated on facial learning abilities, it is a starting point to follow-up comparisons among many more species (Box 5.5).

Box 5.5. SCIENCE AT WORK

What is the research question? Does facial learning occur in paper wasps?

Why is this an important question? Facial learning may provide important fitness-related benefits, but has not been demonstrated in any nonmammalian species.

What approach was taken to address the research question? Paper wasps were exposed to facial images paired up with aversive stimuli to determine whether they were capable of facial learning.

What was discovered? Paper wasps displayed facial learning, but only when images used in the trials mimicked actual paper wasp faces.

What do the results mean? Results from other aversive stimuli trials with geometric objects in paper wasps, in conjunction with the lack of facial leaning in related species, suggest that natural selection may have favored facial learning per se in paper wasps.

Molecular Genetics and Endocrinology of Learning

Modern techniques in both molecular genetic analysis and endocrinology are shedding light on proximate aspects of learning. Both of the studies discussed in this section focus on fear avoidance learning in rats, but the lessons drawn from these studies may apply to learning in a wide variety of contexts.

MOLECULAR GENETICS OF LEARNING IN RATS

Work on learning has attempted to tie together long-term breeding experiments in rats with the molecular underpinnings of various types of learning. Zhang and his colleagues examined the molecular genetics of avoidance learning in two lines of rats that have been selectively bred for over forty years (F. R. Brush, 2003; F. R. Brush et al., 1999; Zhang et al., 2005).

The two lines of rats—known as the Syracuse High Avoidance (SHA) line and the Syracuse Low Avoidance (SLA) line—are descended from a single, large population of rats founded in 1965. Individuals in each generation were tested on their tendency to avoid auditory and visual cues associated with a foot shock. Although the details varied slightly over time, in the basic protocol, a rat was placed in a cage with two compartments and could move freely between these compartments. Just before a series of foot shocks was delivered to the compartment that the rat was in, a light and a tone were set off. A rat underwent ten training sessions in such a protocol and was then tested in sixty "avoidance" trials to see how often it would move to the other compartment once the sound and tone were presented. In each generation, those rats that were best at avoiding shock (SHA) were bred with one another, and those that were poorest at such an avoidance task (SLA) were bred with one another.

Over the course of more than forty years of selective breeding, SHA animals eventually avoided shocks in forty of sixty trials (on average), while the SLA rats typically displayed such avoidance learning in none of the sixty trials. Other work had shown that the SHA and SLA rats were equally active in their normal daily routines and that they did not differ in their ability to detect shock or the visual and auditory cues used during the experiments. But these two strains of rats did differ in "fearlessness," such that the SLA rats showed much higher levels of anxiety in a series of experiments that were separate from the avoidance learning trials described above. It seems that SLA rats were both anxious and poor at learning to avoid unpleasant cues (shocks), while the converse held true for SHA rats. Further support for this association comes from studies that demonstrate that rats that were administered drugs that are known to reduce anxiety became better at avoidance learning (Fernandez-Teruel et al., 2002; Pereira et al., 1989; Sansone, 1975).

To better understand the molecular underpinnings of the learning differences between the SHA and SLA lines of rats, Zhang and his colleagues examined gene expression patterns in the hippocampus—an area of the brain known to be important in avoidance learning as well as anxiety (Zhang et al., 2005). They ran rats from both lines through ten training sessions and then through sixty avoidance learning trials. Then they selected SHA rats that showed avoidance learning in 70 percent (or more) of their trials and SLA rats that displayed such avoidance learning in less than 10 percent of their trials.

After the learning trials, the researchers removed the hippocampus and measured gene expression in each rat. Initially sifting through gene expression in 7,500 genes, and correcting for statistical problems associated with sampling expression patterns in so many genes, Zhang and his team were able to distill their system down to eight candidate genes that were differentially expressed in the SLA and SHA rat lines. Four of these genes—*Veli1*, *SLC3a1*, *Ptpro*, and *Ykt6p*—showed greater expression in the hippocampus of SHA rats, while four others—*SLC6A4/5HTT*, *Aldh1a4*, *Id3a*, and *Cd74*—were expressed in greater quantities in the brains of SLA rats. From these results, Zhang and his colleagues argue that complex traits like avoidance learning may be controlled by many genes, each of which contributes a small amount to phenotypic expression (similar sorts of findings have been found when comparing other strains of laboratory rats that have been selected for high and low anxiety behavior; Sabariego et al. 2011, 2013; Diaz-Moran et al., 2013). Exactly how the differences in gene expression that Zhang and his team found translate into different behavioral phenotypes associated with avoidance learning per se is not yet understood.

ENDOCRINOLOGY OF LEARNING IN RATS

Let’s now review a study in which another proximate factor associated with learning in rats has been examined. Glucocorticoids such as corticosterone are hormones that play a large role in the stress responses and learning of many animals (de Kloet et al., 1999). Glucocorticoids can cross the “blood-brain” boundary and enter the brain, where they can affect emotional state and cognitive abilities: when pregnant female rats are stressed and glucocorticoid levels rise, the offspring of such females show high levels of anxiety and perform suboptimally in learning tests (Lemaire et al., 2000; Weinstock, 1997).

Glucocorticoids bind to receptors in the hippocampal section of the brain, including the mineralocorticoid receptor (MR) (de Kloet et al., 1998). To better understand the relationship between glucocorticoids, stress, and learning, Ana Herrero and her colleagues administered a series of behavioral tests to a group of rats and then measured the level of various hormones. Their results are correlational rather than causal, but they shed light on learning and stress (Herrero et al., 2006).

Herrero and her team first exposed a group of rats to tests designed to examine the fear response: one test involved rats moving through a maze, and the second involved measuring how rats respond to large open fields. Rats fear open environments—environments lacking cover—and both of these tests involve placing a rat in an open environment and examining its stress response to that environment. The researchers assessed the rat's stress by measuring such variables as the amount of time the rat spent frozen (unmoving) and the rate at which the rat defecated. The higher these values, the greater the stress and anxiety attributed to the animal. Some rats were exposed to only one fear test, and others were exposed to both fear tests. Rats exposed to both tests were consistent in that they were either relatively anxious in both or not anxious in either.

Once the researchers had established that rats are consistent in their response to open environments, they ran 140 rats through one fear test, and based on the rats' behavioral responses, they classified them as either "high-anxiety" or "low-anxiety." After this fear test, rats were tested on their spatial learning skills. This involved placing the rats in a water maze and measuring their abilities to find and remember the location of a submerged escape platform on which they could rest. Herrero's team measured either the rats' plasma corticosterone levels—a rough measure of the amount of corticosterone circulating in their blood—and the number of mineralocorticoid receptors in their hippocampus.

Although all animals—both those classified as high- and low-anxiety—eventually learned to swim to the submerged platforms, high-anxiety individuals took significantly longer than low-anxiety animals to learn to do so, mostly because high-anxiety animals spent more time swimming close to the edge of the water tank (Figure 5.29). When blood corticosteroid levels were measured in rats that had been run through the water maze, Herrero found that high-anxiety animals had higher corticosterone levels than did low-anxiety animals (see chapter 3). In addition, high-anxiety animals had *fewer* mineralocorticoid receptors in their hippocampus: having fewer mineralocorticoid receptors results in a reduced ability to bind corticosterone, and indirectly leads to an increase in circulating stress hormones.

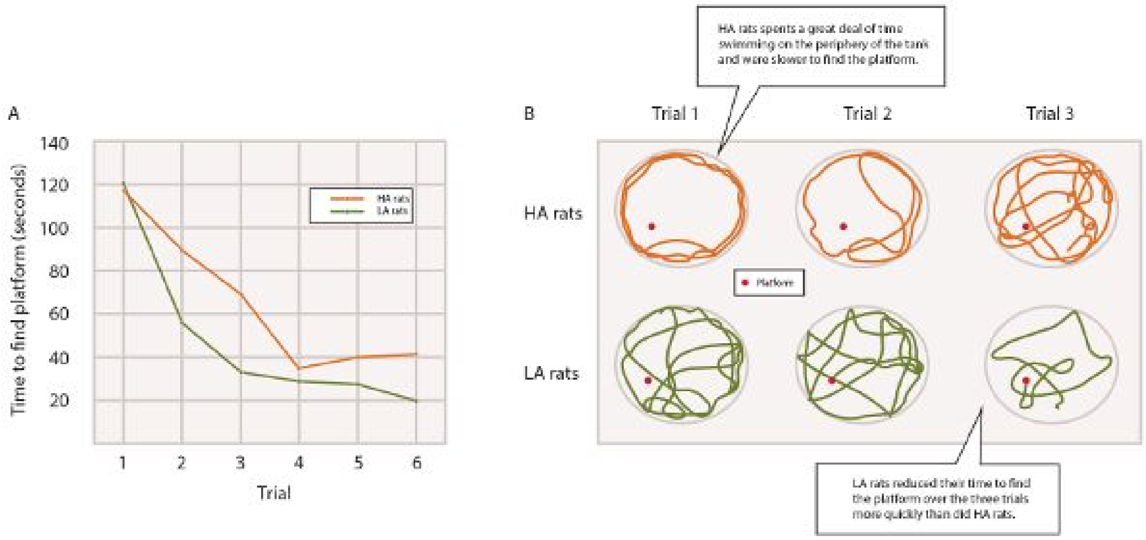


Figure 5.29. Anxiety and learning in a water maze. (A) High-anxiety (HA) rats took significantly longer than low-anxiety (LA) animals to learn to swim to the submerged platform, primarily because high-anxiety animals spent more time swimming close to the edge of the water tank. (B) Diagrams of the rats' swimming paths in their first three training trials. *Reprinted with permission from* Elsevier. © 2006. *(From Herrero et al., 2006)*

It is not clear what the cause-and-effect relationship is in Herrero's studies. It may be that rats with few mineralocorticoid receptors and high-circulating corticosterone became anxious in the open-environment tests, and then scored poorly in the water maze test. Or it could be that the open environment tests caused a change in the availability of mineralocorticoid receptors and circulating corticosterone, and animals with increased circulating corticosterone and decreased availability of mineralocorticoid receptors then did poorly on the water maze test. Further experiments are needed to decipher a cause-and-effect relationship, but the work of Herrero and her colleagues suggests a link between stress hormones, stress hormone receptors, anxiety, and learning.

Interview with Dr. Sara Shettleworth

How did you become interested in studying learning? Were you trained as a psychologist or a biologist?

As an undergraduate, I was drawn to psychology by the introductory course taught by Henry Gleitman. He was a wonderful lecturer who went on to write a popular introductory textbook and win awards for his teaching. Much of the course dealt with the then-current controversies in learning theory, and I found the interplay of theory and experiments fascinating.

In graduate school I was exposed to biological approaches to behavior, which piqued my interest in what role learning played in the natural lives of animals. As it happened, it was at about that time that conditioned taste aversion was discovered by Garcia and his colleagues, and not long afterward Brown and Jenkins first described autoshaping in pigeons. These discoveries were mind-blowing at the time because they seemed to show that animals learn some things with very minimal input and others not at all. To understand these patterns, we might need to take into account the role that learning might play in the animal’s natural life. Although I have worked on quite a number of different species and learning problems since then, it has always been with a commitment to this point of view. As for biological training, I have been fortunate to collaborate or otherwise be associated with biologists who are interested in psychological questions, and I think we have learned a lot from one another.

Do we know of any species of animal that can't learn something?

I don't know of any. Considering that even the single-celled organism *Stentor* can modify its behavior in simple ways, as shown by Jennings 100 years ago, it might be hard to find one that did not at least show habituation or sensitization.

Is there any reluctance in mainstream psychology to study learning from an evolutionary perspective? If so, why?

Historically, learning and memory were studied pretty much in isolation from anything about the biology of the species doing the learning. People have suggested that the prominence of learning in American psychology and its abiological emphasis are attributable to the American faith in the importance of the environment as opposed to hereditary factors in individual development and adult achievement. The relationship between psychology and evolutionary thinking has been changing, partly due to discoveries within psychology like those I mentioned in answering the first question. The increasingly important role of neuroscience and genetics in psychology probably also plays a role in making people think more and more of psychology as, in effect, part of biology. At the same time, behavioral ecologists have brought the evolutionarily based study of behavior full circle, back to an interest in causal mechanisms and development, which tended to be neglected in the early days of that field. Indeed, the term *cognitive ecology* was invented to refer to the study of the role of cognitive mechanisms—perception, learning, memory, and the like—in solving ecological problems. These developments have led to more cross-disciplinary communication, collaboration, and training. This integrated approach is especially evident in the burgeoning subfield of comparative cognition, which deals not only with processes of learning but also with other aspects of cognition, such as social and physical understanding. Many of the questions addressed in contemporary comparative cognition arise from observations of natural behavior, such as tool use by corvids and primates.

How much of a quagmire is the terminology used in the study of learning? To the outside reader it seems as if there are endless definitions and subdefinitions. Is that a fair statement?

No, I don't think it's fair. Fields of science all have their own specialized terminologies, which are necessary to convey specialized ideas and distinctions that can't be expressed concisely in ordinary language. When I ask psychology students to read literature from behavioral ecology, they find terms like *ESS*, *MVT*, *conspecific*, *homology versus analogy*, *phylogeny*, and the like, pretty baffling.

What do you think ethologists can glean from work on human learning?

In his famous paper "On Aims and Methods of Ethology," Tinbergen pointed out that a complete understanding of behavior includes answers to four questions. Two of them are "What is the current (or proximate) cause of this behavior?" and "How does it develop in the individual?" (The others are "How did it evolve?" and "How does it function?" or "What is its survival value?") Causation and development are essentially what psychologists study. So it seems obvious that ethologists and psychologists (whether they study humans or other animals) should have a lot to learn from each other.

Could you weigh in on the "modular mind" debate? Do you think learning is better viewed as one all-purpose algorithm or as a series of smaller programs, each designed by selection to allow animals to cope with particular sorts of problems (foraging, mating, etc.)?

I am definitely of the "modular mind" school because I think it makes more functional sense and because it also makes better sense of some data. It is also a more sensible way to approach a broad comparative psychology than the old idea that species differ in some single dimension like "intelligence." Along with other psychologists of this persuasion, I tend to think of modules more as cognitive subunits that perform distinct information-processing operations rather than as mechanisms for separate biological functions like mating and food-finding. For example, learning and using information from landmarks might be identified as a distinct (modular) part of spatial cognition, but it could be employed in finding food or mates or a nest. Of course, there have been rather few tests of whether this is correct. In laboratory tests, in rats, spatial learning seems to proceed similarly whether the animal is rewarded with food (i.e., foraging) or escaping from a water tank or some other aversive situation. As a key concept in evolutionary developmental biology, modularity also provides a framework for comparing cognition across species. For instance, young human children share basic processes of spatial, numerical, social, and other aspects of cognition with other animals, whereas later-developing abilities such as counting and using maps may be uniquely human.

What’s the next breakthrough to look for in the study of animal learning?

Although there are still many unanswered questions about animal learning and cognition that need to be studied entirely at the level of behavior, at present there is probably more research on learning being done by behavioral neuroscientists and geneticists than by people like me who focus on behavior of normal intact animals. Thus, statistically it is most likely that the biggest breakthroughs will be made in studies of the neural and molecular basis of learning. However, while much work of this kind simply uses traditional behavioral tests like maze learning or Pavlovian conditioning, some behaviorally sophisticated researchers in this area are making novel observations about how animals learn and remember. For example, in a quest to develop simple tests for rats in which the animals would remember many items of information, Howard Eichenbaum and his colleagues discovered that—not surprisingly given their nocturnal way of life—rats are extraordinarily good at olfactory learning. A rat can learn and remember the significance of many different odors and at the same time. As well, when odors are used, rats can easily learn kinds of tasks that they would learn only with great difficulty, if at all, with visual stimuli, which have traditionally been used. This example illustrates how an integrated approach to learning can lead to new findings: by using ethologically relevant stimuli the researchers have revealed new facts about animal learning and memory, as well as making possible investigations of the neural basis of learning that would not be possible otherwise. An important future frontier will be to use knowledge of the neural and molecular basis of cognition with information about species differences in cognition. For example, can we relate cognitive differences among humans, chimpanzees, and bonobos to differences in their brains and ultimately their genomes?

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SUMMARY

1. Here, we define *learning* as “a relatively permanent change in behavior as a result of experience.”
2. The ability of organisms to learn provides them with the opportunity to respond in a very flexible fashion to environmental change. Learning, in the most general sense, is considered a form of phenotypic plasticity.
3. The simplest form of learning involves a single stimulus. Sensitization and habituation are two single-stimulus forms of learning. Habituation is often of concern to experimental ethologists, as experimental results can be difficult to interpret if animals habituate quickly to stimuli.
4. Pavlovian, or classical, conditioning experiments involve two stimuli: the conditioned stimulus and the unconditioned stimulus. A *conditioned stimulus* (CS) is a stimulus that fails initially to elicit a particular response, but comes to do so when it becomes associated with a second (unconditioned) stimulus. Second-order conditioning, excitatory conditioning, inhibitory conditioning, learnability, blocking, overshadowing, and latent inhibition are issues often addressed in Pavlovian conditioning experiments.
5. Instrumental conditioning, also known as operant or goal-directed learning, occurs when a response made by an animal is somehow reinforced. One difference between Pavlovian and instrumental learning centers on the fact that, in the latter, the animal must undertake some “action” or “response” in order for the conditioning process to produce learning.
6. Interpopulation comparisons in learning are a powerful tool employed by ethologists interested in learning. By making comparisons across populations that differ in their abilities to learn, ethologists can address both proximate questions (What are the differences?) and ultimate questions (Why do such differences occur?).
7. Ethologists, behavioral ecologists, and psychologists have long argued that learning is favored over the genetic transmission of a fixed trait when the environment in which an animal lives changes often, but not too often. Work that expands on this idea has investigated within- and between-generation variability. Theory suggests that learning is favored when predictability within the lifetime of an individual is high but predictability between generations is low.

8. Animals learn in many different contexts, including, but not limited to, foraging (what to eat?), habitat selection (where to live?), anti-predator behavior (what's dangerous?), mate choice (what constitutes a mate, and what constitutes a good mate?), and familial relationships (who is genetic kin?).
9. Modern techniques in both molecular genetic analysis and endocrinology are shedding light on learning.

DISCUSSION QUESTIONS

1. Obtain a copy of parts I and II of Tooby and Cosmides's 1989 article "Evolutionary psychology and the generation of culture," in volume 10 (pp. 29–97) of the journal *Ethology and Sociobiology*. After reading this article, explain how "Darwinian algorithms" work and how they relate to our discussion of animal learning.
2. Read Domjan and Hollis's 1988 chapter "Reproductive behavior: A potential model system for adaptive specializations in learning," which appeared in Bolles and Beecher's book *Evolution and Learning* (pp. 213–237). Then outline how classic psychological models of learning can be productively merged with evolutionary approaches to learning.
3. Design an experiment that can distinguish between the two alternative explanations for interpopulational differences in dove foraging, as described in Carlier and Lefebvre's 1996 "Differences in individual learning between group-foraging and territorial Zenaida doves," which appeared in volume 133 (pp. 1197–1207) of the journal *Behaviour*.

SUGGESTED READING

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Krebs, J. R., & Inman, A. J. (1992). Learning and foraging: Individuals, groups, and populations. *American Naturalist*, *140*, S63–S84. A review of learning and its role in foraging studies.

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6

Cultural Transmission

> A man belonging to the Aché tribe sits down on a long log in the clearing of his forest camp in a Paraguayan Forest Reserve to make a bow. He selects that particular log because it affords a place for another person to sit side-by-side with him. He calls to his son as he begins to work, and his son comes to sit down next to him, watching. Carving a notch into the top of the wooden shaft, the man does not speak but does shift position from time to time so that his son can better observe the process. He methodically wraps the sinew string around the notch in the bow and covers it with a sticky resin. By late afternoon, the father has created a new bow and the son has learned something: the steps involved in making a traditional hunting weapon.
>
> Byrne and Rapaport, 2011

Teaching is at the heart of human culture. We teach our children, as well as each other, as a matter of course. In the last chapter we saw abundant evidence for individual learning, but is there evidence of social learning, including teaching, in other animals? Consider foraging behavior in the ant, *Temnothorax albipennis*. When a food source is discovered, pairs of ants head toward it in what is known as a tandem run (Figure 6.1). During these tandem runs, ants appear to signal one another about direction and speed.

Figure 6.1. **Tandem runs in foraging ants.** When food is discovered in *Temnothorax albipennis*, pairs of individuals move toward it in what is called a tandem run. Two marked ants involved in a tandem run on an experimental grid are shown here. Reprinted by permission from Macmillan Publishers Ltd. © 2006. *(From Franks and Richardson, 2006)*

Franks and Richardson designed an experiment to test whether tandem runs involved teaching (Franks and Richardson, 2006). They marked pairs of ants with colored dots: one color-marked ant in a pair knew the location of food, but the other did not (Figure 6.1). The ant that knew where the food was located led the tandem run and the naive ant followed and constantly tapped the legs of the leader: indeed, leaders *only* continued tandem runs when they were tapped often on their legs. Leaders paid a cost for responding to their partner's taps, as they were able to get to food sources four times faster when they were alone than when paired with naive tandem run partners. Despite the costs of being the leader, in tandem runs that were interrupted by investigators, and in which followers were temporarily removed, leaders waited for the followers to return before moving toward the food source, and they waited longer the longer the run had already been in progress.

On the other side of a tandem run, naive ants learned from following leaders. They arrived at the food source much faster when in tandem runs than when foraging alone. They also returned back to their nest more quickly after tandem runs as compared to solo foraging bouts.

Is this teaching? Are leaders teachers and naive follower ants pupils? Perhaps. Leaders paid a cost for leading, yet despite this cost, they modified their foraging runs by waiting for followers who appeared to lag behind (because of their experimental removal). For their part, followers appear to make good pupils, learning from leaders how to find food quickly and then efficiently making their way back to their nests.

This example is not meant to suggest that teaching is common in nonhumans. The verdict on that question is still out, but the evidence so far suggests that it is not common. We will examine reasons why later in the chapter. This opening vignette is instead meant to help you open your mind to the possibility that cultural transmission of information, including that transmitted through teaching, occurs in other species, even species of ants.

* * *

In the discussion of genetics and heritability in chapter 2, we noted that for natural selection to act on a behavior, a mechanism for transmitting that behavior across generations is required. When Mendel’s work on genetics was rediscovered in the early 1900s, it became clear that genes are a means of transmitting traits across generations, enabling natural selection to act on genetically encoded traits. In fact, until recently, evolutionary biologists and ethologists operated under the assumption that genes were not only *one* way to transmit information across generations, they were the *only* way. Slowly, this view is beginning to change. Recall, for example, our discussion in chapter 1 of Jeff Galef’s work on foraging and information transfer across generations of rats. There is now a growing recognition of the importance of the **cultural transmission** of behavior—typically defined as the transfer of information from individual to individual through social learning or teaching—both within and between generations of animals (see below for more on the definition of *cultural transmission*; Bonner, 1980; Boyd and Richerson, 1985; Heyes and Galef, 1996; Laland and Janik, 2006; Odling-Smee et al., 2003; Reader and Laland, 2003; Whiten et al., 2012; Laland and Galef, 2009; Mesoudi, 2011; Henrich, 2015).

Consider the case of Imo, a Japanese macaque monkey that lived on Koshima Islet, Japan, in the 1950s (Kawai, 1965; Kawamura, 1959; Figure 6.2). Imo's story begins when ethologists studying her troop of macaques threw sweet potatoes on the sandy beach for the monkeys to gather and eat. When Imo was a year old, she began to wash the sweet potatoes in water before she ate them. This novel and creative behavior, which was never before seen in Imo's population, allowed her to remove all the sand from the sweet potatoes before she ingested them. But what made this new behavior remarkable is not that Imo found a novel solution to cleaning her food; rather, the key feature of this system is that many of Imo's peers and relatives learned the skill of potato washing from Imo via **social learning**—the process of learning by watching others. By 1959, most young macaques in Imo's troop intently watched their mothers, many of whom had acquired Imo's habit, and they learned to wash their own sweet potatoes at early ages (Figure 6.3).

Figure 6.2. Imo the monkey. Imo, a Japanese macaque, introduced a number of new behaviors, including potato washing, that spread through her population via cultural transmission. *(Photo credit: Umeyo Mori)*

Figure 6.3. Potato washing in monkeys. In Japanese macaques living on Koshima Islet, Japan, the skill of potato washing appears to be transmitted culturally. *(Photo credits: Kennosuke Tsuda/Nature Production/Minden Pictures; © Takafumi Suzumura, Wildlife Research Center of Kyoto University)*

When Imo was four, she introduced an even more complicated new behavior into her group. In addition to the sweet potatoes researchers occasionally treated the monkeys to a food item to which the macaques were partial—wheat. The introduction of this new food source, however, caused a problem for the monkeys in that the wheat was provisioned on a sandy beach, and the wheat and sand mixed together. Imo came up with a novel solution—she tossed her wheat and sand mixture into the water, where the sand sank and the wheat floated. As with the sweet potatoes, her groupmates soon learned this trick from her. It took a bit longer for this trait to spread through the population, however, as monkeys aren't used to letting go of food once they get it, so it was hard to learn to throw the sand-covered wheat into the water. But eventually this new behavioral trait spread to many group members via cultural transmission.

Imo's actions were not the only ones to attract attention about the cultural transmission of behavioral traits in nonhumans, and many similar cases are now on record. Michael Huffman, for example, has been studying cultural transmission in the Japanese macaques of the Iwatayama National Park in Kyoto, Japan (Huffman, 1996; Nahallage and Huffman, 2006). Early in his work, he began to observe a behavior never before noted in macaques—individuals would play with stones, particularly right after eating (Hiraiwa, 1975; Figure 6.4).

Figure 6.4. Stone play in monkeys. In one population of Japanese macaques in the Iwatayama National Park in Kyoto a tradition of "stone play," in which individuals stack up stones and then knock them down, has been observed. *(Photo credit: Michael A. Huffman)*

In the Iwatayama National Park where Huffman studies macaques, stone play behavior was first observed in 1979 when Glance-6476, a three-year-old female macaque, brought rocks in from the forest and started stacking them up and knocking them down. Glance-6476 was very territorial about her stones and took them away when approached by other monkeys. When Huffman returned to study Glance's troop four years later, stone play (also called stone handling) was common and was being transmitted from older to younger individuals. Interestingly, cultural transmission in this system seems to work down the age ladder, but not up. While many individuals younger than Glance-6476 acquired her stone play habit, no one older than her added stone play to their behavioral repertoire (Figure 6.5).

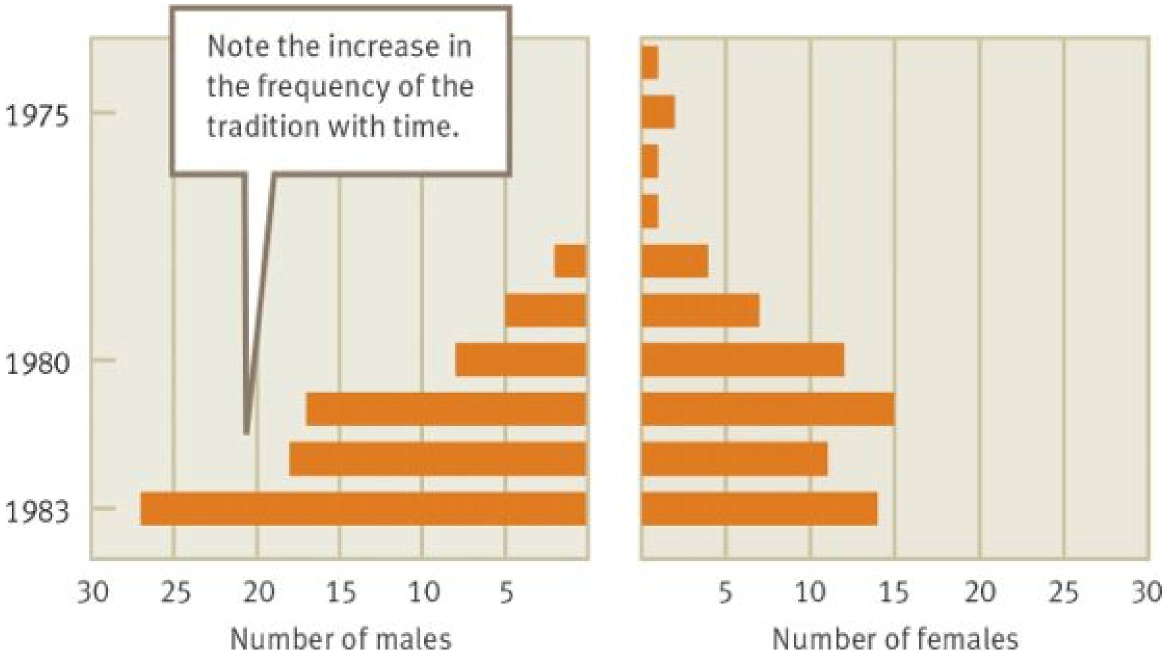


Figure 6.5. Stone play tradition spreads. Orange bars represent verified stone handlers in Japanese macaques. *(From Huffman, 1996, p. 276)*

Charmalie Nahallage and Huffman later examined stone play in a captive troop of macaques in the Primate Research Institute in Kyoto, Japan (Nahallage and Huffman, 2006). When they did a detailed study of the use of stone play in juvenile and adult macaques, they uncovered age-specific differences in the use of culturally acquired behavior. Juveniles tended to engage in many short bouts of stone play that involved vigorous body actions (for example, shaking, running, and jumping). This pattern of behavior is consistent with what is called the “motor training” hypothesis of play behavior (see chapter 16), which suggests that stone play may facilitate the development of perceptual and cognitive skills (Bekoff and Byers, 1981; Leca et al., 2011). Adults, on the other hand, engaged in fewer but longer bouts of stone play, which may help slow down the deterioration of cognitive processes often seen in aging primates (Figure 6.6). More work is needed to fully test these hypothesized benefits of stone play.

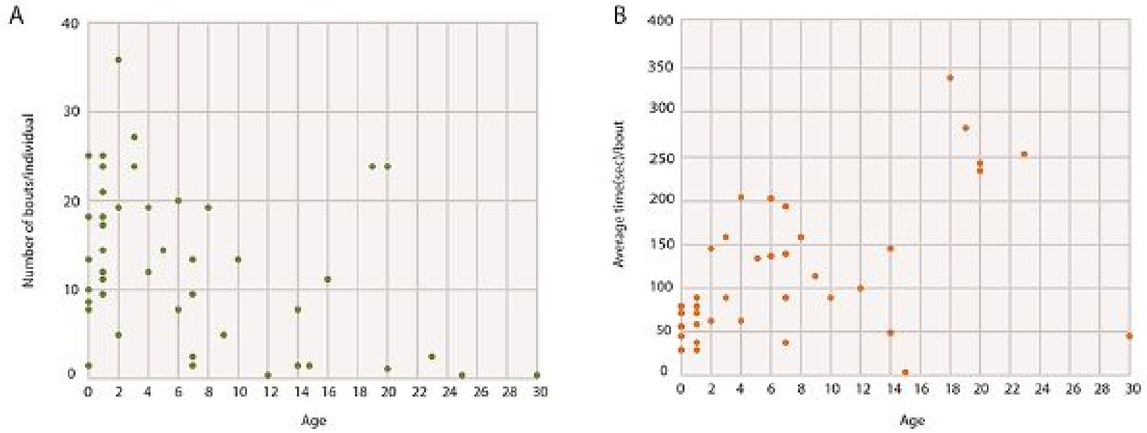


Figure 6.6. Stone play and age. (A) The number of stone play sessions decreases with age. (B) The average time per stone play session increases with age. Reprinted with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc. © 2007. *(From Nahallage and Huffman, 2007)*

Stone play has been uncovered in other captive troops of macaques like the monkeys that Nahallage and Huffman have studied. But this behavior has never been documented in wild populations that are not provisioned by humans. Stone play appears to occur only in populations that have significant “leisure time”—that is, in populations that are freed up because their food is provided for them (Nahallage and Huffman, 2007). What makes this sort of play behavior potentially very important to researchers is that stones—the play objects themselves—remain long after the individuals that used them have died, and if they are found clustered or in unusual combinations, this creates relics that can be used in the newly developed field of primate archeology (Haslam et al., 2009; Kuehl et al., 2016).

Cultural transmission has also been extensively documented in other primates, including chimpanzees (Whiten, 2005, 2011; Whiten and Boesch, 2001; Whiten et al., 1999, 2005). Over the course of the last thirty plus years, six long-term studies of natural populations of chimpanzees have documented an array of culturally transmitted traits, ranging from “swatting flies” and opening nuts with stones, to squashing parasites with leaves. In some cases, researchers have clear evidence of young chimps watching and learning these behaviors from adults; in other cases, the evidence is more indirect (see chapter 16).

When looking across these chimpanzee populations, we see a hallmark signature of cultural transmission: numerous traits are transmitted by social learning in every population, but populations differ from one another in terms of *which* traits are transmitted. For example, hammering open nuts with stones is seen in two chimp populations, but it is absent in four. Hammering nuts, once it arose by such trial-and-error learning, could quickly spread by cultural transmission, but only in the populations in which one of the members stumbles on the solution in the first place (or a population into which such an individual migrates).

What Is Cultural Transmission?

What *exactly* do we mean when we speak of cultural transmission in animals? This turns out to be a more difficult question than it might appear (Figure 6.7). Even back in 1952, anthropologists already had more than 150 definitions of *culture* and *cultural transmission* (Kroeber and Kluckhohn, 1952). Evolutionary and behavioral biologists tend to use the following definition: cultural transmission is a system of information transfer that affects an individual’s phenotype by means of either teaching or some form of social learning (Boyd and Richerson, 1985). Recall the Norway rats discussed in chapter 1. As scavengers, rats often encounter potential new foods. The cost to scavenging is that many novel foods may in fact be dangerous to eat. Scavenging is an ideal behavior in which to examine the cultural transmission of information, as new items are always being encountered, and information on their potential danger constantly needs to be updated. Obtaining some sort of information about food from other rats is one way to update knowledge about the suitability of novel foods. In fact, Norway rats learn what new foods to try by smelling their nestmates and subsequently trying the new food items that those nestmates have recently ingested (Galef, 1996, 2009; Galef and Wigmore, 1983). One aspect of a rat's phenotype—in this case, what sorts of food it eats—is modified by information that it has learned from other individuals.

Figure 6.7. What constitutes cultural transmission? The child is learning to use utensils by watching others (that is, through cultural transmission). The young chimp also has learned its nut-cracking skills from watching others.

WHAT'S SO IMPORTANT ABOUT CULTURAL TRANSMISSION?

We spent a great deal of time on the topic of learning in chapter 5, and if cultural transmission is just one form of learning—that is, learning from other individuals—why not simply consider it a special kind of learning and move on? As Boyd and Richerson ask, "Why not simply treat culture as a . . . response to environmental variation in which the 'environment' is the behavior of conspecifics?" (Boyd and Richerson, 1985). Why not think of cultural transmission as just another means by which organisms adapt to the environment?

The answer to these questions is that learning from other individuals involves the spread of information *from individual to individual*: information can be spread through a population (Figures 6.8 and 6.9). This potentially translates into the behavior of a single individual in a population dramatically shifting the behavior patterns seen in an entire group—recall how Imo's novel food-washing techniques spread via cultural transmission. This is not the case for other types of learning. What an individual learns via individual learning disappears when that individual dies, and perhaps earlier. When cultural transmission is in play what is learned by one individual may be passed down through generations. If Imo had learned to clean her sweet potatoes by washing them in water in a population in which social learning was absent, this foraging innovation would have vanished when she died. Instead, decades later, one can still go to Koshima Islet and see monkeys washing their sweet potatoes.

Figure 6.8. Imitation in infants. Imitation is a form of social learning that begins early in humans. Here an infant claps his hands in imitation of his mother clapping her hands. *(Photo credit: iStock.com/Carey Hope)*

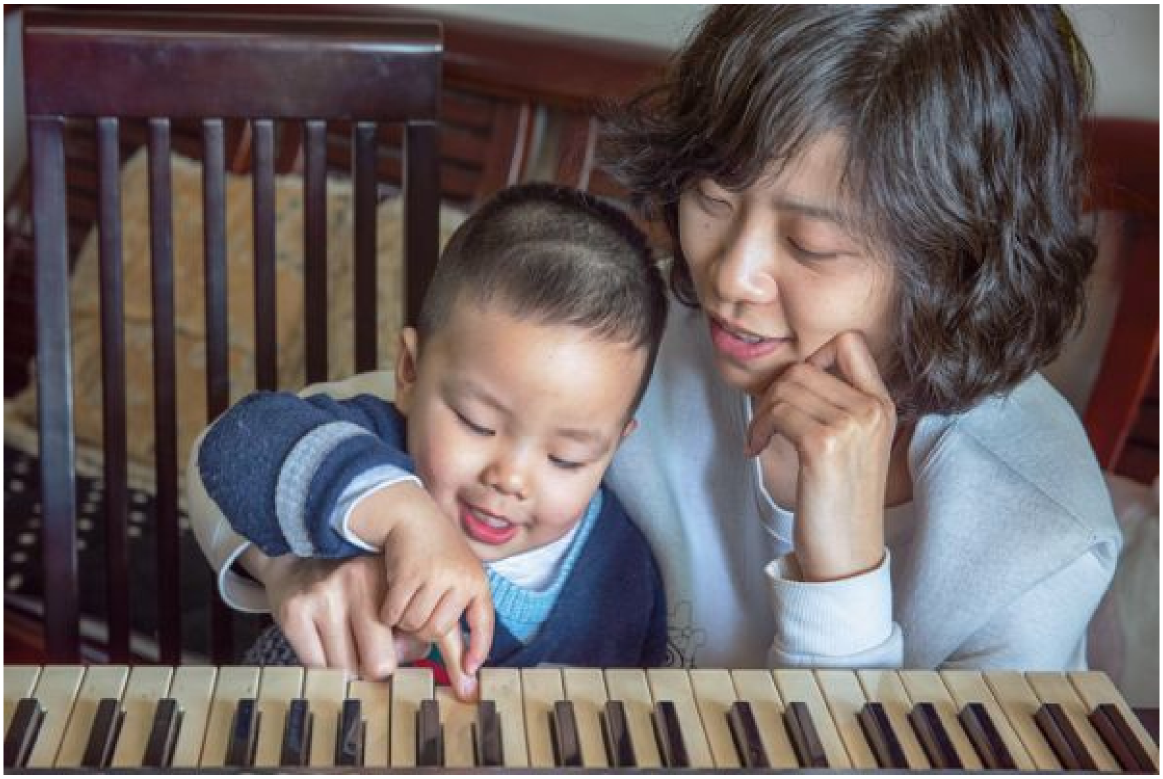


Figure 6.9. Cultural transmission via teaching. Teaching is a form of cultural transmission in which the teacher imparts some information to a student faster than the student could learn it on her own. This piano teacher is introducing her young student to the piano. *(Photo credit: iStock.com/Oktay Ortakcioglu)*

Cultural transmission can spread behaviors throughout a population very quickly, which makes it a particularly potent form of information transfer. When natural selection acts to change the frequency of genes that code for behavior, the time scale can range from a few dozen generations (as in the guppy case we explored in chapter 2) to much longer time scales (thousands of generations). And when natural selection acts on major morphological change, the time scale may be even longer. Cultural transmission of information, on the other hand, operates much faster, and can cause important changes in the behavior seen in populations in just a few generations. In fact, cultural transmission can have a dramatic impact within a single generation (Boyd and Richerson, 1985, 2004, 2005; Henrich et al., 2005; Odling-Smee et al., 2003; Reader and Laland, 2003).

EFFECTS OF OTHERS ON BEHAVIOR

Cultural transmission involves a “model” individual—sometimes called a demonstrator or tutor—and an “observer,” who learns a specific action or series of actions from the model. But there are situations that involve an interaction between observers and models, but that do *not* constitute social learning or teaching. In these cases—labeled local enhancement and social facilitation—the observer is drawn to an area by a model or by the action of a model, or is simply in the presence of models, but the observer does not learn a particular behavior or response from the model, so cultural transmission is not occurring.

Local Enhancement

William Thorpe coined the term **local enhancement** to describe the situation in which individuals learn from others, not so much by doing what they observe, as by being drawn to a particular area because another individual—a model—was in that location (Heyes, 1994; Thorpe, 1956, 1963; Figure 6.10). In other words, a model simply draws attention to some aspect of the environment by the action it undertakes there (for example, digging for worms). Once the observer is drawn to the area, the observer may learn on its own, via individual learning.

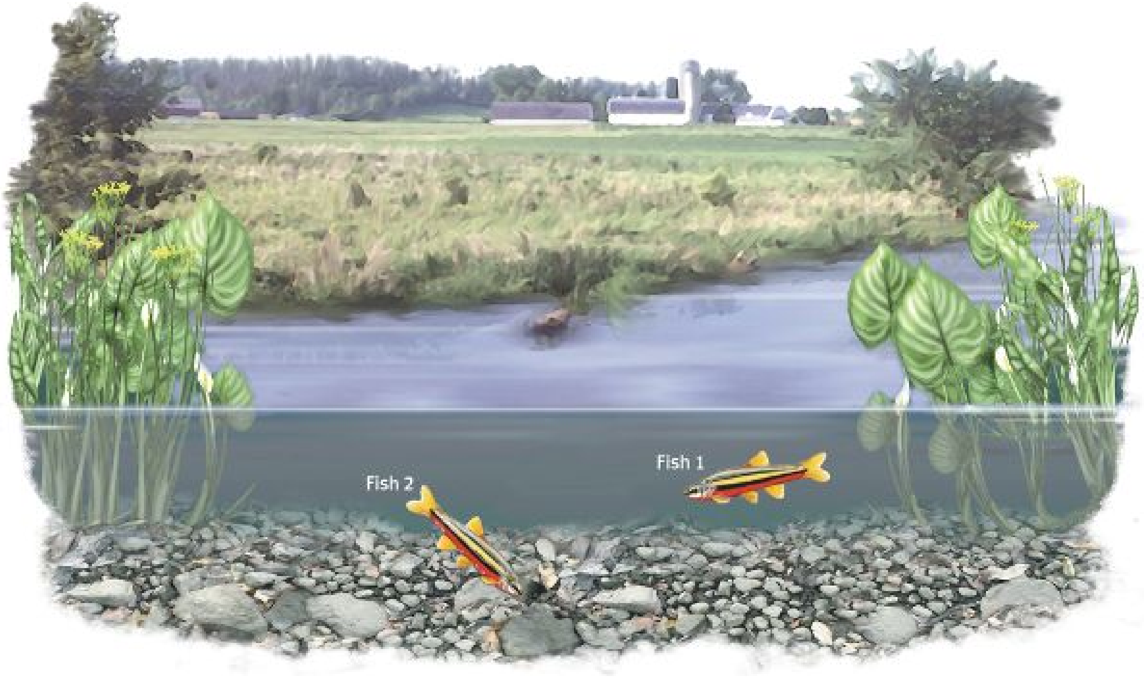


Figure 6.10. Local enhancement. If fish 1 is drawn to the area where fish 2 is foraging (near a stone) local enhancement is at work.

Consider foraging behavior in colonially nesting cliff swallows, birds that feed in groups ranging in size from 2 to 1,000 individuals (see chapter 2). Charles Brown has found that, in addition to the actual transfer of information between groupmates (C. R. Brown, 1986), local enhancement facilitates foraging, as some individuals are drawn to good foraging areas just because other birds are foraging there.

Social Facilitation

Social facilitation differs in a subtle, but important, way from local enhancement. During local enhancement, the *action* of a model draws attention to some aspect of the environment. But under social facilitation, the *mere presence* of a model, regardless of what it does, is thought to facilitate learning on the part of an observer (Zajonc, 1965). For example, there are many instances in the foraging literature in which increased group size caused increased foraging rates per individual, perhaps because the mere presence of others made them safer (Giraldeau and Caraco, 2000; Stephens and Krebs, 1986; Figure 6.11).

Figure 6.11. Social facilitation. In social facilitation, the mere presence of one or more models draws in an observer. Here a lone starling is attracted to a group, not because of what group members are doing or where they are, but simply because it is drawn to the presence of others. “Safety in numbers” might be a benefit to such facilitation.

Social facilitation and local enhancement can be experimentally separated from one another. To see how, let’s examine a series of experiments that Elisabetta Visalberghi and Elsa Addessi ran on foraging behavior in capuchin monkeys (Visalberghi and Addessi, 2000; Figure 6.12). These researchers examined what factors affected a capuchin monkey’s probability of eating a novel food. In treatment I, a *lone* capuchin was tested on its tendency to try a new food type (vegetables that had been color dyed). In treatment II, a capuchin and the novel food type were on one side of a test cage, and a group of capuchins was on the other side of the cage. No food was placed on the side of the cage with the group. Treatment III was identical to the second, except that a familiar food type was placed on the side of the cage with the group, which made it likely that they would eat the food.

Now the lone capuchin saw not only a group, but a group that had individuals eating food, just not the novel food (Figure 6.13). These treatments were carefully designed to create potential for social facilitation (treatment 2: mere presence of others) and local enhancement (treatment 3: presence of others that are eating). Treatment 1 served as the control condition.

Figure 6.12. Capuchin foraging. Foraging in capuchins (*Cebus paella*) has been examined with respect to both local enhancement and social facilitation. These capuchin monkeys are foraging on palm nuts. *(Photo credit: Tui De Roy/Minden Pictures)*

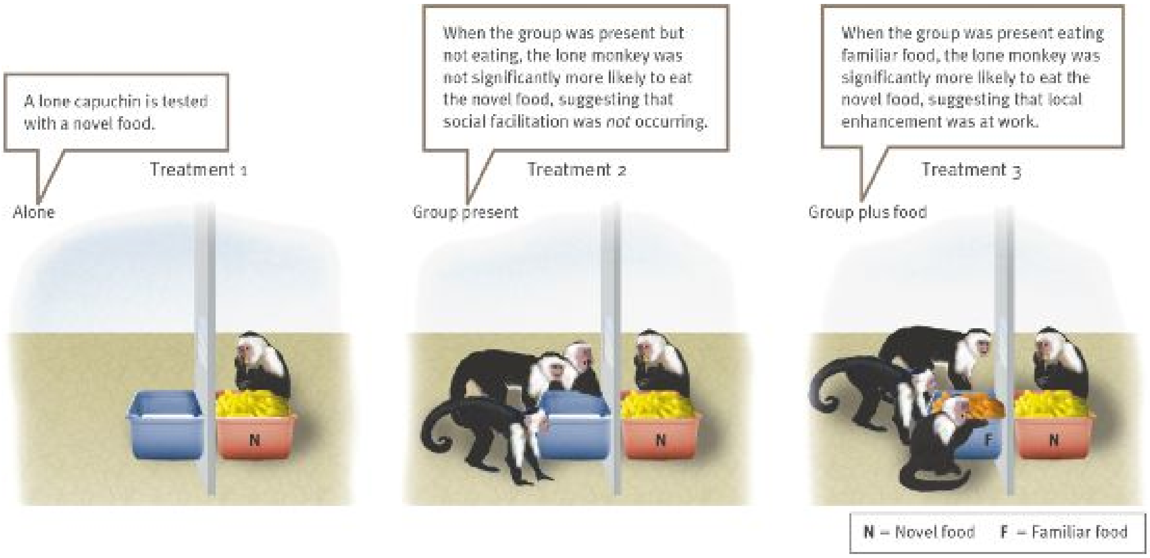


Figure 6.13. Social facilitation and local enhancement in capuchin foraging. The experimental design for the three treatments examining social facilitation and local enhancement. *(From Visalberghi and Addessi, 2000)*

When comparing across their treatments, Visalberghi and Addessi found evidence of local enhancement, but not of social facilitation. Evidence for local enhancement was uncovered in that the test capuchin in treatment 3 (test capuchin + group with food) was more likely to be eating food than capuchins in treatment 1 (test capuchin alone). Local enhancement was occurring as the test capuchin's attention was drawn to the novel food when it saw the other capuchins eating food, and then the test capuchin proceeded to eat more itself. However, no evidence for social facilitation was uncovered.

SOCIAL LEARNING

Social learning, sometimes referred to as "observational learning," can take many forms in both humans and nonhumans (Bandura, 1977, 1986; Dugatkin, 2000; Galef, 2009; Heyes and Galef, 1996; Rosenthal and Zimmerman, 1978; Zentall and Galef, 1988; Figure 6.14; see Box 6.1). Below we examine two forms of social learning: imitation and copying.

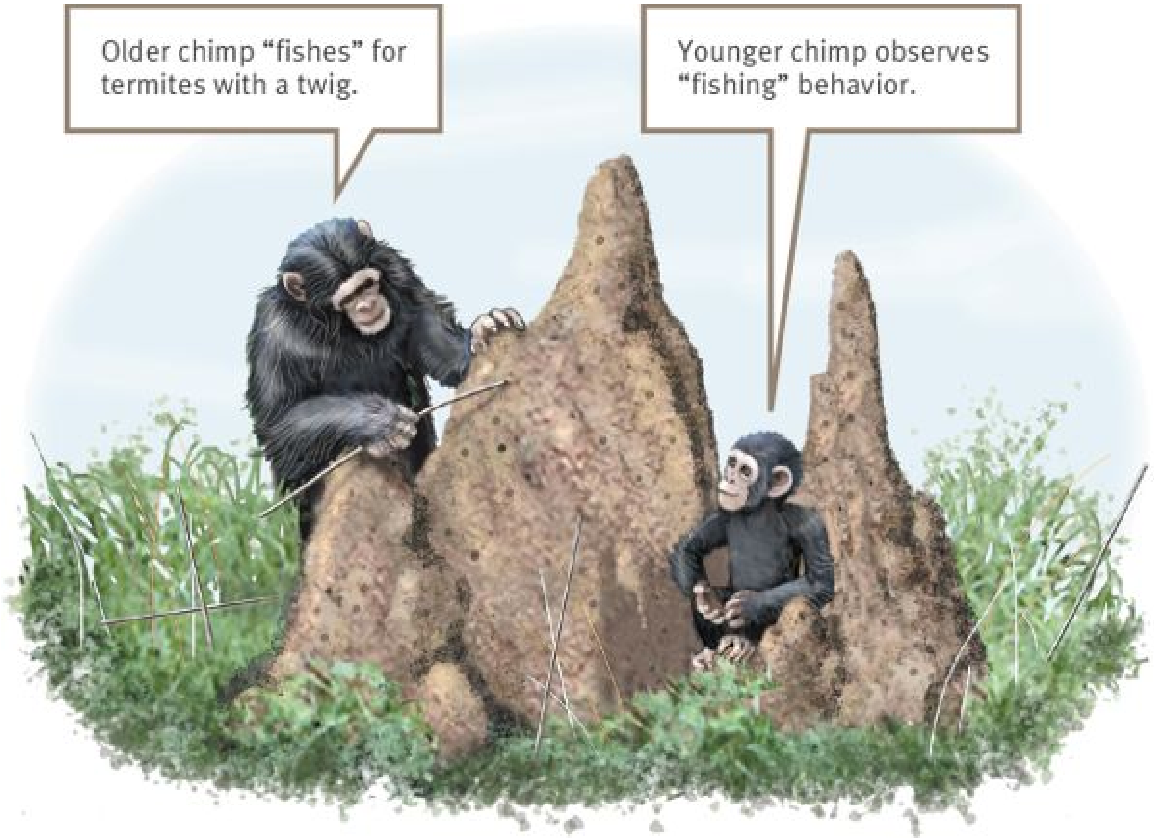


Figure 6.14. Watch, learn and decide. Chimps learn how to “fish” for termites by watching others. Chimps may judge how effective a foraging technique is, and choose whether to add it or not to their behavioral repertoire.

Box 6.1. CONSERVATION CONNECTION

Crop Raiding, Elephants, and Social Learning

Around the world, humans cultivate crops in areas that have not historically been used for agriculture. This can cause conflict between indigenous people and native wildlife that attempt to forage on such crops. For example, around the Amboseli National Park in Kenya, approximately one out of three adult male elephants that have dispersed from their natal groups raid crop fields (Figure 6.15). Raiding crop fields is a dangerous behavior for male elephants, as many are injured or killed by farmers during such raids (Obanda et al., 2008).

Figure 6.15. Crop-raiding behavior in elephants. The role that social learning plays in crop raiding has been studied in elephant populations in the Amboseli National Park in Kenya. *(Photo credit: Martin Harvey / Alamy Stock Photo)*

Elephants live in complex social networks, in which both individual and social learning play important roles (Lee et al., 2011; Plotnik et al., 2011; Goldenberg et al., 2014). Patrick Chiyo and his colleagues tested the hypothesis that male elephants learn how to raid crops—and especially how to be vigilant for farmers when doing so—through some form of social learning (Chiyo et al., 2012). They predicted that males that associated with others that raided crops would raid crops at a higher rate than males that associated with others that did not raid crops and that this effect would be strongest when males associated with *older associates* that raided crops, because such associates would likely be the best models.

Chiyo and his team tested their idea in a population of 1,400 elephants—recognizable by unique tusk and body markings—in the Amboseli National Park. They observed fifty-eight male elephants often enough to rank these individuals in terms of their association patterns and were also able to gather information independently on the crop-raiding behavior of these individuals.

As predicted, a male was more likely to raid crops if the individual it associated with most often was a crop raider: this was also true when its second-closest associate was a crop raider, but not if only a third, fourth, or more distant associate was a crop raider. Also, as predicted by Chiyo and his colleagues, this effect was most pronounced when associates were older.

One of the long-term goals for ethologists involved in such projects is to guide policy makers in the difficult task of developing management practices that simultaneously minimize harm to animals and maximize crop productivity. Much work is being done to develop ideas on this front, but one application from the study on social learning in elephants might be something like this: *If* a plan were developed for providing elephants an alternative food source so that crop raiding is decreased, then this plan should first target older males that serve as models for others in their group.

Imitation

George Romanes was one of the first psychologists to suggest that cultural transmission via imitation plays an important role in animal societies (Romanes, 1884, 1889, 1898). Since Romanes wrote his books on this subject more than a century ago, the term **imitation** has been used in many different ways in the psychological literature (R. W. Byrne, 2002; Heyes and Galef, 1996; Miklosi, 1999; Whiten, 1992). Here, we will adopt Cecilia Heyes's definition of *imitation* as the "acquisition of a topographically novel response through observation of a demonstrator making that response" (Heyes, 1994). To demonstrate imitation, there must be some *new* behavior learned from others, and that behavior must involve some sort of *new spatial (topographic) manipulation* as well as lead to the achievement of some goal (Figure 6.16). We have already touched on a case of imitation at the start of this chapter. When Imo washed her sweet potatoes in water before she ate them, and others in her group observed and then learned this novel behavior, which requires a new sequence of spatial actions, imitation was taking place.

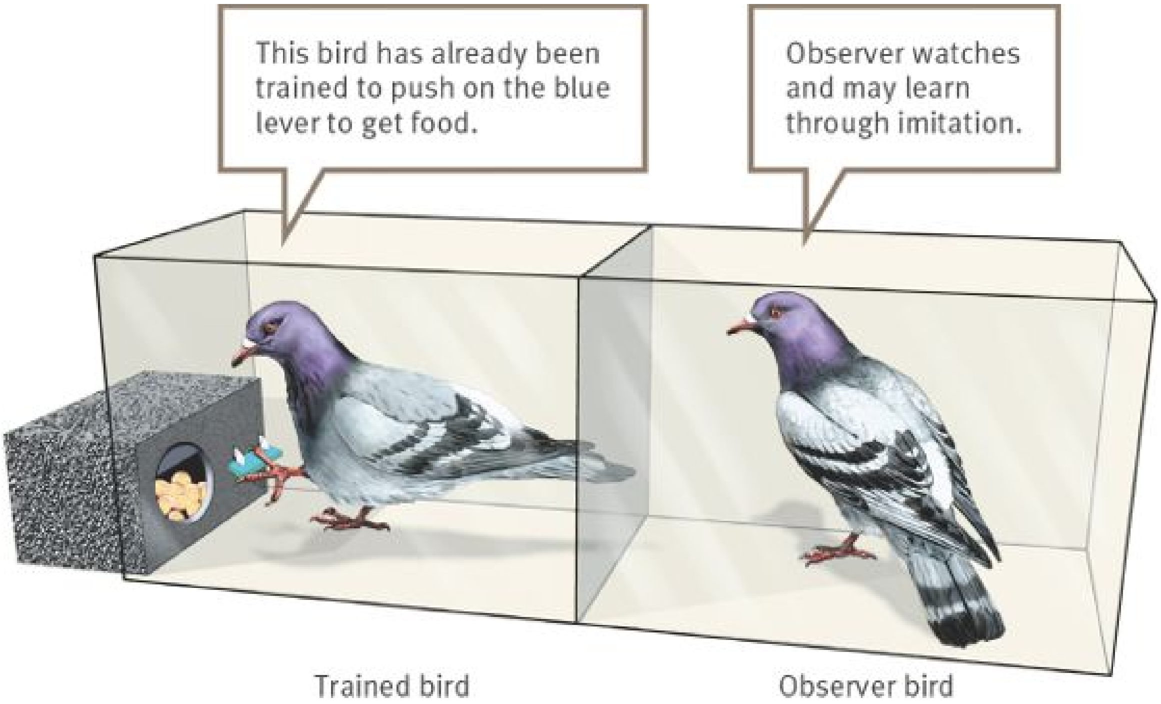


Figure 6.16. Imitation. Here an observer bird watches a trained pigeon that must lift its foot and push on a lever to open a small circular entrance to a food source. Imitation occurs when the observer learns this new task by watching the model lift its leg and push the lever down.

A second example of imitation involves milk bottle opening in birds. In the mid-twentieth century, Brits had their milk delivered to their front porches in bottles with foil caps. In a 1949 paper published in the journal *British Birds*, Fisher and Hinde noted the following observation that they and others had made about these milk bottles:

> In 1921, birds described as tits were observed to prise open the wax board tops of milk bottles on the doorsteps in Swaythling, near Stoneham, Southampton, and drink the milk. This is the first known record of an act which has now become a widespread habit in many parts of England and some parts of Wales, Scotland, and Ireland, and which has to date been practised by at least eleven species of birds. . . . The bottles are usually attacked within a few minutes of being left at the door. There are even several reports of parties of tits following the milkman's cart down the street and removing the tops from bottles in the cart whilst the milkman is delivering milk to the houses.

While seen in many species, this behavior was most common in blue tits (*Parus caeruleus*) (Figure 6.17). In 1949, Fisher and Hinde circulated a survey to 200 members of the British Ornithological Society regarding this behavior (Fisher and Hinde, 1949). From this survey, they pieced together the history of the spread of this novel behavior over a large range of Great Britain (Figure 6.18).

Figure 6.17. Blue tit birds opening milk bottles. Blue tit birds learned to peck open the top of milk jugs decades ago. This behavior may have spread via cultural transmission. *(Photo credit: Kim Taylor/Warren Photographic)*

Figure 6.18. **The spread of a novel behavior.** Each point represents a location where birds have been observed opening milk bottles. Reproduced with permission of British Birds.
(From Fisher and Hinde, 1949)

They found that individuals in all the species opening milk bottles, including blue tits, rarely move more than 10–15 miles from their natal habitat, and so “it would seem, therefore, that new centres and records more than fifteen miles distant from any place where the habit has been recorded previously probably represent new discoveries by birds” (Fisher and Hinde, 1949). Fisher and Hinde suggested that this new behavior is, on occasion, accidentally stumbled upon by a lucky blue tit and that others learned this nifty trick, at least in part, from watching the original milk thief (Fisher and Hinde, 1949), thus explaining the wide distribution of the behavior.

Some evidence supports this hypothesis. Milk of different grades in Britain at this time had different colored foil covers. Birds in an area where milk bottles were opened tended to prefer the same color foils, consistent with the idea that they imitated one another. Which cover foil was preferred varied across a tit population, which is again consistent with cultural transmission via imitation (Box 6.2).

Box 6.2. SCIENCE AT WORK

What is the research question? How did British birds figure out how to open milk bottles, and why has this behavior spread?

Why is this an important question? At the time of the study (1949) there was scant evidence for cultural transmission in wild populations.

What approach was taken to address the research question? A combination of approaches, including behavioral observation and survey questions, was used.

What was discovered? Evidence was most consistent with cultural transmission via imitation explaining how birds learned to open milk bottles and how this behavior spread.

What do the results mean? Even before controlled experiments were undertaken, and long before more sophisticated tools were available to analyze social transmission, it was possible to make inferences about cultural transmission in wild populations.

Imitation raises a number of interesting questions. For example, when individual 1 attempts to imitate individual 2, it can only see individual 2's movements, but not the muscle activation underlying such movements. So how does individual 1 know what to do to make such movements itself? This is referred to as the correspondence problem (Brass and Heyes, 2005). Another issue associated with imitation is that of "perspective taking." Suppose, for example, that you and I are facing one another, and I raise my right hand and move it in circles. If you wish to imitate this action, you need to take into account our positions relative to one another. If you simply raise the hand that was on the same side as the hand I raised, you would be raising your left hand, and not precisely imitating my action.

Behavioral neuroscience is beginning to shed light on both correspondence and perspective-taking problems (Rizzolatti et al., 2006). Studies on these questions in humans often involve subjects who are placed in a magnetic resonance imaging (MRI) device and given some problem to solve while activity in their brain is scanned by the MRI machine. Typically, the problem is very simple—for example, tapping a specific finger a set number of times, or repeating a particular musical chord on the guitar. These studies indicate that certain sections of the brain—the inferior frontal gyrus, the dorsal and ventral premotor cortex, as well as other areas—are consistently active during imitation (Decety et al., 2002; Grezes and Decety, 2001; Grezes et al., 2003; Iacoboni et al., 2001; Koski et al., 2002; Muhlau et al., 2005). Interestingly, our brains respond more strongly to opportunities to imitate an action when we see another human doing it than when we see the same action being performed by a robot (Kilner et al., 2003; Tai et al., 2004).

There is less behavioral neuroscience work on these issues in nonhumans, but that is changing (Rizzolatti and Fogassi, 2014; Ferrari and Rizzolatti, 2014). For example, work on imitation in monkeys has found that a set of “mirror” neurons in the F5 area of the premotor area of the monkey brain becomes very active when a monkey observes an action—such as grasping a piece of food on a tray—and then repeats that action (Molenberghs et al., 2009; Rizzolatti and Craighero, 2004; Rizzolatti et al., 2001). What makes the mirror neurons in the F5 area of the brain particularly relevant is that some of these neurons are motor neurons (neurons that are needed to repeat an act during imitation) and some are visual neurons (neurons that are necessary for watching a model). An action must first be observed before mirror neurons will fire, again suggesting a connection to imitation. Indeed, these neurons will fire if an individual sees a hand manipulating an object, but not if it sees the object alone or if it sees the object being manipulated by a tool (Gallese et al., 1996; Molenberghs et al., 2012; Rizzolatti et al., 1996). Some evidence suggests that mirror neurons in humans also reside in the equivalent of the F5 section of our brain, and that such neurons are involved in human imitation as well, but much work in this area remains to be done.

Copying

When animals **copy** one another, an observer repeats what it has seen a model do. Typically, the copier is then rewarded for whatever behavior it has copied. In the psychological literature, the rewards associated with copying can be extrinsic (the food items in the above case) or intrinsic (related to animal emotions and feelings). Copying differs from imitation in that what is copied need not be novel and need not involve learning some new topographical action—an individual can copy the action of another, even if it already knows how to do what the model is doing, and even if it does not involve learning some new spatial orientation to do what the model does. As a case in point, animals will select a mate in the absence of the opportunity to copy the mate choice of others, but, when the opportunity to copy others arises, they may opt to mate-choice copy.

Some evidence of copying comes from my own work on mate-choice copying, during which a female copies the choice of those around her. I examined female mate-choice copying in guppies (*Poecilia reticulata*) using a ten-gallon aquarium situated between two separate end chambers constructed of clear Plexiglas (Dugatkin, 1992b). A single male was put into each of these end chambers. The observer female—the individual that potentially copies the behavior of other females—was placed in a clear canister in the middle of the central aquarium. At the start of a trial, one male was put into each end chamber (Figure 6.19). Removable glass partitions created left or right sections of the aquarium into which another female—the model female—was placed. To rule out the possibility that one male may have been more attractive than the other and that the model and the observer independently each chose that male, the placement of the model—either near the male in the left end chamber or near the male in the right end chamber—was determined by the flip of a coin.

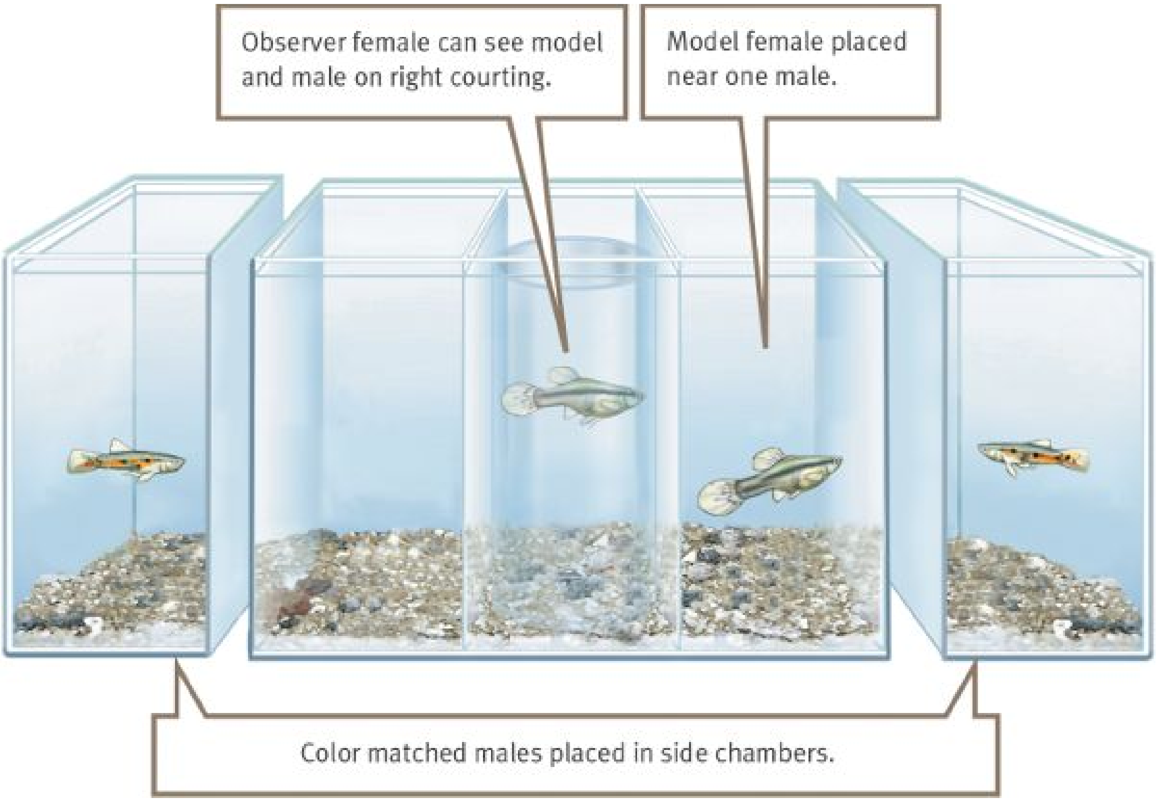


Figure 6.19. Mate-choice copying. The experimental apparatus used in the guppy mate-choice copying experiments. Whether the model is placed near the male on the left or on the right was determined randomly.

Once the model, the observer, and the two males were in place, fish were given ten minutes during which the observer female could watch the model female near one of the two males. The model female and the glass partitions were then removed, and the observer female was released from her canister and given ten minutes to swim freely and choose whichever male she preferred. In these trials, the observer female chose the male that had been chosen by the model female seventeen out of twenty times.

While the results of this experiment are consistent with the hypothesis that females copy the mate choice of others, there are several alternative explanations. Guppies live in social groups (schools of fish), and so it is possible that the observer female was simply choosing the area that had recently contained the largest number of fish (in this case, two). A control treatment was conducted to test this schooling hypothesis. It was identical to the above protocol, except that females were placed in the end chambers. In this case, the observer female chose the female in the end chamber closest to the model in only ten out of twenty trials. The tendency to school (stay near two fish rather than one fish) per se does not explain the results of the first experiment; if it had, observer females would have consistently chosen the end chamber closest to where the model had been placed. Results from other control experiments were also consistent with mate-choice copying. Using a protocol similar to that of the guppy experiments, mate-choice copying has also been observed in a number of different species of fish, as well as in some birds and mammals (see chapter 7).

Copying also plays a role in the fear response of mice to stable flies (*Stomoxys calcitrans*; Kavaliers et al., 1999, 2001). Normally, mice that have been exposed to stable flies do not show any immediate behavioral response to the presence of a stable fly. After an individual has been bitten by a stable fly, one of its defensive responses is to bury itself under whatever debris it can find (Figure 6.20). When a naive mouse observes another mouse being bitten by a fly and then burying itself, the observer quickly buries itself when it is *exposed* to a fly for the first time—it copies the defensive action of the model.

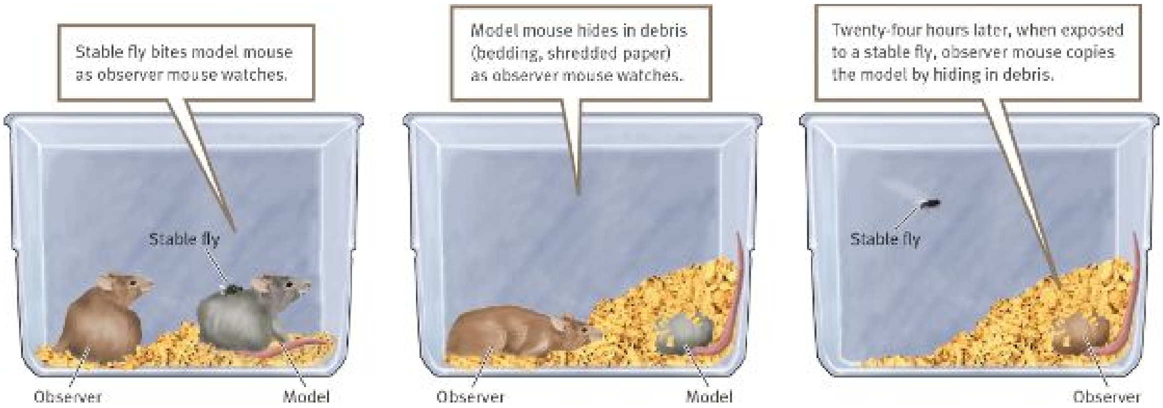


Figure 6.20. Copying a defensive response. After a mouse is bitten by a stable fly, one of its defensive responses is to bury itself under debris. A mouse that observes a conspecific being bitten by a stable fly and then hiding will copy the hiding behavior of the model as soon as it is exposed to a fly.

To better understand the underlying molecular genetics of copying and the fear response in mice, Martin Kavaliers and his colleagues focused on the NMDA receptor, a receptor which plays an important role in neural plasticity (Kavaliers et al., 2001). When Kavaliers and his colleagues blocked the NMDA receptor of an observer mouse, using an NMDA antagonist chemical, they found that the observer did not learn to bury itself as soon as it was exposed to a fly; the NMDA antagonist blocked copying in these mice. A similar experiment with rats that could copy a model’s foraging behavior also found that blocking the NMDA receptor impeded copying (M. Roberts and Shapiro, 2002).

THE RISE AND FALL OF A TRADITION

If a new behavior emerges, and then becomes common within a group as a result of social learning, it is referred to as a **tradition** (Thornton and Clutton-Brock, 2011). In 2009, Alex Thornton and Aurore Malapert ran one of the first controlled experiments on traditions in wild populations, using nine groups of meerkats (*Suricata suricatta*) in the South African Kalahari (Figure 6.21A; Thornton and Malapert, 2009b; see Thornton and Malapert, 2009a and Thornton et al., 2010).

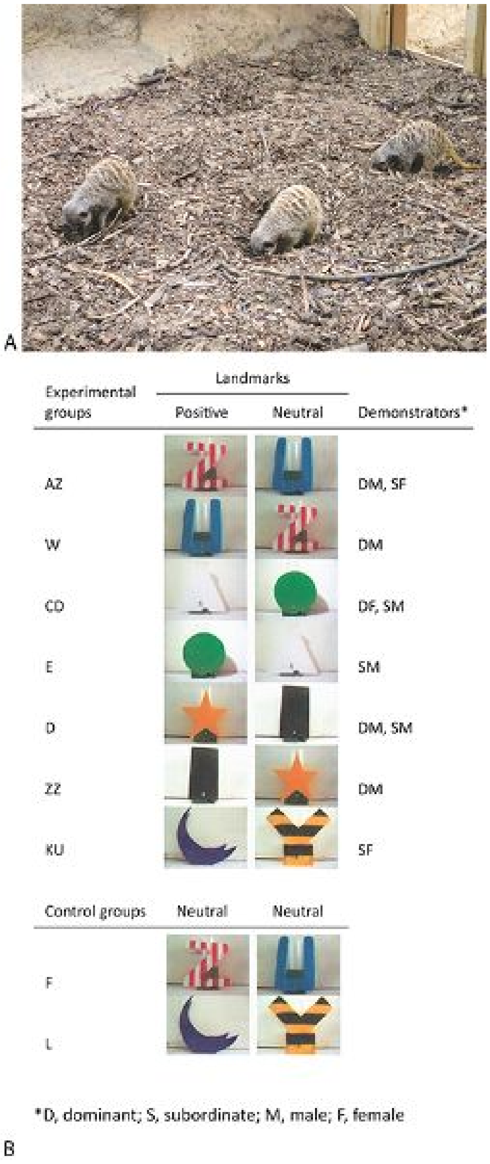


Figure 6.21. Meerkat traditions come and go. (A) Meerkats foraging in a group. (B) The set of visual cues used to create landmarks. Such arbitrary landmarks became attractive to meerkat group members if they observed others feeding there. “Positive” means a trained model preferred the area near this landmark. “Neutral” means no model was associated with this landmark. *(Photo credit: A, Meerkats foraging by Burtonpe, licensed under CC BY-SA 3.0; B, Thornton and Malapert, 2009b, p. 1660, by permission of the Royal Society. © 2009.)*

To experimentally examine traditions, Thornton and Malapert created two arbitrary landmarks in the area of each group of meerkats. These landmarks were plastic geometric objects that differed in color and pattern. Both landmarks were placed near a reliable new water or food source for the meerkats. In seven of the nine meerkat groups, a demonstrator individual was trained by the researchers to show a preference for *one* of the landmarks (Figure 6.21B). Which landmark an individual was trained to prefer in a specific group was determined randomly. In two groups, no demonstrators were trained.

What Thornton and Malapert found was the rise, and subsequent fall, of a tradition. Initially, after seeing a demonstrator at the landmark to which the demonstrator had been trained, meerkats in a group preferred that landmark. A completely arbitrary tradition—both landmarks were equally profitable, but one was preferred by other group members—emerged in the seven non-control groups (the choice of sleeping burrows is another traditions in meerkats; Thorton et al. 2010). This preference for a particular landmark lasted a few days, but then slowly disappeared. What happened was that meerkats initially preferred the landmark visited by the demonstrator, but over time they began to explore the other landmark. Once they learned *themselves* that this other landmark was just as good as the one they had been frequenting, they spent time at both landmarks, eroding the tradition. Social learning produced a tradition, but individual learning led to its demise.

Some traditions in animals do not fade. Lucy Aplin and her team work “seeded” great tits populations with individuals that had been trained to solve a complex foraging task in a specific way, and then examined the diffusion of information in these populations (Aplin et al., 2015a,b). The foraging task involved sliding open a door to access food (mealworms) behind it. A puzzle box was built so food could be accessed by a bird by either sliding the blue colored door on the box from the left to the right or by sliding the red colored door from the right to the left (Figure 6.22). Each time a bird arrived at a puzzle box, an automated system recorded the visit and then reset the puzzle box to be solved by the next bird.

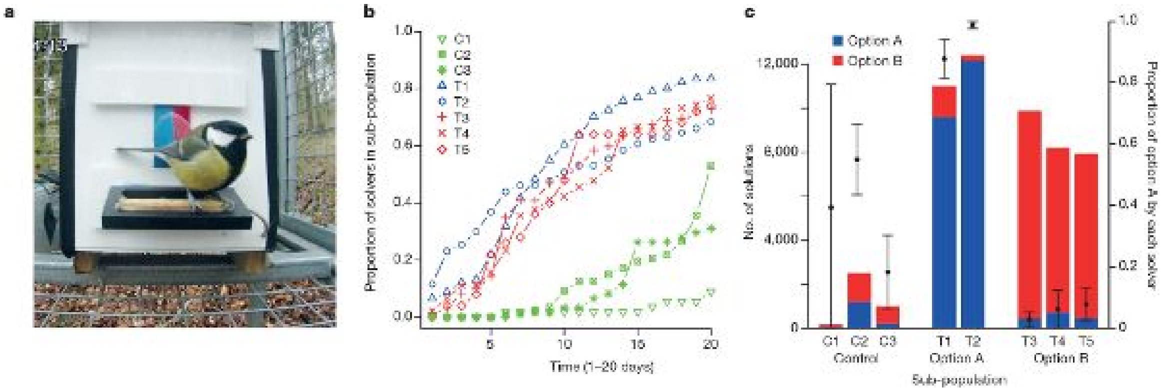


Figure 6.22. **Puzzle boxes.** The puzzle box used to train great tits to either slide a door to the left or right to access food. Reprinted by permission from Macmillan Publishers Ltd. © 2015. *(From Aplin, Farine, et al., 2015)*

The researchers captured two male birds from each of eight different populations. The birds from three of these populations served as controls—they were not trained how to solve the puzzle box and access the mealworms within. Demonstrator birds from the other five populations were trained *either* to open the door by sliding it to the right, or to open the door by sliding it to the left. All demonstrator birds were then returned to their home populations, and Aplin and her colleagues examined whether the door-opening tradition (slide to the right or the left) spread through populations and, if so, whether the tradition persisted.

Information flowed quickly once demonstrator birds were released: within three weeks after the ten trained birds (two birds per five populations, not including the controls) were reintroduced to their home populations, more than 400 birds were solving the puzzle box using the technique introduced by the two demonstrators in their population (Figure 6.23A). A within-population analysis of social interactions using a technique called social network analysis found that birds that associated with demonstrators were more likely to solve the puzzle box task than others, and they most often solved it using the technique employed by their demonstrators. Unlike the meerkat example we discussed above, even after some birds eventually figured out how, via individual learning, to access food using the door-sliding technique not used by demonstrators from their population, they continued to prefer the option they learned from a demonstrator.

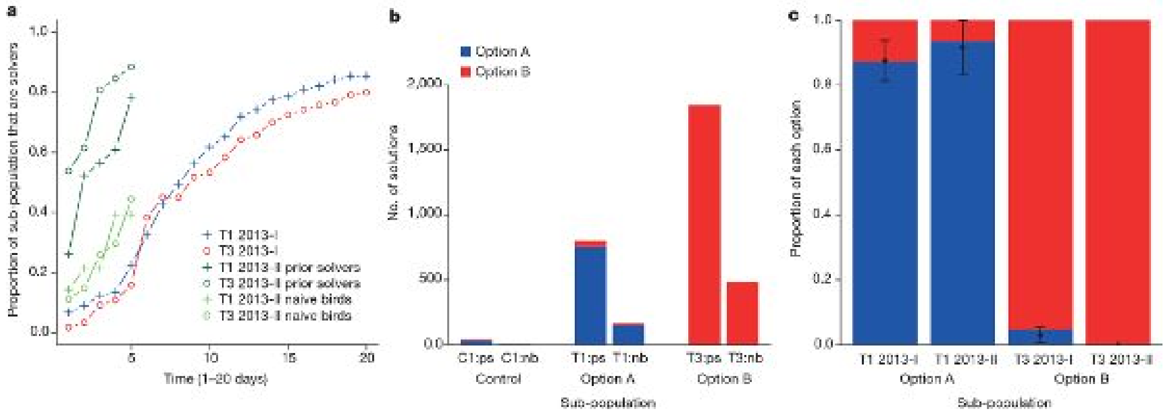


Figure 6.23. **The birth and maintenance of a tradition.** (A) Great tits in a control population showed no preference for sliding to the right or left, and they solved the puzzle box much less often than birds from populations where a demonstrator opened the door either from the left *or* from the right. When demonstrators opened the box by sliding a blue door to the right, birds in their population most often used this solution. Similarly when demonstrators opened the box by sliding a red door to the left, birds in their population did this as well. (B) After the puzzle box feeders had been removed for 9 months and returned a second time, birds in each population still employed the door-opening technique introduced by former demonstrators. I = data from a population at time 1, II = data from the same population nine months later. Reprinted by permission from Macmillan Publishers Ltd. © 2015. *(From Aplin, Farine, et al., 2015)*

This tradition continued for at least two generations. Aplin found that after she and her team had removed the puzzle box feeders for 9 months and then put the feeders back, birds in each population still employed the door-opening technique introduced by former demonstrators, despite significant population turnover (Figure 6.23B; Box 6.3).

Box 6.3. SCIENCE AT WORK

What is the research question? Can researchers introduce new traditions into animal populations? If so, do the traditions persist?

Why is this an important question? Experimental manipulation of culturally transmitted behavior in natural populations opens the door to future work that focuses on causality.

What approach was taken to address the research question? Two different foraging-related traditions were introduced into a series of great tit populations to study whether traditions established themselves via social learning, and then persisted.

What was discovered? Birds copied the new behavior introduced into their population, and the behavior spread quickly. New traditions persisted across generations, and did so despite much population turnover.

What do the results mean? Animal behaviorists now have a powerful new approach to examining cultural transmission in wild populations.

TEACHING IN ANIMALS

The idea that animals teach one another is one of the more contentious in the literature on animal cultural transmission (Caro and Hauser, 1992; Franks and Richardson, 2006; Leadbeater et al., 2006; Thornton and McAuliffe, 2006; Kline 2015a,b; Skerry et al., 2013). While there are many definitions of **teaching**, most have one individual serving as an instructor or teacher, and at least one other individual acting as a student who learns from the teacher (Caro and Hauser, 1992; Ewer, 1969; Fogarty et al., 2011; Fragasy and Perry, 2003; Galef et al., 2005; Maestripieri, 1995).

In an early review on teaching in animals, Tim Caro and Marc Hauser suggested that for a behavior to be labeled as “teaching,” a teacher must provide an immediate benefit to students but not to him- or herself, “students” must be a naive to what is being taught, and a teacher must impart some new information to students faster than they would otherwise receive it. This definition is interesting, not only because of the emphasis on what must take place for teaching to occur, but also for what kinds of behaviors are excluded from the realm of teaching. For example, in the case of the blue tits opening the foil caps of milk bottles in Britain in the 1940s, imitation rather than teaching was taking place. While blue tits learned how to open foil caps by observing others, those that opened the caps did so regardless of who watched them. According to Caro and Hauser's definition, they weren't teaching other birds anything since they opened the milk bottles in the same way even if they were alone and thus they weren't modifying their behavior only in the presence of naive observers. They were obtaining immediate benefits for themselves in that they obtained the milk after they opened the bottles.

What sort of examples might fall under the Caro and Hauser definition of *teaching*? Consider a female cat that captures live prey and allows its young to interact with this prey, making sure that the prey doesn't escape along the way. If mother cats engage in this behavior only when in the presence of young cats, then teaching may be occuring. Anecdotal examples of this kind of teaching have been documented in domestic cats (Baerends-van Roon and Baerends, 1979; Caro, 1980; Ewer, 1969), lions (Schenkel, 1966), tigers (Schaller, 1967), and otters (Liers, 1951). Teaching has been examined in more detail in both cheetahs (Caro, 1994a) and meerkats (Thornton and McAuliffe, 2006). Consider Caro's description of three ways that mother cheetahs used "maternal encouragement" to facilitate hunting skills in their offspring (Figure 6.24):

> Firstly, they pursued and knocked down the quarry but instead of suffocating the victim allowed it to stand and run off. By the time the prey had risen, the cubs had normally arrived. Second, mothers carried live animals back to their cubs before releasing them, repeatedly calling (churring) to their cubs. Third, and less often, mothers ran slowly during their initial chase of a prey and allowed their cubs to overtake them and thus be the first to knock down the prey themselves. (Caro, 1994a, pp. 136–137)

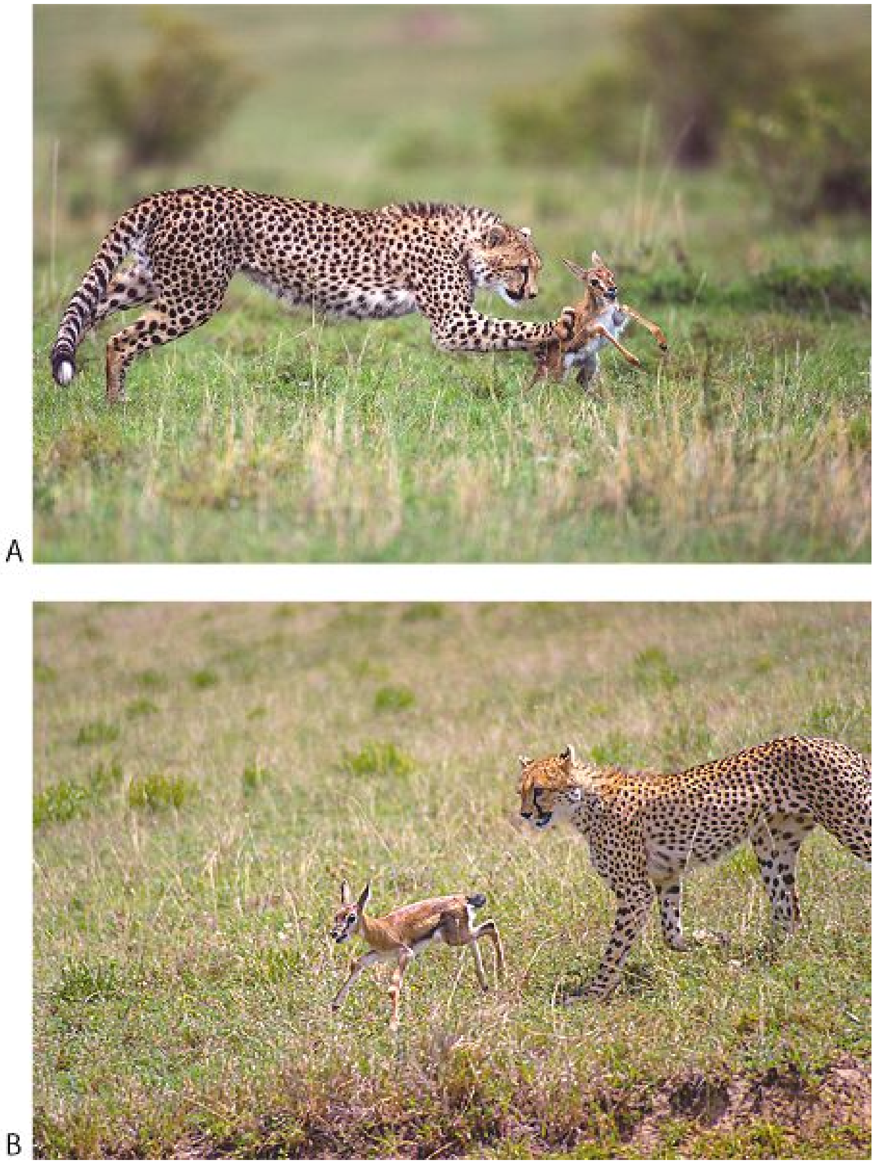


Figure 6.24. Cheetah teaching? (A+B) When a mother cheetah hunts, she sometimes allows her cubs to interact with the prey in a way that facilitates teaching. *(Photo credits: Anup Shah/Minden Pictures; Alex Thornton)*

While this sort of behavior is consistent with teaching, it is not sufficient to demonstrate teaching, as it is unclear whether young cheetahs accelerated their hunting skills as a result of these interactions with their mother or for other reasons (Caro and Hauser, 1992; Galef et al., 2005; Thornton and Clutton-Brock, 2011).

Teaching has been documented in meerkats, where young pups are incapable of catching their own prey. At about a month old, pups begin following groups of foragers, and are assisted in their own foraging attempts by older “helpers” (Figure 6.25). Many of the prey that meerkats eat are difficult to catch and, in the case of scorpions, are also dangerous. Helpers will often incapacitate scorpions by removing their stingers and present them to pups as food. Thornton and McAuliffe observed that very young pups were fed either dead or incapacitated scorpions, but as the pups got older, the helpers presented them more and more often with live scorpions (Thornton and McAuliffe, 2006).

Figure 6.25. Meerkat foraging and teaching. Older groupmates assist younger pups in their foraging attempts and also teach the younger pups to catch prey such as scorpions, as shown here. *(Photo credit: Alex Thornton)*

To experimentally examine whether helpers were teaching pups how to forage on dangerous prey, the researchers took advantage of the fact that helpers respond to the begging calls of pups even when pups cannot be seen, and that such begging calls change in predictable ways as pups age. When Thornton and McAuliffe had a group of young pups, but played the calls of older pups, helpers were more likely to bring live prey over to the pups. When the group contained older pups, but the researchers broadcast the begging calls of younger pups, helpers were more likely to bring over dead or incapacitated scorpions: helpers were changing what type of prey they delivered in a manner that would help and might even teach the pups.

Thornton and McAuliffe found additional evidence for teaching by helpers in that helpers: (1) spent much time monitoring pups after presenting them with food; (2) retrieved prey when pups lost their food; (3) on occasion, further modified a scorpion (removing the stinger, killing the scorpion, and so on) after it was lost but later retrieved by the pups; and (4) nudged pups that were reluctant to eat scorpions, increasing the probability that the pups would eat the scorpion that they had initially rejected. Together, the evidence suggests teaching in that helpers modified their behavior in costly ways—spending time that they could have used to forage for themselves but instead spent with pups—and such modifications helped pups learn how to forage on dangerous prey.

Common Themes in Examples of Animal Teaching

Caro and Hauser, as well as subsequent researchers, found two common themes in nonhuman teaching. First, almost all instances of animal teaching focus on the parent/offspring relationship. This may strike you as intuitive, but remember that in many animal societies, young can learn from others besides their parents. In principle, adult animals could presumably teach other adults, but there is little, if any, evidence that they do. These common themes certainly suggest something special about the costs and benefits of teaching in the parent/teacher, offspring/student relationship. The benefits associated with the genetic kinship that bonds teacher and student—that is, parent and offspring or perhaps between siblings—may be some of the only benefits large enough to make up for the costs of teaching (Caro and Hauser, 1992; Galef et al., 2005).

Box 6.4. COGNITIVE CONNECTION

Parents Teaching Embryos?

Animal behaviorists hypothesize that teaching will be most common in parent-offspring interactions. A fascinating set of studies has been done in fairy wrens (*Malurus cyaneus*), where mothers may teach their *neonate* offspring a "vocal password" associated with feeding (Colombelli-Négrel et al., 2012; Kleindorfer et al., 2014).

Fairy wren females have their nests parasitized by Horsfield's bronze cuckoos (*Chalcites basalis*), who lay their eggs in wrens' nests. Colombelli-Négrel hypothesized that to minimize the amount of food given to brood parasites rather than their own young, fairy wren mothers emit a vocal password that their embryonic young can learn while in the egg, and can then emit when they are chicks, thereby accessing food that cuckoo chicks in the nest cannot. The researchers found a significant correlation between the use of the correct vocal password by young fairy wrens and maternal feeding rate. More importantly with respect to teaching, the more often the female emitted the password when young fairy wrens were in the egg stage, the more accurate the call by fairy wren chicks after they hatched. In addition, a cross-fostering experiment using only fairy wrens found that young tend to produce the call of the females in the nest in which they are raised, suggesting that the call is not innate, but learned.

The key to the vocal password system in fairy wrens appears to be the amount of time that embryos in eggs are exposed to the maternal password. Mothers start to emit the password at about day 10 of incubation. Embryos in cuckoo eggs exposed to vocal passwords hatch at about day 12, and then do a relatively poor job of mimicking the password they heard while in the egg stage, while fairy wren chicks hatch at day 15 and are thus hearing, and learning about, the call for an additional 3 days (Colombelli-Négrel et al., 2012; Figure 6.26).

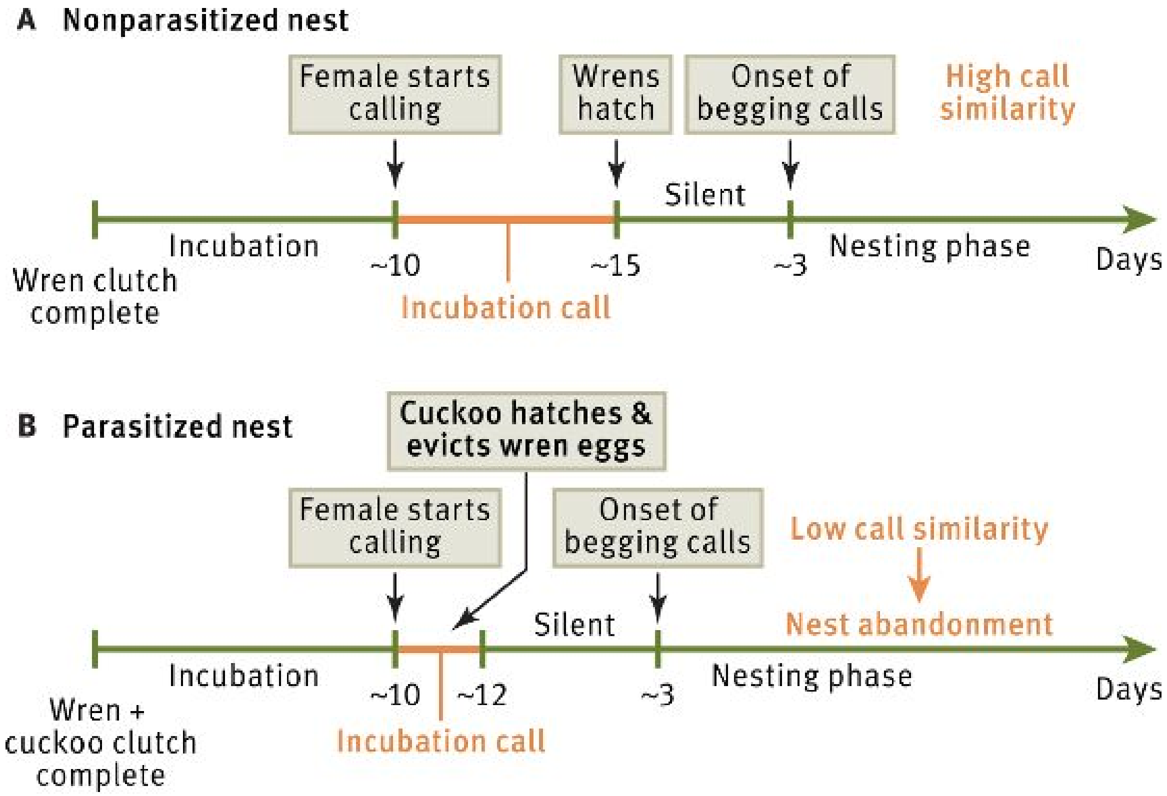


Figure 6.26. **Vocal passwords in superb fairy wrens.** Schematics of incubation and post incubation periods and how they are linked to vocal passwords. Reprinted with permission from Elsevier. *(From Colombelli-Négrel et al., 2012)*

If it allows them the ability to distinguish between their own young and brood parasites, why don't fairy wren females *always* teach their offspring the vocal password? Sandra Kleindorfer and her colleagues examined this question by testing whether there was a cost associated with females teaching their offspring a vocal password. They focused on whether vocal passwords attracted potential predators to a nest. They found that in natural nests, nest predation was higher when females produced more incubation calls/hour. When they experimentally manipulated call rate, using taped calls broadcast over speakers, they also found strong evidence for a cost to emitting vocal passwords. Nests with high incubation call rates (30 calls per hour) suffered eight times as much predation as nests with no incubation calls. Even nests that had relatively low call rates (15 calls per hour) suffered predation rates five times higher than nests with no calls (Kleindorfer et al., 2014; Figure 6.27).

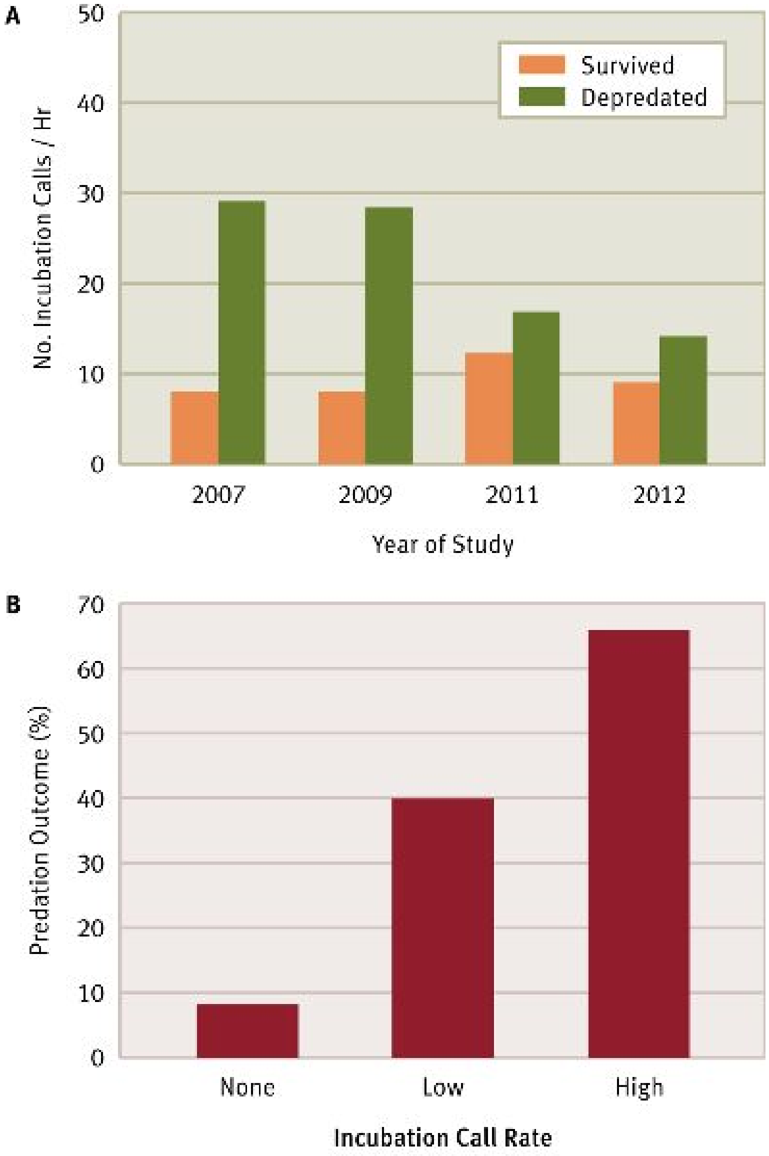


Figure 6.27. **The cost of teaching.** In both natural nests (A), and in nests that were part of an experiment in which superb fairy wren calls were simulated and broadcast (B), a high cost for incubation calls was uncovered. By permission of Oxford University Press. *(From Kleindorfer et al., 2014)*

Second, cases of teaching tend to fall into one of two categories: “opportunity teaching” and “coaching.” In opportunity teaching, teachers actively place students where they can learn a new skill. In contrast, coaching involves a teacher who directly alters the behavior of students by encouragement or punishment. The majority of examples of animal teaching fall under opportunity teaching, presumably because this type of teaching is the simpler of the two. The meerkat example, however, shows nicely how both forms of teaching can be in play in the same system. Meerkats use opportunity teaching by manipulating prey for young pups, while at the same time coaching pups by nudging them and thereby encouraging them to try new, potentially dangerous, food items.

Modes of Cultural Transmission

With a better understanding of what constitutes teaching and social learning, we are now ready to examine three different modes of cultural transmission: vertical, oblique, and horizontal transmission (Cavalli-Sforza and Feldman, 1981).

VERTICAL CULTURAL TRANSMISSION

Vertical cultural transmission occurs when information is transmitted across generations from parent(s) to offspring. This type of cultural transmission might take place through either teaching or social learning—offspring might learn from their parents by observation, or parents might teach a behavior to their offspring. For example, in some finch species, vertical transmission occurs when males learn the song that they will sing from their fathers, as well as when females develop song preferences in potential mates based on the songs their father sang (B. R. Grant and Grant, 1996; Figure 6.28).

Figure 6.28. Cultural transmission in finches. Birdsong in some species of finches is learned culturally. *(Photo credit: Christopher Plummer, Switzerland)*

Researchers have studied vertical transmission of foraging skills in bottlenose dolphins (*Tursiops truncatus*), who display a complex and rich assortment of foraging strategies (Kuczaj et al., 1998; Patterson and Mann, 2011; Sargeant and Mann, 2009; Xitco and Roitblat, 1996). One foraging strategy called “beaching” or “beach hunting” involves a dolphin surging out of the water and onto a beach to catch a single fish, and then quickly returning to the water with its prey (Mann and Sargeant, 2003). This form of beaching of individual fish is a fairly rare behavior—in a long-term study of one bottlenose dolphin population in

Shark Bay, Australia, only four adult females and their calves were observed beaching with any consistency (Sargeant et al., 2005). Another form of beaching among other dolphins, however, has been observed in salt marshes in the southeastern United States, where one to six dolphins isolate a school of fish and herd the fish toward land, creating a wave to send them onto the land and then surging out of the water to capture the stranded fish (Hoese, 1971; Figure 6.29). Although beaching can be profitable when successful, it can also be quite dangerous, as beaching dolphins may get stranded.

Figure 6.29. Beaching behavior. Bottlenose dolphins may trap fish by stranding them on a beach and then surging out of the water to catch them. The dolphins then quickly return to the water with their prey. *(Photo credit: Neil Lucas/Nature Picture Library)*

Janet Mann and her colleagues found that only calves born to mothers that themselves were “beachers” displayed this specialized foraging strategy. Evidence suggests that young calves *learn* beaching from their mothers, likely because the young calves spend a great deal of time with their mothers and learn this dangerous foraging tactic via vertical cultural transmission (Krutzen et al., 2005).

Another case of vertical transmission of foraging strategies involves tool use in the bottlenose dolphins of Shark Bay (Krutzen et al., 2005). Here the foraging behavior, called “sponging,” involves female bottlenose dolphins breaking a marine sponge off the seafloor and placing it over their mouth, and then using this tool to probe the seafloor for fish prey (Smolker et al., 1997; Figure 6.30). This foraging behavior appears to open a novel foraging niche to spongers (Krutzen et al., 2014). Sponging is seen almost exclusively in females, spongers prefer to associate with others who use this behavior, and young females learn sponging primarily from their mothers (Mann et al., 2012).

Figure 6.30. Sponging behavior in dolphins. Female bottlenose dolphins break a marine sponge off the seafloor and place it over their mouth. This sponge tool is used to probe the seafloor for fish prey and to protect them from scrapes and stings as they forage. *(Photo credit: © Janet Mann/Shark Bay Dolphin Research Project)*

OBLIQUE CULTURAL TRANSMISSION

Oblique cultural transmission refers to the transfer of information across generations, but not via parent/offspring interactions: young animals get information from adults that are not their parents. This sort of transmission might be particularly common in systems where there is no parental care, and hence where most interactions between younger and older individuals would be between nonrelatives.

Oblique transmission in nonhumans occurs in the learned snake aversion seen in rhesus monkeys. Early work comparing wild- and laboratory-raised primates found that the lab-raised animals that had never seen a snake before did not respond to snakes in the same manner as wild-raised individuals that had the chance to experience snakes in nature (K. R. Hall and Devore, 1965; Seyfarth et al., 1980; Struhsaker, 1967). Susan Mineka and her colleagues designed an experiment to test whether oblique cultural transmission played a role in the development of the fear of snakes (Cook et al., 1985; Mineka and Cook, 1988; Mineka et al., 1984).

They began with juvenile rhesus monkeys that were not afraid of snakes. Shortly after observing an adult model respond to snakes with typical fear gestures and actions (Figure 6.31), juveniles themselves adopted these same gestures (for at least three months). It made no difference whether the individuals observed were the subjects' parents (vertical transmission) or unrelated adult monkeys (oblique transmission)—exposure to adult models showing fear in the presence of snakes led to observers showing similar fear responses. Mineka and colleagues also found that when observers saw a model that had been trained to display fear in the presence of a neutral object—a flower—the observers did not display fear when they were exposed to flowers, suggesting that a predisposition to fear snakes is interacting with oblique cultural transmission (Cook and Mineka, 1989). In addition, monkeys that had first seen an adult model interact with a snake in a nonfearful manner, but then saw a second model respond with fear to snakes, displayed less fear than individuals exposed only to a model that had displayed fear. These monkeys were culturally "immunized" against associating snakes and fear (Mineka and Cook, 1986).

Figure 6.31. Monkeys and fear of snakes. Rhesus monkeys in the field often fear snakes after watching others respond to such potential danger. Monkeys that do not normally fear snakes can be induced to fear them through observing older monkeys reacting fearfully to snakes in the lab. Young monkeys were shown a video of an older monkey that fled to the back of the cage and cringed in fear at the sight of two snakes. *(Photo credit: Sue Mineka)*

HORIZONTAL CULTURAL TRANSMISSION

Horizontal cultural transmission involves transmission between peers—same-aged individuals—and occurs not only in adults but young individuals as well. Consider the case of horizontal transmission of foraging-related information in guppies. Laland and Williams trained same-aged guppies to learn different paths to a food source—a long path and a short path (it was more difficult to train fish to take the longer path when both paths were present, but the researchers found a clever way to do so) (Laland and Williams, 1998).

Once the “long-path” and “short-path” groups were trained, Laland and Williams sequentially removed the original members of each group and replaced them with new “naive” individuals that didn’t know either of the paths to the food source. Initially, groups contained five trained guppies, then four trained individuals and one untrained, and so on, until none of the original trained group members remained. The question then was this: do the fish remaining at the end of the experiment—none of which were trained to a particular path—use the path taken by the original group members?

Laland and Williams found that in both the short-path and long-path groups, guppies at the end of the experiment still followed the path to which the original fish had been trained. Horizontal transmission of information was operating, as the only models from which to learn were same-age individuals. What makes this experiment particularly interesting is that it demonstrates that cultural transmission can produce "maladaptive" (long-path use) as well as adaptive (short-path use) behavior. In fact, horizontal transmission in the long-path groups not only resulted in guppies acquiring the "wrong" information, it actually made it more difficult for the fish in that treatment to subsequently learn to use the shorter path (C. Brown and Laland, 2002; Reader et al., 2003).

The Interaction of Genetic and Cultural Transmission

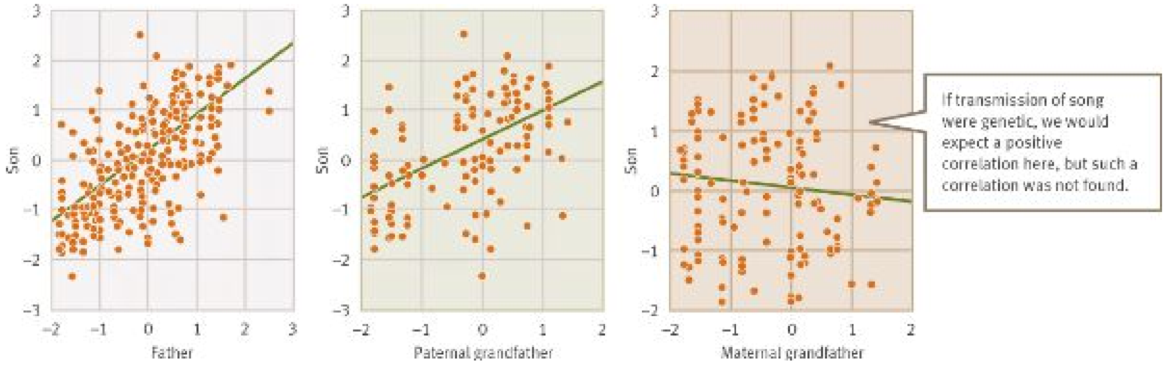
Because cultural and genetic transmission both operate on animal behavior, in principle it is possible to study cases in which they operate concurrently in the same system. To better understand how such interactions work, let's consider two different case studies that examine the interaction of genes and culture in two animal systems: birds and fish.

FINCH SONG

Peter and Rosemary Grant have been studying finches in the Galápagos Islands for more than three decades. Among the many problems they have tackled is the role of cultural transmission in the evolution of finch song. In Galápagos finches, cultural transmission not only shapes birdsong but it interacts in an unexpected manner with the genetics of reproductive isolation and speciation in these birds (P. R. Grant and Grant, 1994, 1997).

The medium ground finch (*Geospiza fortis*) and the cactus finch (*G. scandens*) both live on the Galápagos island of Daphne Major. Although these are classified as different species, some cases of interbreeding between these two finch species have been uncovered, and the hybrids do not appear to suffer a decrease in reproductive success as compared to the matings within species. Yet although there seems to be no cost per se for hybridization, medium ground finches and cactus finches rarely interbreed. Why? Does cultural transmission play a role in inhibiting such interbreeding (Freeberg, 2004; Lachlan and Servedio, 2004; D. A. Nelson et al., 2001; Slabbekoorn and Smith, 2002)?

In finches, males learn the songs they sing. When the Grants studied the songs sung by ground and cactus finches during the mating season, they found that these songs were transmitted across generations via cultural transmission (B. R. Grant and Grant, 1996). Fathers and sons have very similar songs, but this could be due to genetic transmission from father to son, or it could be due to the cultural transmission of the song from father to son. If songs are genetically controlled, then the songs of sons and their paternal and maternal grandfathers should be similar, since they inherit genes from both grandfathers. But if the songs are culturally transmitted from father to son, then the songs of the sons should resemble only those of their paternal grandfather, but not those of their maternal grandfather. This is because the paternal grandfather would have transmitted the song to the father, who would then have transmitted the song to the son. The evidence suggests that the songs of sons resemble the songs of their paternal grandfathers, but not the songs of their maternal grandfathers (Figure 6.32). Birdsong in these finches appears to be culturally transmitted.



If transmission of song were genetic, we would expect a positive correlation here, but such a correlation was not found.

Figure 6.32. Finch songs across generations. Components of male finch song are positively correlated with those of their father and their paternal grandfather, but not their maternal grandfather. This is consistent with cultural transmission of male song. *(From B. R. Grant and Grant, 1996)*

The Grants also found that the songs of ground and cactus finches were different from one another. For example, the song of the cactus finch has shorter components that are repeated more often than the components of the song of the ground finch. These differences in their songs—a culturally transmitted trait—have a dramatic impact on gene flow across species. Of 482 females sampled, the vast majority (over 95 percent) mated with males who sang the song appropriate to their own species, that is, cultural transmission of song allows females to recognize individuals of their own species. In addition, females tend to avoid males who sing songs that are similar to the songs that their own fathers sang, which suggests that song also plays a role in preventing inbreeding. Because song is culturally transmitted from father to son, females may decrease the probability of mating with genetic relatives when they avoid mating with males that sing like their fathers.

In their long-term study, the Grants uncovered eleven cases in which the male of one species sang the song of another species. In most of these cases, cross-species breeding would then occur, resulting in hybrid offspring; remove the normal pattern of cultural transmission and the barrier to breeding across species disappears, suggesting a new and exciting avenue of research in the interaction of cultural transmission and genetics.

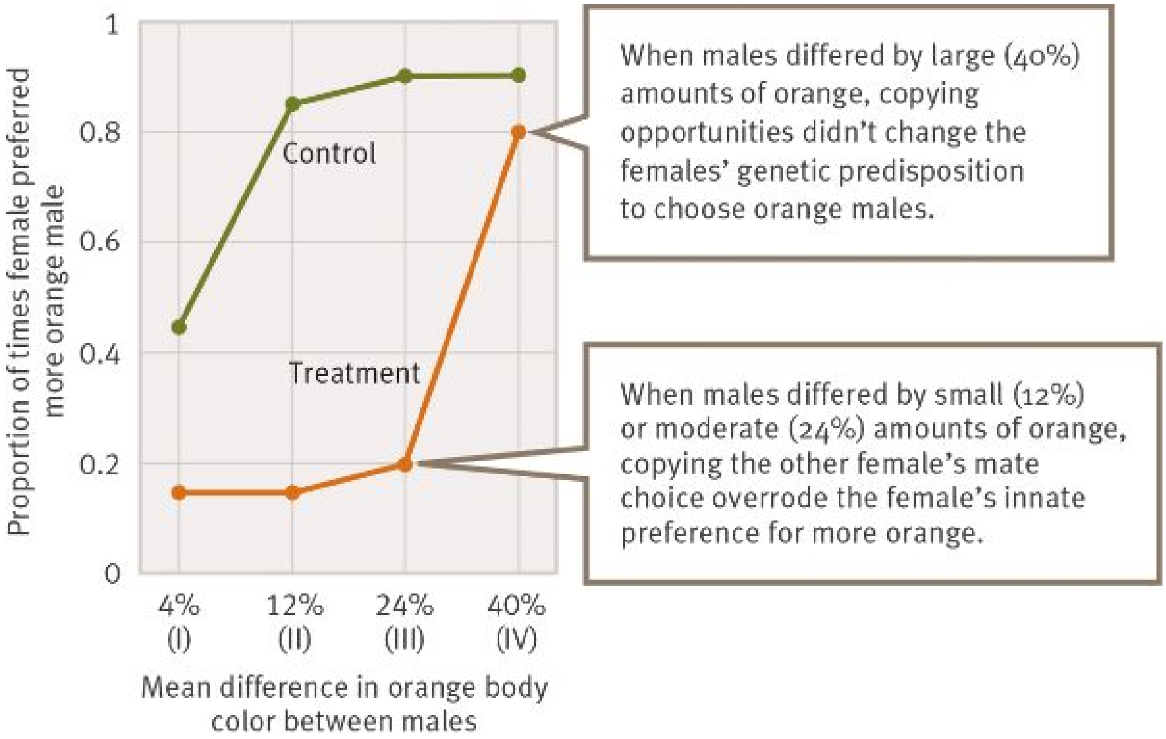
GUPPY MATE CHOICE

As we discussed earlier in the chapter, female guppies copy the mate choice of other females. Observer females that viewed a model female choose one male over another were much more likely to choose that male themselves. In addition to this type of cultural transmission of information, genetic transmission of traits also plays an important role in guppy mate-choice (Houde, 1997; Magurran, 2005).

Guppies from the Paria River in Trinidad and Tobago prefer to mate with orange-colored males. Interpopulational comparisons suggest that this preference of Paria River females for males with more orange body color is heritable (Houde, 1988; Houde and Endler, 1990). In addition, orange body color itself is a heritable trait in Paria River males (Houde, 1992, 1994).

To examine how genetic and cultural transmission interact in shaping mate choice in females from the Paria River, I set up an experiment with four different treatments (Dugatkin, 1996b). In each treatment, a female was exposed to a pair of males. In treatment I, males were matched for orange body color (the mean difference in orange color between the males was less than 4 percent). In treatments II, III, and IV, males differed in total orange body color by an average of 12 percent (II), 24 percent (III), and 40 percent (IV). In each treatment, the experiment was designed such that observer females always saw a model female near the male with less orange body color. That is, the information being culturally transmitted to models was always in direct opposition to a female's genetic predisposition to choose males with more orange body color as mates.

Results of the experiment suggest that females in treatment I—in which males were matched for orange body color—copied each other's mate choice. When males differed in orange body color by an average of 12 or 24 percent (treatments II and III, respectively), females consistently preferred the less orange of the two males, again copying the mate choice of the model female; in these treatments, culturally transmitted information overrode a female's genetic predisposition to mate with males with lots of orange body color. But when male orange body color differed by an average of 40 percent (treatment IV), females consistently preferred the more orange of the two males, thus overriding any effects of mate-choice copying (Figure 6.33).



When males differed by large (40%) amounts of orange, copying opportunities didn't change the females' genetic predisposition to choose orange males.

When males differed by small (12%) or moderate (24%) amounts of orange, copying the other female's mate choice overrode the female's innate preference for more orange.

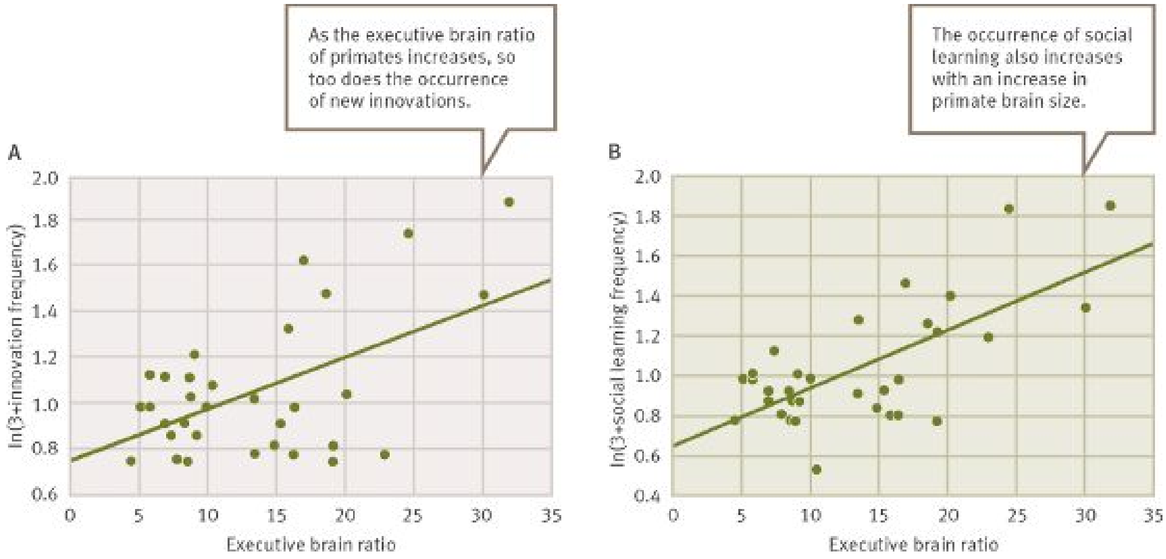
Figure 6.33. Mate-choice copying in guppies. In the control trials, a female chose between males that differed in orange body color and no model female was present. In these trials, females showed a strong preference for more orange males. In the treatment trials, a model female was always placed near the less orange male. *(Based on Dugatkin, 1996b)*

In the guppy system, it appears that whether or not females copy a model's mate choice is affected by a threshold difference in the amount of orange body color in the male. If the male's orange body color is beneath this threshold, the effects of copying are predominant. But if the orange body color is above this threshold, genetic preferences mask any cultural effects.

Cultural Transmission and Brain Size

Many ethologists have suggested that in a population of large-brained animals, new innovations—the discovery of novel solutions to problems—might arise and spread more often than would happen in a population of small-brained animals. In the most comprehensive study to date, Simon Reader and Kevin Laland found that across more than 100 species of nonhuman primates, there was a significant positive correlation between brain size and both innovation and tool-use frequency, confirming the predicted trends (Dunbar, 1992; Reader and Laland, 2002; Sawaguchi and Kudo, 1990).

Reader and Laland defined *innovations* as “novel solutions to environmental or social problems.” They uncovered 533 recorded instances of innovations, 445 observations of social learning, and 607 episodes of tool use that covered 116 of the 203 known species of primates. and mapped out these behaviors against “executive brain” volume, a measure that includes both the neocortex and striatum sections of the brain (Jolicoeur et al., 1984; Keverne et al., 1996). Innovation, social learning, and tool use all had a positive correlation with the absolute value of executive brain volume (Figure 6.34).



As the executive brain ratio of primates increases, so too does the occurrence of new innovations.

The occurrence of social learning also increases with an increase in primate brain size.

Figure 6.34. Effects of increasing brain size in primates. The relationship between the executive brain ratio and (A) innovations and (B) social learning. Both of the relationships shown in the graphs were also found when absolute executive brain size was used. *(From Reader and Laland, 2002)*

A similar trend between large brain size and an increased propensity toward innovation was found for birds in North America, Britain, and Australia (Lefebvre et al., 1997a; Lefebvre et al., 1997; Lefebvre et al., 2004; Sol, Lefebvre et al., 2005). This relationship has interesting implications for questions relating to the conservation and ecology of birds (Overington et al., 2011; Sol, Duncan et al., 2005; Sol, Lefebvre et al., 2005; Sol et al., 2010; Sol et al., 2016). For example, Daniel Sol and his team examined whether the relationship between brain size and innovation affected bird species when they were moved to novel environments through large-scale, human “introduction” programs (where humans introduce a new species to a novel habitat). Using data on more than 600 such introduction programs around the world, Sol and his colleagues found that bird species in which individuals had a high brain size/body ratio were more likely to survive and thrive (that is, to have greater “invasion potential”) after introduction to novel environments than were species with lower brain size/body ratios. In addition, the researchers found that when large-brained species were introduced to novel environments, they increased their rate of innovation—for example, by using a new foraging technique—which in turn increased their probability of success (their “invasion potential”) in their new habitats (Box 6.5).

Box 6.5. SCIENCE AT WORK

What is the research question? Are innovation and tool use more common in large-brained species?

Why is this an important question? While it may seem intuitive that brain size is correlated with complex behaviors such as innovation and tool use, this need not be true: many of our intuitions turn out to be wrong. The only way to know is to do an in-depth analysis.

What approach was taken to address the research question? A literature search of innovation and tool use in more than 100 primate species was used.

What was discovered? The frequency of innovation, tool use, and social learning were positively correlated with executive brain size in primates. Similar results on brain size, innovation, and tool use have been found in comparative studies in birds.

What do the results mean? At least some types of very sophisticated behaviors are positively correlated with brain size. This work has implications for conservation studies in which species are introduced into novel habitats, where innovation and tool use may be particularly important for successful introductions.

Interview with Dr. Cecilia Heyes

Why study cultural transmission in animals? Isn't culture the sort of subject that sociologists examine?

There are many reasons why the study of culture cannot be left solely to sociologists, anthropologists, and other experts on human cultures and societies. Humans are, among other things, animals, so even if culture were a distinctively human phenomenon, it would be essential to understand it at the biological and psychological levels—to find out where it comes from in evolutionary terms, and to identify the proximate biological and psychological processes that make it possible. Comparing human and nonhuman cultures (or, if you prefer, human cultures with animal traditions) helps us to understand what Thomas Huxley, "Darwin's bulldog," called "Man's place in nature" (1863). Each of us is part of at least one human culture, and usually we belong to many. For example, I am soaked in English culture, but I'm also influenced by Western culture, the culture of science, and, as a result of my upbringing, by Roman Catholic culture. Because each of us is embedded in the matrix of one or more human cultures, it can be difficult for us to get an aerial view of what culture really is and how it works. Comparing ourselves with other animals can give us this aerial view. It can reveal the fundamental processes that make culture possible, the ingredients that are and are not needed to make cultural transmission “take off” to become a system of cultural inheritance, analogous to that of genetic inheritance. It might turn out that the full set of ingredients is present only in humans, but on the way to that conclusion we would have learned a great deal, not only about culture but about a type of learning—social learning—that can have a profound influence on behavioral adaptation.

There is a good deal of contention about how to define *culture* in animals. What is your take on this issue?

I think it may be too soon to be using the term *culture* to describe examples of social transmission or traditional behavior in nonhuman animals. The risk is that, if we categorize them as examples of culture too soon, we’ll forget that the critical ingredients of culture have not yet been identified, and then we won’t prioritize the research that would enable us to answer this important question. This kind of maladaptive shortcut is made surprisingly often in the study of animal behavior. For example, field primatologists in the 1980s were so confident that they had seen examples of intentional deception that they claimed quite emphatically that nonhuman apes have “theory of mind”—the capacity to think about the thoughts and feelings of others. As a result, it has been hard in the last twenty years for researchers such as Daniel Povinelli and Michael Tomasello to get the animal behavior community to recognize that more careful research was needed to find out whether animals can really attribute mental states to themselves and others.

So, I’m uneasy about calling socially transmitted behavior “culture.” Having said that, I should also point out that I don’t think the exact content of a definition is terribly important. What’s essential is that a definition should be explicit and reasoned. If it isn’t clearly stated, then there will be cross-talk and confusion. I might say “I believe that fruit bats have culture,” and, if I haven’t said what I mean by culture, you might think I’m claiming that fruit bats go to the opera. When definitions aren’t reasoned—for example, if I describe the behavior of my favorite species as “cultural” without thinking, or just because it sounds more exciting that way—then it’s hard to make real scientific progress. Much of pre-Darwinian biology was about giving arbitrary names to things; it involved the kind of cataloging that goes on in a library. But contemporary biology is about understanding structures and processes. A definition without a reason is a throwback to cataloging science, but a reasoned definition usually represents or leads to a testable hypothesis. For example, if a researcher chooses to call all social transmission in animals “culture” because he believes that the nongenetic transmission process is the most important ingredient of culture, then his definition represents a testable hypothesis, and therefore contributes to progress in the field.

If you had to make an educated guess, how common would you say that cultural transmission is in nonprimates?

There are many kinds of social learning and, although most of them do not require the learner to be especially “clever,” they all have the potential to yield very substantial adaptive advantages. Therefore, if *culture* is understood liberally to mean behavior affected by social learning, then I think it’s very common in nonprimate as well as primate taxa. The phenotype of any animal that lives in a social group, and in an environment that is sufficiently variable to warrant adaptation through learning, is likely to be influenced by social learning.

When I was a graduate student, I had the bright idea that adult Syrian hamsters may have poor social learning ability because they are “solitary”; except when mating, they are highly intolerant of even the presence of mature conspecifics. However, my attempts to show this experimentally, by comparing the social learning ability of adult and predispersal juvenile hamsters, were a rank failure. In each experimental task, the adult hamsters cheerfully learned from their “demonstrators,” and thereby heartlessly proved me wrong.

If *culture* is defined more strictly—for example, as a system of inheritance that allows cumulative, selection-based evolution—then I’m not yet convinced that it is present in any nonhuman species. To answer this intriguing question we would need much more information about the dynamics of social transmission in animals, and particularly about the fidelity with which behaviorial variants are copied across successive links in a transmission chain. If adaptive innovations are not transmitted faithfully, then an inheritance system based on social learning cannot have effects comparable to those of gene-based selection.

How do you see advances in neurobiology affecting the study of animal culture over the next five years?

The discovery of “mirror neurons” in the premotor cortex of macaque monkeys has caused a huge stir among those who study imitation and related processes in humans. These cells fire when the animal executes an action—for example, grasping an object—but also when the animal passively observes a human performing the same action. Curiously, the discovery of mirror neurons does not seem to have had such a dramatic impact on those studying social learning in animals. Part of the reason for this may be that there are still many gaps between research on the functions and mechanisms of animal behavior. The work of neurobiologists, psychologists, and ethologists is becoming ever more integrated, but these are still, to some extent, three separate scientific cultures.

However, there may be another, more specific reason why those studying social learning and culture in animals have not run with the lead provided by mirror neurons. At first glance, it looks like mirror neurons could mediate imitation or copying of very specific features of behavior—the shape or topography of body movements. But, due to doubts that monkeys are able to copy at this level of specificity, many people have rejected this idea, and instead focused on the possibility that mirror neurons are involved in action understanding, theory of mind, or empathy, processes that are not so closely related to culture. I think that was a mistake. Looking into the crystal ball, I predict that the connection between imitation and mirror neurons—in the premotor cortex and elsewhere in the brain, in monkeys and in other taxa—will be “rediscovered,” and that well-integrated behavioral and neurobiological studies will begin to answer important questions about mirror neurons. This will be greatly assisted by more widespread availability of scanners for functional magnetic resonance imaging (fMRI) of primates and rodents. The most important question, in my mind, is: Where do mirror neurons come from? Are some animals born with mirror neurons for a range of behaviors, or are mirror neurons made through associative learning? The answer to this question will tell us a great deal about the origins of the capacity to imitate and, insofar as imitation is involved in cultural transmission, about the origins of culture.

Dr. Cecilia Heyes is a professor at Oxford University in England. Her research focuses on the evolution of cognition. She is a coeditor of *Social Learning in Animals: The Roots of Culture* (Academic Press, 1996) and *Evolution of Cognition* (MIT Press, 2000).

SUMMARY

1. Cultural transmission involves the acquisition and transfer of information via social learning and teaching and affects the acquisition and spread of behaviors both within and between generations of animals.
2. What is learned via cultural transmission is passed on from individual to individual, so that the behavior of a single individual may shift behavior patterns seen in an entire group. When cultural transmission is operating, what is learned by one individual may be passed down through many generations.
3. Cultural transmission involves a “model” individual and an “observer” that learns a specific behavior or response from the model. There are situations, however, that involve an interaction between observers and models, but that do not constitute cultural transmission because observers do not learn any particular behavior or response from models. Two examples of this are local enhancement and social facilitation.
4. Cultural transmission can occur through learning from other individuals via social learning (copying or imitation) and/or teaching.
5. To demonstrate imitation, there must be some new behavior learned from others, and the behavior must involve some sort of new spatial (topographic) manipulation as well as lead to the achievement of some goal. Copying differs from imitation in that what is copied need not be novel and need not involve learning some new topographical action.
6. Traditions can be experimentally examined in animal societies. Traditions can rise and fall over time.
7. Teaching, when rigorously defined, implies that one individual serves as an instructor and at least one other individual acts as a student who learns from the teacher. Teaching provides an immediate benefit to the student but not to the teacher, instructing naive “students,” and imparting some new information to students faster than they would otherwise receive it.
8. Cultural transmission may occur via vertical, oblique, or horizontal transmission. Vertical cultural transmission involves the transfer of information from parent to child; oblique cultural transmission is the transfer of information from older to younger individuals, excluding transfers from parents to offspring; and horizontal cultural transmission occurs when information comes from same-aged peers.
9. Genetic and cultural transmission can operate independently on animals, but may interact in interesting ways.

DISCUSSION QUESTIONS

1. Why do you suppose it took so long for ethologists to focus on the possibility that cultural transmission was an important force in animals? Can you imagine any biases—scientific, ideological, and so on—that might be responsible for this?

2. Suppose I run an experiment in which I take a bird (the observer) and let it view another bird (the demonstrator) opening a sealed cup by pecking at a circle on the cover of the cup. I then test the observer and see that it now opens the cup by pecking at the circle. What can I infer about social learning here? What other critical treatment is missing from this experiment?
3. Imagine that adults in some population of monkeys appeared to pick up new innovations (for example, potato washing, stone play) from observing others. How might you disentangle vertical, oblique, and horizontal cultural transmission as possible explanations?
4. List the pros and cons of Hauser and Caro's definition of teaching. How might you modify this definition to address what you listed on the "cons" side of your ledger?
5. Suppose that after extensive observations, you determine that certain animals in a population appear to rely on social learning much more often than other individuals, and that such differences are due to genetic variation. How might you use the truncation selection technique described in chapter 2 to examine the heritability of the tendency to employ social learning?

SUGGESTED READING

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press. This book can get technical, but it is well worth the effort.

Brass, M., & Heyes, C. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, *9*, 489–495. A paper on the role of neuroscience in explaining a long-standing "perspective-taking" problem in the study of imitation.

Galef, B. G. (2009). Strategies for social learning: Testing predictions from formal theory. *Advances in the Study of Behavior*, *39*, 117–151. An overview of ethological theories of social learning and how these theories have been tested.

Kline, M. A. 2015. How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences*, *38*, e31. This article, along with others in the same issue, provide an overview of modern work on teaching in nonhumans.

Lefebvre, L. (2011). Taxonomic counts of cognition in the wild. *Biology Letters*, *7*, 631–633. A review of the evidence for innovations in natural populations of birds and mammals.

7

Sexual Selection

Few structures are as salient, odd, and beautiful as the elaborate nests that male bowerbirds build to attract their mates. Males build one of two types of nests—a teepee-like nest or an “avenue” nest, which has tall walls running down an open path (Figure 7.1). The nests are surrounded by every trinket males can find—from leaves, bones, shells, acorns, berries, fruits, and shiny rocks to man-made bits like beads, glass, and bottle caps—all neatly placed and arranged by the male. Within and around these nests, males perform elaborate behavioral displays to solicit mating opportunities from females who visit.

Figure 7.1. Great bowerbird avenue nest. An avenue nest with bones, shells, and stones. Reprinted with permission from AAAS. *(From Anderson, 2012)*

John Endler and his colleagues hypothesized that male great bowerbirds (*Ptilonorhynchus nuchalis*) take this already rich mating ritual, and make it even richer, by use of an optical illusion (Endler et al., 2010; Kelly and Endler, 2012). Optical illusions occur if a scene from the environment, when projected onto the two dimensions of the retina, differs from the actual three-dimensional reality of that scene in nature. Kelly and Endler studied what are known as forced-perspective illusions, which occur when an observer is in a stationary position, as are female bowerbirds when they watch males display and bring them shells, bones, and stones from a set position in an avenue nest (Figure 7.2) (see Anderson, 2012; Endler et al., 2012b; and Borgia et al., 2012, for a debate about exactly how these illusions might work).

Figure 7.2. **Female in an avenue nest.** Female bowerbird in the avenue nest looking out at gesso. Reprinted with permission of Elsevier. © 2010. *(From Endler et al., 2010)*

Males arrange their shells, bones, and stones in an area called the gesso and females see the gesso while they are inside the avenue nest. What Kelly and Endler found was that males place shells, etc., on the gesso in a configuration that creates the illusion that items are larger than they actually are. If the researchers changed the position of items on the gesso, males moved them back to the position that creates the forced perspective illusion (Endler et al., 2010). This optical illusion appears to increase the reproductive success of males—the more that the placement of objects on a gesso created the illusion of large-sized shells, bones, and stones, the more mating opportunities a male received (Figure 7.2) (Kelly and Endler, 2012).

* * *

Each of the six primer chapters in this book has focused on a fundamental topic in animal behavior, identified basic theory, and then examined the issue across a whole suite of behaviors. In the remaining chapters, we continue to examine theoretical, empirical, and conceptual questions, but from here forward chapters will focuses on a specific behavior—or more generally, a specific set of related behavioral issues (sexual selection, mating systems, foraging, predation, cooperation, and so forth). We begin with **sexual selection**.

In *The Descent of Man and Selection in Relation to Sex*, Darwin provided the first evolutionary theory of sexual selection, defining this process as one that “depends on the advantage which certain individuals have over other individuals of the same sex and species in exclusive relation to reproduction” (Darwin, 1871). Darwin’s work on sexual selection is typically divided into (1) **intrasexual selection**, in which members of one sex compete with each other for access to the other sex, and (2) **intersexual selection**, in which individuals of one sex choose which individuals of the other sex to take as mates. Because differential reproductive success drives the process of natural selection, intersexual and intrasexual selection are among the most studied topics in ethology (these processes can also be inferred from remains in the fossil record; Knell et al., 2013). (For a discussion of mate choice and conservation biology, see Box 7.1.)

Box 7.1. COGNITIVE CONNECTION

Aggression, Observation, and Gene Expression in Female Fish

Although the separation of sexual selection into intra- and intersexual selection is historically accurate, and is conceptually appealing because of its simplicity, in nature the distinction between these types of selection can be blurry. The most obvious case is when females base their choice of mates, at least in part, on the outcome of direct male-male aggressive contests. Julie Desjardins and her colleagues looked at this in an African cichlid fish, *Astatotilapia burtoni*, a species in which mate choice and male-male aggression have been well studied (Desjardins et al., 2010). In *A. burtoni* gravid, females select between males, and prefer more dominant, aggressive individuals as mates (Fernald and Hirata, 1977; Clement et al., 2005). To study the interface between intra- and intersexual selection, Desjardins's team wanted to know whether observing a fight between males triggers action in certain areas of a female's brain. And if so, what areas, and what does this tell us about associated cognitive processes?

The experimental procedure used was elegantly simple. First, a female was placed in an aquarium. At each end was a male, and the males were matched for size and dominance rank. Which male the female preferred was measured by the amount of time she spent near an individual. Subsequent to this, the female saw a fight between these two males. Because males are territorial, Desjardins et al. knew that when they moved male 1 from the side he was on to the side of the tank with male 2 (still on his home territory), male 2 was likely to win any contest. This allowed the researchers to stage fights in which females saw the preferred male either win or lose a contest. To assess how this observation affected brain activity patterns in females, they measured gene expression levels in two genes, *c-fos* and *egr-1* (Burmeister and Fernald, 2005; Burmeister et al., 2005; see Wilkson et al., 2015, for more on this post–genomic era approach to sexual selection).

Once a female had made a choice between males, seeing her preferred male win or lose a fight had dramatic effects at the level of gene expression in the brain (Figure 7.3). An analysis of *which* brain areas were affected found that when observing a preferred mate win, there was increased gene expression in both *c-fos* and *egr-1* in the preoptic area (POA) and ventromedial hypothalamus (Vm) area of the brain, both of which are known to be linked to reproductive physiology and reproductive behavior. But after watching a preferred male lose a fight, *c-fos* and *egr-1* gene expression was high in the lateral septum (LS) of the brain, which prior work has found is linked to anxiety-like behaviors. It seems then that watching a preferred male win a fight primes a female for reproduction, while watching a preferred male lose a fight triggers anxiety-like responses, which might reduce the likelihood of mating and reproduction (Figure 7.4).

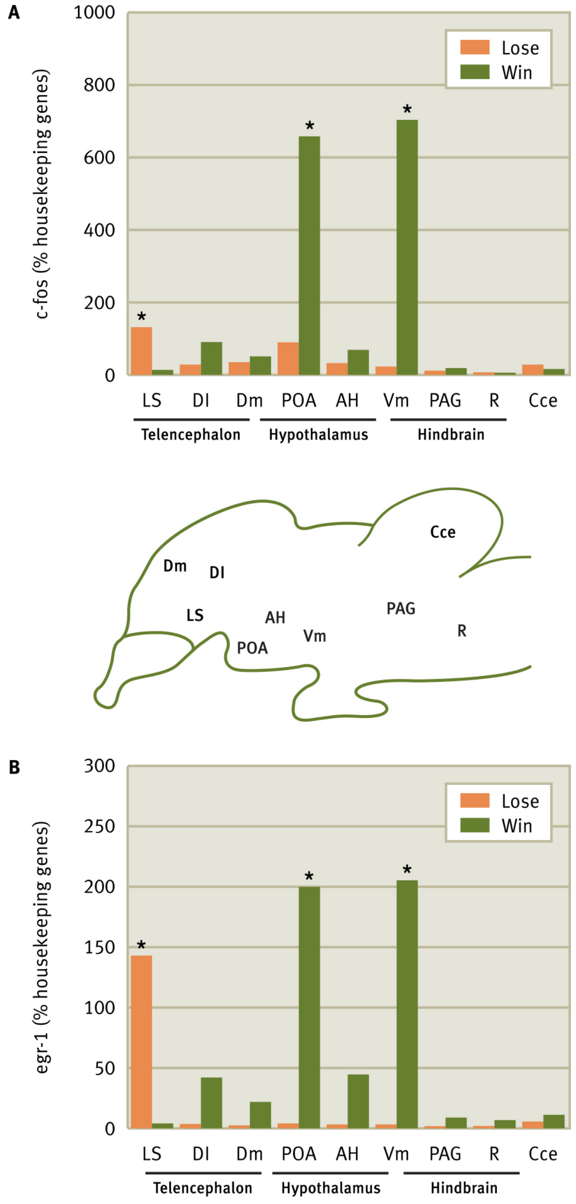


Figure 7.3. Observation of males fighting affects gene expression patterns. Gene expression in *c-fos* (top) and *egr-1* (bottom) in three different areas in each of three sections of the brain of *Astatotilapia burtoni*: the telencephalon, the hypothalamus, and the hindbrain. Asterisks indicate a significant difference as a result of seeing a preferred male win versus lose a fight. The approximate location of the brain areas studied is shown in the middle panel. *(From Desjardins et al., 2010)*

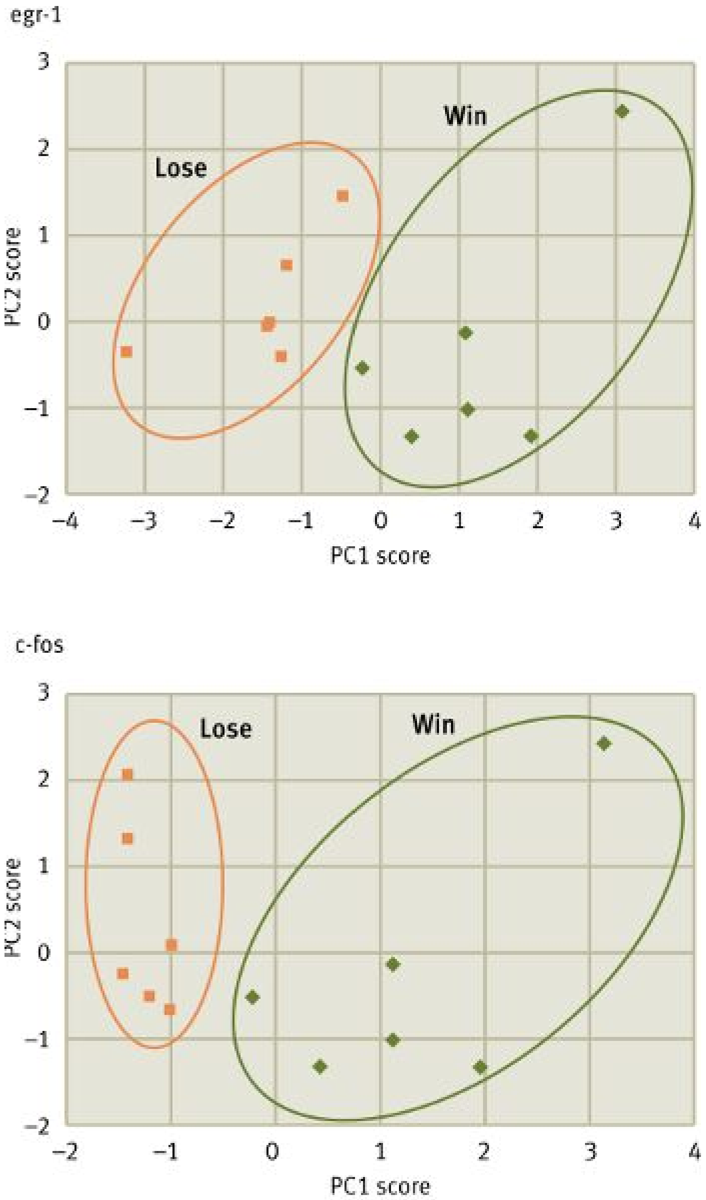
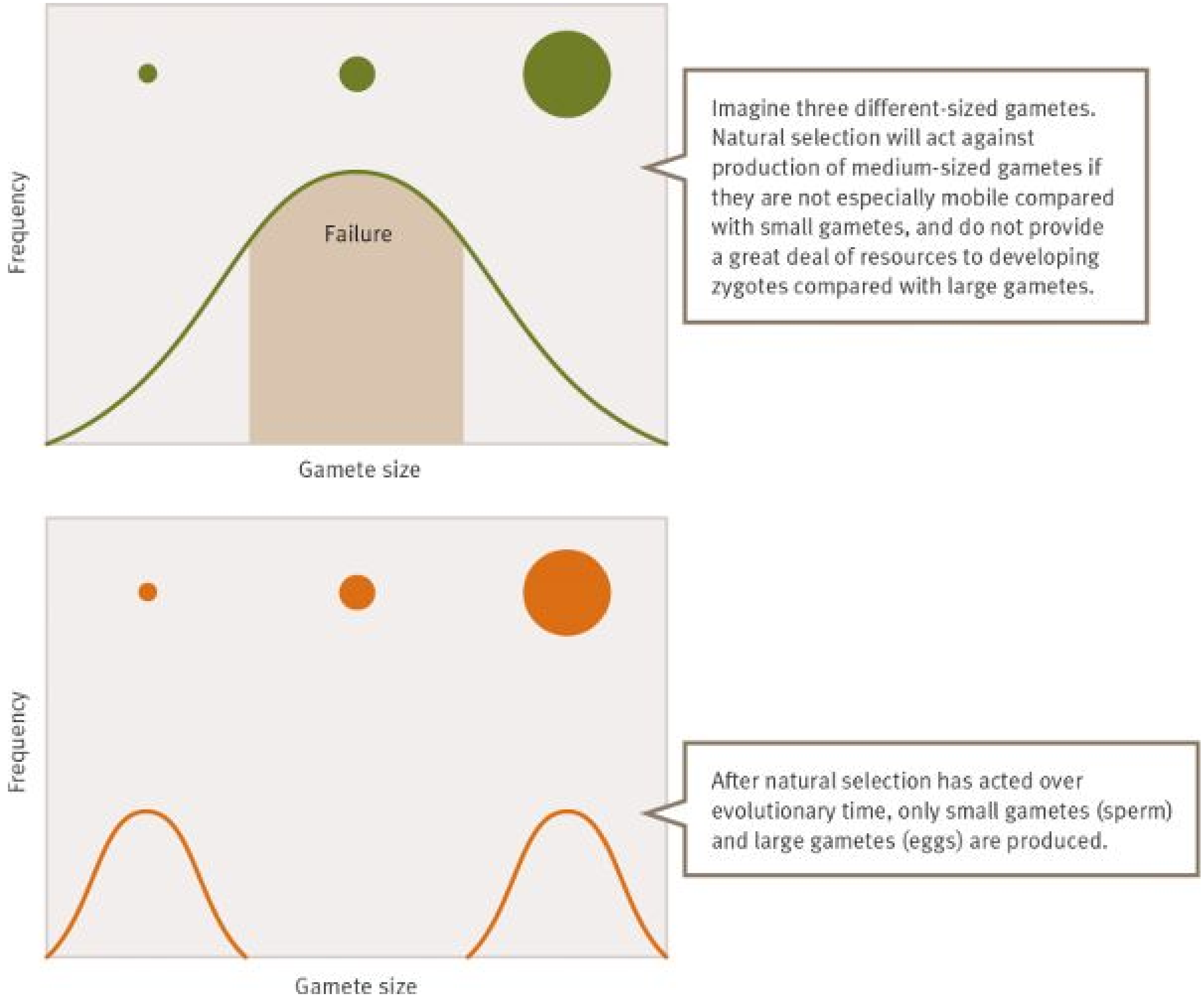


Figure 7.4. **Observing a win or a loss triggers different brain areas.** For both for *egr-1* (top) and *c-fos* (bottom), gene expression was highest in areas of the brain of *Astatotilapia burtoni* associated with reproduction after observing a preferred male win a fight, and highest in areas of the brain associated with anxiety after watching such a male lose a fight. The *x*- and *y*-axis are "principal components" used in the analysis. Moving east to west, the *x*-axis is more strongly associated with the preoptic area (POA) and ventromedial hypothalamus (Vm) area of the brain. Moving south to north, the *y*-axis is more strongly associated with the lateral septum (LS) of the brain. *(From Desjardins et al., 2010)*

In this chapter, we shall examine sexual selection from both proximate and ultimate perspectives, with particular emphasis on (1) the evolution of mating preferences, (2) learning and sexual selection, (3) cultural transmission and female mate choice, and (4) male-male competition.

Intersexual and Intrasexual Selection

Darwin proposed that one important factor leading to differences in reproductive success is differential access to mating opportunities. In most animal species, it is males that compete for mating opportunities. This difference between the sexes is due, in part, to the different type and number of gametes produced by males (sperm) and females (eggs). Females produce fewer, but larger gametes (Figure 7.5). Each egg is extremely valuable, because of both its size and its relative scarcity. Each sperm requires much less energy to produce, and sperm are usually found in prolific quantities. Male reproductive success is limited by the much lower rate of gamete production of females compared with that of males. Males often produce millions of sperm, creating the possibility that some males will have extraordinary reproductive success; females' eggs are much scarcer, causing intense competition for this relatively scarce resource (Trivers, 1985).



Imagine three different-sized gametes. Natural selection will act against production of medium-sized gametes if they are not especially mobile compared with small gametes, and do not provide a great deal of resources to developing zygotes compared with large gametes.

After natural selection has acted over evolutionary time, only small gametes (sperm) and large gametes (eggs) are produced.

Figure 7.5. Natural selection and gamete size. Natural selection favors large and small gametes over medium-sized gametes. *(From Low, 2000)*

According to what is known as **Bateman's principle**, named for geneticist A. J. Bateman, who studied sexual selection in fruit flies: (1) females should be the choosier sex because eggs are expensive to produce and because a female's potential reproductive success is limited compared with that of a male, and (2) females' greater choosiness in mate selection should translate into greater variance in the reproductive success of males (Bateman, 1948).

Any male trait that confers mating and fertilization advantages and is passed down across generations will, over time, increase in frequency in a population, because males with such traits will produce more offspring than their competitors. Darwin's idea about the struggle among males for mating opportunities—one component of intrasexual selection—still informs our current understanding of sexual selection. Competition for mates can take many forms, depending on ecology, demography, and cognitive ability. For example, males may fight among themselves, occasionally in dramatic “battles to the death,” but more often in less dangerous bouts, to gain mating opportunities with females (Figure 7.6). This latter form of male-male sexual competition is illustrated by male stag beetles and red deer (*Cervus elaphus*), who use their “horns” (enlarged jaws) and antlers, respectively, in physical fights over females; the winners of such contests mate more often than the losers.

Figure 7.6. Competition for mates. (A) Male red deer battle with their antlers. (B) Male horses compete for females. *(Photo credits: © shaftinaction / Shutterstock; © mariait / Shutterstock)*

Until the 1970s, much of the work on sexual selection focused almost exclusively on intrasexual competition, rather than intersexual selection (mate choice; Andersson, 1994; Andersson and Simmons, 2006). One reason for this focus may be that intrasexual competition, particularly male-male competition, is very easy to observe in nature. In addition, some prominent evolutionary biologists of the 1930s dismissed mate choice as unimportant and directed research toward male-male competition (J. Huxley, 1938; Prum, 2012).

Just as intrasexual selection, in principle, could involve either males fighting for females or females fighting for males, intersexual selection can involve both female choice of a male and male choice of a female. Both take place in nature, but female mate choice is more prevalent, likely because females stand to lose much more than males by making a bad choice of mates. Females invest much more energy in each gamete they produce, so they should be choosier than males in terms of who has access to their gametes. In addition, in species with internal gestation, females typically devote a great deal of energy to offspring before they are born, and so should be under strong selection pressure to choose good mates that will produce healthy offspring.

Above and beyond the physical genitalia that are necessary for the act of mating, males often possess other traits that play an important role in attracting mates. These traits are referred to as secondary, or epigametic, sexual characteristics, and include ornamental plumage, bright colors, and courtship displays. The underlying genetics of such epigametic characteristics are the subject of much experimental work (Wilkinson et al., 2015). For example, male fruit flies "sing" to females during courtship by vibrating their wings. Their courtship song, which is an epigametic trait, not only influences female mate choice but also may be important in the process of speciation in fruit flies (Spieth and Ringo, 1983; Tomaru and Oguma, 1994). One particular form of song in fruit flies, called "pulse song," is very conspicuous during courtship, and the interval between pulses (the interpulse interval, or IPI) appears to affect female fruit flies' choice of mates (Arthur et al., 2013;Ewing and Bennet-Clark, 1968; Ritchie et al., 1999; Schilcher, 1976a,b). Early work on the genetics of courtship song in *Drosophila* suggested pulse song might be controlled by a large number of different genes, each of which contribute a small amount to the expression of the song. Subsequent work, however, suggests that the genetics of song appear to involve three loci that account for much of variance in courtship song (Gleason et al., 2002).

Both intersexual and intrasexual selection play a role in virtually all mating systems (see chapter 8). Whether the system is *monogamous* (a single male pairs up with a single female), *polygamous* (some males mate with many females), or *polyandrous* (some females mate with numerous males), sexual selection plays a role. Generally speaking, sexual selection will be stronger in polygamous and polyandrous systems than in monogamous systems. In polygamous and polyandrous systems, some individuals may obtain many mating opportunities and others may obtain no mating opportunities, while there is generally less variation in reproductive success in monogamous systems (see chapter 8). This greater variation in reproductive success in polygamous and polyandrous species creates stronger sexual selection pressure.

Evolutionary Models of Mate Choice

There are four different types of evolutionary models of female mate choice: “direct benefits,” “good genes,” “runaway selection,” and “sensory exploitation” models. We will examine the logic of these models, and then look at case studies for each. For all of these models, ethologists attempt to understand how evolutionary change has shaped the process of mate choice. It is important to note that we will focus on case studies in which the evolution of a sexually selected trait is best explained by one of our four models. In many species, of course, the evolution of sexually selected traits might best be explained by a combination of two or more models. The logic of focusing on the more clear-cut cases, where a single model best explains the evolution of a sexually selected trait, is to provide a basic understanding of the dynamics of female mate choice.

Box 7.2. CONSERVATION CONNECTION

Genetic Diversity, Genetic Quality, and Conservation Biology

Conservation biologists have long understood the negative consequences of low genetic diversity in populations, but only recently have they come to realize the importance of mate choice per se for conservation issues (Charge et al., 2014). Suhel Quader has suggested that human disturbances, as well as actions that conservation biologists and managers undertake to protect species, may have a broad spectrum of effects on mate choice, particularly female mate choice (Quader, 2005). Such effects on mate choice may then have implications for genetic diversity as well as the genetic quality of individuals in natural and managed populations of animals. A few examples will help illustrate the sometimes subtle ways in which such effects can occur.

1. **Increasing hybridization:** Many natural environments are being heavily polluted by human activities, from dumping commercial waste products to washing laundry in otherwise pristine water sources. Above and beyond the obvious effects on animal mortality, such pollution also affects mate choice. For example, Lake Victoria is home to many closely related species of cichlid. Females often distinguish between males of their species and those of other species by male color patterns. But with pollution increasing in Lake Victoria, the turbidity of the water has also increased. Females cannot see as well in this turbid water, and research has found that cichlid females mate with males from other species because of their inability to distinguish male color patterns (Seehausen et al., 1997). Pollution, through its effect on increased turbidity, has led to higher rates of hybridization in Lake Victoria cichlid species. The long-term implications of such hybridization on these cichlid species are still not well understood.
2. **Sexual imprinting:** As discussed later in this chapter, sexual imprinting is important in establishing mate preference in some species. Managed animal populations, such as those on conservation refuges or in zoos, may be forced to live under circumstances that reduce, or completely eliminate, suitable models on which to sexually imprint (P. R. Grant and Grant, 1997; Slagsvold et al., 2002). When closely related endangered species are reared together, individuals may even imprint on adults from the wrong species, leading to potentially maladaptive behaviors (M. Wallace, 1997).
3. **Danger and decreased mating:** Individuals from some species may interpret human disturbances from censusing, habitat manipulation, and so on as cues of increased

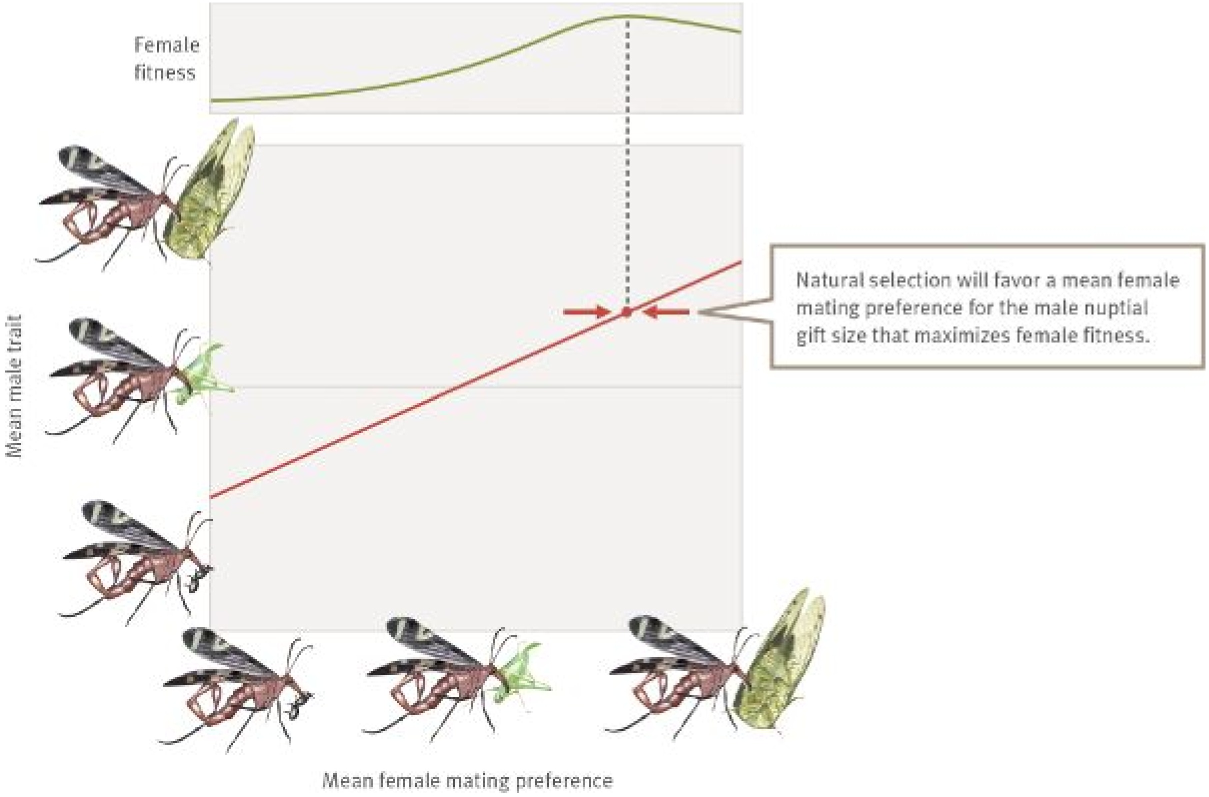
danger. These cues may then cause females to spend more time being vigilant for danger and less time choosing their mates. As a result, low-quality males may have mating opportunities they would not normally (without human disturbance) obtain. Under extreme circumstances, this increased time spent on vigilance could cause females to skip breeding altogether (Mungall, 1978).

4. **Mating and parental investment in managed populations:** The effects of conservation and management practices on female mate choice in animals can be subtle. For example, work on zebra finches has found that when the number of males in a population is low, females may sometimes breed with males that they would not otherwise choose as mates. When females make such a mate-choice decision, there are rippling effects on the next generation. If high-quality males—those best suited to survive and reproduce in their environment—are absent from a population, females may invest fewer resources in their offspring than they do when they mate with high-quality males. When conservation biologists initiate breeding programs that maximize the number of individuals mating (and hence genetic diversity), they may inadvertently force females to mate with low quality males, and the result may be that females devote fewer resources to their offspring. Offspring from such matings may be less healthy and suffer other adverse affects, such as weakened immune systems (Burley, 1986; Burley et al., 1982).

An understanding of mating systems and issues such as increased hybridization, sexual imprinting, the interaction of predation pressure and mating, and parental investment will provide conservation biologists and managers additional tools to foster natural populations, as well as develop reserves, wildlife parks, and managed populations of all sorts.

DIRECT BENEFITS AND MATE CHOICE

The direct benefits model of mate choice hypothesizes that selection favors females that have a genetic predisposition to prefer mates that provide them with tangible resources—above and beyond sperm—that increase their fecundity (Andersson, 1994; Kirkpatrick and Ryan, 1991; Møller and Jennions, 2001; T. Price et al., 1993; Figure 7.7). Females that choose males that provide them with some important resource—food, safe shelter, assistance with parental care, and so on—will do better than their counterparts that are less choosy, and over evolutionary time we expect to see an increase in such phenotypes. One study of direct benefits centers on nuptial gifts in scorpionflies.



Natural selection will favor a mean female mating preference for the male nuptial gift size that maximizes female fitness.

Figure 7.7. The direct benefits model of female mate choice. Here males provide a direct benefit (in this case, food), and females choose males based on how the resource affects their fitness. Prey items are shown in green. *(Based on Kirkpatrick and Ryan, 1991)*

Direct Benefits and Nuptial Gifts

Randy Thornhill and his colleagues have tested the hypothesis that direct benefits provided by males influence female mate choice in the scorpionfly (*Hylobittacus apicalis*; Thornhill, 1976, 1980a). They found that female scorpionflies choose their mates using a simple rule: choose males that bring relatively large prey items—primarily aphids, flies, and beetles—during the courtship process (Figure 7.8). These **nuptial gifts**, consumed during courtship, provide females with a direct benefit in the form of food.

Figure 7.8. Scorpionflies and nuptial gifts. To obtain mates, male scorpionflies present females with nuptial gifts, which are prey items that the females consume during courtship or mating. The male (top) provided the female (bottom) with a blowfly (at arrow), which she eats as they copulate. *(Photo credit: © Trevor Jinks, Queensland, Australia)*

Males that bring no prey are rejected as potential mates by females (Cordero, 1996). But females do more than simply choose a mate based on nuptial gifts: they also determine how long they will mate with a male based on the size of his gift, that is, based on the direct benefit they receive. When the nuptial gift is small—between 3 and 19 mm^2—there is a positive relationship between prey size and copulation time. When nuptial gifts are in this size range, it is the female that always terminates copulation, by pulling her abdominal tip away from the male (Figure 7.9A). Copulation time is important, because there is a positive relationship between it and the number of sperm transferred during such matings: Copulation times of less than approximately seven minutes often involve no sperm transfer (Figure 7.9B).

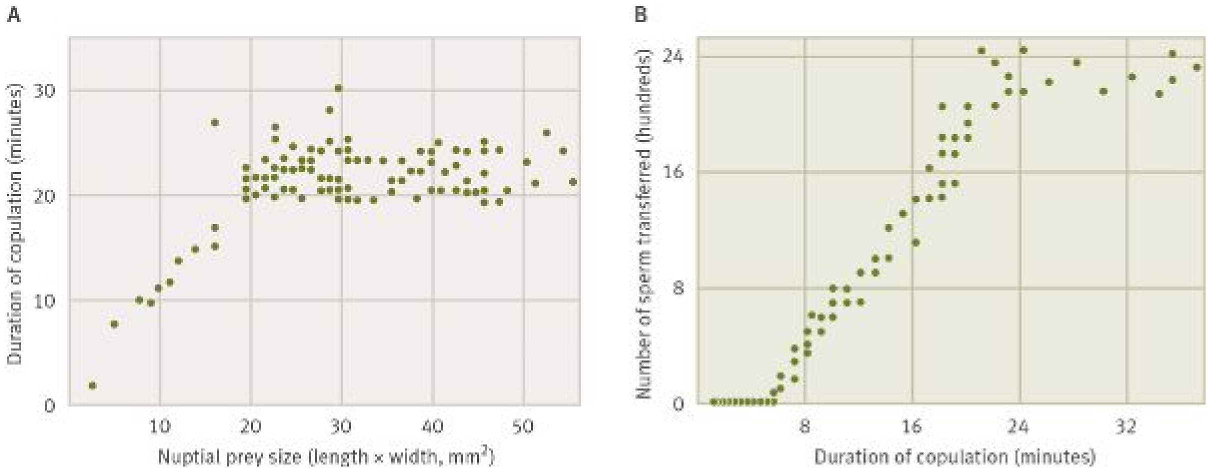


Figure 7.9. The direct benefits model and nuptial prey gifts. (A) Copulation time as a function of direct benefits. Male scorpionflies provide females with a nuptial prey gift. Up to about 19 mm^2, the greater the value of the gift, the longer a male is allowed to copulate with the recipient. (B) Longer copulation time leads to greater sperm transfer in scorpionflies. When males provide large nuptial gifts to females, the added copulation time translates into more sperm transferred to the female. *(From Thornhill, 1976, 1980b)*

Given that females can distinguish males with large gifts from other males, how does food translate into fitness-related benefits? A female that actively chooses males that bring large nuptial gifts produces *more* eggs and, in all likelihood, has a longer life span, both because of the nutrition she receives directly from the nuptial gift and the decreased amount of time she must allocate to hunting (Thornhill, 1976, 1979b, 1980a,b; Thornhill and Alcock, 1983).

Because nuptial prey size has such a strong effect on mating opportunities (and sperm transfer), there is strong sexual selection pressures on males to bring large nuptial gifts to females. Finding prey that are large enough to result in long copulations with a female is both time consuming and dangerous as increased foraging time exposes males to greater risks of predation. At any given time, only about 10 percent of the males in a population are in possession of such prey. These constraints have led to some rather remarkable adaptations in male foraging behavior. Males will often sample, but then discard, prey that are too small to result in long copulation opportunities with females. In contrast, females hunting on their own almost never discard small prey.

Selection pressure on males to bring large nuptial gifts has also resulted in males stealing large prey from one another. In one study, Thornhill recorded such prey theft on 345 occasions; a follow-up study discovered that one way that males manage such thefts is to mimic the behavior of a female and then subsequently steal prey brought to them by other males (Thornhill, 1976, 1979a).

Thornhill's work not only provides evidence that females select among males based on resources that provide direct benefits, but also illustrates the way that such choice shapes foraging (Palmer, 2010) and male mating behavior (Box 7.3).

Box 7.3. SCIENCE AT WORK

What is the research question? Does the indirect benefits model explain female choice in scorpionflies?

Why is this an important question? Though the simplest of the models of mate choice, relatively few experiments have directly assessed the indirect benefits model of female mate choice.

What approach was taken to address the research question? The relationship between the nuptial prey size and copulation length and sperm transfer were examined in the field.

What was discovered? Up to about prey of about 20 mm^2, copulation length and sperm transfer were positively correlated with nuptial prey size.

What do the results mean? Females used the size of the direct benefit they received—the nuptial prey—to determine which males to mate with and how long to mate with them.

GOOD GENES AND MATE CHOICE

Females obtain more than direct resources such as food and shelter from their mates; they also receive sperm, and with it, the genes that will make up half of the genomes of their offspring. Some theory and empirical work suggests that sexual selection favors females choosing mates that possess "good genes" (Andersson, 1994; R. A. Fisher, 1915; Kodric-Brown and Brown, 1984; Kokko et al., 2003; Mays and Hill, 2004). Good genes are those are associated with adaptive traits inherited by offspring of the appropriately choosy female. **Good genes models** propose that selection favors that females choose the males with genes best suited to their particular environment—for example, genes associated with superior foraging skills or the ability to fend off predators. In doing so, the females receive indirect benefits, in the sense that their offspring receive some of the good genes that led their mother to choose a particular male as a mate in the first place (Cameron et al., 2003). Good genes models are sometimes called "indirect benefit models" of sexual selection.

Good genes models of sexual selection apply to mating systems in which the primary benefits received by females lie in the good genes their offspring receive as a result of their mate choice. For example, in pronghorn antelopes (*Antilocapra americana*), males provide females with no direct benefits, and they do not appear to actively coerce females into mating in any measurable way. Instead, many female pronghorns undertake a long and energetic search to find mates by visiting different males that already have harems of females. Early work had shown that females select males as mates based on a male's ability to defend his harem—most females end up mating with a small subset of males in their population (J. A. Byers et al., 1994). This leads to high variance in harem size among males and to males with large harems in prior years siring a disproportionate number of offspring. John Byers and Lissete Waits hypothesized that such males possessed good genes. But how could a female know about a male's prior reproductive success? The researchers hypothesized that females were using current harem defense as an indicator of good genes in males. If so, males with large harems (attractive males) should have offspring that are more likely to survive than offspring from other (nonattractive) males (J. Byers and Waits, 2006).

Byers and Waits tested their hypothesis in a population of individually marked pronghorns that live in the National Bison Range in Montana. They followed females during the mating season and recorded which males were selected as mates. When offspring were born, they were marked, and their survival was measured as a surrogate for fitness. They found that, in accordance with predictions from most good genes models, offspring from attractive males had higher survival rates than offspring from other males, suggesting that females were selecting males based on some measure of a male's genetic quality (Figure 7.10).

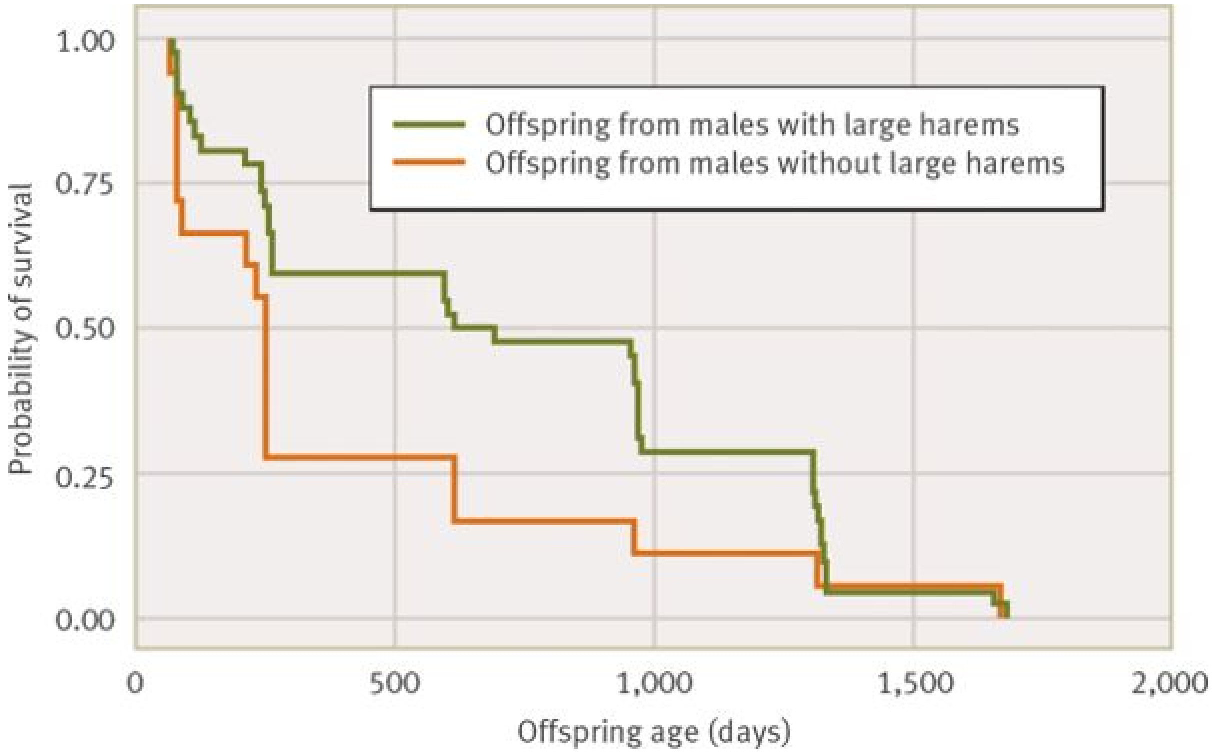


Figure 7.10. Indirect benefits in pronghorns. Offspring from males that had large harems (green line) had higher survival rates than offspring from other males (orange line), suggesting that females were selecting males based on some measure of a male's genetic quality. *(From J. Byers and Waits, 2006, p. 16344)*

In pronghorns, females use harem defense as an indicator of good genes in males, but how do females gauge which males have good genes in other systems? How do females determine whether males have cheated in indicating that they possess good genes, given that sexual selection would be likely to favor males that cheat in such a manner? Shouldn't selection favor males that attempt to give the impression that they possess appropriately good genes, even if they don't? The answer is yes—sexual selection should favor males that do just this. This, in turn, creates new sexual selection pressures on females, such that **honest indicators** of male genetic quality should be used by females when choosing mates.

If females focus on such honest indicators, they might be able overcome the male cheater problem—at least temporarily.

Parasite Resistance and Good Genes

Which male traits should females accept as honest indicators of a male's genetic quality? One theory is that honest indicator traits should be costly to produce. The costlier the trait, the more difficult it is to fake, and so the more likely it is that this trait is a true indicator of good genes (Zahavi, 1975; Zahavi and Zahavi, 1997; Figure 7.11). One such costly trait is resistance to parasites. Females that choose males with strong resistance to parasites, a trait that should be difficult to fake, may receive indirect benefits in that they mate with individuals with genes that confer parasite resistance. The predictions of honest advertising models, when applied to parasites, go under the name of the Hamilton-Zuk hypothesis, after Bill Hamilton and Marlene Zuk, who first applied the idea of good genes to parasite resistance (Hamilton and Zuk, 1982; Balenger and Zuk, 2014).

Figure 7.11. Peacock's tail. An example of an elaborate, costly trait in males. *(© Eky Studio / Shutterstock)*

Consider the case of parasites that live *in* their hosts and can't be seen, that is, endoparasites. How do females know which males have good genes with respect to endoparasite resistance? The answer to this question likely lies in the female's ability to use some other male trait that correlates with the ability of a male to avoid being parasitized. If possessing trait T also means that males are good at fighting endoparasites, females can use trait T as a proxy for judging what they really need to know. If information on internal parasitization is unavailable, then using some other trait (T) that correlates well with the one of interest should be favored by sexual selection. One such proxy cue is body coloration (Figure 7.12), which has been studied extensively in birds and fish. Healthy males tend to be very colorful, while infected males have much duller colors (Milinski and Bakker, 1990; Figure 7.13). Although still the subject of some heated debate, numerous studies in birds and fish have found results that are consistent with the predictions of the Hamilton-Zuk hypothesis, in that females often choose the most colorful (and least parasitized) males (Figure 7.14).

Figure 7.12. Elaborate coloration in males. In many birds, such as the red-knobbed hornbill (*Rhyticeros cassidix*), males are more colorful than females as a result of different sexual selection pressures acting on males and females. *(Photo credit: Arco Images GmbH / Alamy Stock Photo)*

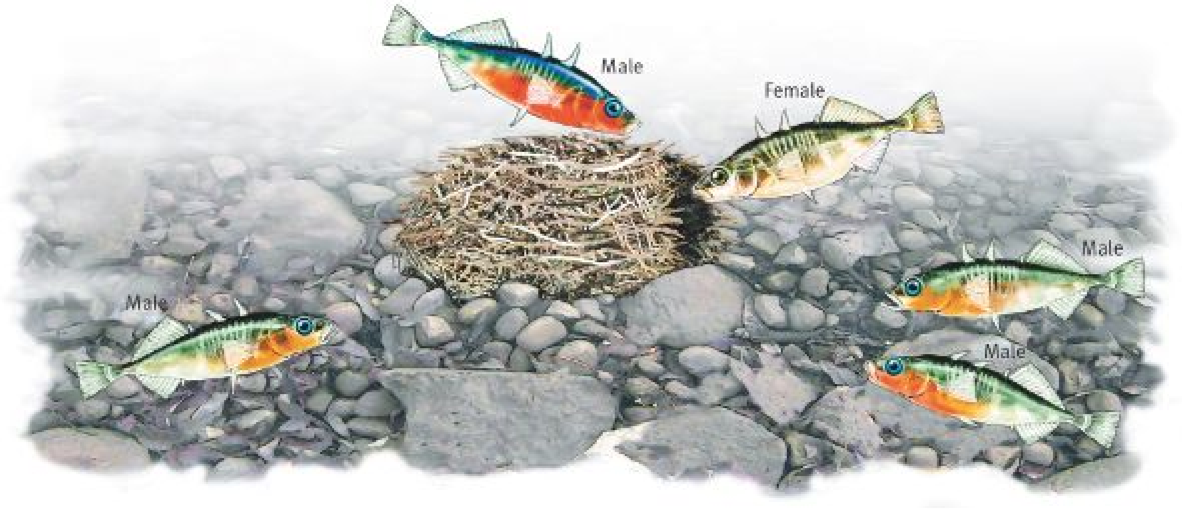


Figure 7.13. Color, parasites, and good genes. One reason stickleback females may prefer the most colorful (red) males is that color intensity is positively correlated with resistance to parasites.

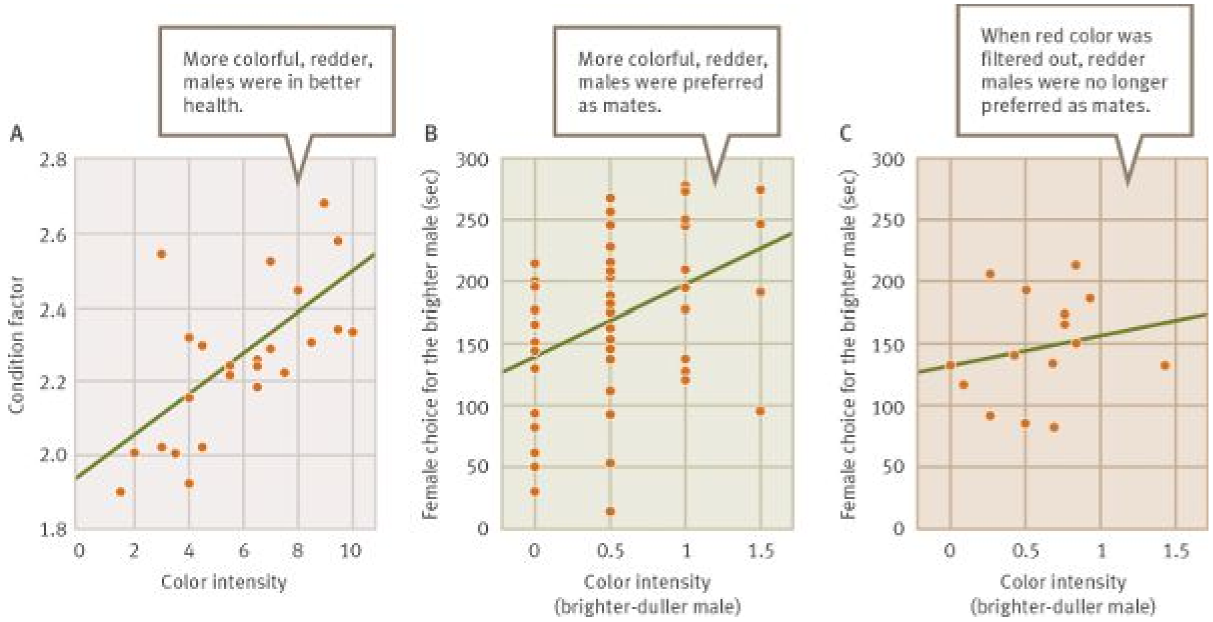


Figure 7.14. Female sticklebacks prefer brighter males. Brighter (redder) stickleback males were healthier and were preferred as mates, but not when red coloration was experimentally filtered out. *(From Milinski and Bakker, 1990, p. 331)*

MHC and Good Genes

If females are searching for honest indicators of good genes in males, the ability to detect disease resistance should be favored by selection. One set of genes that is involved in disease resistance is the major histocompatibility complex (MHC; Milinski, 2006; Penn and Potts, 1998, 1999; Kamiya et al., 2014). Proteins produced by MHC genes guide the body in identifying “self” versus “foreign” cells (Wills, 1991). A unique aspect of the MHC is that it is the most variable set of genes known. Very few (if any) individuals have exactly the same MHC. Given this incredible genetic variability, biologists have predicted that animals may prefer mating with others that have a dissimilar MHC (S. V. Edwards and Hedrick, 1998; Ziegler et al., 2005). Such a preference might lead to offspring with particularly strong immune systems. Why? Because diseases evolve so rapidly that it is as if animals are trying to hit a moving target in trying to combat them. In this case, their weapon against such a moving target is a set of MHC genes that is constantly changing across generations.

How can females determine which males have MHCs that differ from their own? Work using fish and rodents suggests that females use odors to determine whether another individual is a good MHC match (Penn and Potts, 1998; Milinski, 2014). This work has spurred experiments on odor, MHC, and mate choice in humans. To test the hypothesis that humans use MHC when choosing mates, and that odor plays a role in the process, male and female undergraduate students in Switzerland were tested by Claus Wedekind (Wedekind and Furi, 1997; Wedekind et al., 1995). In Wedekind and Furi’s (1997) study, men were instructed to wear a cotton T-shirt for two nights. Blood samples from each of these males were then analyzed to determine MHC. Females also had blood samples taken for MHC analysis. These women were then given T-shirts from males with MHCs similar or dissimilar to their own. Women not on oral contraceptives consistently found the odors of the T-shirts from males with dissimilar MHCs sexier, suggesting that MHC has a significant effect on female mate choice in humans. Indeed, not only do females choose males with dissimilar MHC alleles, but they themselves use perfumes that specifically magnify their own MHC-mediated odors (Milinski and Wedekind, 2001).

Thorston Reusch and his colleagues have hypothesized that to produce disease-resistant offspring, individuals should, all else being equal, prefer mates with many MHC alleles, rather than choosing a mate that is dissimilar in MHC-related genes (S. V. Edwards and Hedrick, 1998; Reusch et al., 2001). They tested their “MHC allele counting” hypothesis using wild-caught stickleback fish from three populations that live in interconnected lakes. Sticklebacks from these three lakes varied in the number of MHC (class IIB) alleles they possessed, ranging from two to eight such alleles. When females were given a choice between males—some of whom had few MHC alleles and some of whom had many such alleles—they consistently preferred males with a greater number of MHC alleles (up to eight; Figure 7.15).

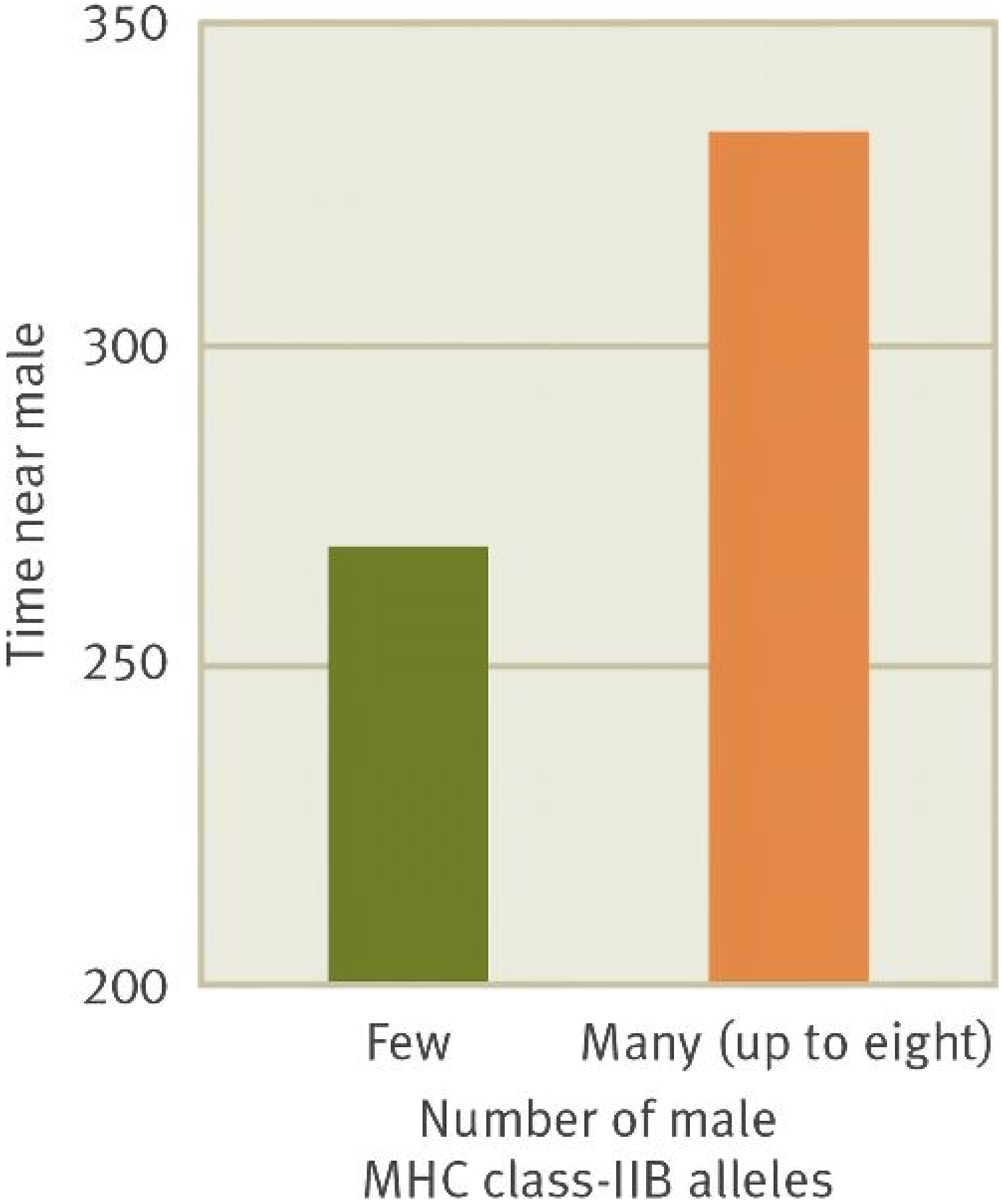


Figure 7.15. Female sticklebacks prefer males with more MHC alleles. Female sticklebacks spent more time on the side of the tank with males that had many different MHC alleles than with males that had few MHC alleles. *(From Reusch et al., 2001)*

In another series of experiments, Manfred Milinski and his colleagues (including Reusch) examined the proximate cues that female sticklebacks may be using to assess the MHC qualities of potential mates (Milinski et al., 2005). They knew from prior work that females can assess the number of MHC alleles a male has using chemical cues alone. The question was, How do female sticklebacks make this assessment? The answer may be that the greater the number of MHC alleles found in an individual, the greater was the number of MHC peptides, which are short strings of amino acids displayed at the cell surface (Rammensee et al., 1997). Milinski and his collaborators hypothesized that female sticklebacks were able to use odor to assess the diversity of MHC peptides for a particular male. More specifically, they proposed that MHC peptide ligands—that is, molecules that bind to proteins—were the key underlying proximate mechanism that females were assessing during mate choice.

The researchers tested their hypothesis by simultaneously exposing a female to two different water columns. One column had water drawn from a tank that had a male swimming in it, and the other column also had water from that male tank, but the water in this column was supplemented with MHC peptide ligands. The MHC peptide ligand diversity of both the male and the female were known, and a given pair together had either the optimal number of peptide ligands (producing offspring with better disease resistance) or a suboptimal number of MHC peptides (Kurtz et al., 2004; Wegner, Kalbe, et al., 2003; Wegner, Reusch, et al., 2003).

What Milinski and his colleagues found was that when a pair had a less-than-optimal number of MHC peptide ligands, the addition of synthetic ligands to one side of the water column made the odor on that side more attractive, suggesting that the number of peptide ligands was the proximate cue being used by females to select males with good genes. Conversely, when a male and a female had the optimal number of MHC peptide ligands, the addition of ligands to one of the water columns made the odor associated with that column less attractive (Figure 7.16).

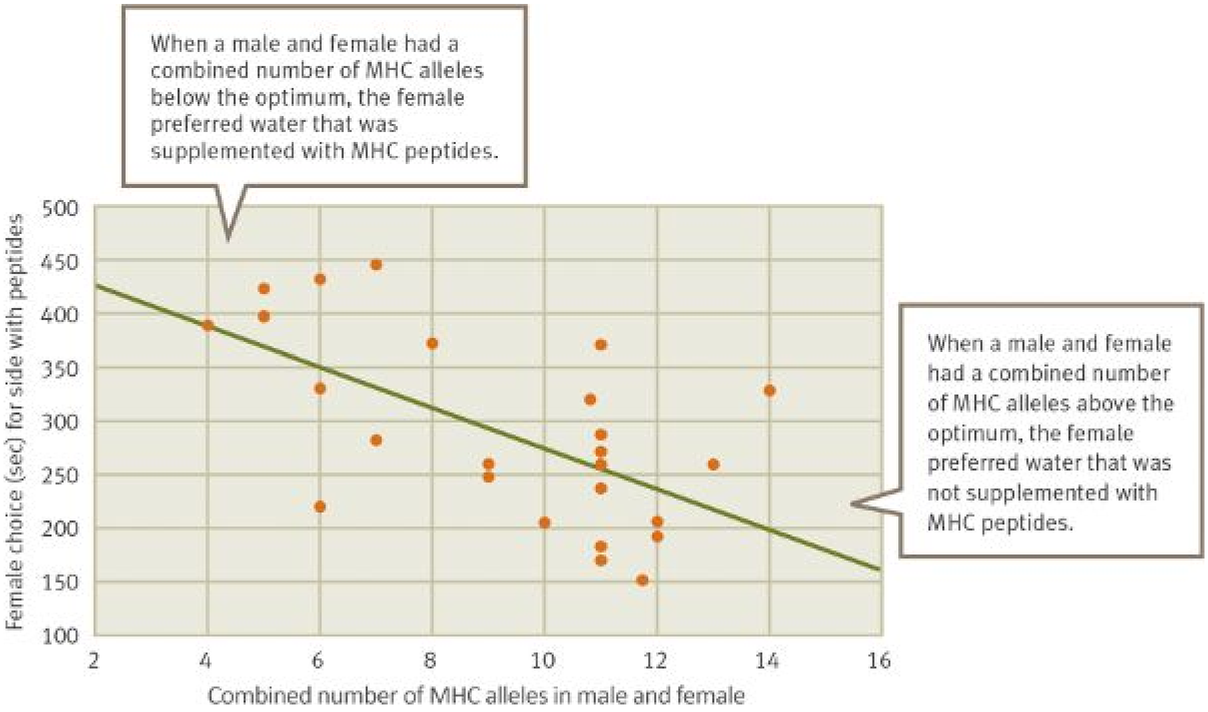


Figure 7.16. Female sticklebacks use peptides to assess MHC. Female sticklebacks were given a choice between water from a tank containing a lone male, or water from a tank with that same male plus added MHC peptides. *(From Milinski et al., 2005)*

In a follow-up experiment, Milinski's group tested another prediction regarding odor and MHC peptide ligands and good genes. Soon after females give birth, they avidly forage, often raiding nests of other sticklebacks and eating their eggs. Males guard nests from such female attacks. Milinski and his team hypothesized that a female should be repelled by the very male MHC peptide ligand odor she was attracted to prior to mating, because such a repulsion would reduce the chance that she accidentally raids the nest of her mate and cannibalizes her own eggs. When they tested whether foraging females were repelled by the MHC peptide ligand odor of their former mates, they found evidence that this was indeed the case.

RUNAWAY SEXUAL SELECTION

Sir Ronald Fisher proposed an idea known as runaway sexual selection. Models of runaway sexual selection center on the relationship between alleles at two loci. In such models, one locus houses alleles that code for female preference, and the other houses alleles associated with the male trait that females prefer. Over evolutionary time specific alleles from the two genes become associated with each other—when one allele is present in male offspring in a clutch, the other allele is likely to be present in female offspring from that clutch (Andersson, 1994; R. A. Fisher, 1958; Kirkpatrick, 1982; Mead and Arnold, 2004).

To see how the runaway selection process works, imagine a population in which some proportion of females have a heritable preference for brightly colored males, and the remainder of females choose males randomly with respect to color. Further suppose that in this population, the degree of male coloration is also a heritable trait and that some males are more colorful than others. So, we have a group of females, some of whom prefer brightly colored males and some of whom don’t, and a group of males, some of whom are more colorful than others. Let’s assume that the loci for both male color and female preference are found in both males and females, but the alleles at these loci are only expressed in the appropriate sex: preference genes in females, color genes in males.

Females that mate with colorful males should produce not only colorful sons, but also daughters that possess their mother’s genetically coded *preference* for colorful males. Over time, the allele in females that codes for the preference for colorful males and the allele in males that codes for color in males become linked in the sense that, as the frequency of one changes, the frequency of the other changes as well. Once this positive feedback loop is set in motion, it can, under certain conditions, “run away,” like a snowball rolling down a snowy mountain. Across generations, selection may produce increasingly exaggerated male traits (for example, male color pattern) and stronger and stronger female preferences for such exaggerated traits.

Stalk-Eyed Flies and Runaway Selection

Empirical evidence of runaway sexual selection comes from Jerry Wilkinson and his colleagues’ work on the stalk-eyed fly (Wilkinson, 1993; Wilkinson, Kahler et al., 1998; Wilkinson and Reillo, 1994). In stalk-eyed flies, females prefer to mate with males possessing eyes that are at the end of long eye "stalks" (Figure 7.17) and eye stalk variation is due, in part, to underlying genetic variation (Birge et al., 2010). In one treatment of their 13-generation experiment, males with the largest eye stalks were selected and allowed to breed with females. In a second treatment, males with the shortest eye stalks were allowed to breed. In both treatments, which females were mated was selected at random. Not surprisingly, in the treatment where long eye stalk length was selected for thirteen generations, the average male eye stalk increased in length, producing a more exaggerated version of this trait. Conversely, in the case where individuals with short eye stalks were selected, the size of the average male eye stalk decreased in length.

Figure 7.17. Stalk-eyed flies and runaway selection. Male stalk-eyed flies show variation in the length of their eye stalks. Lines of flies with long and short eye stalks were bred to test the runaway model of sexual selection. *(Photo credit: Phil Savoie/npl/Minden Pictures)*

The critical finding in this study, however, did not center on the length of the male eye stalk per se. At the heart of the runaway sexual selection model was the finding of a positive link between the length of the male eye stalk and the *female preference for this trait*. Recall that in both treatments—the long eye stalk and the short eye stalk male treatments—the females that mated with males were selected at random. All of the selection pressures were with respect to male eye stalk length. Yet, after just a few generations, when females were given the choice between mating with males with short and long eye stalks, females from the short eye-stalk line preferred males with short eye stalks. This preference for short male eye-stalk length by females in the short eye-stalk line changed in response to selection pressure on *males*, as predicted by the runaway selection model. In the long eye stalk line, females preferred males with long eye stalks, but no more so than females that had not been subject to any selection treatment (that is, females in a control line of flies). In other words, contrary to predictions of the runaway selection model, Wilkinson and his colleagues did not find evidence that selection on males in the long eye stalk treatment produced significant changes in female preference for eye stalk length. While there were a number of possible reasons why results were similar in the long eye stalk length treatment and the control, Wilkinson and Reillo speculate that female preference might very well have been detected had the experiment gone on for a longer period of time.

SENSORY BIAS AND THE EMERGENCE OF MATE CHOICE

The last of the evolutionary models of mate choice that we will consider is the **sensory exploitation**, also known as the **sensory bias**, or **preexisting bias model** (Endler and McLellan, 1988; M. J. Ryan, 1990; West-Eberhard, 1979; Ryan and Cummings, 2013). Sensory bias models posit that when a male trait first emerges it is preferred by females because it elicits a neurobiological response that is already in place in females, and that such a response initially is not associated with mating preferences.

As a hypothetical example, suppose that red berries are the most nutritious food source available to a fruit-eating, blue-feathered songbird species. Females that are best able to search out and subsequently eat red berries survive and reproduce better (Rodd et al., 2002; C. Smith et al., 2004). Natural selection should then favor the neurobiological circuitry in females that allows them best to home in on red items in their environment (Kirkpatrick and Ryan, 1991).

Once a preference for all things red is in place, if red feathers should suddenly arise in males of this normally blue-feathered species, birds with these red feathers may be chosen as mates because the female’s nervous system is already set to respond preferentially to red objects. Males with red feathers, then, are exploiting the preexisting neurobiologically based preferences of females—preferences that evolved as a result of other selection pressures.

The sensory bias model makes a prediction regarding phylogenetic history. On a phylogenetic tree that includes information on both female preference and the male trait preferred by females, the female preference trait should predate the appearance of the male trait (Figure 7.18). In our example of red berries, the preference for red should be in place before red feathers are present.

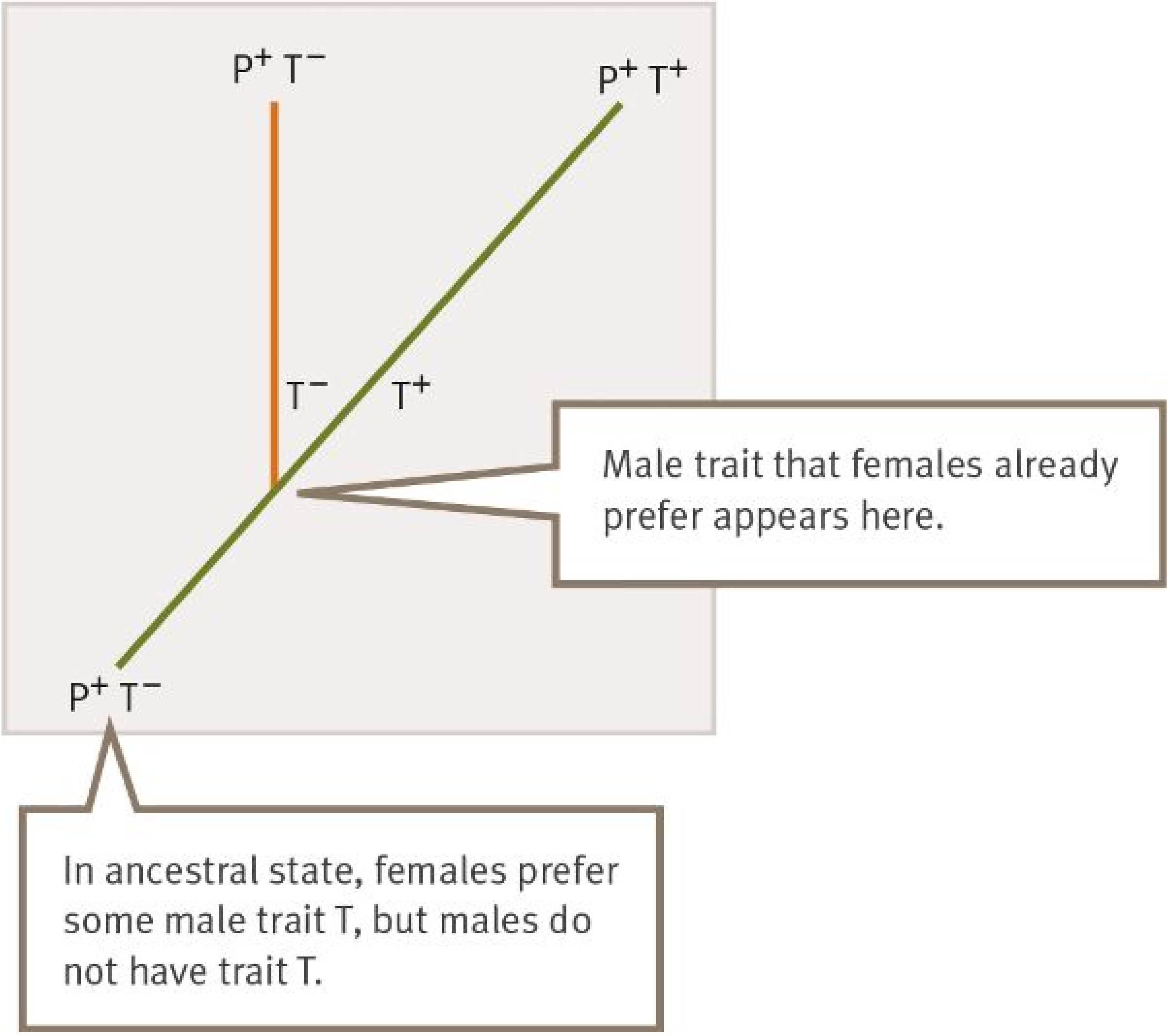


Figure 7.18. Sensory exploitation model. In the sensory exploitation model, female preference (P+) is assumed to predate the male trait (T) that is preferred. In one lineage here (shown in orange), the male trait is immediately preferred once it appears (T+). *(From Ryan and Rand, 1993, p. 189)*

One thing to keep in mind as we discuss the sensory bias hypothesis is that it was designed to explain the *origin*, not the long-term maintenance, of female preference—the sensory bias hypothesis centers on how a female preference initially arose in a population, not how it was maintained in a population by natural selection over evolutionary time.

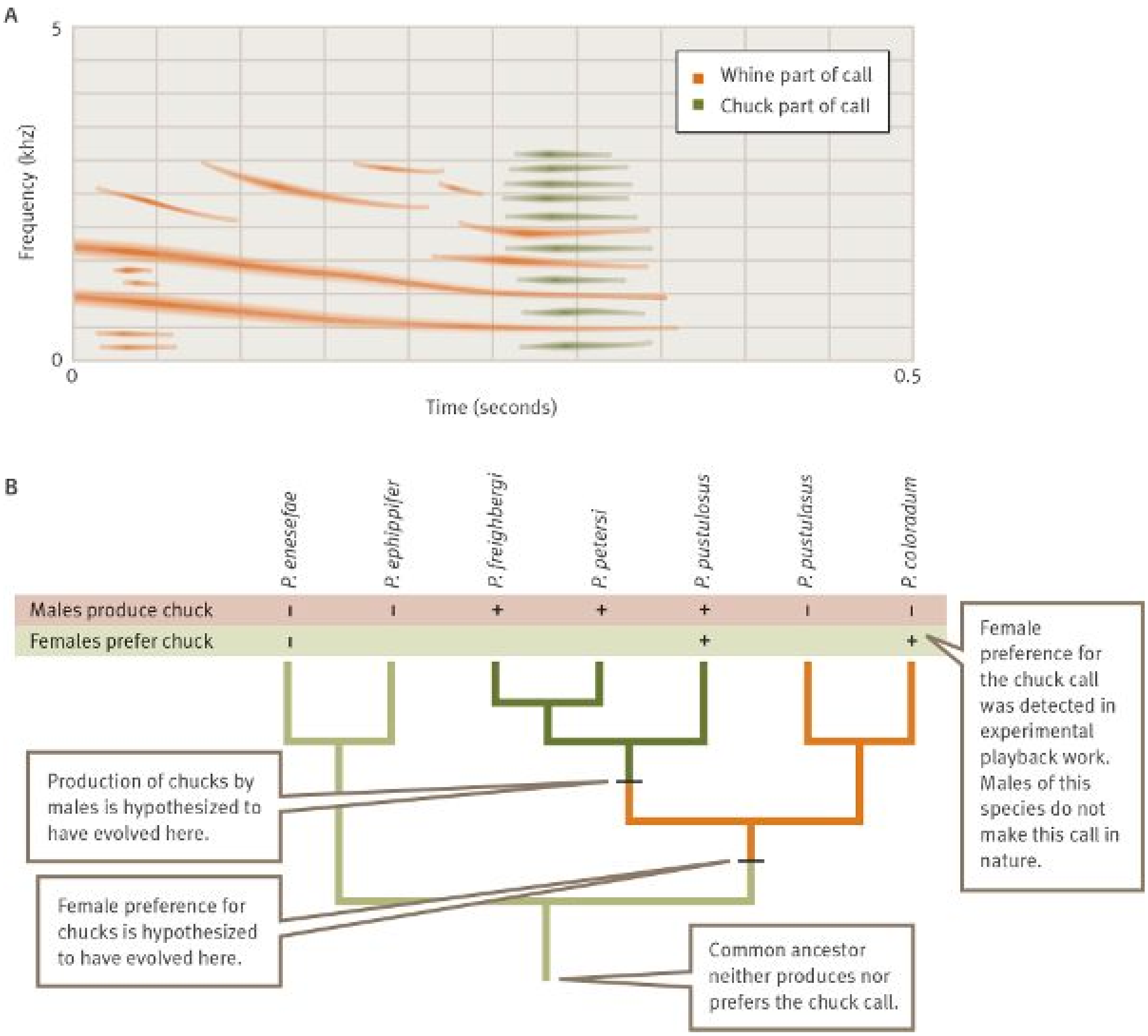
Frogs and Sensory Biases

One of the first studies of sensory exploitation examined mate choice in two closely related species of frogs—*Physalaemus pustulosus* and *Physalaemus coloradorum* (M. J. Ryan et al., 1990; Figure 7.19). Males in both species use calls to attract females. Both *pustulosus* and *coloradorum* males begin their call with a high-frequency "whine." Females pick up the whine part of a male's call through the basilar papilla in their inner ear.

Figure 7.19. Frog calls and sensory bias. *Physalaemus pustulosus* males (shown here) add a unique "chuck" sound to the end of their calls. The calls of *Physalaemus coloradorum* males lack a chuck. The calls of these two species have been used to test models of the sensory bias hypothesis. *(Photo credit: Ryan Taylor)*

Pustulosus, but not *coloradorum*, males may also add a low-frequency "chuck" sound to the end of their call. When *pustulosus* females choose between *pustulosus* males that chuck and those that don't, they prefer to mate with the former. Females detect the chuck through the amphibian papilla section of the inner ear, which is sensitive to low-frequency sounds. Michael Ryan and his colleagues hypothesized that the preference for chucks in female *pustulosus* was the result of an already in-place sensory bias in favor of such low-frequency sounds.

Phylogenetic and behavioral evidence support the contention that the preference for chucks is due to a sensory bias. When Ryan and his colleagues used molecular and morphological data to reconstruct the evolutionary history of the genus *Physalaemus*, they found that the common ancestor of *coloradorum* and *pustulosus* did not use a chuck call. That is, not only do male *coloradorum* not use the chuck call, but the chuck call appears never to have been used in any of the species that make up the evolutionary lineage leading to *coloradorum* (Figure 7.20). Yet when software is used to add a chuck call to the end of prerecorded *coloradorum* male calls, *coloradorum* females show a preference for calls that include a chuck. This experimental manipulation of calls suggests that as soon as chucks appear in a *coloradorum* population, females prefer males that produce such calls, and the auditory circuitry in *Physalaemus* frogs has been designed in such a way as to prefer a certain class of sounds—low-frequency calls like chucks. As predicted by the sensory bias hypothesis, these studies suggest that the preference for chucks predated the actual appearance of chucks in the *Physalaemus* species.



Female preference for the chuck call was detected in experimental playback work. Males of this species do not make this call in nature.

Production of chucks by males is hypothesized to have evolved here.

Female preference for chucks is hypothesized to have evolved here.

Common ancestor neither produces nor prefers the chuck call.

Figure 7.20. Sensory bias in frogs. (A) The whine and chuck components of the call made by *Physalaemus pustulosis*. (B) Preference for the chuck calls arose before the chuck call itself. *(Adapted from Ryan and Rand, 2003)*

Learning and Mate Choice

Psychologists and ethologists have conducted many experiments examining the role of learning in selecting mates (Domjan, 2009; Verzijden et al., 2012; Servedio, 2015). For example, controlled laboratory work on conditioned stimuli (see chapter 5) and mating behavior across many species has found that, after exposure to a conditioned sexual stimulus, males are quicker to copulate, become better competitors with other males, display higher levels of courtship, and produce more sperm and progeny (Domjan, 2006; Figure 7.21).

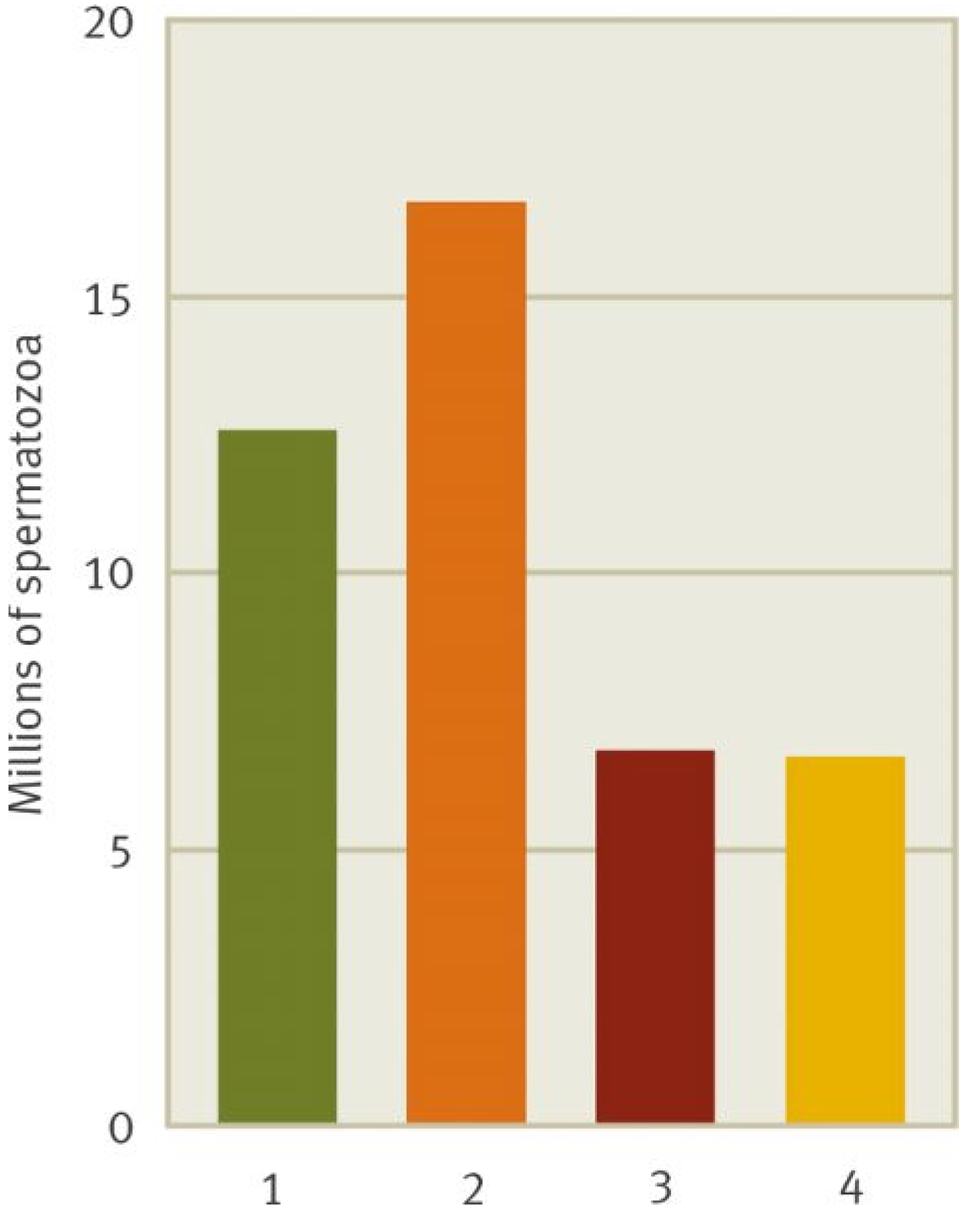


Figure 7.21. Pavlovian conditioning and sperm number. Two different lines of male quail learned to pair a distinctive experimental chamber with the opportunity to mate with a female. Males were then placed in the chamber with a model female. Afterward, spermatozoa samples were taken. Males from both lines that had learned to pair the chamber with the chance to mate produced significantly more spermatozoa than control males (treatments 3 and 4, which consisted of males from the two lines that had not been given the chance to associate these two cues). *(From Domjan et al., 1998)*

SEXUAL IMPRINTING

One type of learning about potential mates is **sexual imprinting** (Bateson, 1978; Lorenz, 1935; ten Cate and Vos, 1999; Chaffee et al., 2013). During sexual imprinting, young individuals “imprint” on the behavior and morphology of adults—almost always their parents—and use these characteristics to guide their subsequent selection of mates. Imprinting is often restricted to some small time window during normal development, but the length of this window varies dramatically across species (including humans) and behavioral contexts (Bereczkei et al., 2004).

Ethologists have developed numerous ways to experimentally examine sexual imprinting, including

1. Cross-fostering (chapter 2). In the case of imprinting, researchers can test the hypothesis that offspring raised by adoptive parents show different mating preferences than those raised by biological parents, and can examine whether such preferences can be linked to something about the behavior or morphology of the adoptive parents (Cooke and McNally, 1975; Cooke et al., 1972, 1976).
2. The “novel trait” approach, in which offspring are raised by parents that have some novel trait introduced by an experimenter.

Klaudia Witte and her colleagues used the novel trait approach to sexual imprinting in their work on the mannikin bird, *Lonchura leucogastroides* (Witte et al., 2000; Plenge et al., 2000). Witte and her team added a novel trait to some adults in her population. The novel trait was a red feather that they attached to the forehead of adult mannikins, so that the feather stood up like a crest. They hypothesized that offspring that were raised in the presence of such adults adorned with a red head feather would display a sexual preference for individuals with red feathers when they matured. They raised juvenile mannikins in one of four groups. Group 1 served as a control in which offspring were raised with their mother and father, both of whom lacked the red feather. In group 2, offspring were raised with their mother and father, each of whom had a red head feather experimentally attached to their forehead. In group 3, offspring were raised with a mother with no feather, but a father with a red feather; and in group 4, offspring were raised with a father with no feather, but a mother with a red feather (Witte et al., 2000).

When offspring reached sixty days of age, they were separated from their parents and their mating preferences were examined.

These birds were given the choice between two members of the opposite sex—one that had a red head feather added, and one that did not. Witte and her team found evidence that young mannikins imprinted on the red head feather of their parents, and expressed a preference for such birds when they themselves matured. Compared with the control groups (in which individuals often preferred unadorned mates), males raised with a mother with a red feather preferred females with red head feathers as mates, and females raised with a father with a red feather preferred males with red head feathers as mates.

Animal behaviorists have also examined the neurobiological underpinnings of imprinting. As an example, let's return to the dendritic spines (on neurons) first discussed in chapter 3. Recall that neuroethologists have argued that an increase in dendritic spines is often associated with learning. If this is correct, it might also be true that when animals rely *less* on learning—including learning about potential mates—we might see a decrease in dendritic spine density. In the context of sexual imprinting, this might manifest itself as a decrease in dendritic spine density soon after an individual has imprinted on the phenotype of those of the opposite sex, as it has now completed one stage of learning about what traits to search for in a mate, and rarely changes such learned preferences after imprinting. Evidence has been found for such a decrease in spine density in the zebra finch.

Following up on early work by Klause Immelmann, behavioral studies have shown that when a male zebra finch is raised by its parents for the first month of life, but then kept in isolation for two months, he often imprints on the phenotype of the first female he encounters after isolation (Bischof and Clayton, 1991; Immelmann, 1972; Immelmann et al., 1991). When Hans Bischof and his colleagues measured dendritic spine density in one area of the zebra finch brain (the media neo/hypostriatum or MNH area), they found a decrease in the spine density after exposure to a female (Bischof and Rollenhagen, 1999; Rollenhagen and Bischof, 1991, 1994; Huchzermeyer et al., 2006). Compared with spine density when males were in isolation, Bischof found fewer dendritic spines in males that had completed the process of sexual imprinting and hence were less reliant on learning about whom to choose as a mate.

LEARNING AND MATE CHOICE IN JAPANESE QUAIL

Michael Domjan and his colleagues have found evidence that classical conditioning (chapter 5) in adults affects mate choice and that adult male Japanese quail will quickly learn to stay in areas in which they have the opportunity to mate with a female (Domjan et al., 1986; Mahometa and Domjan, 2005; Mills et al., 1997). While earlier work had demonstrated that sexual imprinting affects Japanese quail mate choice (Gallagher, 1976), Nash and Domjan found that learning may also play another role in mate choice. They tested the hypothesis that classical conditioning at the adult stage might override the effects of sexual imprinting as a juvenile (Nash and Domjan, 1991).

Nash and Domjan used different strains, or varieties, of Japanese quail. Each trial in their experiment had three subjects: an adult male quail from the standard brown-colored strain, an adult female quail from the brown strain, and an adult female quail from a lighter-colored "blond" strain of quail. The brown males were raised with other brown quail, and these males had already sexually imprinted on the phenotype of brown females. All else being equal, when such males matured, they typically showed a strong preference for brown females as mates. But all else was not equal in the experiment.

In phase 1 of a trial, a brown male was allowed to see a blond female and was then given the opportunity to mate with her. In phase 2 of a trial, the same male could see a brown female quail, but was never in physical contact with her; a male learned that in the laboratory, the presence of a blond female meant a mating opportunity, but the presence of a brown female did not. In the last phase of the experiment, males were tested to see how much time they spent near brown and blond females. The researchers found that blond female quails elicited a much stronger response—adult-stage learning about who was likely to be a receptive mate overrode the effects of early sexual imprinting (Figure 7.22).

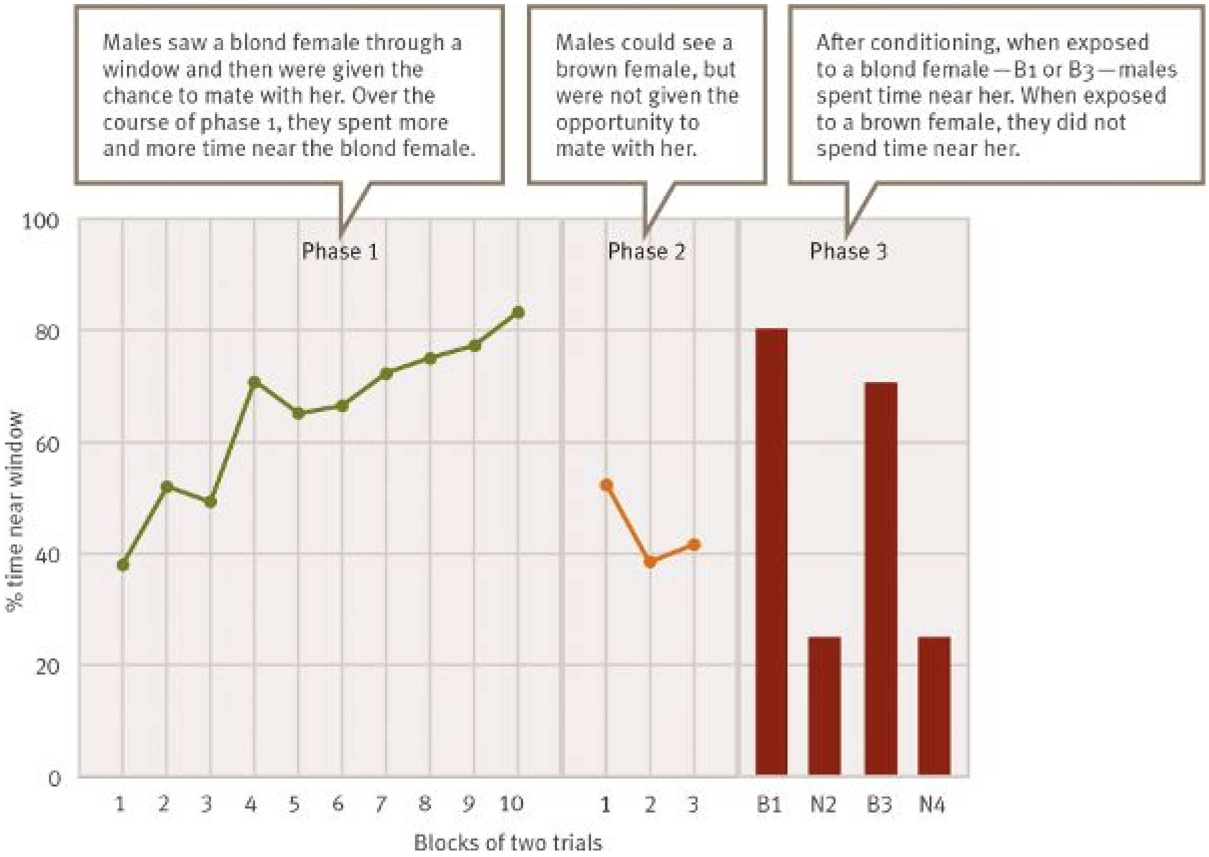


Figure 7.22. Overriding an imprinted sexual preference. Male Japanese quail were raised with brown-colored female quail (prior work had found that under such conditions, male sexually imprint on brown coloration in females). Males were then put through a battery of tests in which experimenters measured the percentage of time they spent near an area associated with mating opportunities. Conditioning—in which males learned that they would have the chance to mate with blond, but not brown, females—overrode sexual imprinting. B = blond, N = brown strain. *(Based on Domjan, 1992, p. 53)*

Cultural Transmission and Mate Choice

Cultural transmission and sexual selection have been studied with respect to song learning and mate choice in birds (Freeberg, 1998, 2004).

MATE-CHOICE COPYING

We will begin our discussion of cultural transmission and mate choice with a definition of mate-choice copying (chapter 6). Following Stephen Pruett-Jones's definition, female mate-choice copying has occurred when a male's probability of being preferred as a mate increases as the result of having been preferred by a female in the past (Pruett-Jones, 1992). If a male has an X percent chance of mating if he has not recently mated, and a Y percent chance if he has recently mated, the effect of mate-choice copying is defined as the difference between Y and X. Mate-choice copying occurs if Y − X > 0; the greater Y − X, the stronger the effect of mate-choice copying.

Mate-Choice Copying in Grouse

Black grouse mating arenas called **leks** are interspersed throughout the bogs of central Finland, Wales, and Scotland (Figure 7.23). Male black grouse (*Tetrao tetrix*) gather together at leks and each individual occupies a small territory, which he defends. To attract females, males display, strutting about with their tail spread out, flapping their wings, jumping in the air, and hissing. As with many lek-breeding species, a single male grouse often obtains about 80 percent of all the matings on a lek. Before mating, females visit leks many times, often in groups that stay together and synchronize their trips to various male territories within an arena (Höglund and Alatalo, 1995). Jacob Höglund and his colleagues found that males that had mated were likely to mate again fairly quickly, suggesting a possible role for mate-choice copying among females (Höglund et al., 1990). In addition, older females mated, on average, three days earlier than younger females, suggesting that mate-choice copying, if it occurred, was most common among younger females.

Figure 7.23. Black grouse and mate-choice copying. Males displaying on leks. This involves strutting, flapping their wings, jumping in the air, and hissing while females observe. *(© Mark Caunt / Shutterstock)*

Höglund and his colleagues placed stuffed “dummy” females on male territories within a lek (Höglund et al., 1995). Each of seven randomly chosen males on a particular lek had stuffed black grouse females (model females) placed on their territories early in the morning, before real females arrived. Males courted these model females and even mounted them and attempted copulations. After observing the males on the lek, females were more interested in mating with a male that had copulated with other females on his territory, even if they were model females. Because models were placed on the territories of randomly chosen males, this finding suggests that mate-choice copying, rather than some set of physical traits possessed by males or some characteristic of their territory, explains the skew in male reproductive success among black grouse.

Mate-choice copying likely plays a role in another species of grouse. In the early 1990s, Robert Gibson and his colleagues studied female mate choice in sage grouse (*Centrocercus* *urophasianus*) in two different leks over a four-year period (Gibson et al., 1991). One of their hypotheses regarding mate-choice copying behavior was that the unanimity of female mate choice would increase as more females mated on a given day, because more opportunities to observe and copy mate choice would exist on such days.

To test this hypothesis, each day Gibson and his team arrived early in the morning before a lek formed and observed all interactions on that lek—when females arrived, which males mated, which males courted, and so on. They tested their mate-choice copying hypothesis using data from fifty-six days of observation and compared their results with a computer simulation that estimated how often females would have chosen the same male on a lek if they had *not* been copying each other. This comparison uncovered support for mate-copying, as the unanimity of female mate choice increased as more females appeared, and this increase occurred more quickly than expected by chance (Figure 7.24).

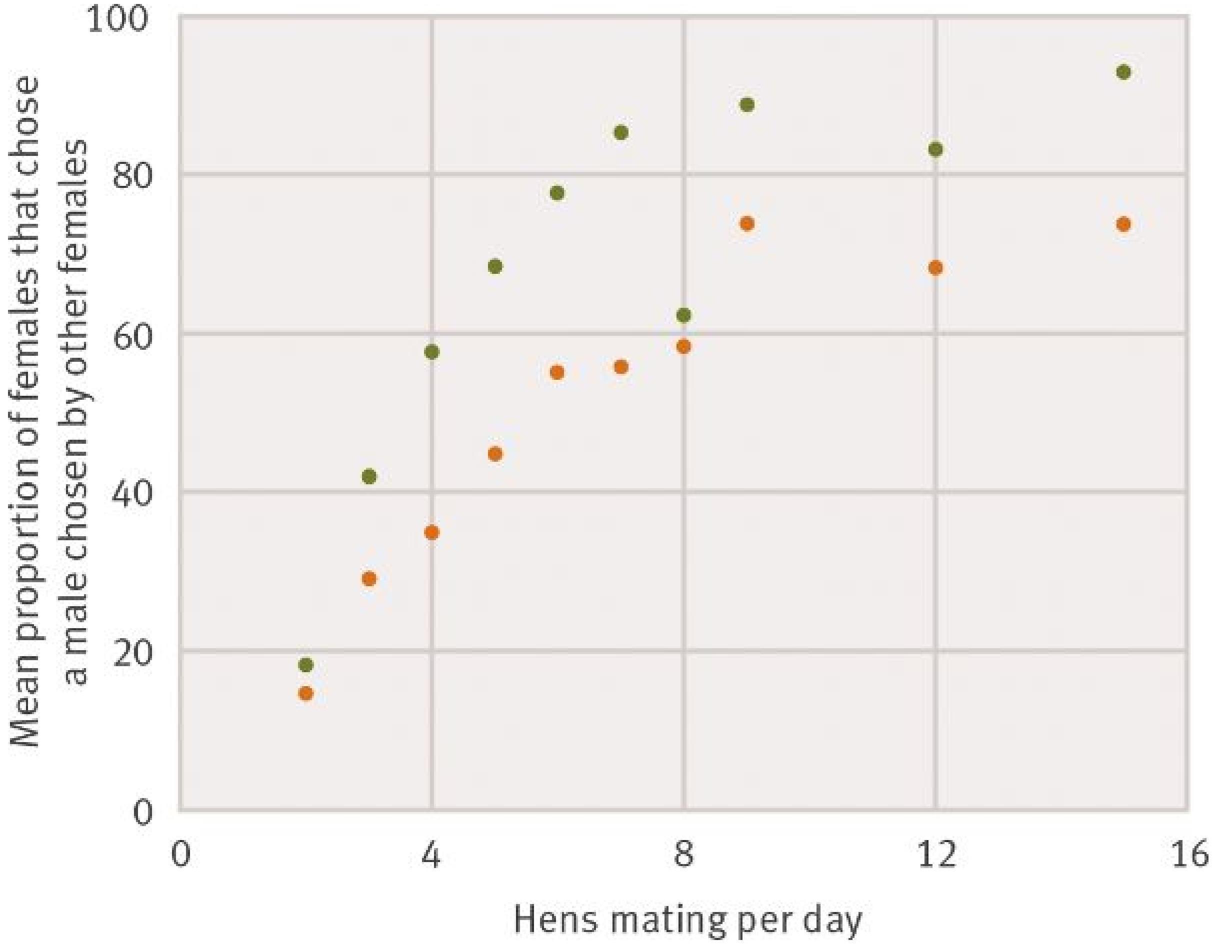


Figure 7.24. Female mate-choice copying in sage grouse. As predicted by models of mate-choice copying, when the number of hens mating per day increased, so too did the proportion of females choosing to mate with a male chosen by other females. The green points are the observed matings, and the orange points are the expected matings if the females had not been copying the mate choices of other females. *(From Gibson et al., 1991)*

Mate-Choice Copying in Mice

Recent work has examined the endocrinological and genetic basis of mate-choice copying. Elena Choleris, Martin Kavaliers, and their colleagues examined the role of oxytocin in facilitating mate-choice copying in mice. Oxytocin (OT) is a neurohormone secreted by the pituitary gland, and it appears to play an important role in social behaviors, including mate choice, maternal bonds, and individual recognition (Choleris et al., 2004; Ferguson et al., 2001; Pedersen and Boccia, 2002). Mice with deletions of the OT gene—called OT “knockout” mice—appear to learn normally, except in the context of social learning and mate choice (Kavaliers et al., 2006).

Choleris, Kavaliers, and their team studied mate-choice copying in three lines of mice, two of which were normal—that is, these mice had the OT gene—and one of which was an OT knockout line of mice. They allowed a female to choose between two males, one of which had recently associated with an estrous female and had traces of the odor of that estrous female in his area, and one of which had not. Females from the two normal lines of mice copied the mate choice of other females—they were attracted to males that had recently associated with estrous females. Females from the OT knockout line, however, did not copy the other females’ mate choice. In conjunction with a number of control experiments run by Choleris and her team that found no difference in other types of learning across the three lines of mice, these results suggest that knocking out the gene for oxytocin has the specific effect of inhibiting mate-choice copying behavior in mice (Box 7.4).

Box 7.4. SCIENCE AT WORK

What is the research question? Does oxytocin play a role in mate-choice copying?

Why is this an important question? The endocrinological and neurobiological underpinnings of cultural transmission are just beginning to be understood.

What approach was taken to address the research question? The mate-copying behavior of a line of mice that had the oxytocin gene knocked out was compared to control lines.

What was discovered? Females in the control lines copied the mate choice of others; however, those in the OT knockout line did not, but showed no other differences in their ability to learn.

What do the results mean? Oxytocin, a neurohormone known to be involved in social bonding, also plays a role in mate-choice copying in mice.

SONG LEARNING AND MATE CHOICE IN COWBIRDS

Mate-choice copying is only one way that cultural transmission might impact the dynamics of sexual selection. Song learning in birds provides another good example of cultural transmission may operate on sexually selected traits (see chapter 6).

One thing that is common to most songbirds is that they learn the songs they sing. In particular, much of the song-learning process involves learning from others that are often referred to as tutors. Todd Freeberg ran a series of experiments with cowbirds to understand cultural transmission and its long-term consequences for mate choice (Freeberg, 2004). He collected juvenile and adult birds from two populations of cowbirds—one population from South Dakota (SD) and one population from Indiana (IN; Freeberg, 1998). Freeberg chose these particular populations because cowbirds display different social behaviors and sing different songs across populations.

Freeberg used the IN and SD birds in a modified cross-fostering experiment designed to examine cultural transmission and mate choice. He raised juvenile SD birds with either SD adults or IN adults (Figure 7.25). In this experiment, if cowbirds behaved like the individuals they were raised with, regardless of whether these individuals were from their native populations, then this would suggest a role for cultural transmission of birdsong.

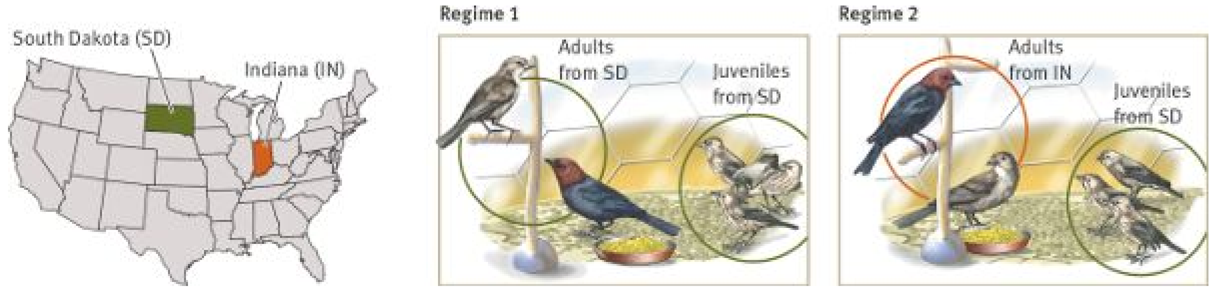


Figure 7.25. Cross-fostering. In one cross-fostering experiment, juvenile cowbirds from South Dakota were raised with adults from South Dakota (regime 1) or adults from Indiana (regime 2).

When juvenile cowbirds matured, they were observed in a large aviary that contained *unfamiliar* birds from both the SD and IN populations. Freeberg found that when placed into such groups, birds paired up and mated with others that came from the same rearing regime (IN or SD) in which they were raised—SD birds raised with SD adults preferred SD birds as mates, and SD birds raised with IN birds preferred IN birds as mates. The mating preferences of the SD birds were strongly dependent on the social environment in which the birds were raised.

Freeberg and his colleagues explored what it was about the social environment during development that might be responsible for SD birds' preference for mates that were like the birds with which they were raised. The answer appears to involve copying and perhaps sexual imprinting. Males copied the songs of the adult males with which they were raised, regardless of whether those adults were from South Dakota or Indiana (Freeberg et al., 2001). Furthermore, female SD birds preferred songs that were like those of the males with which they were raised (M. J. West et al., 1998). This preference either might be an example of females copying the song preferences of adult females in their population, or it might be a consequence of females imprinting on the songs of the males they were exposed to during development. Further work is needed to distinguish between these possibilities.

Male-Male Competition and Sexual Selection

After Darwin introduced the idea of sexual selection, much of the work in this area focused on intrasexual selection in the form of male-male competition for females. Intrasexual selection is often more obvious to ethologists than female mate choice, as it often involves direct competition between males, as in the classic case of various males bashing horns to determine access to a female. But intrasexual selection need not be as dramatic as fierce fights between males. Competition may be less direct, as in the case of male cuckoldry or sperm competition, both of which are examined in detail in chapter 8.

RED DEER ROARS AND MALE-MALE COMPETITION

Tim Clutton-Brock and his colleagues studied male-male competition in roaring behavior in red deer (*Cervus elaphus*; Clutton-Brock and

Albon, 1979; Clutton-Brock et al., 1979). Male red deer stags on Rum Island, Scotland, form harems during the mating season (the rut) and fight off other males to defend their harems. Twenty-three percent of harem holders show some sign of a fighting injury and six percent are permanently injured, suggesting strong selection pressure for accurately assessing an opponent's strength to avoid injury and possible death at the hands of a much stronger rival. Because of the risk of injury associated with fights, Clutton-Brock and Albon hypothesized that male red deer should use honest indicators of each other's fighting ability to determine how much time and energy to invest when competing with other males for access to females (Clutton-Brock and Albon, 1979).

They hypothesized that the main indicator of strength and fighting ability in males was roaring. Evidence suggesting that roaring was being used to assess an opponent's fighting ability in the context of harem holding included

- Roaring and associated activities such as "parallel walks," in which males walk alongside one another to assess their size and fighting ability relative to others, were almost exclusively seen during the mating season (Figure 7.26).
- During the mating season, harem holders roared more than those without a harem (Figure 7.27).
- Roaring rates increased when a harem holder was approached and ownership of his harem was threatened by another male.
- The more a male roared, the more likely he was to win a subsequent fight.
- Roaring contests were much more common between mature stags of approximately equal fighting ability than between stags of unequal fighting ability, and roaring rarely escalated (via the "parallel walk" stage) to fighting except among the most closely matched stags, which suggested that roaring was a good indicator of fighting ability and one upon which stags often relied.

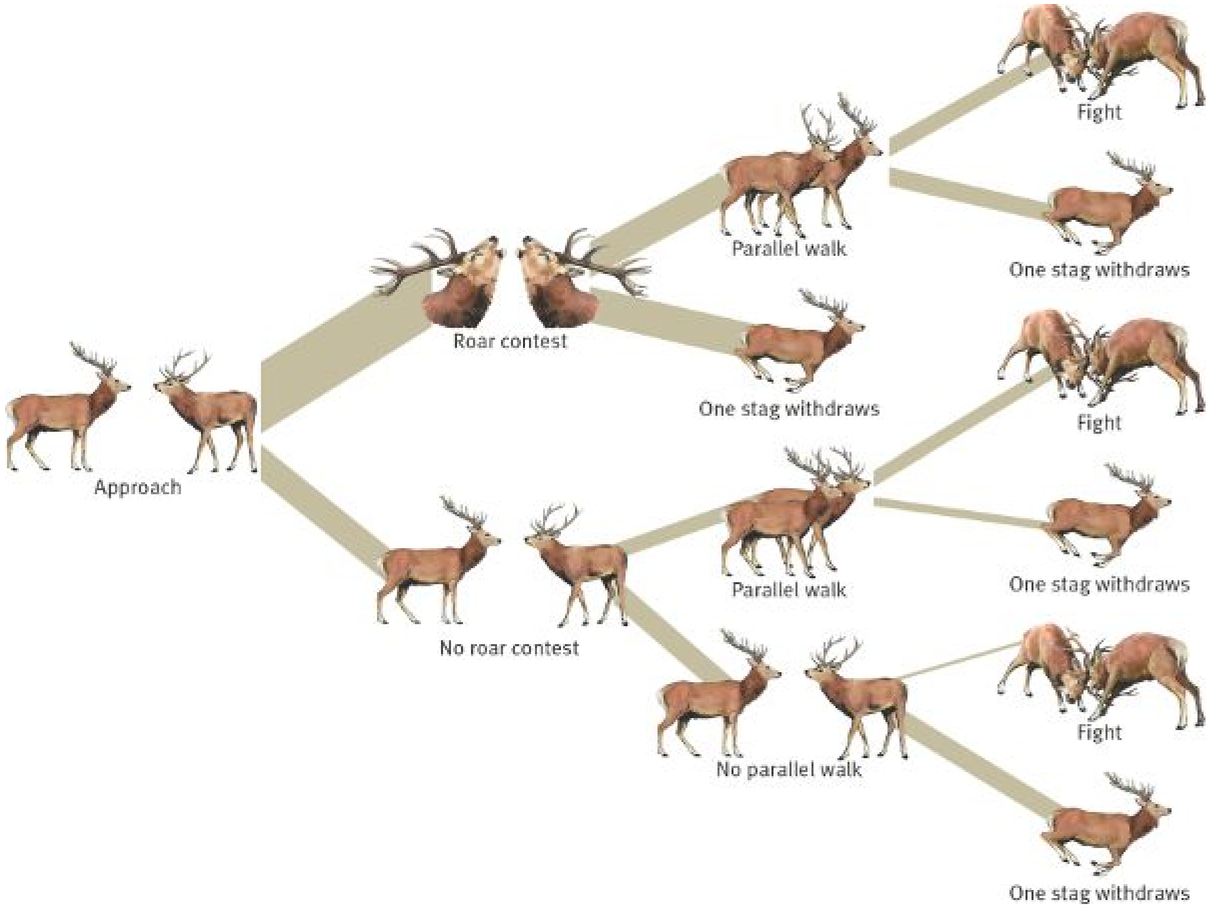


Figure 7.26. Approach and assessment in male red deer. When two male red deer approach within 100 m of each other during the mating season, any number of outcomes are possible. Thicker lines represent more likely outcomes. *(From Clutton-Brock et al., 1979)*

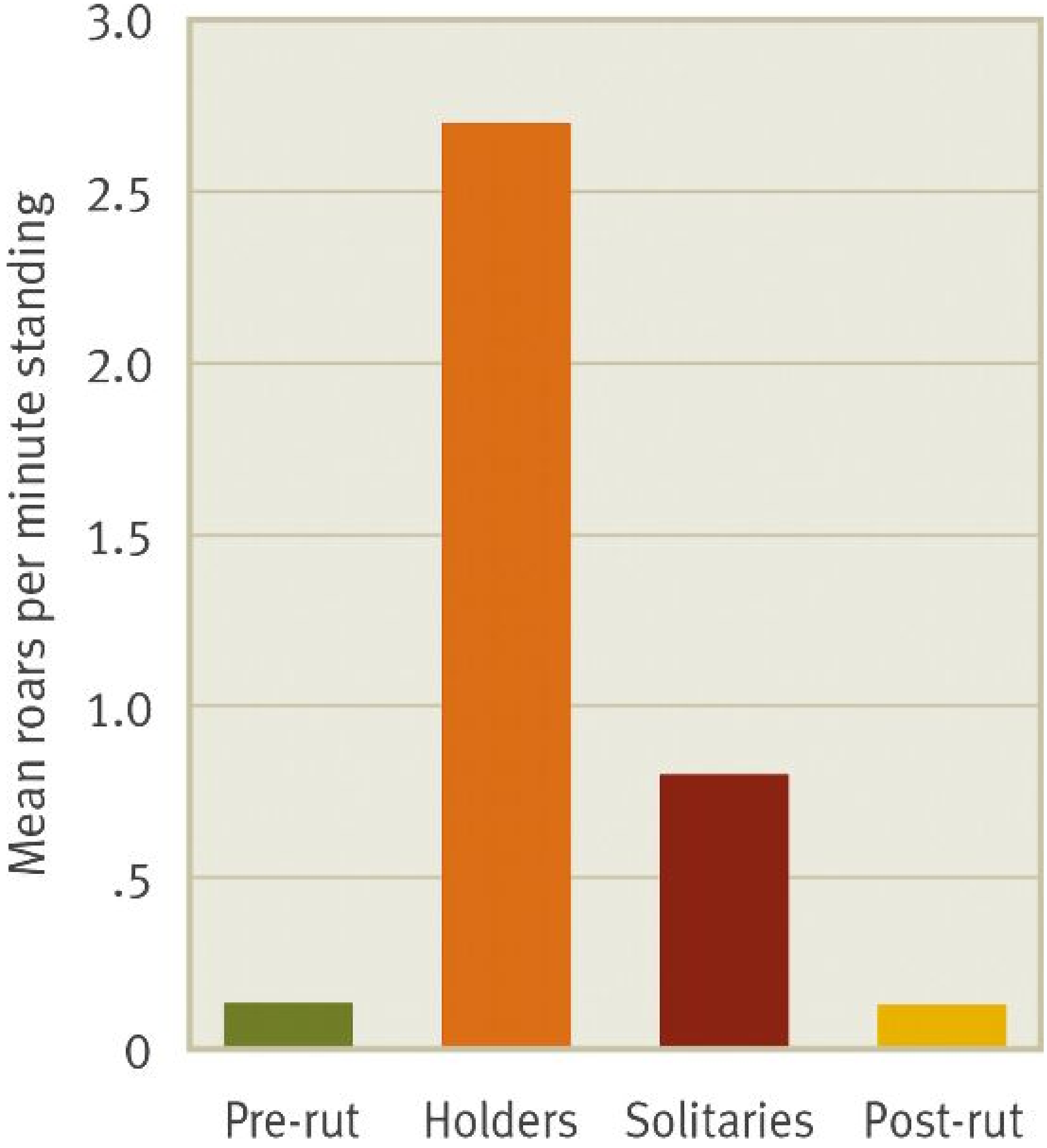


Figure 7.27. Roaring rates in red deer. Males in possession of a harem (holders) roared much more than males not holding a harem (solitaries), as well as more often than males in the pre-rut or post-rut periods. *(Based on Clutton-Brock and Albon, 1979)*

Clutton-Brock and his team also experimentally manipulated red deer roars to examine the hypothesis that males use roar rate to assess opponents. Using stags of different sizes and abilities, the researchers played tapes for red deer males of other males roaring at different rates. They then measured the responses of the stags to the different roars on the tapes. When playback tapes included sounds from a larger opponent, male red deer responded by being more attentive to such calls and increasing their own rate of roaring (Reby et al., 2005).

Together, all of the data above suggest that male-male competition for females has led to a social system involving fine-tuned communication designed to maximize access to females while minimizing injuries that result from serious fights.

MALE-MALE COMPETITION BY INTERFERENCE

Although many examples of male-male competition involve males fighting *before* a female is present, one interesting subset of male-male interactions involves one male interfering with a second who is attempting to mate with a female. This sort of behavior is common in amphibians and insects (Duellman and Trueb, 1994). For example, in the European earwig (*Forficula auricularia*), heavier males often succeed in interrupting copulation between lighter males and females by displacing lighter males to gain access to females (Forslund, 2000).

In at least some cases of male-male interference, females appear to solicit males to try to remove a rival during the actual mating event. Cox and Le Bouef hypothesized that females incite male-male competition because it increases the probability of mating with the highest-ranking male in a group (Cox and Le Boeuf, 1977). They tested this idea in the elephant seal (*Mirounga angustirostris*), where males form large harems of females and in which the males are much larger than the females (Figure 7.28). Harems of up to forty females are defended by a single dominant (large) bull seal, and there is huge variation in reproductive success among males. In one long-term study, only 8.3 percent of males mated, but some males inseminated 121 females (Le Boeuf and Reiter, 1988).

Figure 7.28. Elephant seal fights. Male elephant seals are much larger than females and fight for access to females during the breeding season. *(Photo credit: David Osborn / Alamy Stock Photo)*

Cox and Le Bouef marked 271 estrous female elephant seals and tracked attempted matings (mounts) with these females. Eighty-seven percent of the attempted mounts were “protested” to some degree or another by the females. Protesting included many behaviors, most prominently loud calls and constant back-and-forth movement to prevent the male from copulating. These protests were quite effective, as 61.4 percent of protested mounts were interrupted by another male to some extent, as opposed to 25 percent of mounts that went unprotested. Females rarely protested dominant male mounts, but they often protested mounts attempted by subordinates, which led to an increased probability of copulation between the highest-ranking males in the vicinity and the females that had protested mounts with subordinate males (Table 7.1).

Table 7.1. Female elephant seals protest more when mounted by males that are not top-ranked in dominance hierarchy. Cox

and Le Boeuf found not only that alpha (dominant) males mounted females more often, but that the females protested their mounts less often than mounts by non-dominant adults or sub-adults (Subadult [1], Subadult [2]). *(From Cox and Le Boeuf, 1977, p. 324)*

Age or Social rank of Mounting Male	**Mounts Observed* (N)**	**Totally Protested (%)**	**Partially Protested (%)**	**Not Protested (%)**
Alpha	74	37	43	20
Non-dominant adult	70	49	34	17
Sub-adult (1)	9	78	22	0
Sub-adult (2)	4	100	0	0

*Interrupted mounts are excluded.

The elephant seal example shows how difficult it can be to completely disentangle female mate choice from male-male competition. Clearly, interruption of the copulation attempts of males by other males involves male-male competition, but in the elephant seal example, this competition is likely initiated by a female to increase her probability of mating with the highest-ranking male in the area.

Sexual Size Dimorphism and Male-Male Competition from a Phylogenetic Perspective

Patrik Lindenfors and his colleagues have studied the relationship between sexual size dimorphism and male-male competition in the pinnipeds (seals, walruses, and sea lions), including the elephant seals described above (Lindenfors et al., 2002), from a phylogenetic perspective. They hypothesized that in species in which harem size is large, and hence where male-male competition is usually most intense, sexual size dimorphism (males larger than females) should be greatest. In addition, since sexual selection for large body size in pinnipeds should act more strongly on males than females, Lindenfors and his team predicted that, as harem size increased, female body size would remain fairly constant. The researchers wanted to make certain, however, that if this relationship was uncovered, it was a result of sexual selection pressures, rather than the fact that pinnipeds share a recent common ancestor, and hence share behavioral and morphological attributes because of common descent. To distinguish between these possibilities, they used the independent contrast method we discussed in chapter 2. To test their hypotheses, they first gathered published data on harem size, male size, and female size for thirty-eight species of pinnipeds. Their analysis uncovered a significant positive correlation between harem size and sexual size dimorphism: the larger the average harem size in a species, the larger was the relative size of males compared with females. This analysis also found that the relative size of males increased as harem size increased, but the relative size of females stayed fairly constant (Figure 7.29).

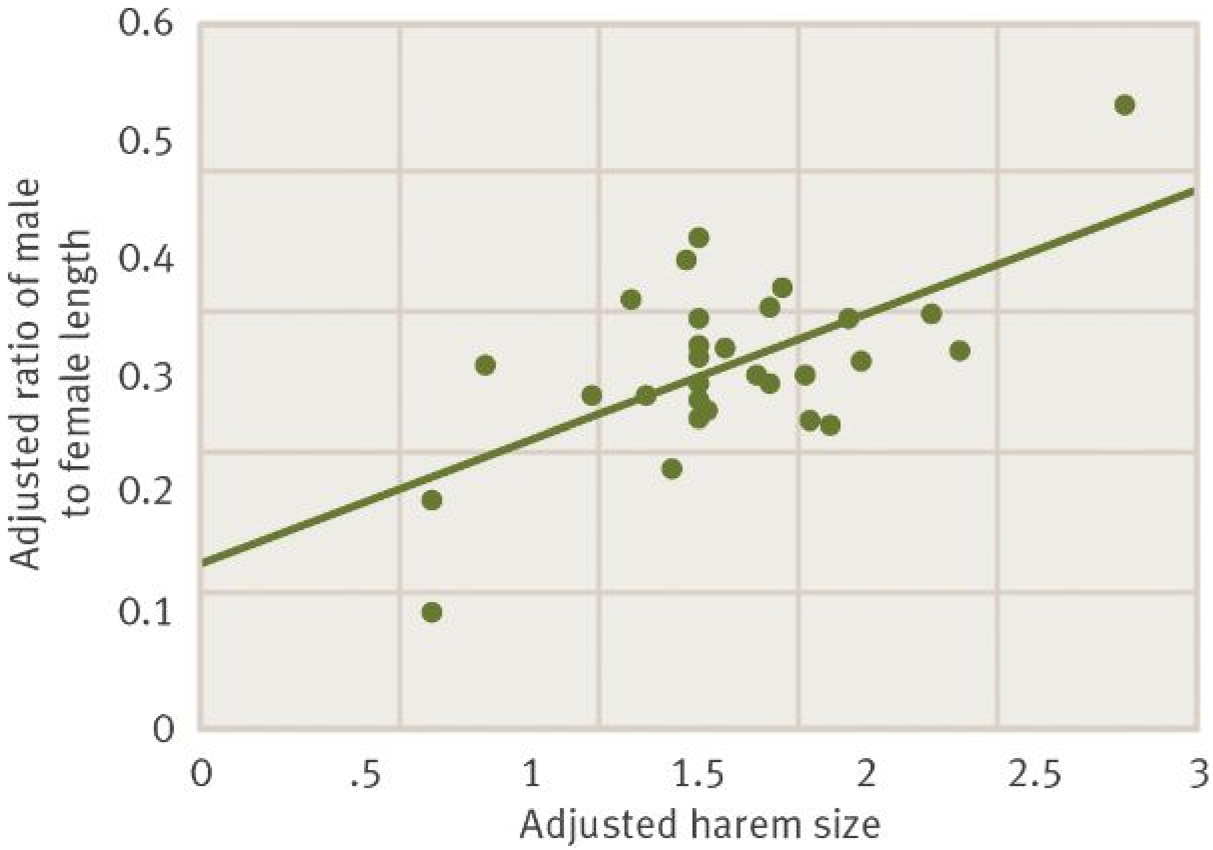


Figure 7.29. Harem size and sexual selection. In pinnipeds, there is a positive relationship between harem size and the relative difference in size between males and females. Each point represents a comparison between two species of pinnipeds. The *x*-axis and *y*-axis are adjusted independent contrast measures. *(From Lindenfors et al., 2002, p. 189)*

MALE-MALE COMPETITION BY CUCKOLDRY

In many species of fish, ethologists have found different male reproductive types, or morphs, that are distinct in structural, physiological, endocrinological, and behavioral traits (Gross, 1985; Gross and Charnov, 1980). In bluegill sunfish (*Lepomis macrochirus*), three male morphs, known as parental, sneaker, and satellite morphs, coexist within populations (Gross, 1982; Neff et al., 2003). Parental males are light-bodied with dark yellow-orange breasts, build nests, and are highly territorial, chasing off any other males that come near their territory. It takes between six and thirteen days for their eggs to hatch, and males exert energy both fanning the eggs to oxygenate them and defending the nest against predators during this time (R. Coleman et al., 1985; Figure 7.30).

Figure 7.30. Parental male bluegill sunfish tending his eggs. Parental male sunfish build nests and care for their eggs by fanning them and defending them against predators. *(Photo credit: Dr. Bryan D. Neff)*

Sneaker males are smaller and less aggressive, and they do not hold territories. Instead, they spend time in hiding places near a parental male and swim quickly into a territory while the parental male and female are spawning. They then shed their sperm and swim away; the whole process takes less than ten seconds (Gross, 1982). Male-male competition here then involves sneakers trying to outcompete others by sneaking into a parental male's territory and cuckolding the parental male (Figure 7.31). Using molecular genetic analysis, researchers have found that, depending on their relative numbers in a population, sneaker males fertilize between 0 and 58.7 percent of all bluegill eggs laid in Lake Opinicon, Canada (Philipp and Gross, 1994).

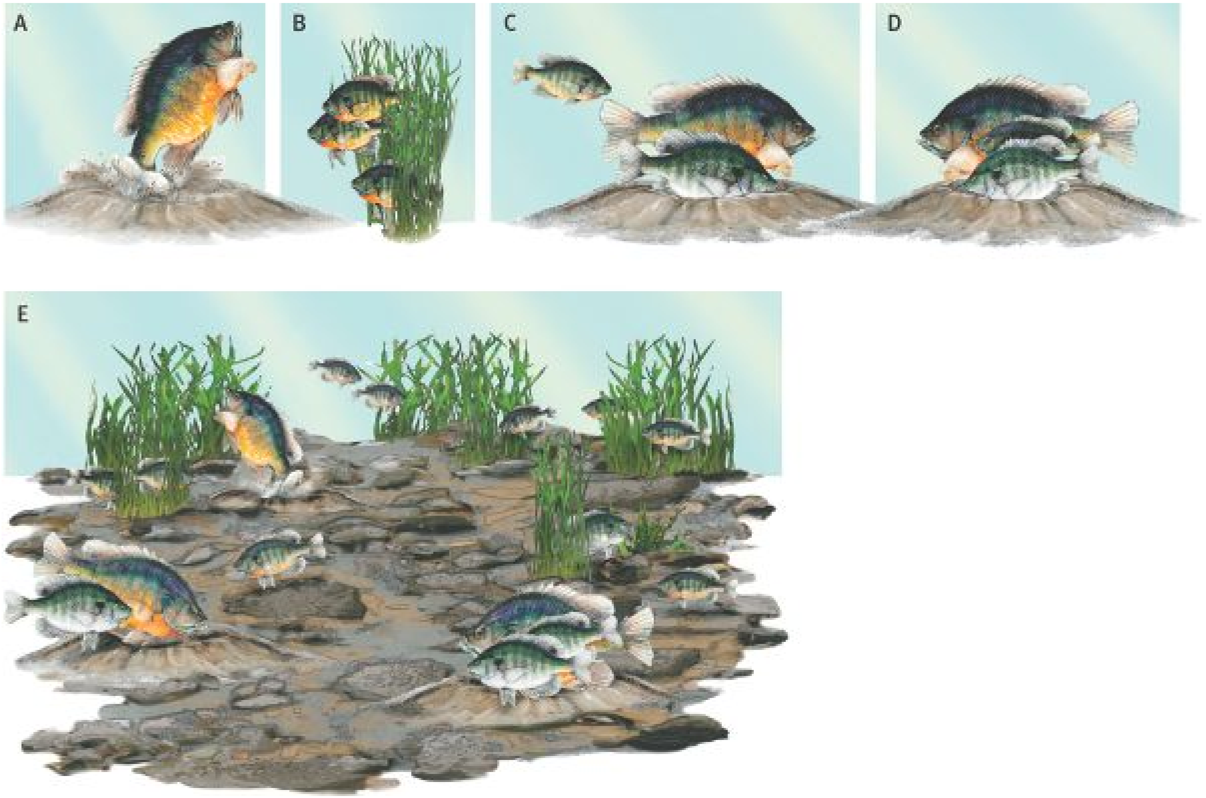


Figure 7.31. Bluegill morphs. (A) A bluegill parental male preparing a nest. (B) Sneaker males hiding behind plants awaiting a chance to quickly sweep into a parental nest. (C) A satellite male swimming over a nest containing a male and female. (D) A satellite male swimming between a parental male and a female. (E) A composite of A–D. *(Based on Gross, 1982)*

A third male morph, labeled a satellite, is also be found in some bluegill populations. Satellite males tend to look like females, and they position themselves between a spawning pair. If the parental male treats the satellite male as another female, he attempts to spawn with both the female and the impostor satellite male, at which point the satellite male releases his own sperm.

Because of the very different reproductive strategies seen among these three bluegill morphs, Bryan Neff and his colleagues tested whether there are also differences in sperm production and sperm quality across morphs (Neff et al., 2003). They predicted that because of their mating strategy, sneaker males might invest most heavily in sperm production. Results are consistent with this prediction. Although parental males are much larger than sneakers and have much larger testes, when Neff and his colleagues examined the ratio of testes size to body size—the relative investment in testes—sneaker males had the highest ratio, followed by satellites and then parentals.

The relative investment in testes size is an indirect measure of sperm production. A more direct measure would be the number of sperm produced per ejaculate. Given that the sperm produced by sneakers are always competing with parental sperm, but parental sperm are not always competing directly with sneaker sperm (not all parentals are cuckolded), a high density of sperm per ejaculate should be more strongly favored in sneaker males. When Neff and his team looked directly at the density of sperm per ejaculate, they found that sneakers produced more sperm per ejaculate. Sneakers do, however, pay costs for investing so heavily in sperm production. Their sperm are shorter lived than sperm from parental males, and when Neff and his colleagues stripped sperm from both sneakers and parentals, and then released the same number of parental and sneaker sperm over eggs, sperm from parental males were more likely to fertilize eggs than were sperm from sneaker males. If we focus on the sneaker and parental morphs, the work on testes and sperm production show two very different reproductive strategies: sneakers invest in producing many short-lived, lower-quality sperm, whereas parentals invest in producing fewer but higher-quality sperm.

As our prior examples illustrate, there are myriad ways that males compete, both directly and indirectly, with one another for access to mating opportunities. In the next chapter (Mating Systems), we will see how in cases where females mate with multiple males, they sometimes employ *post*-copulatory strategies to select between the sperm of different males. For now, however, we examine a different sort of sperm competition—one in which males use *pre*-copulatory sperm allocation strategies to attract females and maximize their chances of mating success.

Many studies have found that males can adjust the number and quality of sperm they produce in response to competition from other males (Wedell et al., 2005; Snook, 2005). These studies, however, often have a confound with respect to male-male competition, because males also adjust sperm quality and number in response to the females they are attempting to mate with (Thomas and Simmons, 2007). Ideally then, researchers would like a system with *pre*-copulatory sperm competition between males, but without direct male-female interactions.

In a some species of insects, sperm transfer is disassociated with male-female interactions, as a male deposits a spermatophore—a capsule of sperm and assorted proteins, which in insects, often sits at the tip of the stalk—in its environment. Some time later, a female selects which spermatophores to pick up in their ovipore, and hence which male will fertilize her eggs.

In the springtail, *Orchesella cincta*, males deposit spermatophores in the absence of females. Females pick up only one spermatophore and they receive indirect benefits from discriminating between spermataphores (Zizzari et al., 2009). Valentina Zizzari and her colleagues tested whether males adjusted the size and quality of their spermataphores in response to male competitors, and whether, if such adjustments occurred, they had any impact on female choice of spermataphores (Figure 7.32) (Zizzari et al., 2013).

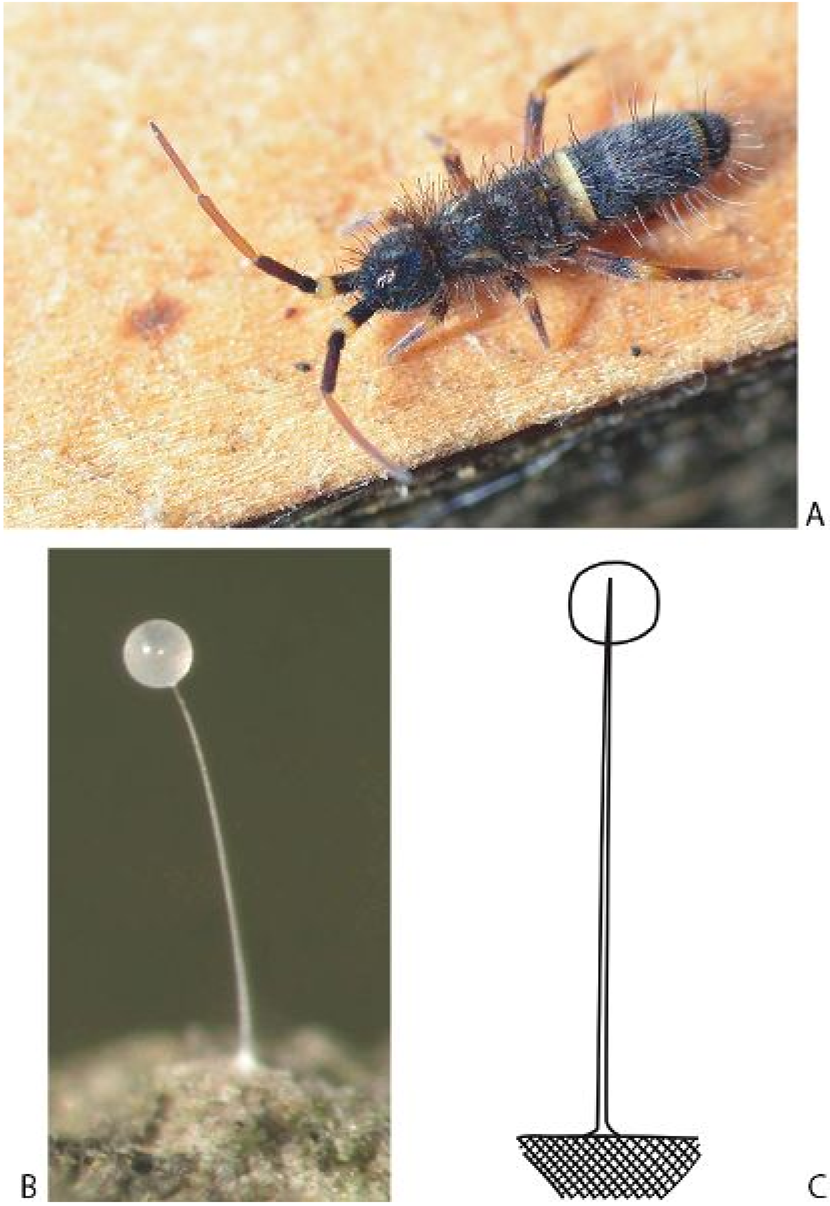


Figure 7.32. **Springtail spermatophores.** (A) A springtail, *Orchesella cincta*. (B) A spermatophore from a closely related species, *Orchesella villosa*, showing stalk and sperm drop. (C) A schematic of a *Orchesella cincta* spermatophore. *(Credits: © Christophe Quentin; © Pietro Paolo Fanciulli)*

They examined spermatophore production in male springtails in three treatments: Treatment 1) a lone male control, Treatment 2) a male placed with a second male who was producing spermataphores, and Treatment 3) a male placed with another male who was at an instar stage where they do not produce spermataphores. Somewhat surprisingly, males in

Treatment 1 produced the *most* spermatophores—that is, instead of producing more spermatophores when in the presence of other males, individuals produced fewer.

What appears to be happening is that when in the presence of other males, males trade off quantity versus attractiveness of spermatophore production. When Zizzari and her colleagues gave a female the choice between two patches with an equal number of spermatophores in each, she showed a strong preference for the patch that contained spermatophores from males in treatment 2 over treatment 1 (Figure 7.33). Males modify the number and attractiveness of their spermatophores as a result of indirect competition from others. What proximate cues females are using to make their choice of male spermatophores is not yet clear, though it is likely mediated by olfactory cues (Box 7.5).

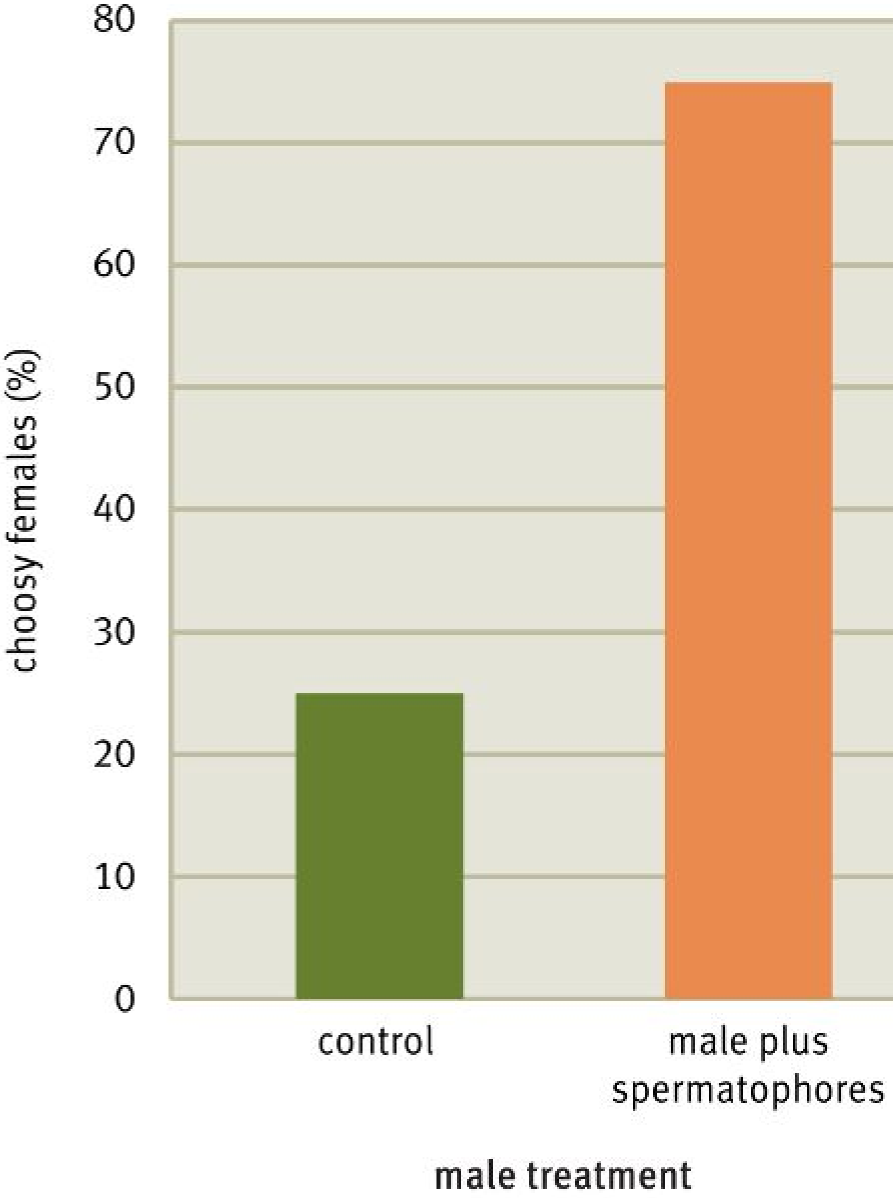


Figure 7.33. **Spermatophore preference in female springtail.** When given a choice between two spermatophores produced by a control male and two spermatophores produced by a male from the treatment where he was paired up with a reproductively active second male, female springtails showed a strong preference for the latter. By permission of the Royal Society. *(From Zizzari et al., 2013)*

Box 7.5. SCIENCE AT WORK

What is the research question? Do males adjust spermatophore number and quality as a function of male-male competition? Does this affect female choice?

Why is this an important question? Much work has examined post-copulatory sperm competition, but very few studies have examined pre-copulatory sperm competition.

What approach was taken to address the research question? Controlled laboratory experiments on spermatophore deposition and female choice in the springtail, *Orchesella cincta*, were undertaken.

What was discovered? Male springtails produce fewer but more attractive spermatophores.

What do the results mean? Male-male competition can be very subtle, yet still affect female mate choice.

Interview with Dr. Anne Houde

You've done extensive research on sexual selection in guppies. Why have you studied that species? How did you first get interested in working with these small fish?

An aspiring scientist can choose a study system in two different ways. First is to sit at your desk and read the literature for a while, find a research question, and then find a study system to help answer it. Second is to start by getting involved with organisms that interest you, either in the field or in the lab. Once you know your system, you can start asking questions. This is what I did: started with the system and then thought of the questions. Of course, to think of good research questions, I needed to have a good grounding in my field, animal behavior, and its literature.

I started out working on birds—terns—but found them to be so long-lived that it was hard to answer questions that interested me in a reasonable amount of time. Then I went in the opposite direction and started looking at the sexual behavior of *Drosophila*, but I did not find flies very exciting (I did not know about their songs and pheromones). When David Reznick came to study life history evolution in my department and gave me some guppies, I started looking at their sexual behavior. I soon realized that I could address some important questions about sexual selection simply by recording male color patterns and observing behavior. I turned out to be correct about this, and have been working on guppies for the last twenty-five years!

Back in 1871 Darwin proposed that females might exert some choice in choosing their mates. Why do you think it took so much longer to study this form of sexual selection compared to studying male-male combat?

The study of mate choice by females did not really get going until the late 1970s, more than 100 years after Darwin's book about sexual selection. I think there are a few reasons for this. People did not take the idea of natural selection seriously until decades later, people had difficulty imagining that nonhuman animals could do things like choose their mates, and science itself has had a long history of being biased toward a male perspective.

When most people think of male-male competition they envision two rams butting heads. Is it possible for male-male competition to be more subtle?

Just as “survival of the fittest” does not only mean that the strong survive by beating up the weak, male-male competition can take many forms. Darwin’s classic distinction says that sexual selection (differences in mating success) can occur if female behavior results in greater mating success of some males than others (female choice), or if interactions between males lead to differences in mating success (male-male competition). So yes, two rams might butt heads until one emerges the victor and the other leaves the area. Presumably the winner then has greater access to reproductive females while the loser risks being beaten up if he comes near the females again. But the combat does not need to be overtly physical.

What else can males do to increase their own success at the expense of others? In many species, male-male interactions are mediated by signals such as coloration, visual displays, or songs and calls rather than fighting, which can be very costly. Males are able to communicate their prowess and likelihood of winning in physical combat through signals like these. Amazingly, these signaling systems seem to work in lieu of combat, perhaps because the signals evolve to be “honest.” Animal behaviorists have been fascinated by the seeming paradox of how signals can be “honest”—evidently, males who “bluff” still face the risk of getting beaten up.

The effect of symmetry on mate choice has proven to be quite a contentious issue. Where do you come down on the importance of symmetry when it comes to choosing mates?

There certainly seems to be something to the idea that mate choice can be based on symmetry—the question is, Why? There are plenty of empirical studies in which the researchers have related mate choice to some measure of symmetry, including studies of humans. The implication is that there must be some benefit to choosing a symmetrical mate if this preference has evolved. The argument goes that an individual with "good genes" will be developmentally stable and be more symmetrical than an individual with lower genetic quality. Thus, an animal choosing a mate should be able to use symmetry as a signal of good genes, and a preference for symmetry should be favored. Perhaps certain sexual ornaments like tail plumes or bright color patterns have evolved because they show off symmetry particularly well.

The problem I see is that there can be circularity in this reasoning. Let's suppose that "good genes" do result in greater symmetry (a point that needs more study). But individuals with good genes might show other signs of this too. Perhaps they are especially vigorous and athletic and potential mates can detect this. So, in studies that find a correlation between symmetry and attractiveness, choice might just be based on a different, unrelated correlate of good genes so that the correlation with symmetry is spurious. A case in point is a study of scorpionflies by Randy Thornhill showing that females prefer the odor of more symmetrical males, even with no chance to assess male symmetry. There is a way out of this problem, and there are studies that convince me that there are preferences for symmetry per se.

How far can we extrapolate from animal studies of mate choice to human mate choice? Are there warning signs one can look for that tell us we have crossed some line we shouldn't cross?

We can learn a great deal from animal studies to understand mate choice in humans. The now-famous "sweaty T-shirt" studies, in which mate choice based on odors has been detected in humans, are a good example. These are adaptations of studies done on rodents, and they reach similar conclusions about, for example, the role of relatedness or MHC genotype in mate choice, despite humans' notoriously poor sense of smell. So mate choice, narrowly defined, has some clear similarities between humans and other species. What are the pitfalls?

First of all, it is too easy to forget that the role of culture in human behavior is vastly more complex and important than in any other species. Studies of classified ads reveal that men prefer youth and beauty in women, while women prefer wealth in men. Do these preferences maximize reproductive success by identifying women with high reproductive value and men who are good resource providers, similar to many animal species? Maybe, but we need to think harder about the interplay of biological and cultural evolution in how men and women construct classified ads.

Second, there is a danger of falling into the “naturalistic fallacy,” especially when thinking more generally about patterns of sexual behavior in humans. Yes, most animal species show the stereotype of macho males and choosy females. The same stereotype in humans probably has an evolutionary origin. Does this mean oppression of women by men is morally justified and inescapable? No, of course not. The answer to this paradox is to think more deeply about human moral systems (themselves the product of natural selection) and also the interplay of natural selection and cultural evolution in shaping the roles of men and women in human society.

How do you think the current focus on brain function will affect our understanding of the evolution of mate choice over the next five years?

It is always hard to see into the future, so let me start with two areas I think are especially promising right now. For several years, we have been seeing studies using various kinds of brain scans (e.g., PET scans), in which “active” parts of the brain are visualized. Mostly these are studies of humans, comparing brain activity in different contexts or between different people. I think this approach could be potentially useful in studies of sexual behavior and mate choice. For example, we might be able to look at the interplay between attraction, fear, and aggression when an individual responds to different potential mates. This kind of “whole-brain” imaging approach can lead to more detailed, neuron-level studies of specific brain circuits involved in producing or modulating behavior.

An even more powerful genomic approach to understanding brain function during mate choice involves directly assessing gene expression in the brain. Scientists are beginning to use this method to understand which genes are involved in a variety of behavioral activities and contexts, including mate choice. Ultimately, perhaps, we will be able to look at how local and global gene expression patterns and neural activity interact in the context of sexual behavior.

Dr. Anne Houde is a professor at Lake Forest College. Her work on sexual selection in guppies is summarized in her book, *Sex, Color and Mate Choice in Guppies* (Princeton University Press, 1997).

SUMMARY

1. When developing his theory of sexual selection, Darwin outlined two processes: intersexual selection and intrasexual selection.
2. Intrasexual selection involves competition among one sex, usually males, for mating access to the other sex.
3. Intersexual selection involves mate choice in which individuals from one sex, usually the female sex, choose their mates from among members of the opposite sex.
4. There are four types of evolutionary models of female mate choice: “direct benefits,” “good genes,” “runaway sexual selection,” and “sensory exploitation” models.
5. Females may learn how to select mates through sexual imprinting and classical conditioning in which they are rewarded with the opportunity to mate.
6. Mate choice is one of the more active areas of ethology in terms of studying the cultural transmission models of behavior. Work in this area includes studies of mate-choice copying, as well as song learning and mate choice in birds.
7. Male-male competition for access to females with which to mate can occur in many ways, including, but not limited to, fighting, roaring, interfering with another male as he attempts to mate a female, and cuckolding another male by fertilizing his mate’s eggs.

DISCUSSION QUESTIONS

1. Suppose that a group of males was engaged in a series of fights, and that male A emerged as the dominant individual. Now suppose that a female assessed all the males involved in fights and chose male A. Why might this example blur the distinction between intersexual selection and intrasexual selection?
2. Find a copy of Kirkpatrick and Ryan’s 1991 paper “The evolution of mating preferences and the paradox of the lek,” in *Nature* (vol. 350, pp. 33–38). Drawing from this paper, list the similarities and differences between sexual selection models in terms of both assumptions and predictions.

3. Why do you suppose it is so difficult to demonstrate mate-choice copying? Choose a species and design an experiment that would examine whether mate-choice copying is present in that species. How many controls did you need to construct to rule out alternative hypotheses to mate-choice copying?
4. Read over Lindenfors, Tullberg, and Biuw's 2002 paper entitled "Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds," in *Behavioral Ecology and Sociobiology* (vol. 52, pp. 188–193). Explain why pinnipeds are a good group for a phylogenetic analysis that examines the relationship between sexual dimorphism and sexual selection.

SUGGESTED READING

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press. This book is considered the modern reference guide for work on sexual selection.

Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: J. Murray. The book in which Darwin outlined his theory of sexual selection.

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Houde, A. E. (1997). *Sex, color and mate choice in guppies*. Princeton, NJ: Princeton University Press. A book-length case study of sexual selection in a model system: the guppy (*Poecilia reticulata*).

Ryan, M. J., & Cummings, M. E. 2013. Perceptual biases and mate choice. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 437–459. A review of the work done in testing sensory bias hypothesis and related ideas.

Kraaijeveld, K., Kraaijeveld-Smit, F. J. L., & Maan, M. E. (2011). Sexual selection and speciation: The comparative evidence revisited. *Biological Reviews*, *86*, 367–377. A review of the relationship between the strength of sexual selection and the rate of speciation.

8

Mating Systems

In some mammal species a leading cause of infant mortality is infanticide by males (Palombit, 2012). Males typically kill unrelated infants, and a number of hypotheses have been proposed to explain the distribution of infanticide by males (Palombit, 2015). The sexual selection hypothesis of infanticide proposes that male-based infanticide will be most prevalent when intense male-male competition is at work (Blaffer-Hrdy, 1979, 1999; van Schaik, 2000).

To test this hypothesis, Dieter Lukas and Elise Huchard examined the relationship between infanticide by males and male-male competition across 260 species of mammals—119 species in which infanticide by males occurred, and 141 species in which it did not (Figure 8.1; Lukas and Huchard, 2014). Their analysis found infanticide by males was more common when male-male competition was strong. Infanticide rates were relatively high when males had access to multiple females, and were behaviorally dominant to other males, and hence likely to be the sire of such females' offspring. It appears that infanticide in such scenarios led to females going into estrous, creating a pool of potential mates for infanticidal males. Support for such an interpretation is also found in that infanticide was much more common where females were *not* seasonal breeders, and hence could go into estrous relatively quickly if they lost offspring, than in species in which females were seasonal breeders.

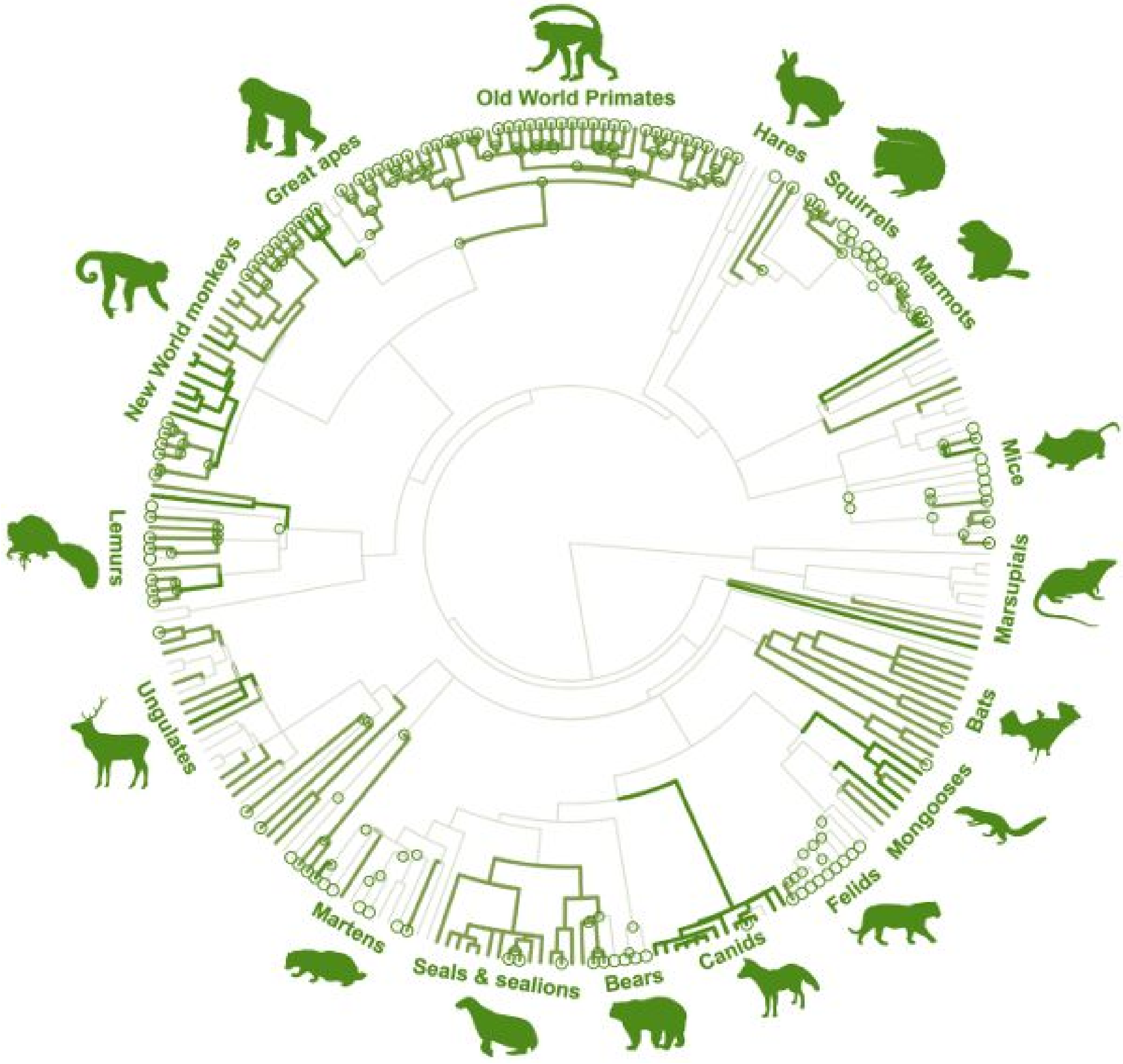


Figure 8.1. **The distribution of infanticide by males.** A phylogeny showing male infanticide in mammals. Reprinted with permission from AAAS. *(From Lukas and Huchard, 2014)*

An understanding of the selective forces that shape infanticide by males raises this question: what counterstrategies have been favored by females? Females, for example, might be favored to associate more strongly with one another to fend off dangerous males (Nunn and van Schaik, 2000). Lukas and Huchard's analysis, however, found no support for that hypothesis. After systematically examining various counterstrategies that might be favored in females, they found support for what is known as the "paternity dilution" hypothesis (van Noordwijk and van Schaik, 2000; Wolff and Macdonald, 2004), which proposes that since males target unrelated offspring, females increase the uncertainty of paternity and hence reduce the benefits of infanticide by males by mating with multiple males. Phylogenetic analysis found that such paternity dilution tended to evolve *after* infanticide by males was already in place (Figure 8.2).

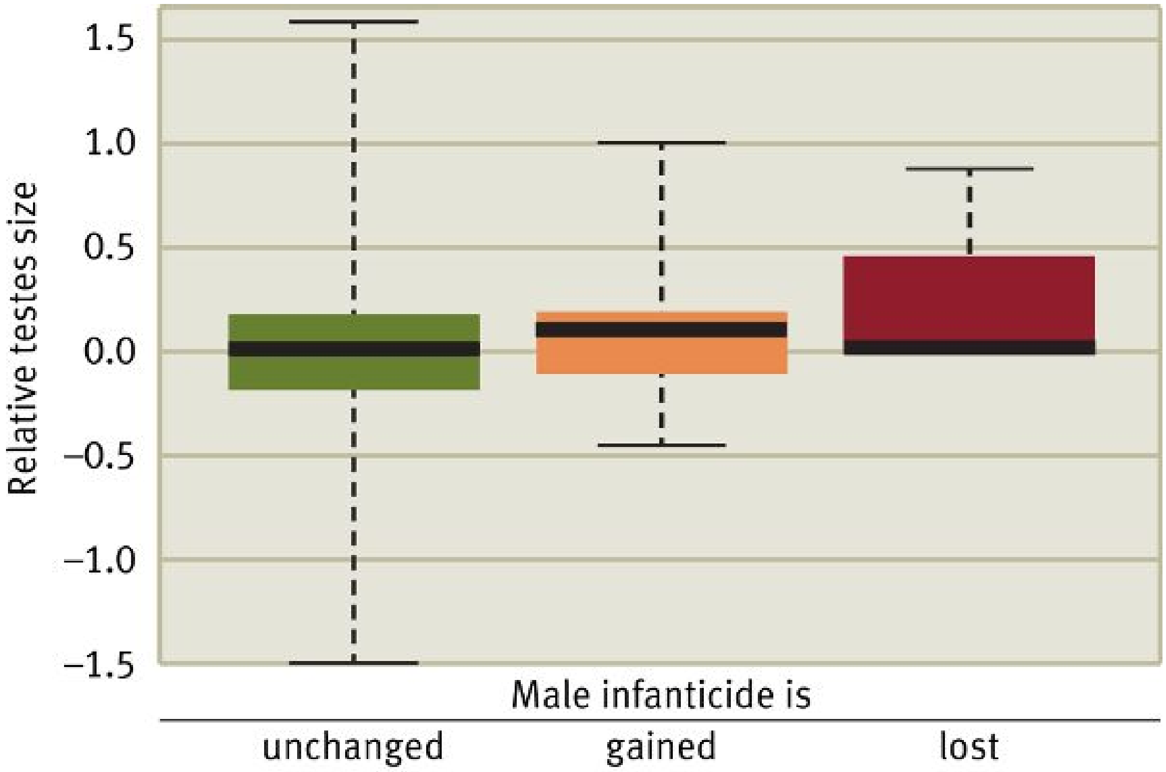


Figure 8.2. **Paternity dilution as a counterstrategy by females.** Phylogenetic analysis found evidence for a link between paternity dilution and infanticide by males. Because prior work has found that in mating systems in which females mate with multiple males, males have relatively large testes, researchers used testes size as a proxy for such mating systems. The analysis found that paternity dilution tended to evolve *after* infanticide by males was in place. Reprinted with permission from AAAS. *(From Lukas and Huchard, 2014)*

* * *

In chapter 7, we examined intersexual and intrasexual selection, and worked through a number of theories on how and why individuals choose particular types of mate(s). In this chapter, we will examine a related question: How can we understand the diversity of *mating systems* that we observe in nature? Why, for example, do some animals choose a single mate for life, while others mate with a single partner each breeding season, but switch partners across breeding seasons? Why do some mating systems involve a male (or female) having two (or more) opposite-sex partners during a single breeding season?

Mating systems occur in many forms and gradations (Shuster and Wade, 2003). Before we examine different mating systems in animals and the underlying proximate and ultimate factors that shape these systems, it is important to understand that mating systems are not static and change over time, as a result of selection pressures. And change can occur quickly, if selection pressures are strong. For example, over the course of a ten-generation experiment, when female *Drosophila pseudoobscura* fruit flies were placed with some males that carry a deleterious allele, which decreases the reproductive success of the male and the reproductive success of females who mate with him, and some males who did not carry this deleterious allele, the tendency for females to mate with more than a single male increased in frequency, compared with control populations (T. A. R. Price et al., 2008). In ten generations, the mating system itself evolved in these populations.

Different Mating Systems

We begin with a brief survey of different forms of mating systems. A general classification of mating systems is shown in Table 8.1 and Figure 8.3.

Table 8.1. Mating combinations. Various mating combinations and how they map onto potential mating success for males and females. *(From Davies, 1992, p. 29)*

	Mating success	
Mating combination	**For a male**	**For a female**
Polyandry (e.g., 2 ♂ 1 ♀)	Share one female	Sole access to several males
Monogamy (1 ♂ 1 ♀)	Sole access to one female	Sole access to one male
Polygynandry (e.g., 2 ♂ 2 ♀)	Share several females	Share several males
Polygyny (e.g., 1 ♂ 2 ♀)	Sole access to several females	Share one male

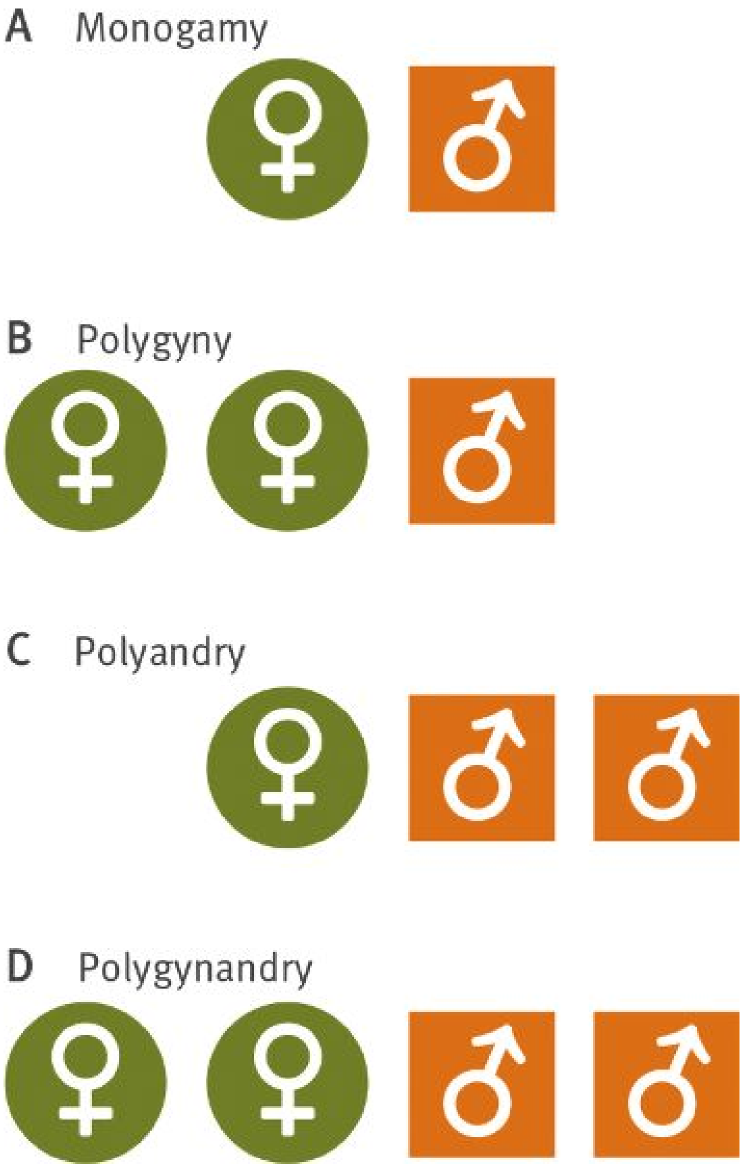


Figure 8.3. Four mating systems. (A) Monogamy (1 male, 1 female), (B) polygyny (1 male, more than 1 female), (C) polyandry (1 female, more than 1 male), and (D) polygynandry (more than 1 male, more than 1 female). Each mating system can be further subdivided.

MONOGAMOUS MATING SYSTEMS

A **monogamous mating system** is one in which a male and female mate with each other, and only each other, *during a given breeding season*. As such, we can have animal societies in which pairs mate only with one another during season 1, but in subsequent years find new mates (serial monogamy)—indeed, this sort of mating system is very common in territorial animals.

In some animal populations, a male and female will mate only with one another during their entire life span (more precisely, the life span of the individual that dies earlier). As an example of this type of lifetime monogamy, let us look at the oldfield mouse, *Peromyscus polionotus* (Dewey and Dawson, 2001; Foltz, 1981; Figure 8.4).

Figure 8.4. Oldfield mouse. Long-term monogamy has been studied in the oldfield mouse.

Early studies suggested that monogamy was rare in mammals (Eisenberg, 1966; Kleiman, 1977), but in the early 1980s, David Foltz hypothesized that though monogamy was uncommon in large, conspicuous, diurnal species (those active in the daytime), it was more common in smaller diurnal groups, particularly rodents (Foltz, 1981). Behavioral work suggested that Foltz might be correct, although the genetic evidence for monogamy in rodents at the time was much weaker (Kleiman, 1977). Foltz studied the breeding system of the oldfield mouse (*Peromyscus polionotus*), because they were relatively easy to study in both the laboratory and the field, and because other work suggested that a great deal of genetic variation existed in this species (Selander et al., 1971).

He excavated more than 500 oldfield mouse burrows, captured the individuals in each burrow, and then brought them into the laboratory. One hundred and seventy-eight families were collected from these burrows, and a genetic analysis was conducted. From a subset of these families, Foltz calculated that 90 percent of the time offspring found in a family group were fathered by the male in their burrow (Figure 8.5). Even higher rates were found in the closely related species *Peromyscus californicus* (Gubernic and Nordby, 1993). Furthermore, behavioral observations of both males and females found that most females remained with the same mates across litters, suggesting long-term, perhaps lifetime, monogamy to be the rule, rather than the exception, in this species.

Figure 8.5. Who fathers whom? In the oldfield mouse (*Peromyscus polionotus*), 90 percent of the time, the male found in the burrow is the father of the pups in that burrow.

Monogamy and Fitness Consequences

In mating systems like that of the oldfield mouse, where most individuals pair with a mate across multiple breeding seasons, there should be significant fitness consequences associated with choosing a high-quality mate. Karen Ryan and Jeanne Altmann tested this idea in a series of mate-choice trials involving oldfield mice (K. K. Ryan and Altmann, 2001). A male was given the choice between two virgin, but sexually mature, females, and the male's preference was recorded. In one treatment, males were paired with the female for which they had expressed a preference, and in a second treatment, males were paired with the female that they had not preferred.

When Ryan and Altmann examined the number of pups that survived in each treatment, they found significantly more pups were born to pairs made up of a male and his preferred mate than to males who mated with females they did not prefer (Figure 8.6A). They then ran a fascinating set of follow-up experiments: after allowing a male to choose between two females, and then recording which female the male preferred, a naive male—a male that had no experience with either of the females—was paired with either the female that had been preferred in the first part of the experiment (in one treatment) or the female that had been rejected in part 1 (in a second treatment). They found that the number of offspring raised in these two treatments was approximately equal, suggesting that what constituted a good mate was different for each individual oldfield mouse—otherwise we would have expected to see more offspring from matings involving females that been preferred in the first part of Ryan and Altmann's experiment (Figure 8.6B).

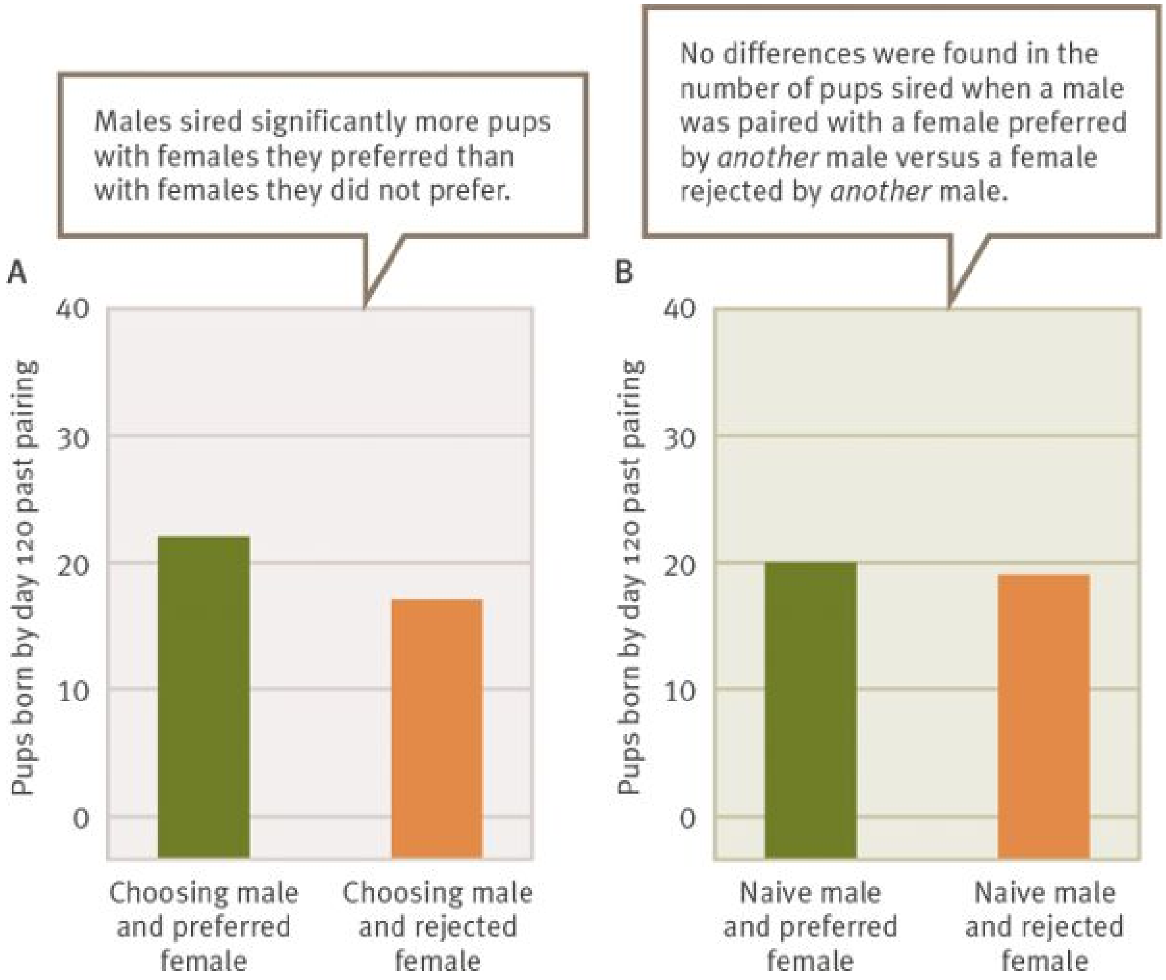


Figure 8.6. Fitness consequences of choice in monogamous oldfield mice. A comparison between the number of pups sired by a male in two different treatments in each of two experiments (as shown in A and B). *(Based on K. K. Ryan and Altmann, 2001, pp. 438, 439)*

Animal behaviorists continue to examine the costs and benefits associated with monogamy. From an adaptationist perspective, ethologists predict that monogamy should occur in ecological situations that create significant benefits to a male that opts to remain with a single female. Later in the chapter, we will see some research that suggests what those circumstances may be. In general, when resources are relatively scarce, a male's reproductive success may be highest when he is part of a monogamous pair and provides some sort of care for the offspring. In such situations, males may help raise offspring by bringing food to the nest and defending the offspring from potential predators. This is often referred to as the mate-assistance hypothesis of monogamy (S. T. Emlen and Oring, 1977; Kenter et al., 2011; Woodroffe and Vincent, 1994).

Proximate Underpinnings of Monogamy

Animal behaviorists have also studied the proximate underpinnings of monogamous mating systems (Donaldson and Young, 2008; McGraw and Young 2010; L. J. Young et al., 2005). Much work has been done understanding the neurobiology of monogamy and pair bonding in the prairie vole (*Microtus ochrogaster*) that we have discussed at length in chapters 3 and 4. In this species, males and females that are courting approach one another, and this affiliative behavior is a prerequisite to partner choice. Once individuals mate and form a strong pair bond, they are aggressive to other members of the opposite sex (Carter et al., 1995). Brandon Aragona and his colleagues studied how this change from affiliative to aggressive behavior occurs (Aragona et al., 2006; McGraw and Young, 2010).

Aragona and his team focused on changes in dopamine in the nucleus accumbens (n.a.), a section of the brain linked to dopamine transmission and both affiliative and aggressive behavior in the prairie vole (Aragona et al., 2003; Liu and Wang, 2003). They first established that a specific area of the n.a. called the rostral shell was most associated with affiliative, mating-related behavior. Within the rostral shell, activation of two dopamine-related receptors—labeled D1 and D2—was critical to the formation of long-term monogamous relationships. When D2 receptors were activated by dopamine, pair bonding was facilitated, but when D1 receptors were activated, pair bonding was inhibited (Hostetler et al., 2011). Aragona and his colleagues hypothesized that D2 receptors mediated pair-bond formation, while D1 receptors played a role in aggression seen toward unfamiliar, opposite-sex individuals after two individuals had formed a pair bond.

To partially test their hypothesis, they examined D1 receptors in males that had recently formed pair bonds with females. These males showed a surge in D1 receptor activation, as well as aggression toward any female that was not their mate. When Aragona and his team experimentally blocked D1 receptor activation in the male prairie voles, aggression toward unfamiliar females disappeared.

These studies are a good launch point for understanding how the proximate underpinnings of monogamy can be examined experimentally at the level of brain receptors (Resendez and Aragona, 2013).

POLYGAMOUS MATING SYSTEMS

Polygamy refers to a mating system in which either males or females have more than one mate during a given breeding season/cycle. Polygamy includes **polygyny**, in which males mate with more than one female per breeding season, and **polyandry**, in which females mate with more than one male per breeding season. Polygamy can also be subdivided temporally, in that it can be simultaneous or sequential. Simultaneous polygamy occurs when individuals maintain numerous mating partners in the same general time frame, whereas sequential polygamy involves individuals forming many short-term pair bonds in sequence during a given breeding season.

Polygamy increases the variance in reproductive success in the sex that has more than one mate per season (see chapter 7). For example, in polygynous systems, there is often intense competition among males, and this typically produces a distribution of mating success in which a few males do extraordinarily well, but many obtain no mates whatsoever (Figure 8.7). The converse holds true for the case of polyandry, although variance in reproductive success is usually less dramatic in polyandry than in polygyny.

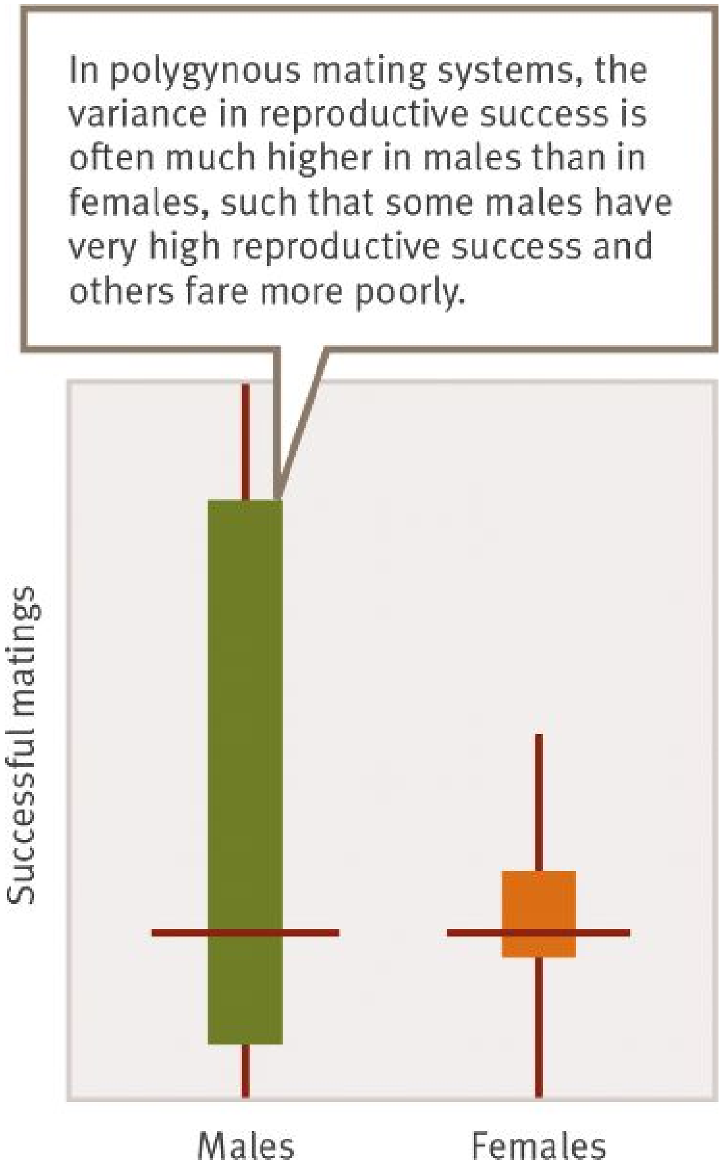


Figure 8.7. Variance and polygyny. Since every successful mating involves a male and a female, the average reproductive success must be equal in both sexes. But the variance in reproductive success differs across mating systems. (Horizontal lines represent average reproductive success.) *(Based on Low, 2000, p. 55)*

Polyandry has been well studied in jacanas, a group of shorebirds in which the males incubate the eggs and care for the young and the females compete aggressively for multiple mates. Stephen Emlen and his colleagues studied polyandry in the wattled jacana (*Jacana jacana*) in Panama (S. T. Emlen and Wrege, 2004a,b; S. T. Emlen et al., 1998; Figure 8.8). While polyandry in some species of jacanas is simultaneous, and females nest with numerous males at one time, wattled jacana females are usually sequentially polyandrous. In this species, males have small territories (40 meters in diameter) that abut one another; female territories are considerably larger and contain anywhere from one to four male territories. In the wattled jacana, a female lays clutches of eggs sequentially, after mating with males on her territory, with intervals of less than two weeks often separating the production of sequential clutches.

Figure 8.8. Polyandrous birds. In the wattled jacana (*Jacana jacana*), polyandry is the typical mating system. The male bird incubates the eggs and cares for the young after they hatch. Here we see a male bird defending his two young chicks. *(Photo credit: © Natalie Demong-Emlen)*

Female Defense Polygyny

We will return to the evolution of polygamous mating systems later in this chapter, but for a moment, let's examine the polygynous mating system in a very small Australian (unnamed) wasp in genus *Epsilon* (A. P. Smith and Alcock, 1980). In this species, males mature earlier than females. When they mature, males search for unopened brood cells from which females will emerge. Such cells are often clustered together, and males are very territorial once they uncover such a cluster of females. Once a virgin female wasp emerges from her cell, the closest male present climbs on her back and mates with her. The benefits to males that guard against intruders may be mating opportunities with as many as two dozen virgin females (Figure 8.9). Because males mate with many females and they defend females from mating attempts by other males, the mating system of these wasps is referred to as **female defense polygyny**.

Figure 8.9. Epsilon wasps and female defense polygyny. Male wasps wait at the nest for females to emerge from their brood cells. Pictured here is one male (left) on the nest and a female (at arrow) that is starting to emerge from a hole in the mud nest. *(Photo credit: © Bonnie Heim, 2008. All rights reserved)*

Randy Thornhill and John Alcock suggest three characteristics associated with female defense polygyny in insects. Females (1) are short-lived and have low fecundity, receiving all the sperm they will ever use from a single male; (2) mate shortly after becoming adults; and (3) are grouped close together in space (Thornhill and Alcock, 1983). These three characteristics make female defense polygyny beneficial for males. This mating system’s effects on female fitness remains less well understood.

Leks

In chapter 7 we touched on one form of polygyny called **lekking**, or **arena mating**. Lekking, which has been studied in birds, mammals, amphibians, fish, and insects, occurs when males set up and defend small arenas called leks—temporary territories specifically for mating—that contain no apparent resources (food or shelter, for example). Females come to these leks and select mates from among the males present. As we have seen, often a single male will obtain a very large proportion of all the matings at that lek, leading to a great deal of variation in reproductive success across males in a population (Hoglund and Alatalo, 1995; Mackenzie et al., 1995).

Leks have long fascinated ethologists, and they have been studied from many different perspectives. Here we shall focus on two questions: (1) What benefit(s) do females obtain from this form of polygyny? and (2) What benefit(s) do males obtain?

The benefit(s) that females receive from choosing among males on a lek has been a contentious issue in ethology, in part because females appear to receive sperm, but few direct, material benefits, from lekking males (see chapter 7). One possibility is that females select among males using indicators of male condition—for example, size, number of parasites, and other indicators of health and vigor—and that such choice results in offspring with higher survival probabilities because they possess good genes with respect to health. An alternative explanation is that females may use these same indicators to select among mates because such choice will lead to the production of male offspring that are themselves attractive to the next generation of females—an idea sometimes referred to as the **sexy-son hypothesis**. Through a series of experiments using the sandfly (*Lutzomyia longipalpi*), Theresa Jones and her colleagues designed an experiment to test between these two hypotheses (T. M. Jones, 2001; T. M. Jones and Quinnell, 2002; T. M. Jones et al., 1998).

Sandflies form leks where males defend small areas that measure about 4 cm in diameter. Males give off a chemical attractant called a pheromone, and females can choose freely among courting males. As in many lekking species, a single male on a lek will often obtain all matings with visiting females, and neither males nor females provide parental care to the young.

Jones and her team set up sandfly leks in the laboratory, and they ran a two-part experiment. In the first part of the experiment, five randomly selected males were put together, and once a lek was established, a single, virgin female sandfly was allowed to choose among these males. After that female mated with a male, she was removed from the lek, and a second female was allowed to select a mate. This process was repeated until ten females had selected mates and had been inseminated in a given lek. In the second part of their experiment, Jones and her colleagues took the males that had rarely been selected by females in the first part of their experiment, and they put them in new leks. They then allowed a sequence of ten females to select among males at these new leks, so that in this second part of the experiment, females could only select among males that other females had rejected as potential mates. By comparing the results obtained in the two parts of the experiment, they could begin to piece together what benefits females might receive when selecting males in a highly polygynous lek mating system.

To distinguish between the good genes and sexy-son hypotheses, the researchers first compared the survival of offspring that were the product of females choosing among a random sample of males (part I) and the offspring of females that chose between males that had been rejected by other females (part II). No evidence for the good genes model was uncovered, as offspring from both part I and part II survived with approximately the same probability. Jones and her team, however, did find support for the sexy-son hypothesis. When male offspring from part I and part II were placed in a lek, females showed a strong mating preference for the former, suggesting that first-generation females were receiving sexy-son-related benefits as a result of their choice among lekking males (Box 8.1).

Box 8.1. SCIENCE AT WORK

What is the research question? Does the good genes or the sexy-son hypothesis better explain lekking behavior in male sandflies?

Why is this an important question? The evolution of lekking has been a perennial paradox in animal behavior and this work tested two of the leading hypotheses for the evolution of lekking.

What approach was taken to address the research question? Researchers built experimental sandfly leks in the laboratory. In the first part of the experiment, a series of ten females sequentially selected among males on a lek. In the second part of the experiment, males who were rarely selected in part 1 were used to create new leks, and a series of females sequentially selected among them.

What was discovered? When comparing survival and attractiveness of offspring produced in part 1 and 2 of the experiment, evidence was found in support of the sexy-son, but not the good genes, hypothesis for the evolution of leks.

What do the results mean? Rather than experimental work that focuses on testing single models for the evolution of lekking, whenever feasible, experimenters might be better served testing among multiple hypotheses.

The benefits that males might obtain from a lek mating system have been investigated in birds (also see chapter 7, where we discuss lekking in grouse). From the perspective of a male on a lek, the fitness benefits are huge *if* you are the individual chosen as a mate by most females. But there are other potential benefits that males on a lek might receive—for example, a male may receive benefits from helping his genetic relatives on a lek (Hoglund, 2003; Hoglund et al., 1999; Kokko and Lindstrom, 1996; Petrie et al., 1999).

Peacock (*Pavo cristatus*) females are often drawn to leks that contain the most males (Alatalo et al., 1992; Kokko et al., 1998; Figure 8.10). If only one or a few males at a given lek obtain matings, and the lek is composed of many males that are genetic relatives, these relatives may receive indirect benefits from the matings that their kin receive.

Figure 8.10. Peacocks on leks. The benefits to mating on leks have been measured in the peacock. (A) Four males gather on a lek before any females arrive (one of the males is under the brush in the top left corner). (B) When a female appears on the lek, the male displays his tail in an attempt to get her to select him as her mate. *(Photo credit: © Buckeye Sailboat / Shutterstock; © Nicole Bouglouan* www.oiseaux-birds.com)

Marion Petrie and her colleagues studied a group of 200 peacocks living in Whipsnade Park in England (Petrie et al., 1999). These peacocks were scattered across many different leks, and males defended their temporary territories within the leks all day during the breeding season. Petrie and her team did a molecular genetic analysis to determine whether individuals in a lek were genetic kin, and they found that indeed they were, with the average genetic relatedness within the groups being equivalent to that of half-siblings. They then ran an experiment in which they released a group of peacocks raised elsewhere into Whipsnade Park. These males were raised in such a way that they did not interact with their genetic relatives any more than they interacted with strangers during their development. Petrie's group found that when the birds that had been raised without interactions with their genetic relatives formed their own leks, genetic relatives set up their temporary territories much closer to one another than one would expect by chance—even without the opportunity to learn about who is kin and who isn't during their development, the peacocks were able to gauge genetic relatedness and clustered near genetic kin within their leks.

Phylogenetic History of Polygyny in Warblers

The origin of polygyny has been studied from a phylogenetic perspective in Acrocephaline warblers, a group that includes the Seychelle warbler, the moustached warbler, and three species of reed warblers. Mating systems in these species vary from monogamous to polygynous. Warblers in monogamous systems show much higher levels of parental care than do warblers in polygynous systems, with monogamous males providing much more food to chicks than do polygynous males. Warbler species in this family of birds also differ in terms of the quality of the habitats they inhabit, ranging from poor habitats with little food to much better habitats that contain significantly more and better food types for warblers.

To examine the evolution of mating systems in warblers, Bernd Leisler and his colleagues used molecular genetic data to build a phylogeny of seventeen warbler species (Leisler et al., 2002). They also gathered published data on habitat quality, parental care, and mating system (monogamous versus polygynous) in warblers (Figure 8.11). Habitat quality was scored from poor (few, poor-quality food items) to medium (more, larger prey) to good (highly productive areas with quickly renewing food sources), and paternal care was scored as "full paternal care," "reduced paternal care," or "no paternal care." They then took the data on habitat quality, male parental care, and mating system and superimposed them onto their phylogenetic tree.

Figure 8.11. Warbler mating systems. The phylogeny of mating systems has been studied in warblers, including (A) the polygynous great reed warbler (*Acrocephalus arundinaceous*) and (B) the monogamous Seychelle warbler (*Acrocephalus sechellensis*). *(Photo credit: Brent Stephenson/npl/Minden Pictures)*

From an ecological and behavioral perspective, Leisler's work found a strong correlation between mating system and habitat quality. Most monogamous systems were found in poor habitats, and most polygynous systems were found in better habitats. In addition, males were more likely to provide parental care to developing chicks in poor habitats. These findings suggest that monogamy is associated with poor habitat quality because in such habitats food is scarce enough that it may take two parents to gather enough food to provision developing chicks.

This phylogenetic analysis also examined which type of mating system—monogamy with male parental care or polygamy with reduced male parental care—was ancestral, and which was derived (see chapter 2). To do so, researchers used a statistical technique called maximum likelihood analysis, which allowed them to take data from their phylogenetic tree and calculate probable ancestral states of various traits. They found evidence that the ancestral state in warblers in this family was a monogamous system in which males displayed parental care and the birds lived in poor habitats. Polygynous systems with reduced care are derived from this ancestral state. In warblers, it appears that, through evolutionary time, some species began inhabiting better-quality habitats. Once this occurred, and it was possible for chicks to receive enough food from a single parent, males were freed from parental care duties, and the evolution of polygyny was favored (Figure 8.12); other paths to polygyny and reduced parental in birds have also been studied by ethologists (Remes et al., 2015; Box 8.3).

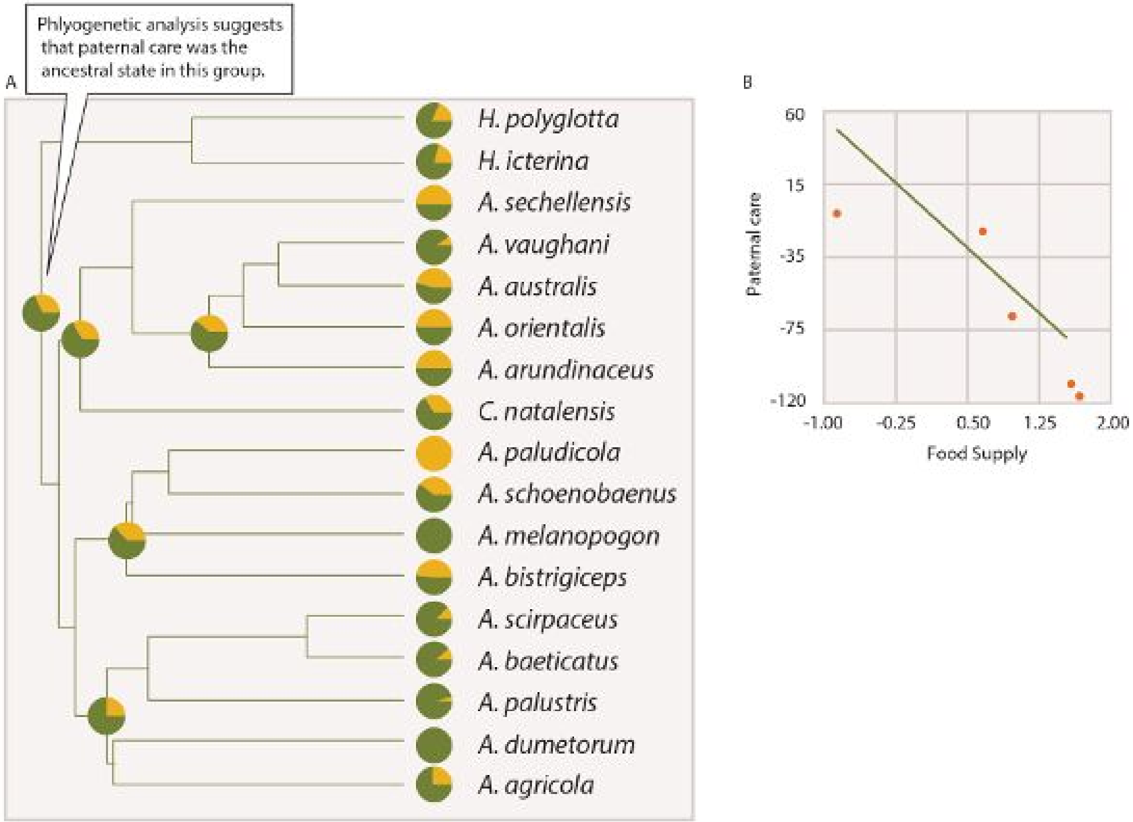


Figure 8.12. Phylogeny of warbler mating systems. (A) Paternal effort is represented as the proportion of a pie chart that is green (when the pie chart was more than 60 percent filled, researchers classified the system as full paternal care). This paternal effort was mapped onto the warbler phylogeny. (B) The relationship between paternal care and food supply in several species of warblers is shown. Where there was less food, there was greater paternal care; where there was more food, there was less paternal care. Values on the *x*-axis and the *y*-axis can be negative because of statistical transformations associated with this analysis. Reprinted by permission of the American Ornithologists' Union. *(From Leisler et al., 2002, p. 384)*

Box 8.3. SCIENCE AT WORK

What is the research question? Does biparental care favor larger brain size in birds?

Why is this an important question? Results will shed light on the general applicability of the social brain hypothesis, which proposes that larger brain size is a result of social dynamics favoring cognitive complexity.

What approach was taken to address the research question? Researchers used published data to examine the relationship between brain size, parental care, pair bonding, and development in 135 species of birds.

What was discovered? Partial support for the social brain hypothesis was found, as biparental care was indirectly linked to larger brain size.

What do the results mean? Larger brain size might be favored in a suite of behavioral venues that require complex social dynamics.

Polyandry in Social Insects

A polyandrous mating system is one in which females mate with more than one male per breeding season. This type of mating system has been well studied in social insect species, where a single queen will often mate with many worker males.

Compared to nests where a single male mates with a queen, polyandrous nests often have greater levels of within-group conflict. The reason that within-group conflict is higher in the nests of polyandrous queens is the presence of numerous patrilines—offspring descended from a common mother, but different fathers. When polyandry is absent, all workers have the same mother and father, and hence the same genetic interest. With the establishment of patrilines, genetic interests are more divergent, and each patriline competes with the others for greater representation in the next generation (Seeley, 1995, 1997). While this situation increases within-group conflict, the decreased genetic relatedness among offspring that comes from polyandry does provide a queen with at a number of benefits. In honeybees, nests with more patrilines are more successful at establishing new colonies and have a more diverse colony microbiome (Mattila and Seeley, 2007, 2010, 2011; Girard et al., 2011; Mattila et al. 2012). High genetic diversity also increases the odds that some of the offspring in a colony will have a genotype that allows them to survive attack by some disease-causing agent (Seeley and Tarpy, 2007; Figure 8.15).

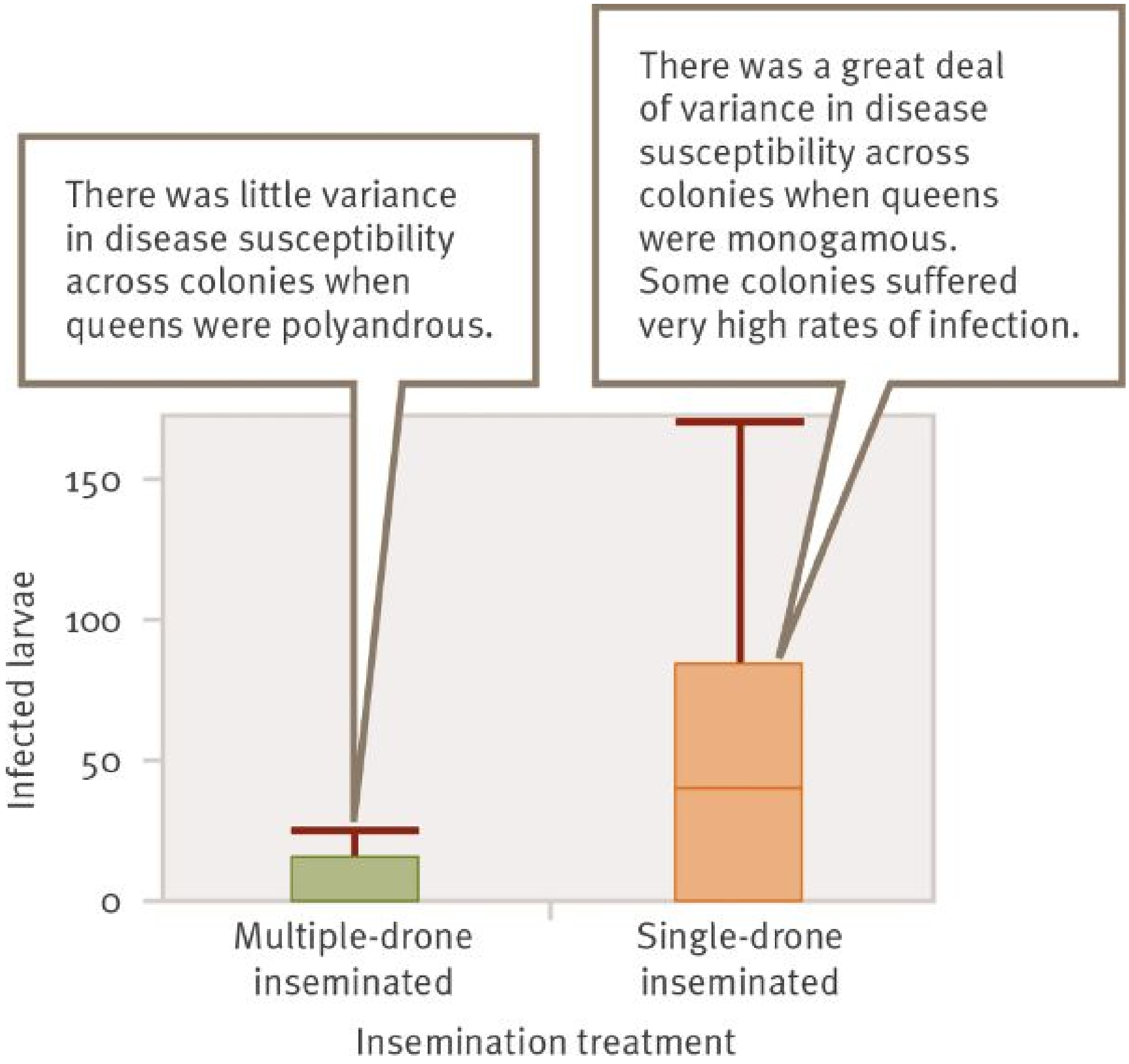


Figure 8.15. Polyandry and disease resistance in honeybees. One benefit of polyandry is resistance to disease. When honeybee colonies were inoculated with spores of *Paenibacillus larvae*, a bacterium that causes a highly virulent disease called American foulbrood, the mean number of brood infected did not differ among treatments, but the variance was significantly greater in colonies in which queens were inseminated by only one male. *(Adapted from Seeley and Tarpy, 2007)*

Thornhill and Alcock have suggested other possible benefits that female insects accrue when in a polyandrous mating strategy (Thornhill and Alcock, 1983). These benefits include:

1. Sperm replenishment

- Female adds to depleted or low sperm supply
- Female avoids the cost of storing sperm

2. Material benefits
    - Nutrients
    - Reduced predation
    - Protection from other males
3. Genetic benefits
    - Replacement of “inferior” sperm
4. Convenience
    - Female avoids the costs of fending off copulation attempts by male

Box 8.2. COGNITIVE CONNECTION

The Social Brain Hypothesis

The social brain hypothesis posits that larger brain size is, in part, a result of social dynamics favoring cognitive complexity (Byrne and Whiten, 1988; Dunbar, 1998). This idea was first proposed for, and tested in, primates, where positive correlations have been found between group size and brain size, as well as between brain size and grooming clique size, deception rates, and coalition formation patterns (Dunbar, 1992, 1995; Byrne and Corp, 2004; Kudo and Dunbar, 2001; Dunbar and Shultz, 2007; Shultz and Dunbar, 2007).

Parental care and pair bonding provide another venue to test the social brain hypothesis. In particular, biparental care of young requires sophisticated coordination and pair bonding between parents. In birds, for example, males and females often alternate between remaining at the nest and caring for the young, and leaving the nest to procure food. If one parent is away from the nest for too long, the remaining parent must decide whether to remain at the nest and care for the young, or leave to find food, potentially placing offspring at great risk. Coordination between parents is clearly important in such scenarios (Dunbar, 2009) (Figure 8.13).

Figure 8.13. **Parental care in birds.** A male and female gray jay (*Perisoreus canadensis*) feed their chicks. *(Photo credit: Dan Strickland at the English language Wikipedia; licensed under CC BY-SA 3.0 Unported)*

Shultz and Dunbar examined the relationship between brain size, parental care, pair bonding, and development in 135 species of birds (Shultz and Dunbar, 2010). They gathered published data on brain size (absolute and relative size), parental care (biparental or not), mating system (pair-bonded or polygynous; and if pair bonded, the duration of the pair bond) and development of chicks (precocial: “well-developed, young covered in down”; or altricial: “poorly developed, naked, eyes closed,” with young dependent on their parents for long periods of time). They then did a path analysis, a type of multiple regression analysis designed to untangle relationships when multiple variables affect a behavior of interest. Their results indicate that 1) Biparental is correlated with altricial development in young, which in turn is correlated with large brain size, likely because a longer development period is needed for a large brain to develop. 2) Biparental is correlated with pair bonding, and pair bonding is correlated with large brain size. 3) Pair bonding favors larger brain size, rather than larger brain size favoring pair bonding (Figure 8.14).

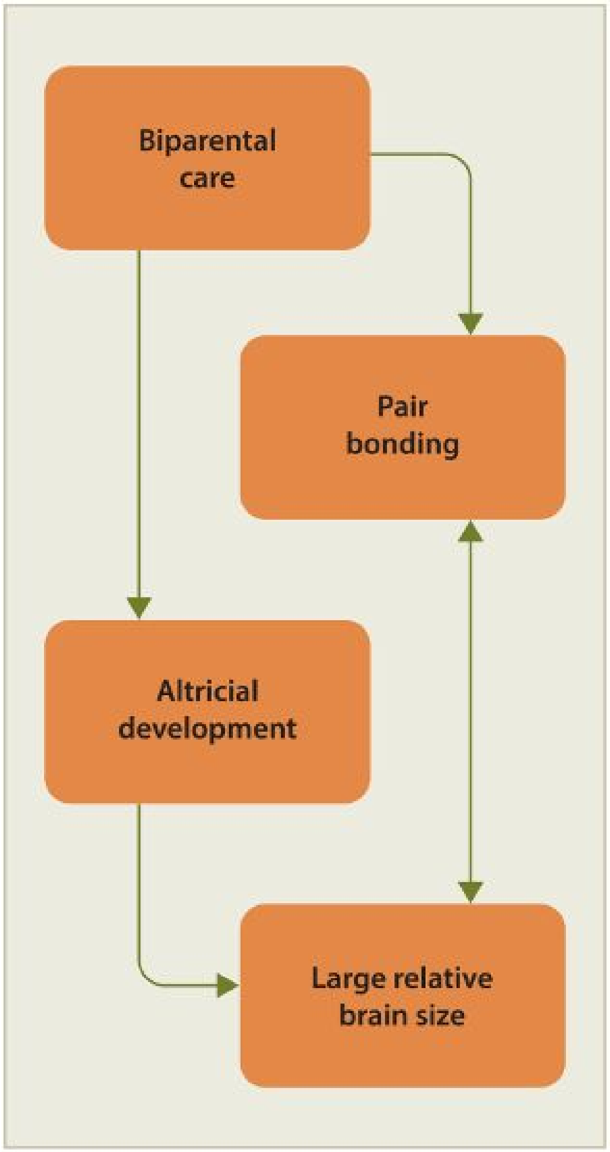


Figure 8.14. **The relationship between biparental care, brain size, and other variables.** This path diagram shows correlations between biparental care, altricical development, pair bonding, and brain size. When two boxes are not linked by an arrow, there is no direct correlation between them. By permission of Oxford University Press. *(From Shultz and Dunbar, 2010)*

In support of the social brain hypothesis biparental care was linked to larger brain size. This link, however, was indirect rather than direct. The link was mediated by biparental care's effects on pair bonding and altricial development—both of which involve sophisticated types of behavioral coordination and presumably a degree of cognitive complexity—and the effects of these variables on brain size.

Of these, Thornhill and Alcock hypothesize that material benefits account for most of the polyandry seen in insects. These benefits include (1) seminal fluid that sometimes contains chemicals that a female can sequester and use; (2) nutritious spermatophores—sperm-encompassing packets filled with nutrients and produced by some male insects; (3) nuptial gifts such as prey items presented by courting males (chapter 7); (4) access to superior feeding sites and oviposition (egg-depositing) sites; and (5) male parental care.

PROMISCUOUS MATING SYSTEMS

When polyandry and polygyny are present in the same population at the same time a breeding system is **promiscuous**. There are two forms of promiscuity, based on the presence or absence of pair bonds between mating individuals. In one form of promiscuity, both males and females mate with many partners and no pair bonds are formed. For example, a male may defend a territory that contains food, and females may visit such territories, obtain food, mate with a male, and then repeat this sequence many times (Davies, 1991). Promiscuity need not be tied to male territoriality. In many primate species, such as the Barbary macaques (*Macaca sylvanus*), when females are in estrous, both males and females mate repeatedly, often in rapid succession, with many opposite-sex partners.

In the second type of promiscuous breeding system, **polygynandry**, several females form pair bonds with several males simultaneously. For example, in the dunnock (*Prunella modularis*), pairs of males will often jointly defend the territory(ies) of a pair of females (Figure 8.16). Nick Davies has studied the dunnock mating system and the help provided by males to females (Davies, 1986). He observed cases in which one or two males were resident on a female’s territory, and found that females received help from one of the males, from both, or from neither of them, but that, on average, polygynandrous females received the equivalent help that a female with only a single mate would receive (Davies, 1992; Figure 8.17). The more help a polygynandrous female received, the higher the mean nestling weight of the chicks in the brood and the lower the chick mortality rate due to starvation.

Figure 8.16. Dunnocks. Here we see a female with newly hatched offspring. *(Photo credit: imageBROKER / Alamy Stock Photo)*

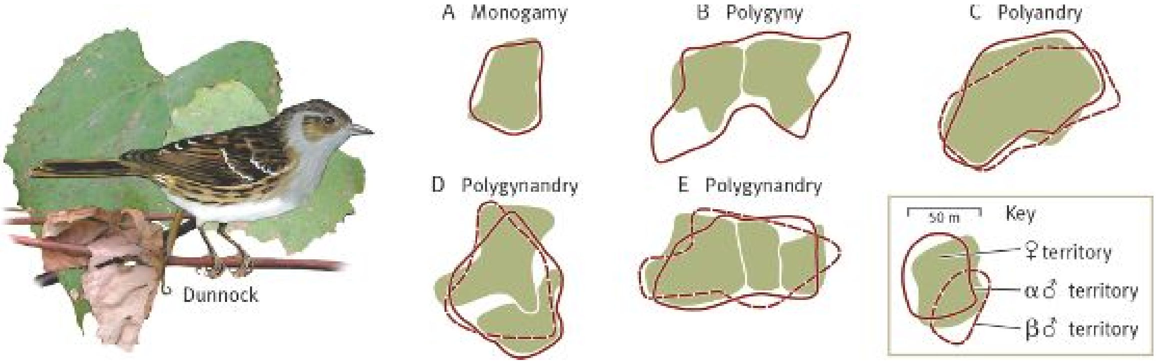


Figure 8.17. Incredible variation in dunnock breeding systems. Female territories are shown in green, while alpha male territories are depicted by solid red lines and beta male territories are shown by dashed red lines. In a single dunnock population, mating systems range from monogamy to polygamy, polyandry, and polygynandry. *(From Davies, 1992, p. 27)*

The Ecology and Evolution of Polygynous Mating Systems

After our brief survey of different mating systems, let's now address questions about the ecology and evolution of these different mating systems. We will first look at the role of resource dispersion on female mating decisions and then at a model to predict when polygyny is favored by natural selection.

POLYGYNY AND RESOURCES

Female dispersion patterns—how females move about in relation to one another and their environment—affect the type of mating system in a population (Bradbury and Vehrencamp, 1977; S. T. Emlen and Oring, 1977). A female can often fertilize all her available eggs by mating with one or a very few males, which means that female fecundity is not so much tied to the availability of mates as it is to the availability of resources like food, defense, and so forth (Krebs and Davies, 1993). The more resources that are available, the more offspring females can produce. Males, in contrast, can potentially fertilize large numbers of females, so that male reproductive success is more tightly associated with access to females than with access to resources. This difference generates a prediction; female dispersion patterns should track the distribution of resources, whereas male dispersion patterns should track the dispersion of females.

If females track resources and males track females, then the mating system in a population is linked to the distribution of resources because resource distribution will affect whether males monopolize more than one female at a time. If resources are dispersed fairly homogeneously and/or if females must cover large areas to obtain enough resources to survive, it may not be economically feasible, in terms of costs and benefits, for males to mate with and potentially defend more than one female.

When resources are clumped—for example, when food is located in discrete groupings—the economics of mating systems may shift, and males may be able to mate with and defend several females at once (see Box 8.4). For example, seal populations can be found aggregating on both ice packs and beaches. On ice packs, females are widely dispersed, and males typically guard and mate with one or a small number of females. In contrast, when the seals are on land, females cluster tightly in particularly safe areas on the beach, and males are able to defend herds of females against the approach of other males, leading to a more polygynous mating system (Le Boeuf, 1978).

Box 8.4. CONSERVATION CONNECTION

Anthropogenic Effects on Animal Mating Systems

Jeffrey Lane and his colleagues (2011) reviewed four anthropogenic effects—effects caused by humans—that have been shown to have important consequences on animal mating systems: (1) habitat fragmentation, (2) climate change, (3) pollution, and (4) sport hunting (Colborn et al., 1993; Lurling and Scheffer, 2007; E. M. Olsen et al., 2004; Parmesan, 2006). Let's examine two of these: habitat fragmentation and climate change.

In an influential paper, S. T. Emlen and Oring (1977) hypothesized that habitat fragmentation produces clumped resources. Emlen and Oring then proposed that clumped resources create an environment in which females, that track such resources, also clump together in space. Under such conditions, it becomes possible for males to guard numerous mates simultaneously, producing a polygynous mating system. Emlen and Oring were originally considering environmental factors that might lead to clumped resources, but their hypothesis applies just as well when anthropogenic effects lead to such clumping.

Emlen and Oring's hypothesis has been indirectly tested in two populations of the brushtail possum (*Trichosurus cunninghami*) that live adjacent to one another (J. K. Martin and Martin, 2007). In the population residing in an unfragmented forest, females have large home ranges, which are necessary to obtain sufficient food in such an environment. Monogamy, the most common mating system in the brushtail possum, was found in this forest population. An adjacent population of brushtail possums lived alongside a road in a more fragmented, piecemeal habitat. In this fragmented population, food was clustered and females had smaller home ranges, allowing males the potential to defend numerous females during breeding season. Polygyny was found in this fragmented population with more clustered resources and more clustered females. In the case of the brushtail possum, anthropogenic road building led to a fragmented population in which the typical monogamous mating system seen in brushtail possums was replaced by polygyny (García-Peña et al., 2009). The implications of such changes to an evolved mating system are not yet understood.

Climate change—including anthropogenic climate change—may affect the evolution of paternal care. Using the phylogenetic techniques discussed in chapter 2, researchers have examined the relationship between migration distance and paternal care in shorebirds (García-Peña et al., 2009; Figure 8.19). As in previous studies on migratory shorebirds, García-Peña et al. found that longer migration routes were correlated with reduced paternal care, presumably because the energy used in migration was not available to care for the young. Subsequent phylogenetic analysis found that changes in migration distances tended to precede changes in paternal care patterns. In terms of anthropogenic climate change, global warming may affect the distance that migratory species must travel to reach an appropriate end point. In some instances, human-caused climate change may lead to increased migratory distances (and reduced paternal care); in others, it may lead to decreased distances (and increased paternal care)—the specifics will depend on the species and whether migration is linked to changes in temperature, rain level, or other factors.

Figure 8.19. Migration, climate change, and mating systems. The relationship between migration patterns, climate change, and mating systems has been studied across many migratory species of birds. Pictured here are black-bellied plovers (*Pluvialis squatarola*) during their spring migration. *(Photo credit: Jamie Roach / Alamy Stock Photo)*

Climate change may affect animal breeding systems in ways that we are only just beginning to understand.

The effect of female dispersion on male mating patterns has been examined experimentally. Rolf Ims manipulated the distribution of grey-sided vole (*Clethrionomys rufocanus*) food sources and found that female dispersion patterns in voles changed in the predicted manner—when resources became more clumped, females clustered themselves together in the area of their resources (Ims, 1987). Ims then introduced the grey-sided vole to a small island in Norway. In one treatment, he used caged female voles to simulate an environment in which females moved about a home range and were fairly spaced out. In a second treatment, caged females were clustered together. As a control, Ims ran a reverse experiment in which males were in cages and their distribution was manipulated. As predicted, Ims found that males tracked the distribution of caged females across treatments, but female dispersion was unaffected by the distribution of caged males.

THE POLYGYNY THRESHOLD MODEL

When males have territories that can sustain numerous mates simultaneously, females can decide which territory they settle on. Female choice, then, affects whether polygyny evolves. In 1969, Gordon Orians built the **polygyny threshold model (PTM)** to predict the behavior of females in such a scenario (Orians, 1969; more detailed and complicated versions that consider such factors as the genetic relatedness among females have subsequently been developed; Ptak and Lachmann, 2003; Gronstol et al., 2015).

How the PTM Works

To see how the PTM works, imagine that ten males each have their own territory. Let's refer to these territories as territories 1–10 (T1–T10), and let's call the males on these territories males 1–10 (M1–M10). These territories vary with respect to some resource that is valuable to females—for example, food. Before females begin selecting mates, T1 has the most food, T2 the second most, down to T10, which has the least amount of food. The first female arriving to choose a male territory on which to settle can base her choice simply on what territory is optimal with respect to food intake, so she should choose male 1's territory, T1. A second female choosing between male territories now must make a decision in an environment that is slightly different, in that T1 is now occupied by a male and another female (not just a male). If this second female chooses T1, she will only get some fraction of the food available there. If the food still available on T1, even though it is already occupied by another female, is greater than the food available on any of the other nine male territories, our second female should choose to settle with M1 on his territory, T1. In so doing, she has passed the "polygyny threshold"—opting to be on a territory with another female and thus to be part of M1's polygynous relationships.

Suppose that the resources still available on T1 are not greater than that on T2, and our second female settles on T2 (M2's territory). A third female now comes in and chooses between T1 (another female present), T2 (another female present), and the territories of males 3–10 (no other females present). Her situation is slightly different from that of female 2 when she arrived, however, because the best open territory is now T3—M3's territory—and that may not be as profitable (in terms of fitness effects) as male 2's territory. If female 3 chooses to settle on T1 or T2, then the polygyny threshold has been crossed for whichever of these she settles on. This sort of logic can be applied to all subsequent females (J. L. Brown, 1982). Figure 8.18 shows a graphical representation of the PTM with four females deciding where to settle.

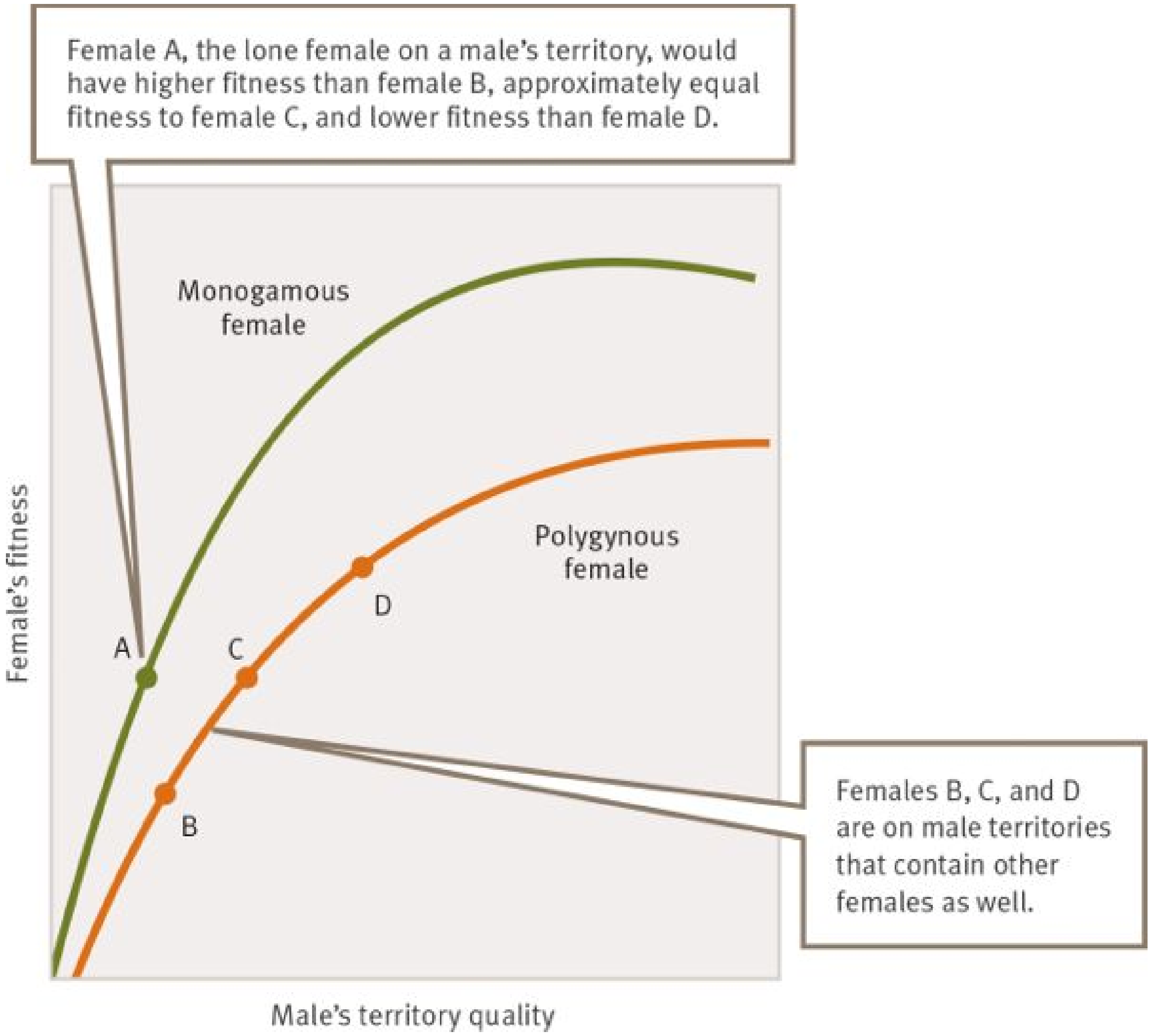


Figure 8.18. Female choice of territories. Imagine a female deciding among territories. Theory suggests she should choose the territory with the highest quality, that is, with the most food available or the most shade and so on, regardless of whether she would be the lone female (monogamous territory) or one of several females (polygynous territory), because such a choice would provide her with the greatest fitness.

The PTM makes a prediction about female fitness. When two females settle at about the same time and hence face the same sort of economic decisions regarding the availability of resources and where to settle, a female that opts to settle on a territory on which she is the lone mate of the male (a territory that then has a monogamous mating pair) and a female that decides to settle on a territory that already contains a male and one or more females (a territory where there is now polygamy) *should have approximately equal fitness* (Krebs and Davies, 1987). It is this equivalency of fitness among monogamous and polygamous females that makes the PTM stable. Because monogamous females and females in polygamous relationships settle in such a way as to produce approximately equal fitness, there is no temptation for females to move from territory to territory once this state has been reached, as any such move would in fact lower an individual's reproductive success (see Borgerhoff-Mulder, 1990, for some limitations of the PTM).

The PTM and Mate Choice in Female Birds

Wanda Pleszczynska used lark buntings (*Calamospiza melanocorys*) in one of the first experimental tests of the PTM. In lark buntings, the resource that primarily determines female settlement onto male territories is shade cover, as the main cause of nestling mortality in lark buntings is overheating. The more shade on a territory, the better the territory, and this shade effect can be shown experimentally by artificially increasing the shade in a given territory, which leads to an increase in nestling survival (Pleszczynska and Hansell, 1980).

Because shade protection is such a critical resource, some of the male territories that are best suited to provide shade will likely have been settled by other females (Figure 8.20). Settling on a territory in which there already is a male and a female and becoming a "secondary" female allows a female access to shading. The cost of becoming such a secondary female is that a male provides paternal care only to the nestlings of his "primary" female, the mate that arrived first (Krebs and Davies, 1987). Pleszczynska and Hansell found that increasing shade availability on a territory not only made it much more sought after by females, but that as the PTM predicts, secondary females that bred in areas with lots of shade cover (but that did not receive male aid) had about the same reproductive success as did monogamous females that bred on territories with less shade cover (but that did receive male aid) (Box 8.5).

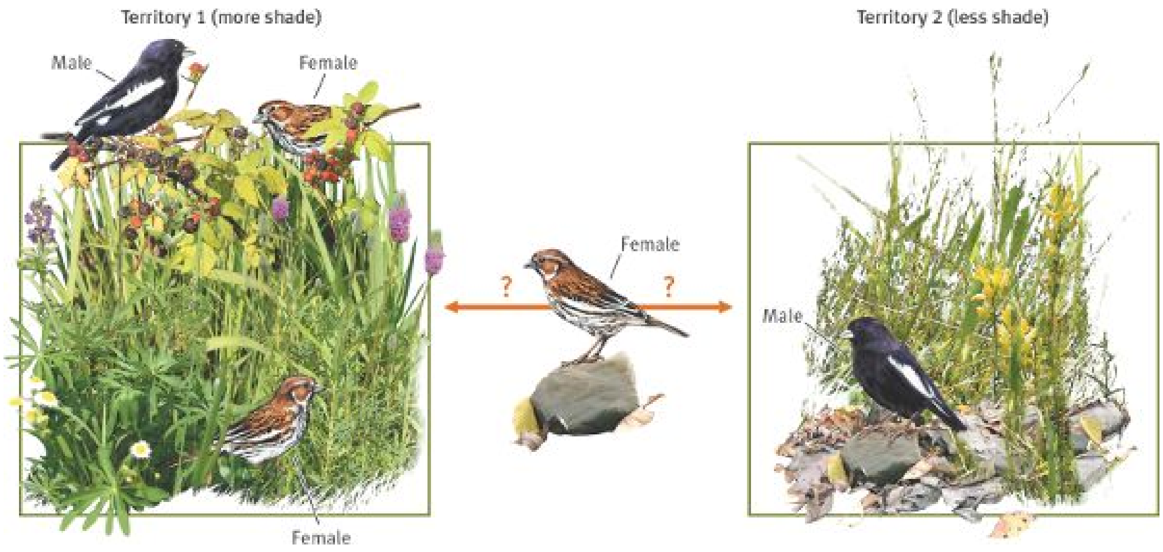


Figure 8.20. The polygyny threshold model. In the lark bunting, shade is a limiting resource that affects nestling survival. Females choose the territory of a male with good shade cover (territory 1) over a territory with less shade cover (territory 2), even if this decision means entering a polygynous relationship rather than a monogamous one.

Box 8.5. SCIENCE AT WORK

What is the research question? How well does the polygyny threshold model (PTM) explain the mating system of lark buntings?

Why is this an important question? The PTM is a conceptually powerful model for the evolution of polygyny. At the time, this was the first experimental test of this idea.

What approach was taken to address the research question? Male nests in shade provide females a territory on which their eggs are less susceptible to desiccation. To test the PTM, researchers experimentally manipulated shade and looked at the pattern in which females settled on male territories and the reproductive success that emerged from such choice.

What was discovered? Female settling patterns and reproductive success were as predicted by the PTM.

What do the results mean? Females settle on male territories in ways that maximize individual fitness given the decisions made by other females.

EXTRAPAIR COPULATIONS

Male and female birds often form pair bonds—involving courtship, and often joint territory defense and sometimes mutual feeding—at their nest during breeding season. It was once thought that such pairings implied a monogamous pairing. Starting in the early 1980s, however, ornithologists began to uncover more and more instances of **extrapair copulations**, or **EPCs** (R. Ford and McLaughlin, 1983; McKinney et al., 1984). They were finding that even when pair bonds were in place, males and females were leaving their territories during the mating season and mating with other individuals, usually those in nearby territories. EPCs prompted some animal behaviorists to make a distinction between social monogamy and genetic monogamy. Most bird species in which EPCs were recorded formed pair bonds with just a single partner during a mating season, and as such displayed what is referred as social monogamy. Yet, genetically, these systems resembled promiscuity more than monogamy, as mating occurred both with the social partner and with other individuals during the mating season.

The increased reproductive success of males that leave territories and engage in EPCs seems clear, as they can fertilize more females. But why would a female be involved in EPCs? The answer depends on the particular species and its ecology and demographics, but in general, females engaging in EPCs may (1) increase the probability that all their eggs are fertilized (the fertility insurance hypothesis); (2) maximize genetic diversity in their offspring, thereby increasing the chances that some of the offspring fare well in the environment in which they mature (Blomqvist et al., 2002, 2003; Griffith and Montgomerie, 2003); (3) use EPCs to select males that have good genes (see chapter 7) but that might not be willing to form a pair bond and provide direct benefits to their offspring (Griffith et al., 2002; Neudorf, 2004); and (4) increase the amount of direct benefits—food, protection, and so on—that they receive from males.

David Westneat was among the first researchers to examine EPCs in nature. His behavioral observations of indigo buntings suggested that about 13 percent of all matings were EPCs, but such observations might underestimate the actual percentage of all offspring that were sired via extrapair copulations (Westneat, 1987b; Figure 8.21). Because buntings were hard to follow for long periods at a time, a significant number of EPCs may have been missed. Furthermore, it was not clear how many extrapair *matings* translated into extrapair *fertilizations*. For example, indigo bunting females generally resisted EPCs to a greater extent than mating with their nesting partner:

Females resisted EPCs in 34 out of 43 attempts, but only resisted mating with their pairmates in 72 out of 320 attempts (Westneat et al., 1987).

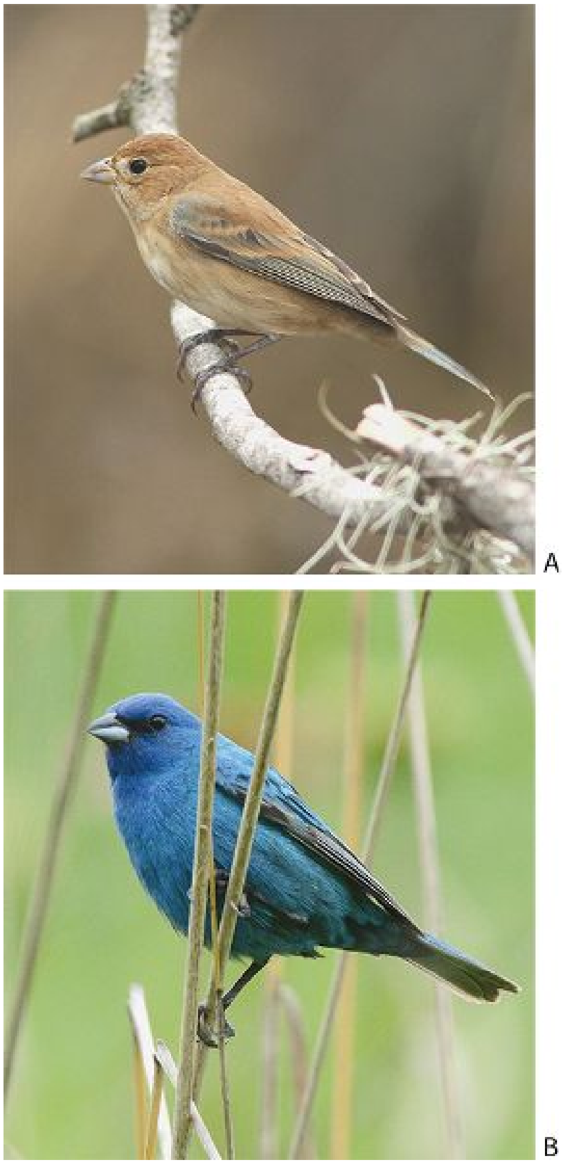


Figure 8.21. Indigo buntings. (A) A female indigo bunting. Although socially monogamous, female indigo buntings are often involved in extrapair copulations. (B) A male indigo bunting. Males defend their territories against intruders. *(Photo credit for B: "Indigo Bunting" by Jim Hudgins/USFWS, licensed under CC BY 2.0)*

To examine what impact EPCs had on mating dynamics in buntings, Westneat ran a genetic analysis of parentage done in conjunction with a detailed behavioral study (Westneat, 1987a; Figure 8.22). This study was conducted before DNA fingerprinting techniques were widely available, and it relied on a technique called electrophoresis, which, although less powerful than DNA fingerprinting, does allow ruling out a particular adult individual as the parent of a particular offspring.

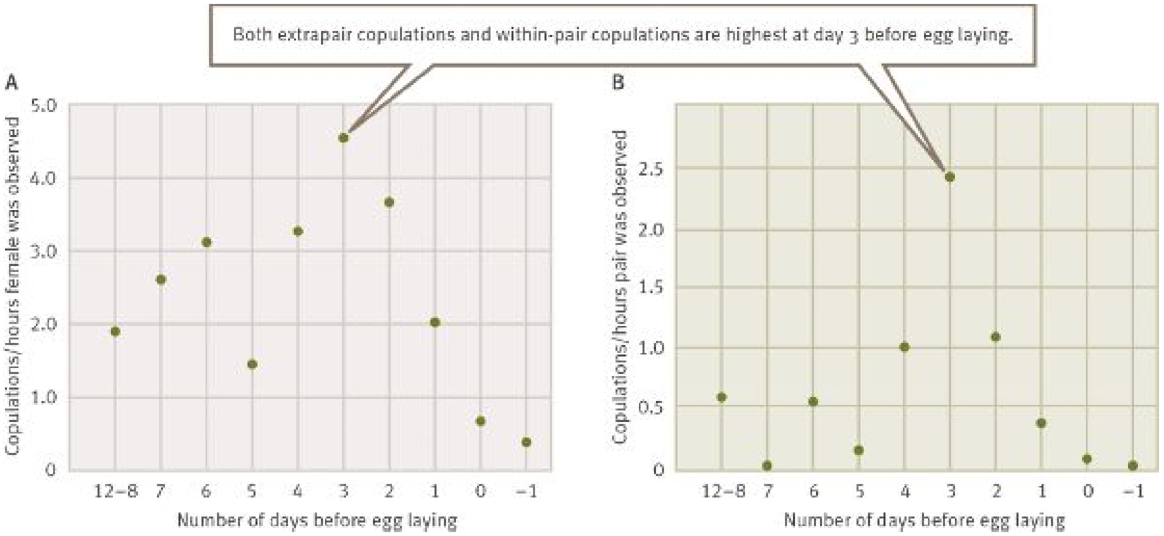

Both extrapair copulations and within-pair copulations are highest at day 3 before egg laying.

Figure 8.22. Copulations in indigo buntings. Occurrence of copulations in (A) extrapair and (B) within-pair matings. The day the egg was laid is shown as day 0 on the *x*-axis. *(Based on Westneat, 1987b)*

Over the course of two years, Westneat obtained DNA samples from hundreds of buntings. Using electrophoretic comparisons, and plugging that data into existing mathematical models, he found that, of the 257 young that were examined, 37 had genotypes that were *not* consistent with the genotype of one of their presumed parents (Westneat, 1987a), so at least 14 percent (37 out of 257) of all young were sired via an extrapair copulation—in line with the 13 percent Westneat had predicted based on his behavioral observations. After that analysis, however, updated mathematical models showed that electrophoretic estimates of the percentage of young fathered by extrapair fertilizations in buntings were underestimates. Plugging Westneat's numbers into these newer models uncovered extrapair fertilization rates between 27 to 42 percent (depending on the year) in buntings (Westneat et al., 1987).

Since Westneat's work, many studies have documented EPC frequency in birds (for example, Adler, 2010; C. E. Hill et al., 2011; Schmoll, 2011), and have found that EPCs account for 76 percent of all young in one population of the superb fairy wren (*Malurus cyaneus*;

Mulder et al., 1994; M. S. Webster and Westneat, 1998; Westneat et al., 1990). Given that monogamy was long considered to be the norm in birds, these are staggering numbers—numbers that are available only because of the revolution in molecular genetics that is still underway today.

SPERM COMPETITION

In chapter 7, we saw how both male-male competition and female mate choice can affect which males are on the upper and lower ends of this mating curve distribution. Here, we will look at the effect of **sperm competition**—that is, the direct competition between the sperm of different males to fertilize a female's eggs—on mating success and the evolution of mating systems (Birkhead and Møller, 1992, 1998; Birkhead and Parker, 1997; G. A. Parker and Pizzari, 2010; Tourmente et al., 2011; Wedell et al., 2002).

In some promiscuous (as well as some polyandrous) mating systems, males compete not only for access to mating opportunities with females, but directly for access to eggs. In these systems, competition also occurs *after* a female has mated with numerous males. If females store sperm from numerous matings, sperm from different males may compete with one another over access to fertilizable eggs (Figure 8.23). When sperm competition exists, natural selection can operate directly on various characteristics of sperm, such as sperm size, shape and swimming abilities.

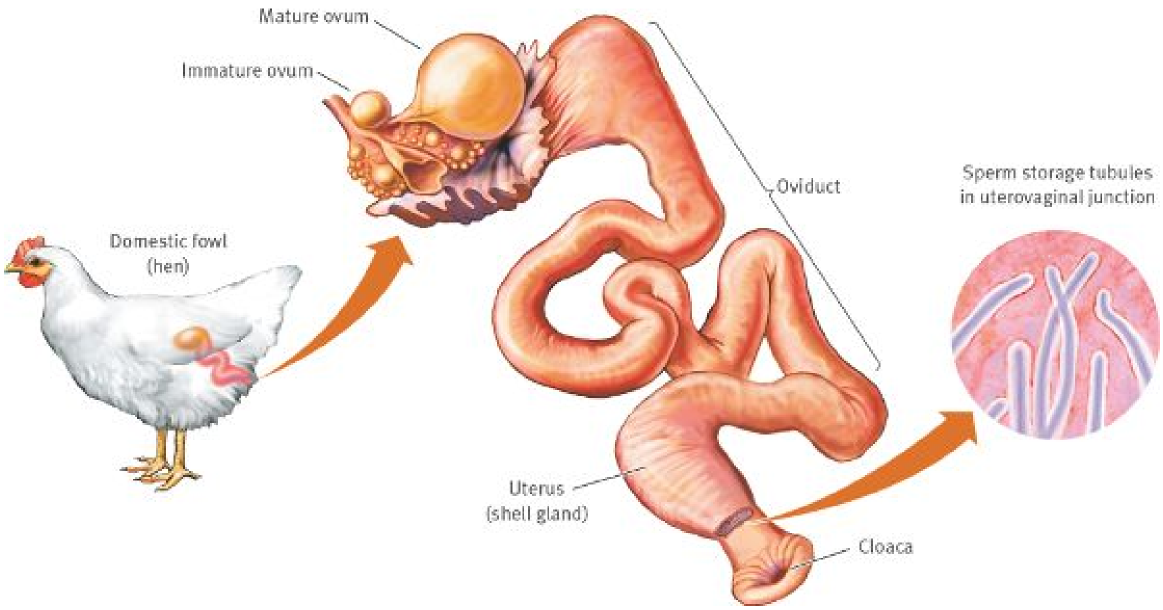


Figure 8.23. Sperm competition. The reproductive system of domestic fowl. Sperm storage occurs in sperm storage tubules (SST) at the uterovaginal junction. Females in many species can store sperm from multiple males, setting the stage for sperm competition. Only a small proportion of sperm makes it into the SST. *(Based on Birkhead and Møller, 1992)*

Sperm competition has been extensively documented in many groups of animals, and a similar sort of competition, known as “pollen competition,” is known to occur in plants (Delph and Havens, 1998).

Sperm Competition in Dungflies

Geoff Parker studied sperm competition in dungflies, who use the droppings of large, often domestic, animals for breeding sites (Immler et al., 2011; G. Parker, 1970b, 2001; G. A. Parker and Pizzari, 2010). While in most insects, copulations often last a matter of seconds, in dungflies they can last more than thirty minutes. When a new dung pat is created and females begin to arrive, there is intense male competition for mating opportunities. A thousand or so males can descend on a single dung pat, all in search of females. Males that find a female and begin copulating are under constant physical attack from other males trying to break up their pairing and start their own round of copulating (Figure 8.24).

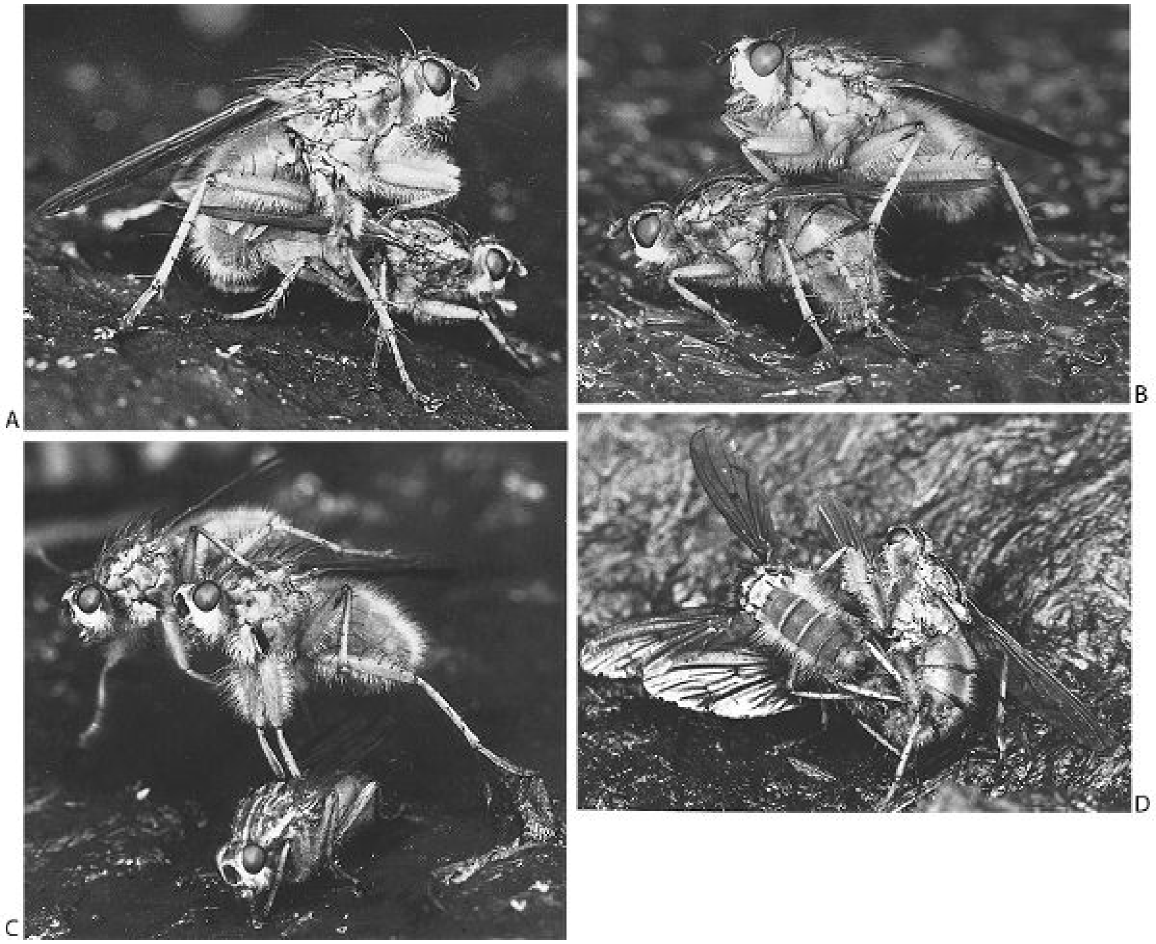


Figure 8.24. Dungfly mating. In dungflies, sperm competition can be intense, with the last male copulating with a female fathering up to 80 percent of her offspring. *(Photo credits: © Geoff Parker)*

To test for the role of sperm competition in this mating system, Parker relied on a technique that entomologists had been using in various biocontrol programs (G. Parker, 1970a). He irradiated the sperm of certain males, creating males whose sperm was otherwise normal, but would then fail to produce eggs that hatched. Working with pairs of males and irradiating one of them, Parker examined the relative success of each male by determining the proportion of eggs that failed to hatch—that is, the proportion of fertilizations attributable to the irradiated male.

Parker found that the number of eggs fertilized by the last male to mate with a female was proportional to how long such a mating lasted. The longer the last mating, the greater the reproductive success of the male. More specifically, the longer a copulation, the greater the extent to which the last male's sperm displaced the sperm of males that had copulated with the female earlier (Figure 8.25). Such "last male precedence" is common when sperm competition is in play, but it is not ubiquitous. In some mating systems, sperm competition appears to favor the first, rather than the last, male to mate with a female.

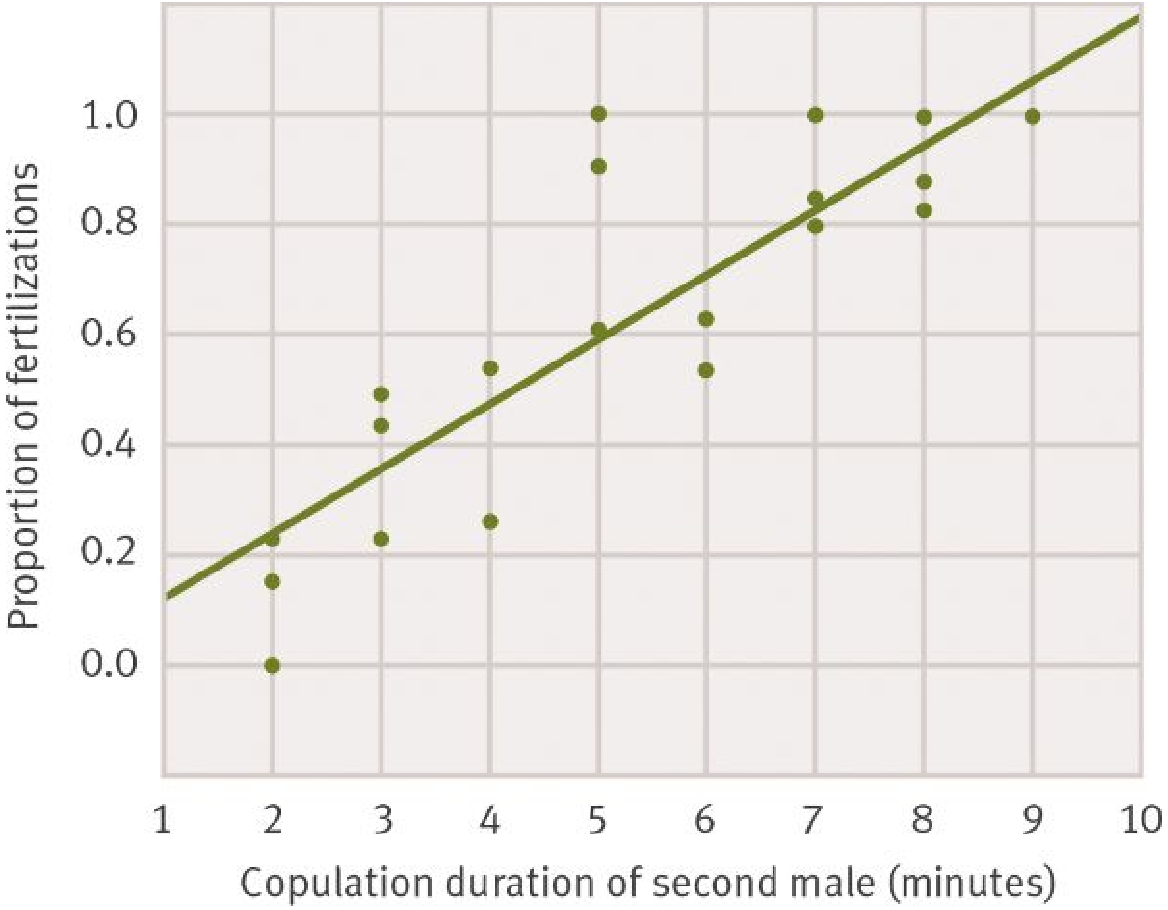


Figure 8.25. Sperm competition in dungflies. The longer a male dungfly mates with a female dungfly, the greater his fertilization success. *(From Simmons, 2001)*

In the dungfly system, the last male to mate with a female copulated on average for thirty-six minutes, and fathered approximately 80 percent of the young in the clutch of eggs deposited by a female (G. Parker, 1970a). But, if copulation time correlates with greater displacement of a competitor's sperm, why don't males copulate for even longer periods and thereby attempt to displace 100 percent of a competitor's sperm? The answer appears to be that males must weigh such an option against what else could be done with the time in question. While increasing the time spent with female A will increase the displacement effect, it is also time that the male could have used to find another female with whom to mate. Because the rate of sperm precedence slows down with time, it will often benefit a male to use such additional time to find other potential mates (G. A. Parker, 1974b; G. A. Parker and Stuart, 1976).

Sperm Competition in Sea Urchins

Sperm competition can also play an important role in species that do not have internal fertilization. To see how, let's consider Don Levitan's work on sperm velocity and fertilization rates in the sea urchin, *Lytechinus variegatus* (Levitan, 2000). Levitan hypothesized that variation in the speed at which sperm traveled correlated with fertilization rate in *L. variegatus*. Using sea urchin sperm makes this task a bit easier than using sperm from birds or mammals, because sea urchins secrete their sperm and eggs into seawater. Using a video camera that can tape sperm swimming along and a microscope to see which eggs are fertilized, Levitan was able to measure the sperm's swimming speed and fertilization success.

Levitan found that to fertilize the same number of eggs, males that produced slow-moving sperm needed to release up to 100 times more sperm than males that produced fast-moving sperm (Figure 8.26). Levitan then examined what happens to sperm as they age. In so doing, he was testing for a predicted trade-off between the speed at which a sperm moves and how long that sperm survives. Because swimming fast and swimming for a long time both require energy, fast-moving sperm shouldn't live as long as slow-moving sperm.

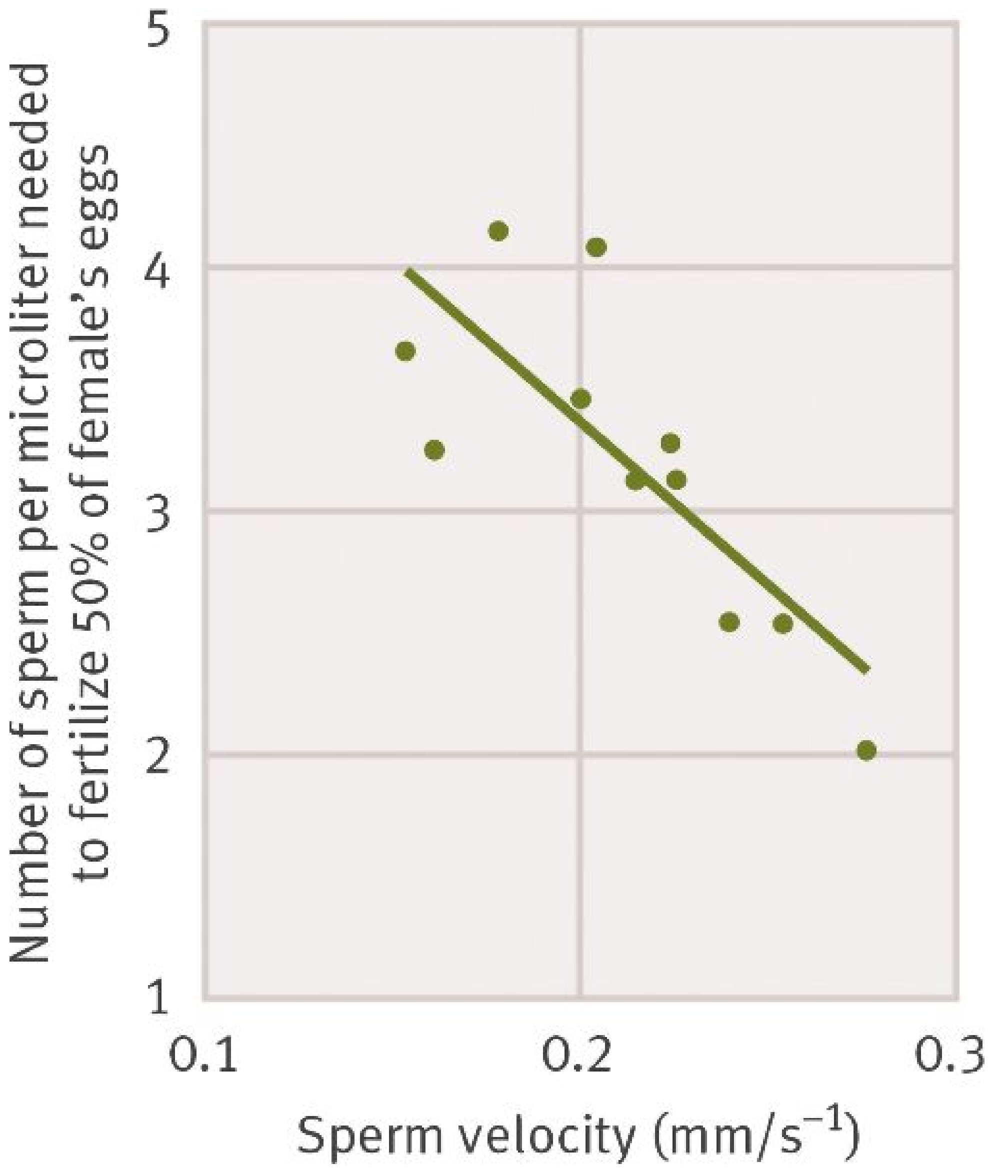


Figure 8.26. Sperm velocity and fertilization. In sea urchins, slower sperm fare poorly. The slower the sperm, the more sperm needed to fertilize a female's eggs. *(Based on Levitan, 2000)*

When examining the expected trade-off between speed and longevity, Levitan first found that *all* sperm slow down as they get older (Figure 8.27). Not only did sperm decrease their swimming speed with age, but as they aged, they were much less likely to fertilize an egg, even when they encountered one. For example, sperm that were only an hour old could be up to 100 times less likely to fertilize an egg than were newly released sperm. After two hours, sperm fertilized no eggs at all.

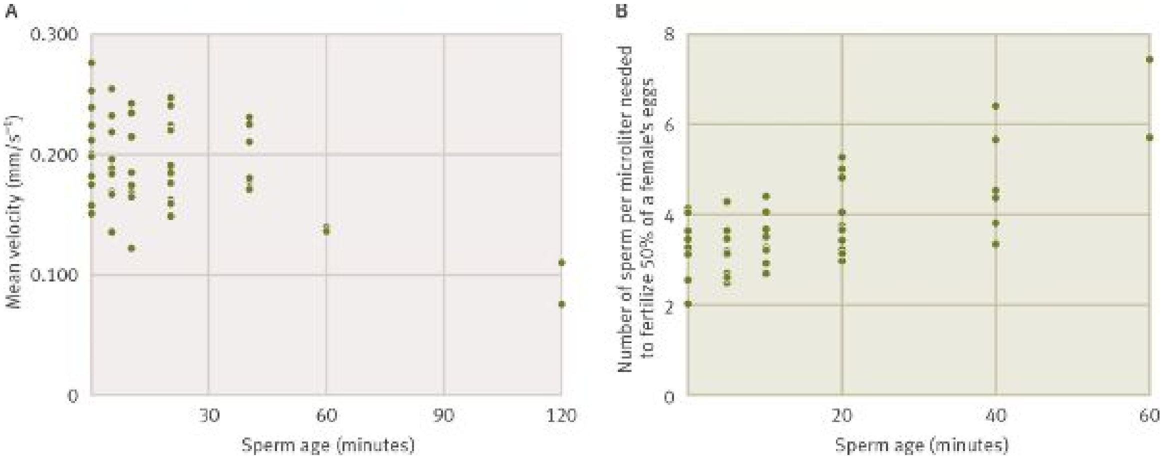


Figure 8.27. Older sperm fare poorly. (A) In sea urchins, older sperm swim more slowly, and (B) a greater quantity of such sperm is needed to achieve high fertilization rates. *(Based on Levitan, 2000)*

With data on longevity and speed, Levitan could return to the question raised earlier: Is there a trade-off between sperm speed and sperm life span for individual sea urchins? The answer appears to be yes, as Levitan found a negative correlation between velocity and endurance. Individuals that produced fast-moving sperm had their sperm become ineffective at much quicker rates than other individuals. The energy used up in swimming fast resulted in less energy for swimming for a long time, as well as a shorter life span for sperm.

Other Effects of Sperm Competition

Sperm competition not only affects the speed at which sperm swim but also affects shape and function in sperm (Bellis et al., 1990; Gomendio et al., 1998; Holman and Snook, 2006; H. Moore et al., 1999; Tourmente et al., 2011). For example, Roger Baker and Mike Bellis's **kamikaze sperm hypothesis** suggests that natural selection might favor the production of some sperm types that are designed to kill other males' sperm rather than fertilize eggs (Baker and Bellis, 1988).

While the evidence for kamikaze sperm in humans is equivocal, sperm competition has had clear effects on sperm morphology in insects, frogs, mammals, birds, fish, and worms (Baer et al., 2009; Birkhead and Møller, 1992, 1998; Eberhard, 1996; Firman and Simmons, 2010; Stockley et al., 1997; Tourmente et al., 2009, 2011; Figure 8.28). In a phylogenetic analysis of 100 species of Australian (myobatrachid) frogs, Philip Byrne and his colleagues found that males in species with intense sperm competition produced sperm with relatively long tails (P. G. Byrne et al., 2003). While the exact advantage of longer-tailed sperm in these frogs is not yet known, other studies have found that sperm with longer tails swim faster than their shorter-tailed competitors, and hence have an increased probability of fertilizing an ovum (Oppliger et al., 2003).

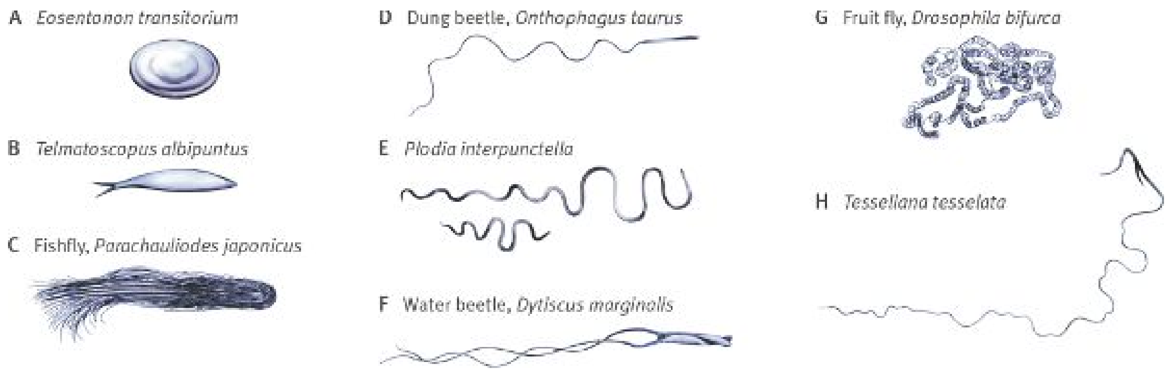


Figure 8.28. Variability in sperm morphology. Sperm competition is one of the many forces that have led to incredible variability in insect sperm morphology. Pictured here are (A) sperm from *Eosentonon transitorium*, (B) sperm from *Telmatoscopus albipuntus*, (C) a sperm bundle from the fishfly *Parachauliodes japonicus*, (D) 1 mm sperm from the dung beetle *Onthophagus taurus*, (E) short and long sperm from *Plodia interpunctella*, (F) paired sperm from the water beetle *Dytiscus marginalis*, (G) giant 58 mm sperm from *Drosophila bifurca*, and (H) hook-headed sperm from *Tessellana tesselata*. *(Based on Simmons, 2001)*

Sperm competition also has effects on the number of sperm produced per ejaculate. One prediction from sperm competition theory is that the number of sperm per ejaculate should be a function of the probability that a female has recently mated with other males (Baker and Bellis, 1993). To see this, consider two males, M1 and M2. Suppose that M1 is about to copulate with a female. The greater the chance that such a female has mated with M2 in the recent past and that his sperm are still present, the greater the chance that M1’s and M2’s sperm will be in direct competition to fertilize the eggs of the female. Sperm competition theory then predicts that M1 will ejaculate more sperm in an attempt to increase the chances that he will fertilize the female’s eggs.

Baker and Bellis tested this hypothesis in humans. They obtained data on the interval between copulations in a given pair of individuals, and assumed that the longer this interval, the greater the chances that a partner would have had a sexual encounter with someone besides their partner. They then obtained sperm samples from individuals the next time they copulated with their partner. Baker and Bellis found that not only did sperm number increase as a function of time since last copulation (which could be due to many different factors), but that even when absolute time was statistically removed from the equation, the relative amount of time couples spent together predicted sperm volume as well (Figure 8.29). When couples spent more time together, and hence the risk of extrapair copulations was low, sperm count was significantly lower than when couples spent less time together.

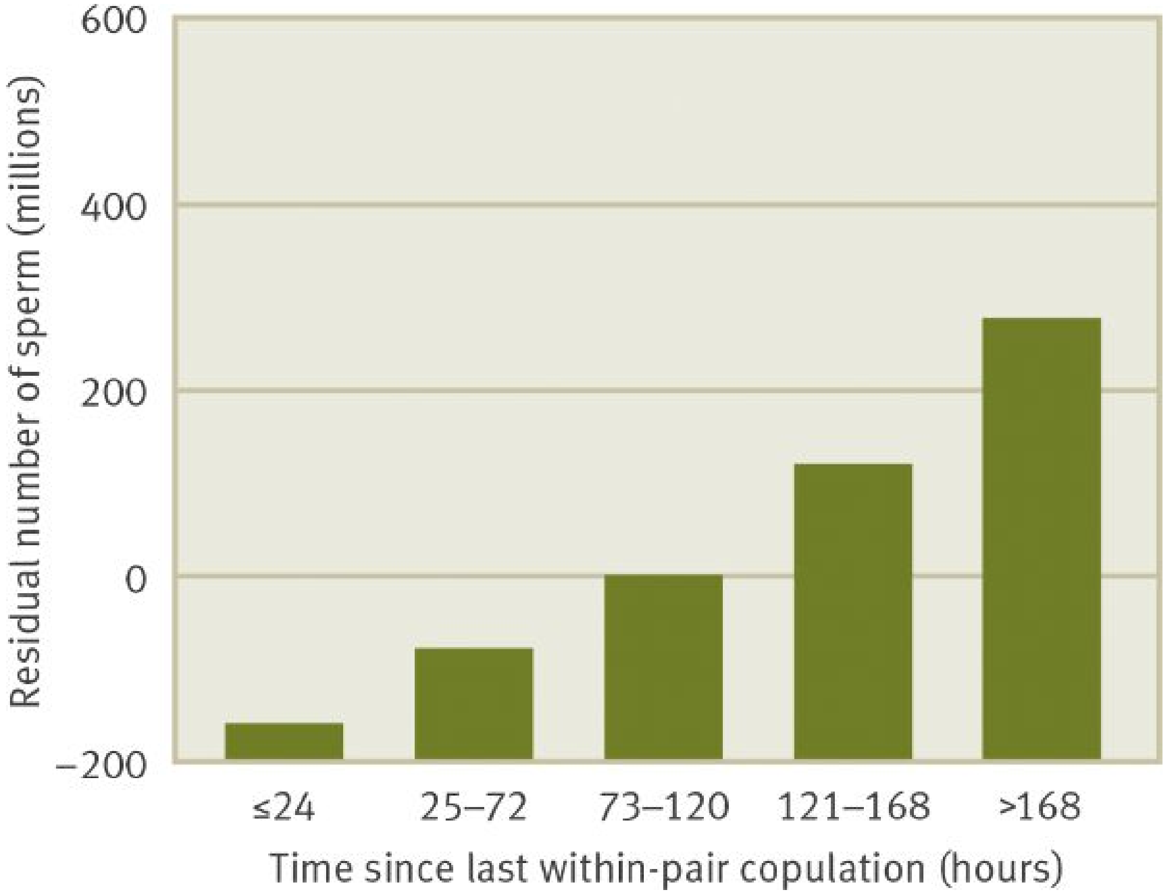


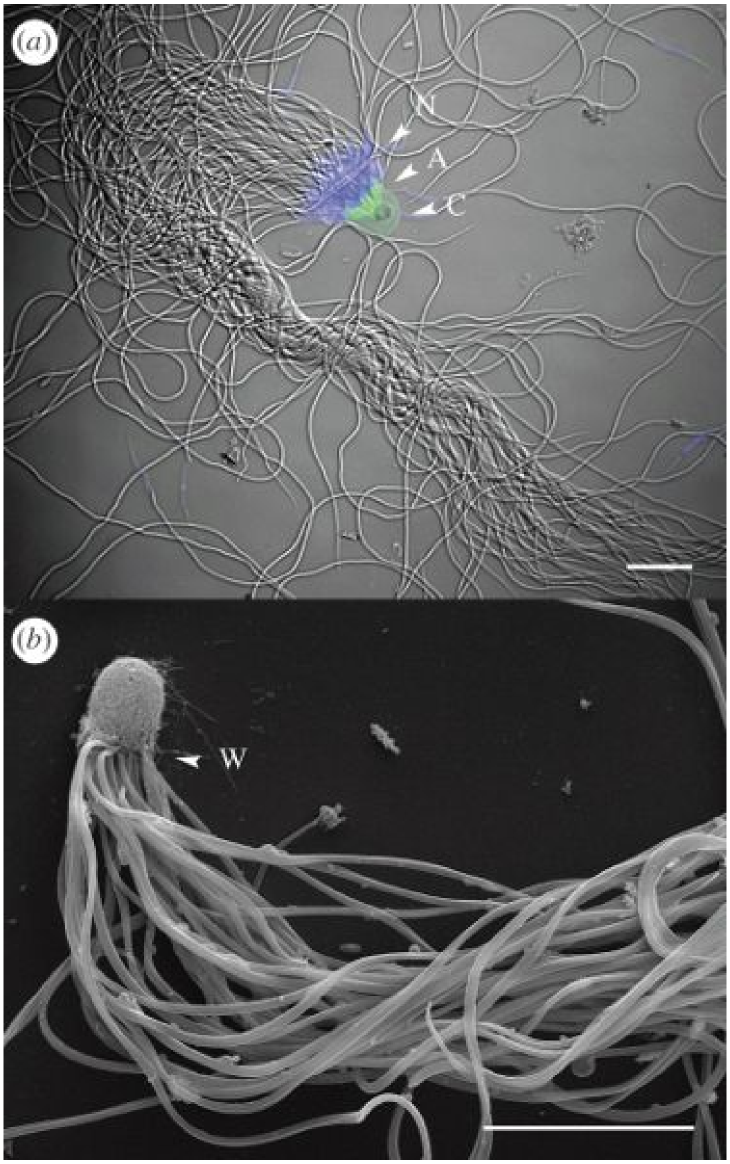
Figure 8.29. Sperm number in humans. In humans, the number of sperm ejaculated during a copulation is a function of the time since a pair last copulated. Note that the *y*-axis is a measure of “residuals,” hence negative values are possible. *(Based on Baker and Bellis, 1993)*

With respect to sperm competition, females are not simply “inert environments” that serve as receptacles of male sperm (G. Parker, 1970b). Rather, females themselves may play an active role in sperm competition via **cryptic mate choice**—that is, female mate-choice behavior that is not obvious to males. William Eberhard has argued that, among other things, cryptic choice may affect how much sperm a female allows a copulating male to inseminate her with, how she goes about transferring such sperm to the organs where sperm are stored, and which sperm she may select for actual fertilization (Eberhard, 1996). Precisely how females select among sperm remains unknown in most cases, but this is an active area of study within animal behavior research.

SPERM COOPERATION

It is possible that sperm from a given male might cooperate with one another to increase the probability that one or more of them fertilize ova (we will examine cooperation in much more detail in the next two chapters). Pearcy et al. (2014) tested for such sperm cooperation in the desert ant *Cataglyphis savignyi*, reasoning that it might be especially likely when the number of mating opportunities is limited, and females mate promiscuously, as is often the case in social insects. While males typically die after a single mating flight in such species, their sperm can survive in the queen's spermatheca for many years.

When the researchers looked at male ejaculates, they found that sperm were often found in bundles (mean sperm number per bundle = 73), and that sperm in a bundle were oriented in the same direction and held together by a "cap" made of glycoproteins (Figure 8.30). But just because sperm are found in bundles does not mean they are cooperating, in the sense of being better off than if they were to swim on their own. To examine cooperation per se, Pearcy and colleagues compared the velocity of sperm bundles to individual sperm, as a proxy for success in reaching and then fertilizing eggs. Velocity in sperm bundles was greater than in single sperm when comparisons were made across different males or across a sperm bundle and a solo sperm from the same male. Taken together, the researchers suggest that such sperm cooperation increases a male's "posthumous fitness."


(a)
N
A
C
(b)
W

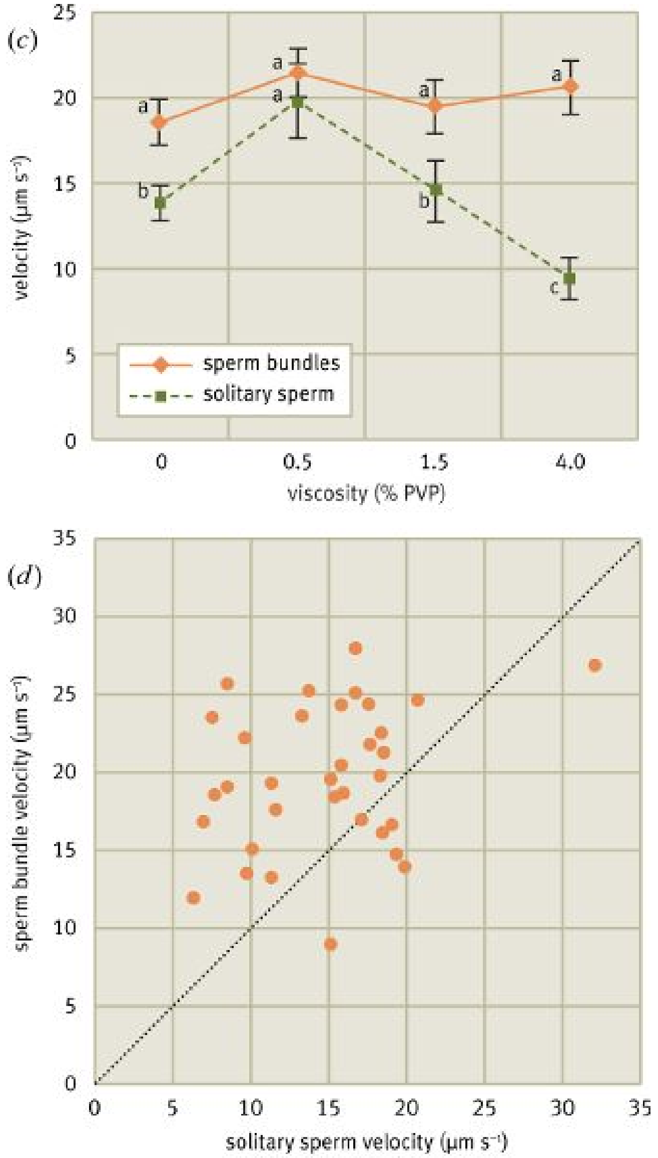


Figure 8.30. **Sperm bundles.** (A) A sperm bundle of *Cataglyphis savignyi* with the sperm nuclei (N) stained in blue and the cap (and acrosome) in green. Scale bar, 10 mm. (B) A scanning electron micrograph showing the cap that bundles sperm and the sperm flagella. Scale bar, 10 mm. (C) Average velocity of sperm bundles in *C. savignyi* is great than that of single sperm in mediums of different viscosities. Comparisons made across males. (D) For a given viscosity, the velocity of a sperm bundle of a male is greater than a solo sperm from that same male. By permission of the Royal Society. *(From Pearcy et al., 2014)*

Multiple Mating Systems in a Single Population?

Nick Davies and his colleagues have a long-term study on a population of about eighty dunnocks that reside in the Botanical Gardens of Cambridge University and it provides a portal into such a complex mating system (Davies, 1992). What makes the dunnock breeding biology so fascinating from a mating systems perspective is the long-term persistence of monogamy, polygyny, polyandry, and polygynandry *in the same population*.

Underlying much of the variance in mating systems, including that of the dunnock, is the fact that the fitness of males and females is affected in different ways by the mating system. Reproductive success of the most successful males will often be lowest when they share access with other males to a single female (polyandry), and then increase in the following order: sole access to a single female (monogamy), joint access to two females (polygynandry), and sole access to numerous females (polygyny). That is, male reproductive success increases as a function of both the number of mates and the degree to which a male has sole reproductive access to such mates.

The reproductive success of the most successful females increases in precisely the opposite direction, with polyandrous and polygynandrous females having the highest reproductive success. As such, a conflict of interest between the sexes—sometimes referred to as a “battle of the sexes”—exists with respect to what constitutes the optimal breeding system (Arnqvist and Rowe, 2005; Hosken et al., 2009; King et al., 2013). In dunnocks, females appear to be winning this battle of the sexes (at least for now), as over the course of ten years, 75 percent of females and 68 percent of males observed by Davies and his team were involved in either polyandrous or polygynandrous mating groups (Davies, 1992).

The battle of the sexes, in conjunction with the dispersal patterns of dunnocks, helps us better understand the complex breeding system found in this bird. Early in the breeding season, females compete with one another to establish territories, and female territories are chosen independently of the position of males. Males then attempt to build their own territories so that they overlay as many female territories as possible. Given these conditions, Davies argues that the difference between monogamy and polygyny is a function of *male* territory size. Polygynous males had larger territories than monogamous males, but when these two breeding systems were compared, the territory size of females remained constant. In contrast, the difference between polyandry and polygynandry was a function of female territory size. Male territory size remained constant across these systems, while female territory size was significantly larger in the former.

Because all individuals in this population were marked (with color rings) and rarely moved more than two miles from the Botanical Gardens, Davies was able to gauge more precisely how resource defense and territoriality influenced the dunnock mating system. Davies and Arne Lundberg hypothesized that because females were in strong competition with one another for territories with the best resources, if the resources available on a territory were experimentally supplemented, territory size should shrink, as females would then be able to obtain the same amount of resources without having to defend as large an area (Davies and Lundberg, 1984).

To test their hypothesis, Davies and Lundberg placed artificial feeders on a randomly selected set of female territories, and they did indeed find that the female territories shrank as predicted. Moreover, they found that the male territories that overlay the manipulated female territories did not change in size. What did occur, however, was a shift in the distribution of mating systems, in such a manner as to favor males. When female territory size shrank as a result of supplemental resources, males were better able to monopolize more than one female, and a shift away from polyandry and toward polygynandry occurred. In the dunnock, females track resources, males track females, and the resulting interaction helps us better understand the incredible variation in mating systems in this bird.

Interview with Dr. Catherine Marler

How did you get involved with your own work on animal mating systems? What has been the most surprising thing you have learned from that work?

My work on animal mating systems has been a confluence of many research experiences, as well as approaches and ideas from many researchers. My dad, Dr. Peter Marler, an internationally renowned animal behaviorist, fostered in me a love of animal behavior, not because we talked about animal behavior, but because I grew up surrounded by all sorts of birds and mammals. At one of my dad's research sites, my brother and I became one of the few examples of human children being hunted by a chimpanzee. Needless to say, that did not deter me. I first started to seriously consider a career in animal behavior after a field animal behavior class as an undergraduate with Dr. Paul Sherman at Cornell University. My sense of curiosity was piqued and I began to view animal behavior as a series of mysteries to solve. In between undergraduate and graduate school, I spent a summer working for Dr. John Wingfield, a close colleague of my dad at Rockefeller University, studying hormones and paternal behavior in an avian species, and my career in behavioral endocrinology began. A paper by Dr. Wingfield that caught my attention involved a simple physiological tweak, just a modification in testosterone levels that could shift a mating system from being monogamous to polygynous. This demonstrated to me the power of hormones on behavior. The ease with which behavior was altered led me to think about how hormones could be influenced by selection not only to shape general categories of mating systems, but also to result in individual variation in behavior. Because my interest in behavioral endocrinology had been piqued, I then began my graduate career with Dr. Michael Moore. The research involved tweaking hormone levels again, but this time in a polygynous species, the Mountain spiny lizard, *Sceloporus jarrovi*; we increased testosterone levels of males in the field earlier than it would naturally occur (prior to the breeding season) and examined the costs of the resulting increased aggression and territoriality, traits involved in male-male competition for obtaining access to mates. From there I went to study with Drs. Walter Wilczynski and Michael Ryan for a postdoctoral position to research polygynous frogs including cricket frogs, *Acris crepitans*, that switched between two male mating tactics, calling and satellite behavior, and found corresponding differences in the neuropeptide distribution in brain areas associated with social behavior within a species! My study of mating systems continued when I accepted a tenure track position at the University of Wisconsin-Madison. My laboratory has returned to studying a strictly monogamous species, the California mouse, *Peromyscus californicus*, in which both parents are territorial and care for the young. It is a fascinating species and we have revealed many behavioral and hormonal mechanisms that influence expression of characteristic behaviors associated with monogamy. We have also revealed significant plasticity in response to social experience and the environment that can then influence future aggressive and paternal behavior. I continue to be intrigued by the diversity of hormonal mechanisms that have evolved to provide the physiological underpinnings for a great diversity in mating systems; these hormones increase the probability that a species will express species-specific social behaviors and at the same time be fine-tuned by the surrounding social conditions and past experience.

Sexual selection and mating systems are often presented as two distinct topics. Is it possible to understand one without the other?

Mating systems have classically been described as discrete categories of behavioral interactions that encompass a species' mating interactions. Drs. Stephen Emlen and Lewis Oring contributed significantly to the perspective that sexual selection is integral to understanding mating systems. We now know, that males and females can have different, even conflicting, behavioral strategies within a species. There was originally a tendency to characterize mating systems solely on male behavior, then female choice also became a common topic of research, and most recently topics such as advantages of multiple mating by females and cryptic female choice have emerged. I find it useful to teach sexual selection prior to mating systems so that students first understand some of the basic processes that contribute to mating systems.

Why is it important for animal behaviorists to study mating systems from both proximate and ultimate perspectives?

If we understand the mechanisms shaping the current expression of behaviors associated with a mating system, we can gain new insights into how these mechanisms have evolved, culminating in the diversity of mating systems that we see in the animal world. For example, the classic work by Larry Young and colleagues found that altering gene expression for a neuropeptide hormone receptor, vasopressin, could induce a polygynous species of vole to become more like a monogamous species in both the pattern of receptors in the brain and in displaying a preference for a familiar mate. Further research in mammals has reinforced the concept that neuropeptides strongly influence bonding behavior. We can take this research approach a step further and ask whether closer proximity or social bonding and its associated neuropeptide underpinnings contribute to sociality in general; this has been supported in avian research conducted by Dr. James Goodson and colleagues. The proximate studies therefore shed light on understanding how important social bonding is to the evolution of mating systems.

Within my laboratory (in collaboration with outstanding graduate students), we have studied the underpinnings for many of the hallmarks of monogamy using the California mouse as a model system. Male paternal behavior is one hallmark that is increased by the hormone testosterone via conversion to estrogen. Paternal behavior can also alter the paternal and aggressive behavior of the sons, as well as the pattern of neuropeptide distributions in brain regions associated with the social behavior of future generations, illustrating the concept that fathers in monogamous species can significantly influence the behavior and not just survivorship of their offspring. Additionally, territorial behavior is often expressed in monogamous species to maintain the exclusive pair-bond and defend the nesting area and its resources from conspecifics. We have found that territorial aggression is very responsive to social conditions and the combination of testosterone pulses and previous winning behavior can increase future probability of winning a male-male competitive encounter and increase androgen receptors in reward-related brain areas. Finally, males that are bonded versus non-bonded can respond very differently to both social and hormonal cues. For example, we revealed a mechanism for male fidelity that occurred through rapid testosterone suppression of ultrasonic vocalizations in bonded but not non-bonded males. Moreover, bonded males will spend significantly more time in a location in response to testosterone pulses when they have established residency associated with a mate; non-bonded but not bonded males will form a conditioned location preference to an unfamiliar area in response to testosterone pulses. We see that bonding in this strictly monogamous species can dramatically alter how individuals interact with their social and physical environments and influence the behavioral hallmarks of monogamy.

Dr. Catherine Marler is a professor in the Department of Psychology at University of Wisconsin, Madison. Her long-term work demonstrates the complexity of mating systems and shows nicely how one can test important hypotheses in this area of animal behavior.

SUMMARY

1. Animal mating systems are classified as monogamous, polygynous, polyandrous, polygynandrous, or promiscuous, depending on the number of mates that males

and females take and the timing of such mating in relation to breeding season.
2. A female can often fertilize all her available eggs by mating with one or a very few males, so female fecundity is not so much tied to the availability of mates as it is to the availability of resources, such as food, defense, and so on. Up to a point, the more resources available, the more offspring females can produce.
3. Males can potentially fertilize many females, so their reproductive success is tied more to access to females than to access to resources. Male dispersion patterns should track the dispersion of females.
4. Recent work in neurobiology and endocrinology has provided animal behaviorists with a better understanding of the proximate underpinnings of both monogamy and polygamy.
5. Phylogenetic work has shed light on the relationship between mating systems and habitat quality. Monogamous systems are often found in poor habitats, and polygynous systems are found in better habitats.
6. The polygyny threshold model predicts under what conditions polygyny should occur in nature. In this model, females weigh the costs and benefits associated with being in a polygynous relationship on a good territory versus a monogamous relationship on a poorer territory.
7. While extrapair copulations and extrapair matings were once thought to be rare in birds, genetic evidence suggests that this is not the case in many species.
8. In some mating systems, males compete not only for access to mates but directly for access to eggs. If females store sperm from numerous matings, sperm from different males compete with one another over access to fertilizable eggs in what is known as sperm competition.

DISCUSSION QUESTIONS

1. Define and distinguish among serial monogamy, serial polygyny, simultaneous polygyny, promiscuity with pair bonds, and promiscuity without pair bonds.
2. Read Jenni and Colliers's 1972 article "Polyandry in the American jacana (*Jacana spinosa*)" in *Auk* (vol. 89, pp. 743–765). What selective forces favored polyandry in jacanas?
3. Why do you think that polygamous mating systems more strongly favor the evolution of virulent diseases in animals and humans than do monogamous breeding systems? Think about this from the perspective of the disease-causing agent.
4. Define an extrapair copulation (EPC). How does this differ from an extrapair mating? Why did it take ethologists so long to recognize the extent of EPCs in nature? How has molecular genetics revolutionized the way we think of mating systems in birds?
5. How has natural selection via sperm competition shaped both sperm morphology and male behavior? Create a list of potential ways in which females may affect sperm competition and its outcome.
6. What is a lek, and why is that form of polygyny especially interesting to ethologists? How has knowledge of kinship bonds contributed to an understanding of why males form leks?

SUGGESTED READING

King, E. D. A., P. B. Banks, & R. C. Brooks. (2013). Sexual conflict in mammals: consequences for mating systems and life history. *Mammal Review*, *43*, 47–58. A review

of sexual conflict and how it shapes mating systems.

Davies, N. B. (1992). *Dunnock behaviour and social evolution*. Oxford: Oxford University Press. A delightful book about Davies's long-term work on dunnock behavior, with an emphasis on dunnock mating behavior.

Lane, J. E., Forrest, M. N. K., & Willis, C. K. R. (2011). Anthropogenic influences on natural animal mating systems. *Animal Behaviour*, *81*, 909–917. An overview of how four anthropogenic factors may affect animal mating systems.

Orians, G. (1969). On the evolution of mating systems in birds and mammals. *American Naturalist*, *103*, 589–603. This is the paper in which Orians presents the polygyny threshold model.

Parker, G. (1970a). Sperm competition and its evolutionary consequences in insects. *Biological Reviews of the Cambridge Philosophical Society*, *45*, 525–567. The seminal paper (no pun intended) of sperm competition and animal behavior.

Shuster, S. M. (2009). Sexual selection and mating systems. *Proceedings of the National Academy of Sciences, U.S.A.*, *106*, 10009–10016. A review of mating systems in a special issue devoted to the 150th anniversary of the publication of Darwin's *On the Origin of Species*.

9

Kinship

Parental care occurs where one or both parents provide care for their developing offspring (Royle et al., 2012). The vast majority of the work in this area centers on extant species, where parental care can be studied in detail. But evidence from the fossil record is also important for our understanding of the origin, evolution and diversity of parental care (Siveter et al., 2014; Caron and Vannier, 2016; Briggs et al., 2016).

Waptia fieldendis, an extinct shrimp-like arthopod, was common during the middle Cambrian Period, approximately 500 million years ago (Figure 9.1). Much of the fossil evidence from this period comes from the famous Burgess Shale Deposit in Canada, and it was here that Caron and Vannier (2016) uncovered fossil evidence of one of the oldest examples of parental care, in *W. fieldendis*. They found numerous fossils of *W. fieldendis* in which brood care was provided by females carrying about two dozen eggs in yolks sacs between the inner surface and the “bivalved” carapaces that sit behind small antennae near their eyes.

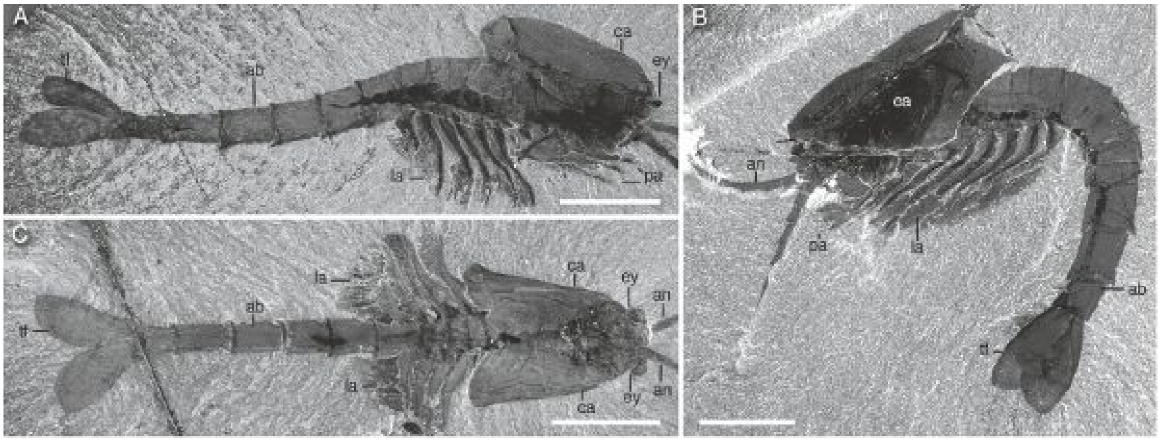


Figure 9.1. ***Waptia fieldensis*, an arthropod from the Cambrian Period.** *Waptia fieldensis*, a species in which brood care has been uncovered from 500-million-year-old fossils, has a head with stalked eyes, a pair of long antennae, a body with four pairs of short appendages, and a fanned tail. Reprinted with permission of Elsevier. © 2016. *(From Caron and Vannier, 2016)*

While *W. fieldendis* sets the origin of brood care at least 500 million years ago, other fossils, some of which also come from the Burgess Shale, demonstrate that a diverse array of brood care strategies arose relatively quickly (Figure 9.2). *Kunmingella douvillei*, another extinct arthropod that lived about the same time as *W. fieldendis*, shows a different brood care strategy, in which eggs are carried on three pairs of posterior appendages. *K. douvillei* also carried more (eighty or so), but smaller, eggs than *W. fieldendis*. And fossil evidence from about 50 million years later, in the Ordovician Period, shows a third type of brood care, in which eggs are kept in a single cluster in a chamber within the carapace (Box 9.1).

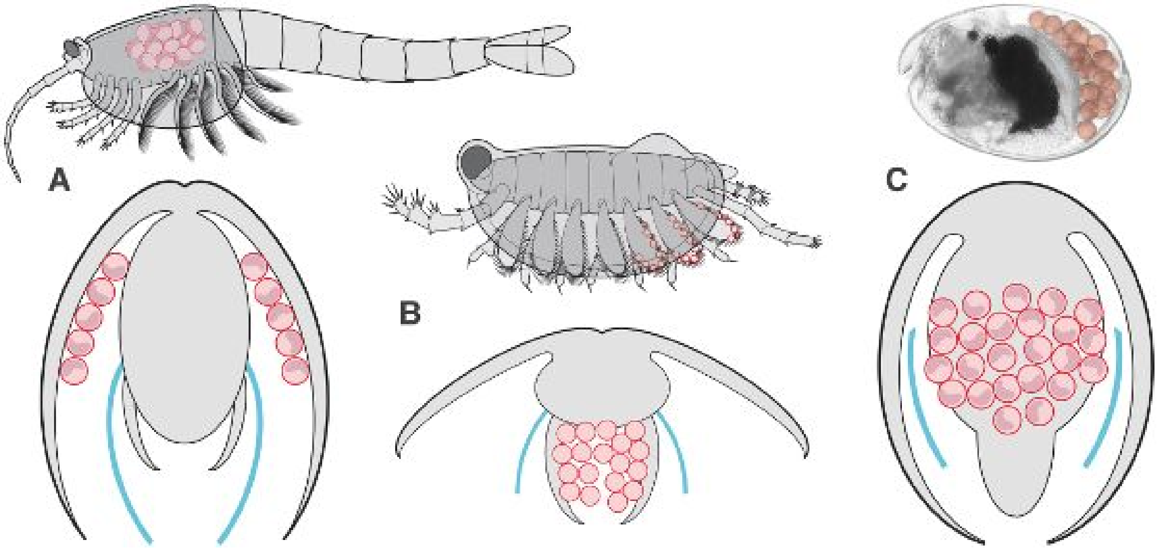


Figure 9.2. **Ancient diversity in brood care.** Brood care in (A) *Waptia fieldensis* (Cambrian), with eggs that are brooded between two carapaces and the inner surfaces of the body, (B) *Kunmingella douvillei* (Cambrian) with eggs on three pairs of appendages, and (C) *Myodocopid ostracod* (Ordovician to modern) with eggs in a single carapace brood chamber. Eggs are shown in pink. Reprinted with permission of Elsevier. © 2016. *(From Caron and Vannier, 2016)*

Box 9.1. SCIENCE AT WORK

What is the research question? Can we use the fossil record to better our understanding of the origin and diversity of parental care?

Why is this an important question? The fossil record has been underutilized in studying the evolution of social behavior.

What approach was taken to address the research question? Fossils from a number of locales were examined for evidence of brood care.

What was discovered? Brood care was found in a number of different species dating from 450–500 million years ago. At least three different brood care strategies were uncovered

What do the results mean? The fossil record can be a useful depository of information relating to the evolution of social behavior.

Kinship and Animal Behavior

In an open field somewhere, a group of ground squirrels feed. Seemingly out of nowhere, a long-tailed weasel (*Mustela frenata*) appears, targeting the squirrels in the field as its prey. Suddenly an alarm call given by one squirrel alerts others of the impending danger. The field comes to life with squirrels making mad dashes everywhere, running to reach their burrow, or at least some safe haven. Later, when the predator has departed, the squirrels reemerge.

Why should natural selection ever favor giving alarm calls? Emitting alarm calls as loud as possible, if nothing else, should make the alarm caller the single most obvious thing in the entire field. Why would the alarm caller do anything to attract a predator in its direction and make itself the predator's most likely next meal? Why not let another squirrel take the risks? In other words why do the squirrels display altruistic behavior, defined as behavior that is costly to self, but beneficial to others?

Paul Sherman has been addressing these sorts of questions in long-term studies of alarm calls in Belding's ground squirrels (*Urocitellus beldingi*; Sherman, 1977, 1980, 1981, 1985; Figure 9.3). He has found that genetic relatedness plays an important role in how natural selection favors squirrels emitting alarm calls when a predator is detected.

Figure 9.3. Alarm calling in squirrels. In Belding's ground squirrels, females (A) are much more likely than males to emit alarm calls when predators are sighted. Such alarm calls warn others, including female relatives and their pups (B). *(Photo credits: Richard Hansen/Photo Researchers; Marie Read/Photo Researchers)*

To understand why Belding's ground squirrels give alarm calls at the risk of their own lives, we need to recognize that alarm calls in these squirrels are most often emitted by females. Female squirrels give alarm calls when a predator is in the vicinity more often than expected by chance, whereas males give fewer alarm calls than expected by chance (Figure 9.4). The question of interest then is not "Why are alarm calls emitted?" but "Why do females give alarm calls so often?" The answer lies in gender differences in migration and proximity to genetic kin.

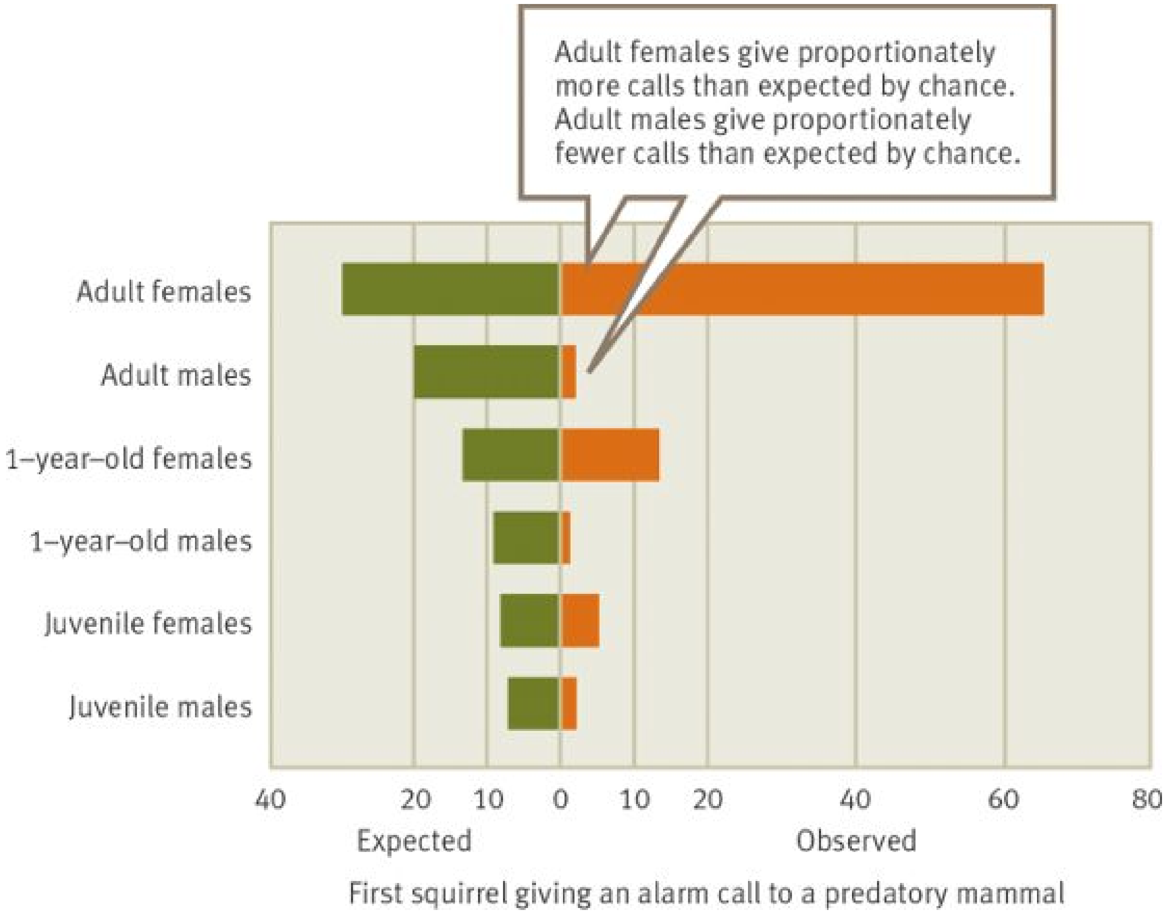


Figure 9.4. Ground squirrel alarm calls. When comparing the observed (orange bars) versus the expected (green bars) frequencies of alarm calls in Belding's ground squirrels, females emit such calls at a rate greater than that expected by chance ($p < .001$). As a result of dispersal differences across sexes, females, but not males, are often in kin-based groups. *(From Sherman, 1977)*

In Belding's ground squirrels, males emigrate from their group to find mates, but females live their entire lives in their natal area (i.e., their place of birth). Male-biased dispersal creates an imbalance in the way males and females are related to the individuals that live in their groups—females find themselves amongst many genetic relatives, while adult males are in groups that do not contain many genetic relatives (Figure 9.5). When females give alarm calls, they are preferentially warning genetic kin. Any alarm calls given by adult males, however, primarily warn unrelated individuals. Kinship, then, lies at the heart of female alarm calling. Further support for the kinship-based alarm-calling hypothesis includes Sherman's finding that, in the rare instances in which adult females do move away from their natal groups and into groups with fewer relatives, they emit alarm calls less frequently than do native females.

Figure 9.5. Kin selection and ground squirrels. Belding's ground squirrel groups are typically made up of mothers, daughters, and sisters that cooperate with one another in a variety of contexts. Males that emigrate into such groups cooperate to a much smaller degree. *(Based on Pfennig and Sherman, 1995)*

In this chapter, after an introductory section on how genetic kinship affects animal behavior, we will examine:

- the theoretical foundation underlying inclusive fitness theory, or the kin selection theory of social behavior;
- the evolution of the family unit;
- parent/offspring conflict and sibling rivalry; and
- how and why animals recognize kin.

Kinship Theory

In the early 1960s, W. D. Hamilton, one of the leading evolutionary biologists of the twentieth century, published his now famous papers on genetic kinship and the evolution of social behavior (Hamilton, 1963, 1964). These papers formalized the theory of "inclusive fitness" or "kinship" theory and revolutionized the way scientists understood the evolution of behavior. Recall from chapter 1 that inclusive fitness is a measure of an individual's total fitness based both on the number of its own offspring and the contribution it makes to the reproductive success of its genetic relatives.

But *why* is kinship so powerful an evolutionary force in promoting social behaviors like cooperation and altruism? In his seminal paper Hamilton wrote:

> In the hope that it may provide a useful summary we therefore hazard the following generalized unrigourous statement of the main principle that has emerged from the model. *The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbors' fitness against his own according to the coefficients of relationship appropriate to that situation* [Hamilton's italics]. (Hamilton, 1964, p. 19)

Although rightly credited with being the founder of modern kinship theory, Hamilton was not the first to recognize the power of kinship to shape behavior (Dugatkin, 2006). Before Hamilton, Charles Darwin suggested that the suicidally altruistic defense behavior that he observed in social insects like bees may have evolved as a result of bees defending hives filled with their relatives—under certain conditions, natural selection could favor such extreme altruism if the recipients of the altruistic act were genetic relatives (Figure 9.6). About seventy-five years later, population geneticist J. B. S. Haldane discussed altruism and genetic kinship (Haldane, 1932). It is rumored that at The Orange Tree pub in London Haldane once said that he would risk his life to save two of his brothers or eight of his cousins (Harman, 2010; Segerstrale, 2010). Haldane, a brilliant mathematician, made this rather surprising statement by counting copies of an allele that might code for cooperative and altruistic behavior. Such a gene-counting approach to kinship and the evolution of cooperation has been formalized by theoreticians, but in its most elementary form, it is at the core of inclusive fitness theory. Let's see how it works.

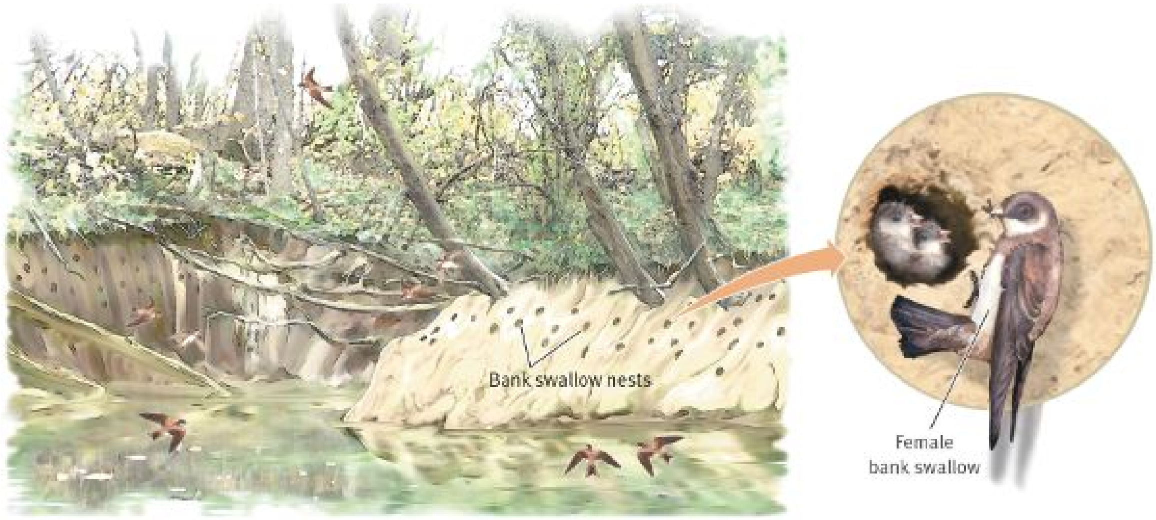


Figure 9.6. Helping offspring. One classic case of helping genetic relatives is that of mothers feeding their young. In bank swallows, young chicks remain at the nest, and mothers remember the location of their nests and return after foraging to feed youngsters there. When chicks learn to fly, mothers learn to recognize their offspring's voices. *(Based on Pfennig and Sherman, 1995)*

RELATEDNESS AND INCLUSIVE FITNESS

The *Random House Dictionary* defines kinship as "family relationship," but an evolutionary definition is narrower. In evolutionary terms, kinship centers on the probability that individuals share copies of alleles that they have inherited from common ancestors—parents, grandparents, and so on. Alleles that are shared because of common ancestry are referred to as "identical by descent." For example, you and your brother are kin because you share some of the same alleles and you inherited them from common ancestors—in this case, your mother and father. You and your cousins are kin because you share alleles in common; but in this case your most recent common ancestors are your grandparents. In general, the most recent common ancestors are those individuals through which two (or more) organisms can trace alleles that they share by descent.

Once we know how to find the common ancestor of two or more individuals, we can calculate their genetic relatedness, labeled *r*, which is equal to the probability that they share alleles that are identical by descent. For example, two siblings are related to one another by an *r* value of 0.5. To see why, recall that all of the alleles that siblings share come from only one of two individuals—their mother or father. As such, there are two ways, *and only two ways*, that siblings can share a copy of an allele—via mother or father. If sibling 1 has allele X, then there is a 50 percent chance she received it from her mother; if sibling 2 has allele X, there is again a 50 percent chance that her mother passed this allele to sibling 2, so there is a 1 in 4 chance that the siblings share allele X through their mother. Similarly, there is a 1 in 4 probability siblings share allele X through their father. To calculate the chances that the siblings share allele X through *either* their mother or their father, we add the probabilities for each and obtain 1/4 + 1/4 = 1/2, or 0.5. This value—labeled *r*—can be calculated for any set of genetic relatives, no matter how distant. For example, the genetic relatedness between cousins is 1/8 ($r = 0.125$), between grandparent and grandchild is 1/4 ($r = 0.25$), and between aunts/uncles and their genetic nieces and nephews is also 1/4 ($r = 0.25$; Figure 9.7).

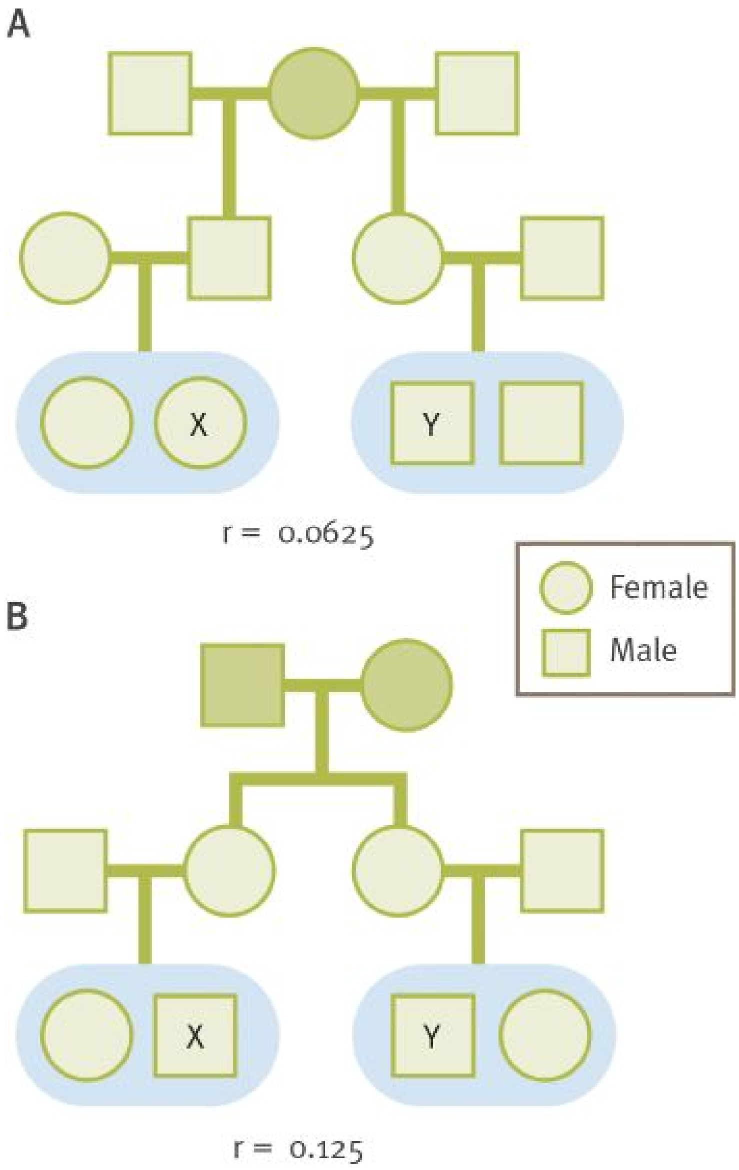


Figure 9.7. Pedigrees for calculating relatedness. Individuals X and Y may have one or two most recent common ancestors (dark shading). (A) X and Y have the same grandmother but different grandfathers. Thus, their grandmother is their sole most recent common ancestor. (B) X and Y have the same maternal grandmother and the same maternal grandfather. Thus, maternal grandparents are their most recent common ancestors. *(From Bergstrom and Dugatkin, 2012)*

Let’s work through a few more examples of calculating genetic relatedness. In Figure 9.8A, individuals X and Y are half siblings, with the same mother but different fathers. To compute the coefficient of relatedness (*r*) between X and Y, we first must find the most recent common ancestor or ancestors. In this case, there is one: their mother. Second, we compute the probability that a given allele copy in the mother is passed to both offspring. The probability is 0.5 that the allele will be passed to 1, and the probability is 0.5 that it will be passed to 2, so the probability that it will be passed to *both* is 0.5 × 0.5 = 0.25. Because the mother is the sole most recent common ancestor, this is their coefficient of relatedness (*r*).

In Figure 9.8B, individuals X and Y have a single most recent common ancestor who is 1’s maternal grandmother and 2’s mother. The chance that a given allele copy in this ancestor reaches 1 is 0.25, because there is a 0.5 chance that it will reach X’s mother, and if it does, there is an additional 0.5 chance that it will go on to reach X, for a net chance of 0.25. The chance that a given allele will reach 2 is 0.5. Thus, the chance that the given allele copy will reach *both* 1 and 2 is 0.25 × 0.5 = 0.125. The coefficient of relatedness between X and Y is therefore 0.125. (If B had been a full sibling to 1’s mother, the coefficient of relatedness between 1 and 2 would have instead been 0.25.) Similar calculations allow us to compute the genetic relatedness between any pair of individuals with a known pedigree.

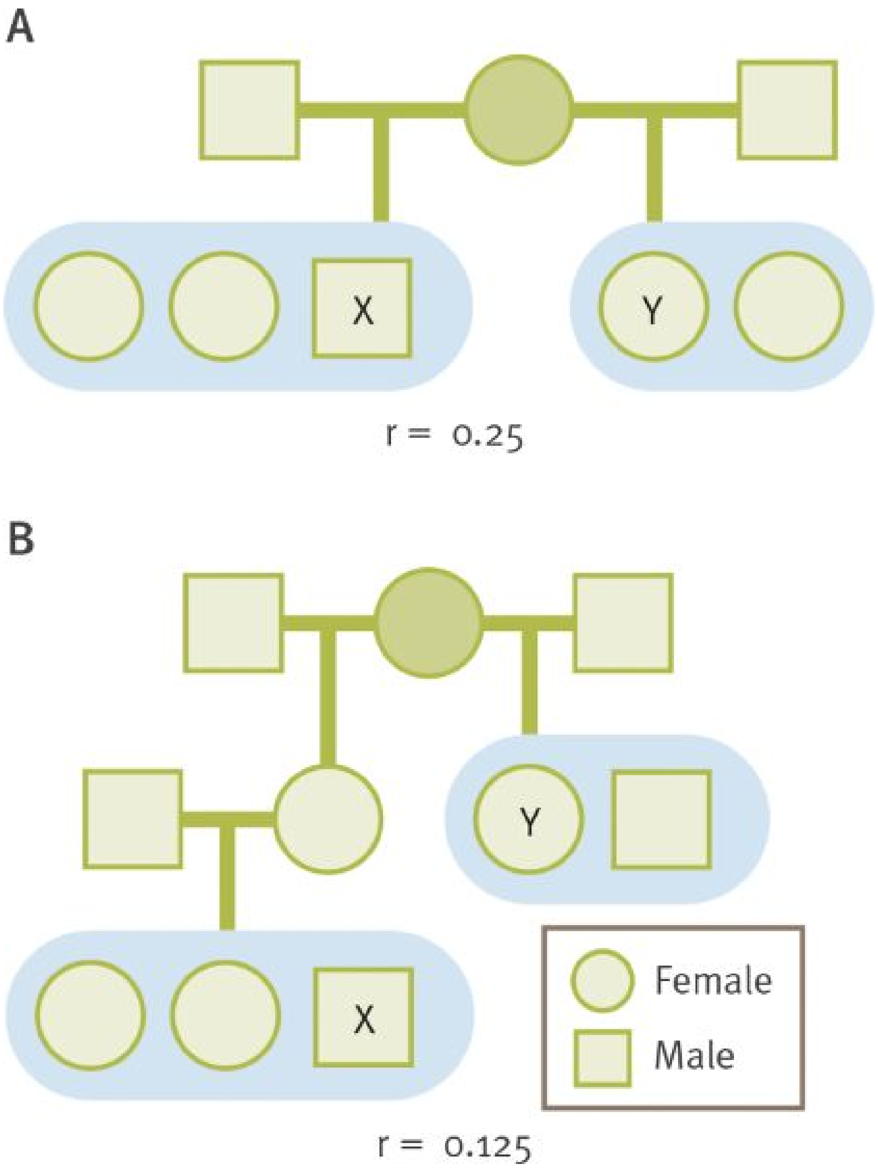


Figure 9.8. Example pedigrees for computing coefficients of relatedness. (A) X and Y are half siblings. (B) A more complicated scenario, in which X and Y come from different generations. Here, Y is X's aunt. *(From Bergstrom and Dugatkin, 2012)*

In previous chapters we have been examining the effect of alleles in terms of the effect on the *individual* in which they reside, but that this is an overly restricted view. Given that genetic relatives, by definition, have a higher probability of sharing allele X through common descent than do nonrelatives, then allele X may increase its chances of getting copies of itself into the next generation by how it affects not just the individual in which it resides, but that individual's genetic relatives as well.

Think about it like this: When an individual reproduces and its offspring survive, copies of that individual's alleles make it into the next generation. But that is not the *only* way that alleles can increase their representation in future generations. If an allele codes for preferentially aiding genetic kin, then that allele can increase its representation in the next generation by coding for aid to individuals who are likely to have a copy of that allele that is identical by descent as well (Hamilton, 1963). How likely a recipient is to have that allele that is identical by descent is equal to r, the genetic relatedness of the donor and recipient (0.5 probability for siblings, 0.25 probability for uncle and nephew, and so on). When we consider both direct and indirect components to fitness, we are talking about **inclusive fitness**.

With an understanding of how *r* is calculated, we can now examine inclusive fitness theory in more detail. Hamilton addressed the question of kinship and animal behavior in a pair of papers, "The Genetical Evolution of Social Behavior, I and II" (Hamilton, 1964). The essence of inclusive fitness models is that they add on to "classical" models of natural selection by considering the effect of an allele, not only on the individual in which it resides, but on individuals (genetic kin) carrying alleles that are identical by descent. The equations in some of Hamilton's papers on kinship can be daunting, even to those with a mathematical background. Fortunately, these equations can be captured in what is now referred to as "Hamilton's Rule" (Hamilton, 1963). This rule states that an allele associated with some trait being studied increases in frequency whenever:

$$\left(\sum_{1}^{A}\right) rb - c > 0$$

where *b* = the benefit that others receive from the trait in question (Rodrigues and Kokko, 2016), *c* = the cost accrued to the individual expressing the trait, *r* is our measure of relatedness, and *A* is a count of the individuals affected by the trait of interest. In Hamilton's Rule, the decision to aid family members is a function of how related individuals are, and how high or low the costs and benefits associated with the trait turn out to be. When genetic relatedness is high, then *r* times *b* is more likely to be greater than *c* than when genetic relatedness is low—

natural selection more strongly favors kin helping one another when *r* is high. In addition, as the benefit that recipients obtain (*b*) increases, and/or the cost (*c*) to the donor decreases, the probability that *r* times *b* is greater than *c* increases and so natural selection should favor kin helping one another when *b* is high and/or *c* is low. Finally, as the number of relatives helped by an act of altruism (A) increases, selection more strongly favors altruism.

Inclusive fitness theory has had a profound impact on the work of ethologists, behavioral ecologists, and comparative psychologists. The effect of these ideas has been even greater as a result of Jerram Brown's reformulation of Hamilton's equation. Field workers in animal behavior had found the *b* and *c* terms of Hamilton's model difficult to measure in nature. To address this problem, Brown proposed the "offspring rule," which used the number of offspring that were born and survived as the currency of measure (J. L. Brown, 1975). This formulation set up the possibility of field manipulations in which Hamilton's and Brown's ideas could be tested by counting the number of offspring across different experimental treatments. For example, if an ethologist wanted to know the positive effects that young "helpers-at-the-nest" might have on raising their siblings, she could examine the difference in the average number of chicks that survive in the presence and absence of such helpers (J. L. Brown et al., 1982; Figure 9.9). In terms of measuring the costs to the helper of helping, ideally ethologists would measure the number of offspring produced by individuals that did not help versus those that did help. All else being equal, the difference between these values allows for an estimation of the cost of helping.

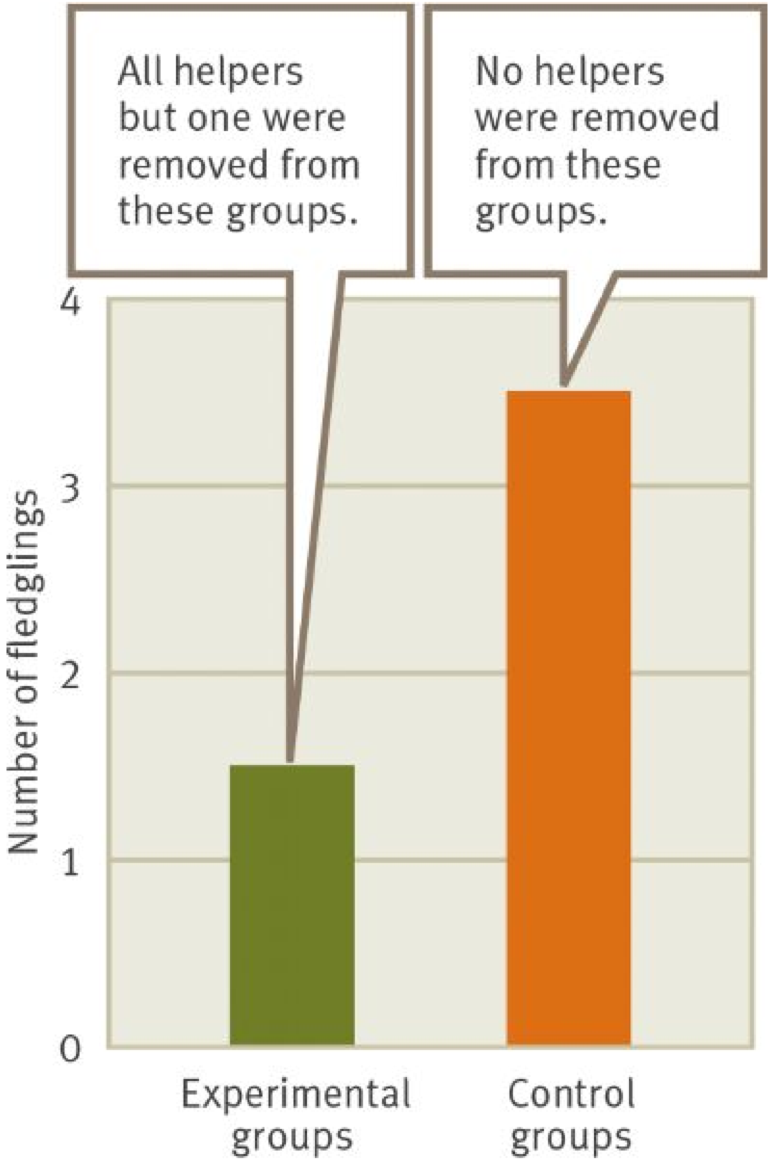


Figure 9.9. The effects of helping kin. In grey-crowned babblers (*Pomatostomus temporalis*), reproductive success, as measured by the number of fledglings, was significantly lower in experimental groups that had fewer helpers. Helpers increased the reproductive success of others—their kin—in their group. *(Based on Brown et al., 1982)*

Ben Hatchwell and his team quantified *r*, *b*, and *c* in a population of long-tailed tits (*Aegithalos caudatus*) to test whether the conditions of Hamilton's rule were met in these birds (Hatchwell et al., 2014) (Figure 9.10). Long-tailed tit breeders who lose their nest to predation (or other causes) often join another nest and help the breeders there raise their young. Hatchwell's team focused on male helpers and male breeders, because male tits are philopatric (remain in their natal areas), while females tend to disperse. The question they addressed was whether, when joining nests to help, $r \times b > c$ for helpers.

Figure 9.10. **A long-tailed tit.** Long-tailed tits have been studied to test predictions that arise from inclusive fitness theory. *(Photo credit: © Martin Mecnarowski / Shutterstock)*

Using a marked population of 100 breeding adults, Hatchwell et al. set out to measure the three variables in Hamilton's rule. They took blood samples from the tits and genotyped them at nineteen loci to estimate genetic relatedness (*r*). A mean r value of 0.20 was found between helpers and the breeders they assisted, and a mean *r* value of 0.16 was found between helpers and the chicks they helped (Figure 9.11).

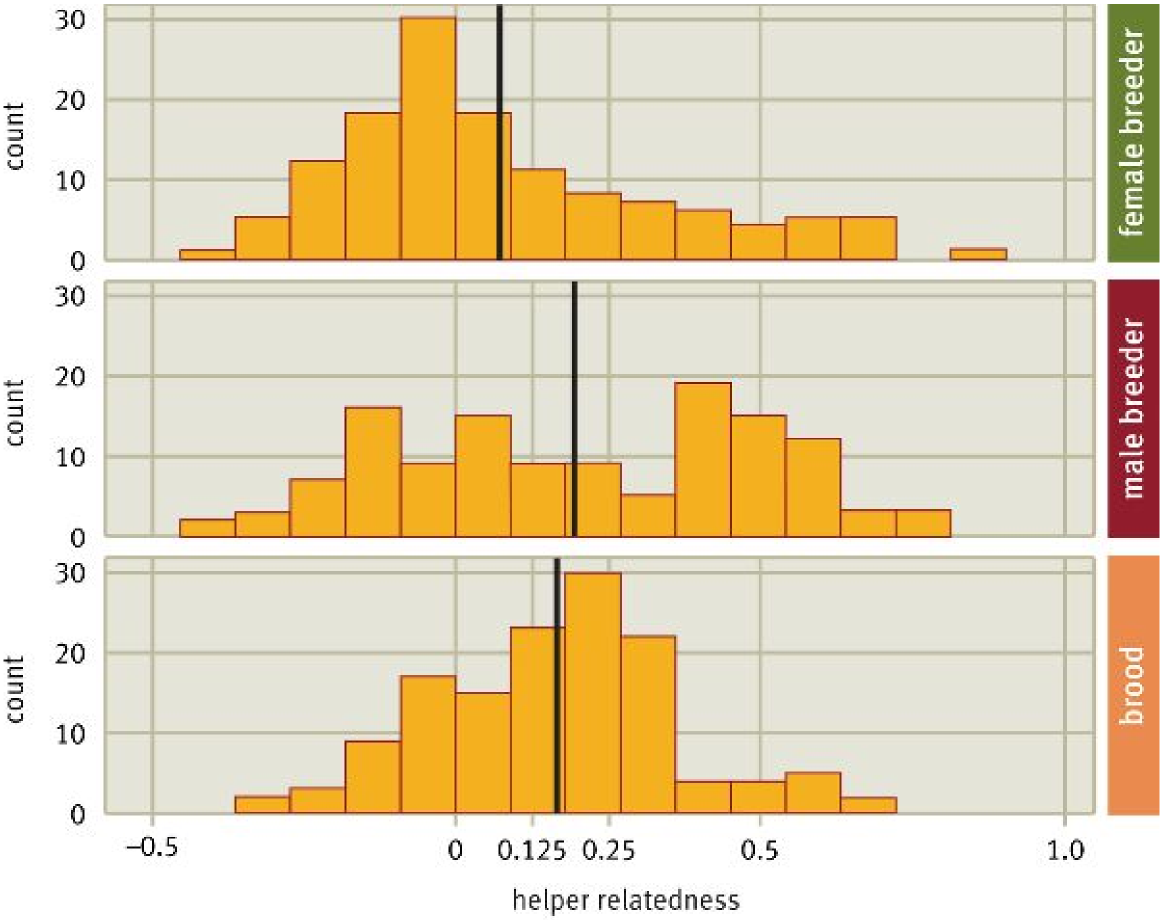


Figure 9.11. **Measuring *r***. A frequency distribution of *r* between helpers and male breeders and helpers and the chicks they help in long-tailed tits. *(From Hatchwell et al., 2014)*

They next measured the benefit that helpers receive from their actions. There were two key components to benefits received by helpers:

1) The increased probability that chicks who are helped survive their first year and make it into the breeding population the next year: this is referred to as the recruitment rate. Detailed multiyear analysis found that the increase in survival rates of young that are helped versus not helped averaged 6.2%. The mean clutch size of clutches that received assistance was 8.9, and 53% of chicks in the nests were male. From these values, Hatchwell et al. were able to calculate the number of additional male recruits attributable to helpers: 8.9 × 0.53 × 0.062 = 0.292.
2) The increased survival of male breeders who are helped. Here, an increase of 5% was found. The probability that a male breeder who survives produces a male chick that survives the subsequent year was 26%, and the average genetic relatedness between a breeder and the male chicks in his nest was 0.48 (lower than 0.5 because of a low-level of extra-pair mating). As such, the number of additional male recruits attributed to helpers here is 0.05 × 0.26 × 0.48 = 0.0062.

Table 9.1. Calculations used to test Hamilton's rule in long-tailed tits. The components of inclusive fitness in long-tailed tits. *(Modified from Hatchwell et al., 2014)*

TERM	MARGINAL EFFECT OF HELPER ON CURRENT BROOD PRODUCTIVITY	MARGINAL EFFECT OF HELPER ON FUTURE PRODUCTIVITY OF MALE BREEDER	MARGINAL EFFECT OF HELPING ON HELPER'S FUTURE PRODUCTIVITY
r	relatedness of helper to brood, → r_{h-b} = **0.16**	relatedness of helper to helped male, → r_{h-m} = **0.20**	relatedness of helper to self, r_{h-h} = **1**
b	brood size = 8.9 proportion of brood male = 0.53 Δ recruitment rate = +0.062 → b_c = 8.9 0.53 0.062 = **+0.292 male recruits**	Δ survival rate = +0.05 probability of producing male recruit in year *n* + 1 = 0.26 → 0.05 0.26 = +0.013 male recruits relatedness of breeder to recruits = 0.48 → b_m = 0.48 0.013 = +0.0062 genetic equivalents	none
c	none	none	Δ survival rate = –0.23 probability of producing male recruit in year *n* + 1 = .026 → –0.23 0.26 = –0.0598 male recruits relatedness of helper to recruits = 0.48 → *c* = 0.48 –0.598 = **–0.0287 genetic equivalents**

The total *r* × *b* for helpers is then 0.20 × .0.292 (*r* × *b* for chick survival component) plus 0.16 × 0.0062 (*r* × *b* for breeder survival component), which sums to 0.0479.

The cost for helping in the long-tailed tit system was calculated in a similar manner. Helpers reduce their own survival rates by a mean of 23%. As mentioned above, if a male survives, the probability of producing a male chick that survives the following year is 26% and the average relatedness between a male breeder and the male chicks in his nest is 0.48. The cost is then the product of these values, or 0.23 × 0.26 × 0.48 = 0.0287.

Table 1 summarizes the inputs used in testing Hamilton's rule. What emerges is that in this system, the conditions of Hamilton's rule are met as $r \times b = 0.0479 > c = 0.287$.

FAMILY DYNAMICS

While Hamilton's Rule makes some very general predictions about animal social behavior, subsequent work by animal behaviorists and behavioral ecologists has generated more specific predictions about family dynamics (S. Emlen, 1995b). In particular, Stephen Emlen has developed an evolutionary theory of family that aims to test specific predictions regarding "the formation, the stability, and the social dynamics of biological families" (S. Emlen, 1995b, p. 8092).

The building blocks for Emlen's work on family dynamics are (1) inclusive fitness theory; (2) ecological constraints theory, which examines dispersal options of mature offspring, and specifically the conditions that favor dispersal from home rather than remaining on a natal territory (J. L. Brown, 1987; S. Emlen, 1982a,b; Koenig and Pitelka, 1981; Koenig et al., 1992); and (3) reproductive skew theory, which examines how reproductive opportunities are divided among potential breeders by predicting conditions that should favor conflict or cooperation with respect to breeding decisions (R. Johnstone, 2008; Nonacs and Hager, 2011; Shen-Feng et al., 2011; Reeve and Shen, 2013; Figure 9.12).

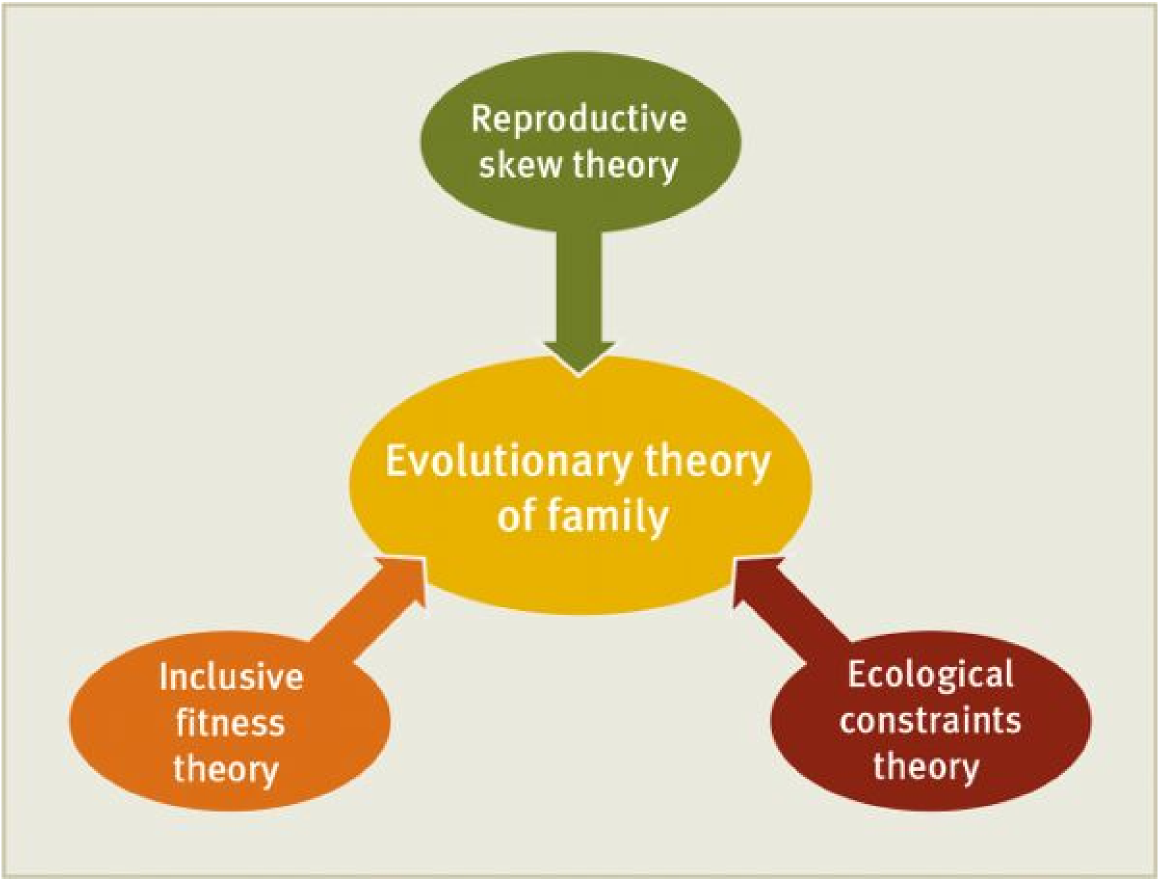


Figure 9.12. Evolutionary theory of family. Emlen's evolutionary theory of family is generated by combining inclusive fitness, reproductive skew, and ecological constraints theory.

Emlen made fifteen specific predictions about animal family dynamics, and for each of these, he reviewed the evidence from the animal literature, both for and against his predictions (S. Emlen, 1995b; Table 9.2). Two years after publication of Emlen's paper, Jennifer Davis and Martin Daly tested Emlen's fifteen predictions as they relate to human families (J. Davis and Daly, 1997). Whereas Emlen's data are from a wide variety of animals, Davis and Daly's analysis is necessarily restricted to one species—*Homo sapiens*. Most of their data came from the Canadian General Social Survey, a telephone survey that amassed information on family dynamics in 13,495 households. Such a survey is probably reflective of modern Western society, but, of course, it does not represent all societies.

Table 9.2. Predictions generated by Emlen's evolutionary theory of the family model. The table lists the fifteen hypotheses associated

with Emlen’s evolutionary theory of the family. *(From Emlen, 1995b, p. 8093)*

No.	Abbreviated prediction
1	Family groupings will be unstable, disintegrating when acceptable reproductive opportunities materialize elsewhere.
2	Family stability will be greatest in those groups controlling high-quality resources. Dynasties may form.
3	Help with rearing offspring will be the norm.
4	Help will be expressed to the greatest extent between closest genetic relatives.
5	Sexually related aggression will be reduced because incestuous matings will be avoided.
6	Breeding males will invest less in offspring as their certainty of paternity decreases.
7	Family conflict will surface over filling the reproductive vacancy created by the loss of a breeder.
8	In stepfamilies, sexually related aggression will increase because incest restrictions do not apply to replacement mates. Offspring may mate with a stepparent.
9	Replacement mates (stepparents) will invest less in existing offspring than will biological parents. Infanticide may occur.
10	Family members will reduce their investment in future offspring after a parent finds a new mate.
11	Stepfamilies will be less stable than biologically intact families.
12	Decreasing ecological constraints will lead to increased sharing of reproduction.
13	Decreasing asymmetry in dominance will lead to increased sharing of reproduction.
14	Increasing symmetry of kinship will lead to increased sharing of reproduction.
15	Decreasing genetic relatedness will lead to increased sharing of reproduction. Reproductive suppression will be greatest among closest kin.

A review of the papers by Emlen and by Davis and Daly provides us with an opportunity to examine and test evolutionary theories of family in both humans and nonhumans. We will examine a subset of three of Emlen’s predictions (his predictions numbered 1, 2, and 4) in more detail. These three predictions were chosen to show the diversity of issues that kinship touches upon within animal and human behavior.

Prediction 1

“Family groupings will be unstable, disintegrating when acceptable reproductive opportunities materialize elsewhere.”

This prediction focuses on costs and benefits associated with family life. Broadly speaking, individuals who have a higher inclusive fitness when remaining with their family should stay as part of the family unit, while those who have opportunities for increasing their inclusive fitness elsewhere should depart (see Box 9.2). Evidence in support of this prediction in animals comes from many species of birds and mammals.

Box 9.2. CONSERVATION CONNECTION

Nonbreeding Groups and Inclusive Fitness Benefits in Gorillas

The Louke population of western lowland gorillas (*Gorilla gorilla gorilla*) in the Congo has approximately 400 individuals. Over the course of their ontogeny males may find themselves in one or more social conditions: (1) a solitary male; (2) a member of a nonbreeding group (NBG), which contains younger individuals (usually males) and often one older, “silverback” male; and (3) a member of a breeding group (BG), in which they are the lone mature male and the remainder of the group are adult females and sexually immature males.

The gorillas in the Louke population are individually recognizable (primarily by fur patterns), and many have been genotyped (from dung samples). This population of gorillas, along with others, has been studied for decades, and although the social dynamics of breeding groups in the wild is fairly well understood, little is known about NBGs (Fossey, 1983; A. Harcourt, 1978; Robbins, 1996). What is known is that males shift from being solitary to being part of NBGs and BGs (Figure 9.13). Florence Levrero and her team were interested in whether there might be inclusive fitness benefits associated with being part of an NBG, both for immature males in the group and for the single male silverback in an NBG (Levrero et al., 2006).

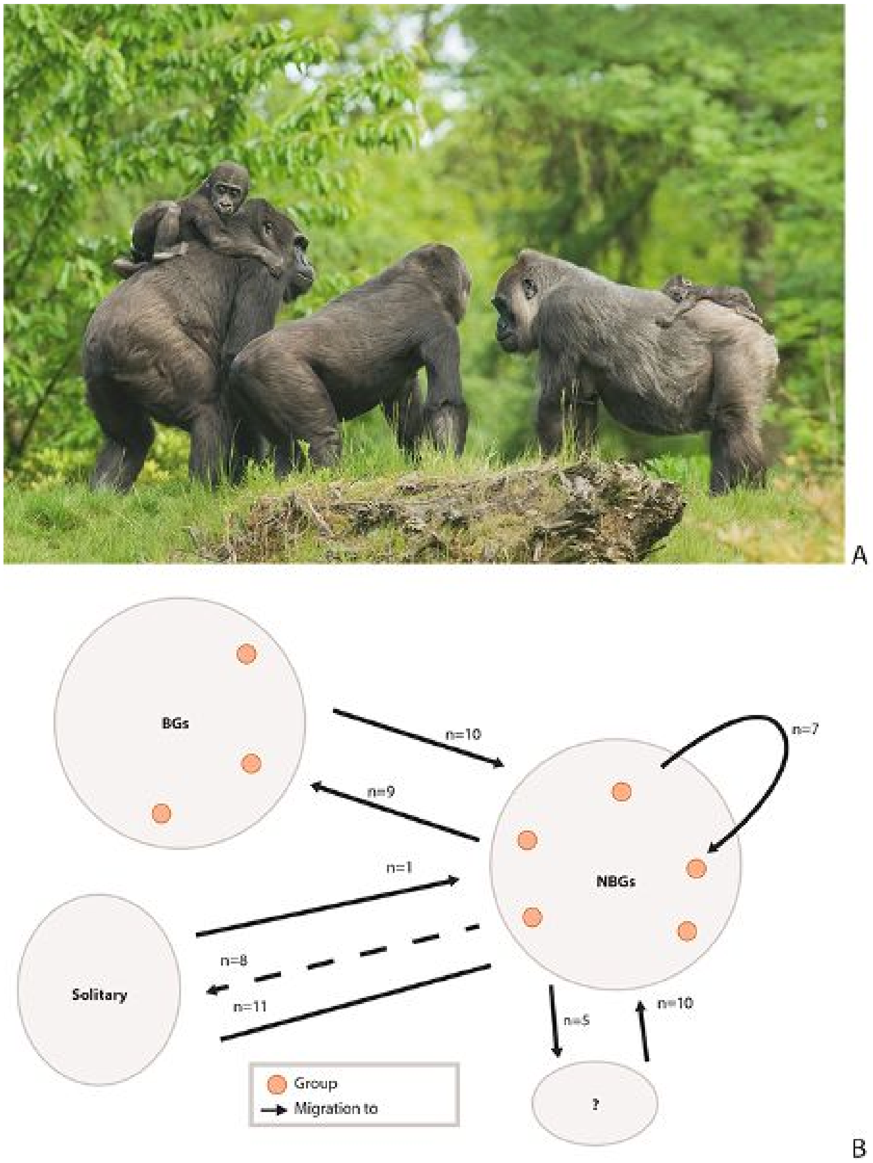


Figure 9.13. Group structure of lowland gorillas. (A) A group of lowland gorillas. (B) BG = breeding group, NBG = nonbreeding group, ? =unknown group structure. Over the course of their lives, most males will be part of all three group structures. *(Photo credits: Terry Whittaker / Alamy Stock Photo; from Levrero et al., 2006, reprinted with permission, © 2006.)*

To examine whether inclusive fitness benefits were important in the formation and stability of NBGs, Levrero and her colleagues first determined levels of genetic relatedness between immature males in NBGs. They found no evidence that males preferentially joined or remained in groups in which other nonbreeding males were their relatives. Males did, however, show a strong preference for joining NBGs that contained a silverback male—such groups tend to be safer and associated with more food than NBGs with no silverback.

Among NBGs that contained a silverback, immature males preferred to join groups in which they were related to the silverback. Silverbacks in NBGs, then, receive indirect benefits by providing food and protection to their genetic relatives, many of whom will go on to form their own breeding groups later in life. In some populations of gorillas, there is evidence that the silverback in an NBG preferentially provides support to relatives in his NBG when such relatives are in aggressive interactions with those not related to the silverback in that group (D. P. Watts, 1990).

While Levrero and her colleagues were able to study the inclusive fitness benefits to silverbacks in NBGs, the inclusive benefits to young males joining an NBG group that contains a related silverback are unclear. It may be that such emigrating young males find that NBGs with a related silverback are simply easier to join. For example, young males may encounter less resistance when attempting to join these groups than when trying to join NBGs that contain silverbacks to whom they are not related.

Gorilla populations are dwindling quickly and are severely endangered. Understanding the role of the indirect fitness benefits that silverback males in NBGs receive may help provide some guidance when developing conservation plans for these populations, both in the wild and in captivity. When managing such populations, attempts to manipulate NBGs in any way that undermines their social structure may interfere with the inclusive fitness benefits that the silverback in such groups normally receives.

One technique for experimentally examining prediction 1 is to create new, unoccupied territories and examine whether mature offspring leave their natal area to live in such newly created areas, as Stephen Pruett-Jones did with superb fairy wrens (*Malurus cyaneus*), an insectivorous (insect-eating) Australian bird species (Pruett-Jones and Lewis, 1990; Figure 9.14). In superb fairy wrens, a breeding pair is often helped by its nonbreeding young male offspring, who provide their siblings with additional food and protection. In contrast, female superb fairy wrens emigrate from their natal territory and do not help raise siblings at their parents’ nest. To test the prediction that families will break down when suitable territories emerge for young helper males, Pruett-Jones and Lewis removed the breeding males from twenty-nine superb fairy wren territories.

Figure 9.14. Superb fairy wren. In superb fairy wrens, young males often act as helpers-at-the-nest. When breeding males are removed from their territories, almost all potential male helpers that could have dispersed to newly opened territories did so. *(Photo credit: © CoolR / Shutterstock)*

When they removed breeding males from their natal territories, all but one of the thirty-two potential male helpers that could have dispersed to the newly opened territories did so, and they did so quickly—new territories were usually occupied by former male helpers within six hours. But why did males immediately leave home when reproductive opportunities emerged? A shortage of females and breeding territories created an environment in which reproductive opportunities were exceedingly rare, so male helpers took the opportunity for a breeding territory and thus disbanded family life when the chance arose (Figure 9.15). Pruett-Jones and Lewis's work suggests that helping-at-the-nest may raise the inclusive fitness of young males when territories are limited, but not otherwise.

Figure 9.15. Family breakup. In the superb fairy wren, male helpers often assist their parents. If a vacant territory opens up, however, male helpers are quick to leave the family unit and attempt to start their own family.

The picture is not as clear-cut with respect to what the data tell us regarding prediction 1 in humans. In their analysis of the Canadian General Social Survey (GSS) data, Davis and Daly found that married individuals were more likely to live away from their parents than were single individuals in the same age/sex category. This suggests that new marriages cause existing family units to dissolve. When new opportunities for reproductive success materialize, they are, on average, taken. It need not have turned out that way. Davis and Daly *might* have found that married individuals were *more* likely than single individuals to live with one set of their parents.

While the above data on dispersal and residence patterns suggest that marriage causes the dissolution of existing family units, while creating other new family units, prediction 1 was not supported when Davis and Daly used other data to test this prediction. When they examined whether married and single individuals living away from their parents differed in terms of contact with parents or grandparents—differences we might expect if marriage did break up already existing families—very few differences were uncovered. For most age/sex categories, married individuals living apart from either set of parents were just as likely to stay in contact via phone, visits, and letters with parents and grandparents as were single individuals living away from home, in clear contrast to prediction 1.

Davis and Daly tested prediction 1 in other ways as well, and they argue that as a whole, the data from the Canadian GSS do not support Emlen's first prediction. Rather, they suggest that, with some exceptions, it appears that human parents act as post-reproductive helpers to their own offspring, which may select for strong family bonds that do not easily dissolve when offspring get married.

Prediction 2

"Families that control high-quality resources will be more stable than those with lower-quality resources. Some resource-rich areas will support dynasties in which one genetic lineage continuously occupies the same area over many successive generations."

Inclusive fitness theory predicts that individuals will, under some circumstances, remain in their natal territory if there are enough resources for them to mate and provide for their own offspring. If the benefits associated with remaining on a natal territory are sufficiently great—lots of food and the space to attract a mate and breed, for example—then those benefits, in conjunction with the indirect benefits of helping relatives, create incentives for keeping families intact. Over the long run, this will create dynasties in families that occupy the very highest-quality territories (see chapter 14). Not only are the offspring that remain on high-quality territories receiving a benefit, but their parents are as well, since they then pass down the best-quality territories to their genetic kin (J. L. Brown, 1974).

Data from six species of birds are in line with the dynasty-building hypothesis in that birds from high-quality family territories are indeed less likely to disperse from the natal territory than their counterparts from families with inferior territories. For example, in cooperatively breeding acorn woodpeckers (*Melanerpes formicivorus*), the critical measure of territory quality is the number of storage holes (Koenig et al., 2011; Figure 9.16). In a New Mexican population of acorn woodpeckers studied by Peter Stacey and David Ligon, territories varied from less than 1,000 to greater than 3,000 storage holes for acorns.

Figure 9.16. Dynasty building in acorn woodpeckers. In cooperatively breeding acorn woodpeckers (*Melanerpes formicivorus*), young birds not only survive better on territories with more storage holes, but also are more likely to remain on their natal territories throughout their life, creating a “family dynasty.”

Individuals on territories with many storage holes produced a greater average number of offspring (Stacey and Ligon, 1987; Figure 9.17). More critical to testing Emlen’s prediction, in areas with more than 3,000 storage holes, 27 percent of the young remained on their natal territories and helped their relatives, while only 2 percent of the young on territories with fewer than 1,000 holes stayed and helped. One of the benefits of remaining on a high-quality territory is that males that served as helpers had a relatively high probability of eventually entering the breeding population, often breeding in turn on their natal territory, either at the same time as their parents or after their parents had died (Stacey and Ligon, 1987).

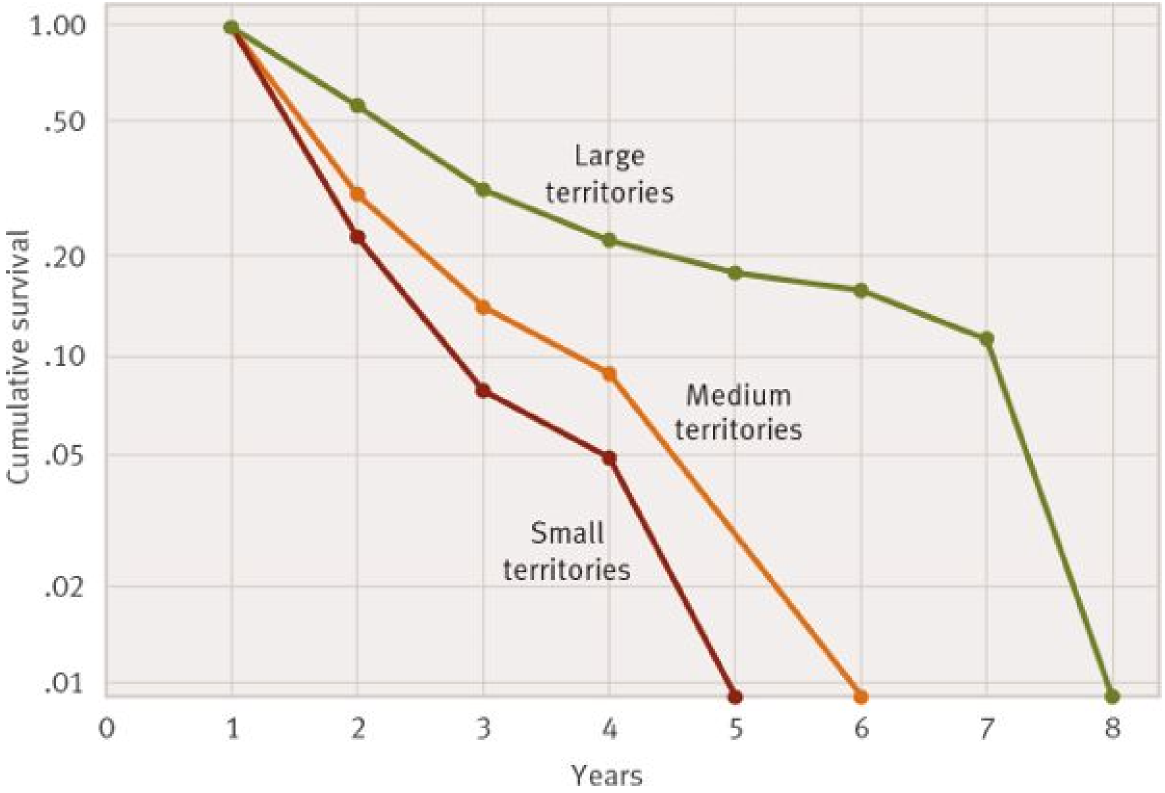


Figure 9.17. Territory quality and survival in acorn woodpeckers. Increasing territory size, and hence increasing number of storage holes, led to increased rates of survival. *(Based on Stacey and Ligon, 1987, p. 663)*

In terms of human family dynamics, prediction 2 translates into the hypothesis that well-to-do families will be more stable than poorer families. Davis and Daly found that if a stable family is defined in terms of co-residence (as in the nonhuman case), then this prediction is not supported. To cite just one of Davis and Daly’s examples, young adults from wealthy families tend to be *less* likely to be living with their parents than are same-age individuals from poorer families (White, 1994). But, since resources are very mobile in today’s economies, it might be argued that familial co-residence is an inappropriate yardstick for measuring family stability. If the measure of stability is defined in terms of maintaining family contacts and providing social support during adulthood, the data are more supportive of prediction 2.

At the most general level, data suggest that contact and support are indeed found more often in wealthy families (Eggebeen and Hogan, 1990; Taylor, 1986; White and Reidmann, 1992). Davis and Daly used GSS data to address the more detailed question of whether contact with kin is not only more likely but more frequent, as a function of wealth. Using letter, phone, or face-to-face conversations as a measure of contact, they examined whether individuals in wealthier families kept in contact more often with parents, grandparents, and siblings than did individuals in poorer families. The GSS data suggest that for most age/sex cohorts, wealthier individuals did keep in touch with relatives more often than did lower-income individuals.

Prediction 4

"Assistance in rearing offspring (cooperative breeding) will be expressed to the greatest extent between those family members that are the closest genetic relatives."

Inclusive fitness theory suggests that, *all else being equal*, when given the choice between helping individuals that differ with respect to r (the coefficient of relatedness), more aid should be dispensed to the closest genetic kin than to more distantly related kin.

Many studies published on cooperation in birds or mammals that live in extended families find that individuals do extend aid as a function of genetic relatedness. For example, in white-fronted bee-eaters (*Merops bullockoides*; Figure 9.18), helpers chose to aid individuals they were most closely related to in 108 of 115 opportunities (Figure 9.19).

Figure 9.18. White-fronted bee-eater kinship. Inclusive fitness models of behavior have been tested extensively in white-fronted bee-eaters. *(Photo credit: Arco Images GmbH / Alamy Stock Photo)*

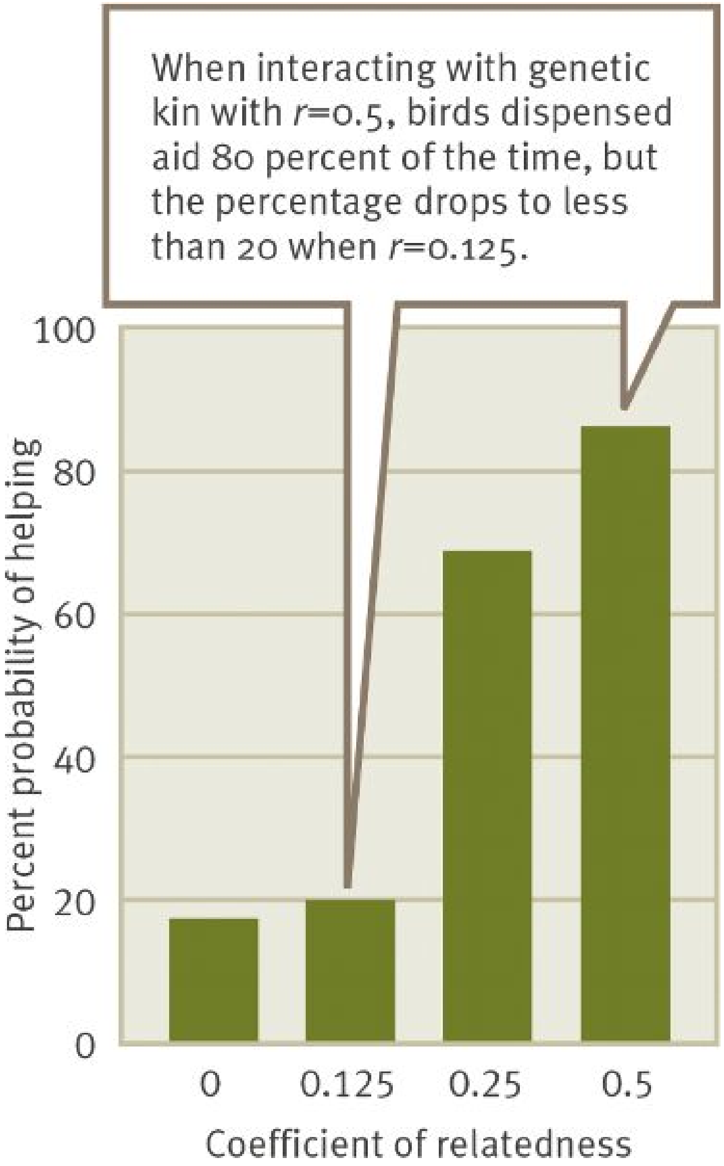


Figure 9.19. Helping close relatives. In white-fronted bee-eaters, individuals are more likely to help those to whom they are more closely related (as indicated by *r*, the coefficient of relatedness). *(Based on S. Emlen, 1995a)*

In addition to supporting a basic prediction of kinship theory, results from the study on bee-eaters helped resolve a thorny issue surrounding Hamilton's Rule. Beginning in 1975, a number of animal behaviorists had suggested a "proportional altruism" model in which individuals should dispense altruistic aid to relatives in *direct proportion* to their genetic relatedness (Barash, 1975; West-Eberhard, 1975). For example, imagine that an individual has nine units worth of aid that it can dispense to relatives. Suppose then that this individual interacts with one sibling ($r = 0.5$) and one uncle ($r = 0.25$). Since siblings share an *r* value twice as great as that between uncle and nephew, the proportional altruism model predicts that six units of aid should be dispensed to the sibling and three units of aid should be dispensed to the uncle.

Stuart Altmann argued that the proportional model rested on faulty logic, because an individual always increases its inclusive fitness most when it is altruistic toward its closest genetic relative (Altmann, 1979). Instead, Altmann predicted that an individual should dispense *all* of its aid to the recipient that is its closest genetic relative (let's call this the "all-or-nothing" model). In our hypothetical case, Altmann's model predicts that all nine units should be dispensed toward the donor's sibling. In principle, Altmann is right, but the question is whether animals actually behave in accordance with Altmann's predictions. Emlen's work on white-fronted bee-eaters allows us to address this question in one species, because it allows behavioral and evolutionary biologists to determine which of these two models better fits data gathered in the wild. In support of Altmann's model, Emlen found that helpers not only overwhelmingly chose to help their closest genetic relative, but that once a helper made a choice, it dispensed all of its aid toward the chosen individual (S. Emlen, 1995b).

Many studies of kin-based cooperation and altruism have been done in eusocial insects, like bees, ants, and wasps (chapter 2), which are part of the insect order Hymenoptera. Hymenoptera have an unusual genetic architecture. Normally, we think of all individuals in a species as being either diploid (possessing two copies of each chromosome) or haploid (possessing only one copy of each chromosome). In haplodiploid species, males are haploid, while females are diploid.

Haplodiploidy produces sisters that are, on average, more related to each other than in more classic diploid animal systems: sisters are related to one another on average by a coefficient of relatedness of 0.75, which has the effect of making females more related to their sisters than to their own offspring. This value differs from the standard average relatedness of sisters in diploid species ($r = 0.5$), because in haplodiploids, full sisters inherit exactly the same alleles from their father, while in diploid species, females have only a 50 percent chance that an allele that they inherited from their father is identical to an allele that their sister inherited from their father. Not only are female social insects highly related to one another, but social insect colonies tend to have very high female: male sex ratios, leading to many females potentially interacting with and helping one another (Trivers and Hare, 1976).

With an *r* of 0.75 between sisters, one would expect high levels of aid giving, and indeed it is the highly related female workers in many species that go to great lengths to defend a hive full of their sisters (for more on kinship and altruism in social insects, see Abbot et al., 2010; Herbers, 2009; Nowak et al., 2010; Ratnieks et al., 2011). In many social insect species, the stinger is often ripped from the body of a worker bee defending the hive, causing death.

The hypothesis that high genetic relatedness is important to the evolution of eusociality in at least some Hymenoptera can also be tested using phylogenetic analyses. Genetic relatedness is highest in social insect groups when queens are *monandrous*—they have a single mate. When females are *polyandrous* (see chapter 8), and have many mates, the average genetic relatedness in groups goes down, as not all individuals in a group share the same father. Because of this difference, ethologists have predicted that eusociality in bees should often be associated with a monogamous mating system.

To test this prediction, William Hughes and his colleagues used already published data that eusociality has independently evolved five times in bees, three times in wasps, and once in ants (W. Hughes et al., 2008; Ratnieks and Helantera, 2009). Today we see both monandry and polyandry in these eusocial lineages. But Hughes and his colleagues hypothesized that for eusociality to have taken hold in these groups to begin with, their evolutionary histories should indicate that the ancestral mating system in most of these lineages was monandrous. A phylogenetic analysis of eight of the nine lineages (data were not available to test one lineage of bees) indicates that, as predicted by inclusive fitness theory, monandry was the ancestral state in *all* eusocial lineages examined (Figure 9.20; Box 9.3).

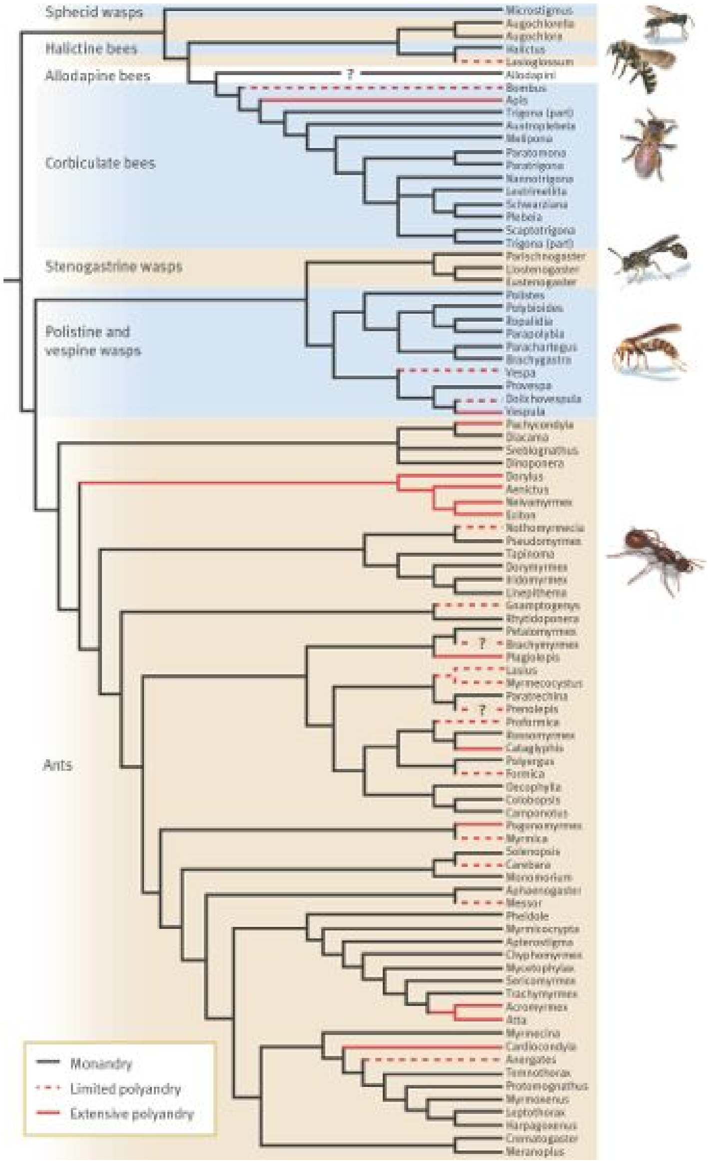


Figure 9.20. Phylogeny of ant, bee, and wasp species. Ethologists have predicted that eusociality should often be associated with a monandrous mating system. The phylogeny shown here is for ants, bees, and wasps for which data on female mating frequency are available. Each independent origin of eusociality is indicated by alternately colored—blue or orange—clades. (A clade is a taxonomic grouping including an ancestral group and its descendants.) Cases of high polyandry are depicted by red branches, and completely monandrous groups are shown with black branches. All eight clades here have monandry as the predicted ancestral state. *(Adapted from Hughes et al., 2008)*

Box 9.3. SCIENCE AT WORK

What is the research question? Is high genetic relatedness important for the evolution of eusociality?

Why is this an important question? The evolution of extreme forms of altruism, such as eusociality, has been a long-standing question in animal behavior.

What approach was taken to address the research question? A phylogenetic comparison of nine independent origins of eusociality in social insects.

What was discovered? Monoandry, which increases genetic relatedness in groups, was found to be the ancestral state in eight independent origins of eusociality in this phylogenetic analysis.

What do the results mean? High levels of genetic relatedness were critical in the origin of eusociality in social insects.

Another example of how genetic kinship can influence behavior in eusocial insects can be seen in **worker policing** in honeybees (*Apis mellifera*), in which worker bees use information associated with genetic relatedness to “police” their hive, and destroy eggs that have low genetic relatedness to them, resulting in an increase to their inclusive fitness (Ratnieks and Visscher, 1989; Olejarz et al., 2016).

In honeybee hives, queens produce most of the offspring, but workers can also produce unfertilized eggs that always develop into males. Using the mathematics of inclusive fitness theory, Francis Ratnieks and P. Kirk Visscher found that in honeybee colonies with a single queen that mates one time, female workers are more related to their nephews (their sisters’ sons, $r = 0.375$) than to their brothers (the queen’s sons, $r = 0.25$; Ratnieks and Visscher, 1989). But honeybee queens typically mate with ten to twenty different males and when multiple mating takes place, workers may be more closely related to brothers (males produced by the queen) than to nephews (males produced by their sister workers), with the exact values of relatedness depending on the number of different males with whom a queen mates. Under such conditions—when female workers are more related to brothers than to nephews—Ratnieks has hypothesized that worker policing of honeybee reproduction may evolve (Ratnieks and Visscher, 1988, 1989). Such policing, for example, may take the form of workers favoring those eggs to which they are most highly related (Figure 9.21).

Figure 9.21. **Honeybee egg-laying.** While the queen (designated by the numeral 39 on her back) typically lays the eggs in a honeybee colony, workers also attempt to lay unfertilized eggs. *(Photo credit: Jens Brüggemann / Alamy Stock Photo)*

Ratnieks and Visscher examined the possibility that honeybee workers may favor brothers over nephews. They found that honeybee workers showed remarkable abilities to discriminate between worker-laid eggs, which produce nephews, and haploid queen-laid eggs, which produce brothers. Largely as the result of worker policing behavior, after twenty-four hours, only 2 percent of the worker-laid eggs were alive, while 61 percent of the haploid queen-laid eggs survived (Figure 9.22). Workers appear to use a specific egg-marking pheromone produced only by queens to distinguish which eggs to destroy and which eggs to leave unharmed, and in so doing, they police the hive in a manner that increases their inclusive fitness (Ratnieks, 1995; Ratnieks and Visscher, 1989).

Figure 9.22. Honeybee policing. When an egg laid by a worker is detected by worker police, it is eaten or destroyed. Workers are much more likely to destroy eggs produced by other workers than eggs produced by the queen. Such "policing" has inclusive fitness benefits associated with it. *(Photo credit: Jens Brüggemann / Alamy Stock Photo)*

Wenseleers and Ratnieks extended the logic of policing behavior to further explore the relationship between kinship and reproduction in insects (Wenseleers and Ratnieks, 2006). If policing is effective at removing the eggs laid by workers, they hypothesized that it should produce strong selection pressures against worker reproduction. Wenseleers and Ratnieks tested this idea by examining policing behavior in ten species—nine species of wasps and the honeybee (Figure 9.23). They found that the more effective policing was at removing worker eggs, the less often workers attempted to reproduce in the first place (Figure 9.24).

Figure 9.23. Wasp policing. In the wasp *Dolichovespula saxonica*, workers often lay (haploid) eggs, in nests with both single-mated and multiply mated queens. Such eggs are often eaten when detected by other workers. Here a worker is eating another worker’s egg. Policing is much more common in wasp colonies where the queen has mated with many males. *(Photo credits: © Francis Ratnieks)*

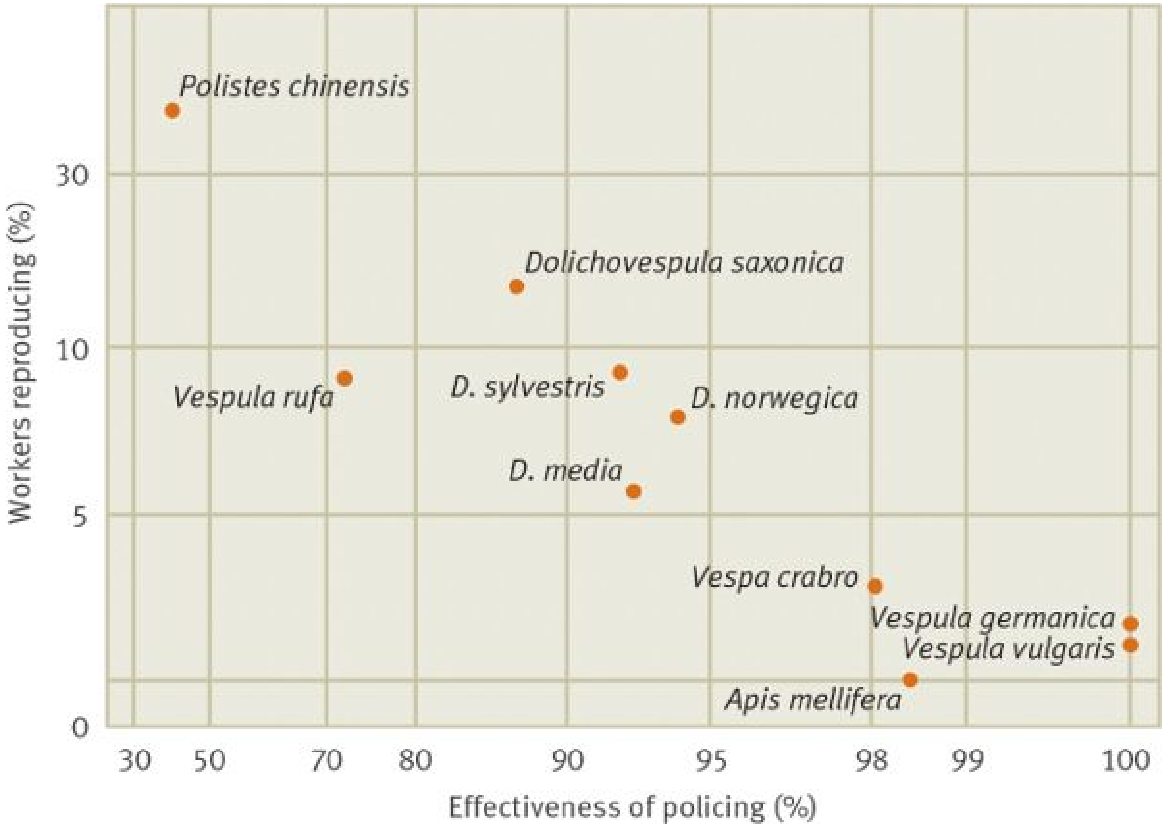


Figure 9.24. Effective policing. The more effective policing was at removing worker eggs, the fewer the workers that attempted to produce eggs. *(From Wenseleers and Ratnieks, 2006)*

Eusociality in social insects is not *completely* explained by the high genetic relatedness that comes about because of their haplodiploid genetics. All hymenopteran species are haplodiploid, but only *some* hymenopteran species are eusocial, and there are also examples of eusociality in diploid species such as naked mole rats and termites. While haplodiploidy alone does not explain the evolution of eusociality, it does help explain, in part, why eusociality is overrepresented in social hymenopterans.

Unfortunately, in Davis and Daly's examination of prediction 4 in humans, the GSS data were not collected in a way to address this question. For the most part, individuals in the GSS study were either related by an *r* value of 0.5 or 0.0, and therefore the distinction between how different relatives—that is, individuals with different positive values of *r*—are treated could not be addressed.

Conflict within Families

Inclusive fitness theory is most often used to understand why relatives cooperate with one another, but it can also be used to study conflicts within families. To see how, we now turn to the subjects of parent-offspring conflict and sibling-sibling conflict.

PARENT-OFFSPRING CONFLICT

Inclusive fitness theory predicts that parents should go to great lengths to help their offspring because parents and offspring have an average r of 0.5. Furthermore, parents are almost always in a better position to help offspring than vice versa. As such, parental aid should be seen in many contexts. And indeed it is. Hundreds of studies have shown that parents, mothers in particular, provide all sorts of aid to their offspring.

Yet there are limits to this aid, as first conceptualized by Robert Trivers in his parent-offspring conflict theory (Trivers, 1974). **Parent-offspring conflict** arises with respect to a parent's decisions about how much aid to give to any particular offspring. From the perspective of the parent, these decisions are affected both by how much energy is available for helping current offspring, and by how many offspring it is likely to have in the future.

In principle, a parent could dispense all of its energy to provide offspring 1 with all the benefits at its disposal. But if such an effort hampers the parent from producing more offspring in the future, then natural selection may not favor such behavior, as it might not maximize the *total number of offspring* that the parent is able to produce over the course of his or her lifetime. To see why, remember that every offspring has an r of 0.5 to its parent, and natural selection should favor parents that raise as many healthy offspring as possible over the course of their lives. So, there are limits on parental investment with respect to any given offspring.

Now, let us look at **parental investment** from offspring 1's perspective. Offspring 1 will receive some inclusive fitness benefits when its parent provides aid to both current and future full siblings, each of whom has an average r of 0.5 to it. Yet, an individual offspring 1 is more related to itself ($r = 1$) than to any of its siblings. As such, in terms of inclusive fitness, an offspring values the resources it receives from its parent more than the resources that its parent provides to its siblings (current or future). The conflict between parent and offspring arises because, although each offspring will value the resources it receives more than those dispensed to its siblings, all offspring are equally valuable to a parent, in terms of the parent's own inclusive fitness. This then sets up a zone of conflict between how much offspring want, and how much a parent is willing to give (the former always being greater than the latter). This zone is where parent-offspring conflict takes place (Figure 9.25).

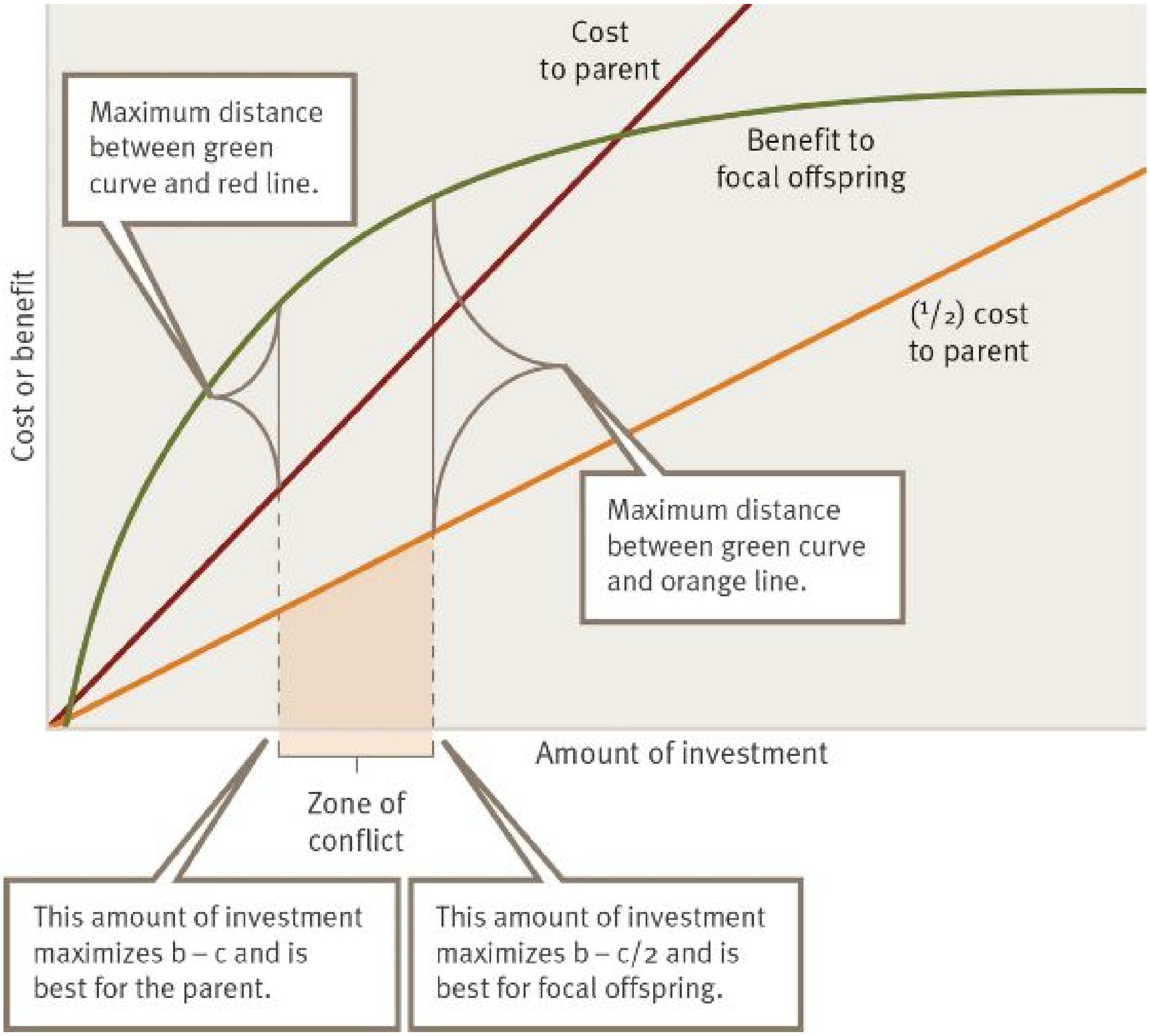


Figure 9.25. Parent/offspring conflict. Parents can provide resources to a “focal” offspring or use those resources on other current or future offspring. The *x*-axis shows the resources invested in the focal offspring, and the *y*-axis shows fitness costs (c) or benefits (b). The parent is equally related to all of its offspring, but the focal offspring is only half as related to its full siblings as it is to itself. As a result, parent and offspring prefer different amounts of resource allocation. This zone of conflict is shaded in the figure. To the left of the zone, parents and offspring alike benefit from increasing allocation to the offspring. To the right of this zone, parents and offspring alike benefit from decreasing allocation to the offspring.

Parent-Offspring Conflict and Mating Systems in Primates

The degree of parent-offspring conflict predicted is in part a function of the mating system because the degree of relatedness between current offspring and future offspring is a function of the mating system (see chapter 8) in place (Hain and Neff, 2006; Long, 2005). To see why, recall that natural selection favors offspring that weigh (1) the inclusive fitness benefits associated with receiving continued parental assistance versus (2) the inclusive fitness benefits of curtailing the degree of parental assistance received, and leaving a parent with more resources to produce future offspring.

In species with long-term monogamy, current offspring and future offspring will have an average genetic relatedness of $r = 0.5$, because they are likely to have the same mother and the same father. But in, for example, a polyandrous system (see chapter 8), the genetic relatedness between current and future offspring will be somewhere between 0.5 (for full siblings) and 0.25 (for half-brothers or half-sisters). Compared with the case of long-term monogamous mating systems, in polyandrous mating systems, natural selection will favor offspring that attempt to extract more in the way of parental assistance. Parent-offspring conflict should then be more intense in polyandrous versus monogamous mating systems (Macnair and Parker, 1978; Mock and Parker, 1997; G. Parker and Macnair, 1979; Trivers, 1974).

Tristan Long tested this hypothesis by examining whether fetuses grew faster in utero—taking more maternal resources—in polyandrous primate species. In utero parent-offspring conflict is particularly fascinating, as it shifts the balance of power between parent and offspring. In most cases of parent-offspring conflict, a mother has the upper hand, as she is almost always behaviorally dominant to her offspring. When the offspring is still in utero, however, it is more difficult (but not impossible) for mothers to deprive offspring of resources without depriving themselves too, thus shifting the balance of power away from the mother and toward the developing fetus.

To examine this possible in utero parent-offspring conflict, Long used the independent contrast phylogenetic method discussed in chapter 2 (Felsenstein, 1985, 2004). He asked whether, if he controlled for phylogenetic effects, strong parent-offspring conflict would be more likely to occur in polyandrous or in monogamous primate species

(Mastripieri, 2002). Long began by using a well-established phylogenetic tree for primates. From this tree, he was able to find sixteen pairs of primates to use in his independent contrast analysis. Each pair was made up of species that had diverged from a recent common ancestor—one of these species was monogamous, and the other was polyandrous. Long then compared already published data on fetal growth rates for each of the species in his pairwise comparison and predicted that in polyandrous mating systems, a fetus would attempt to sequester more resources during development, and would show faster rates of growth, than fetuses in species that were monogamous. The independent contrast analysis found such a relationship.

Long also examined how mating systems were connected to parent-offspring conflict in a different way. Because sperm competition (see chapter 8) is more intense in polyandrous species, males in such species tend to have larger testes. Testes size, then, can often be used as a proxy for the degree of polyandry. When Long examined the relationship between testes size and parent-offspring conflict (measured by fetal growth rate), a phylogenetic analysis found a positive relationship, demonstrating again how parent-offspring conflict can be mediated by the type of mating system in place (Figure 9.26).

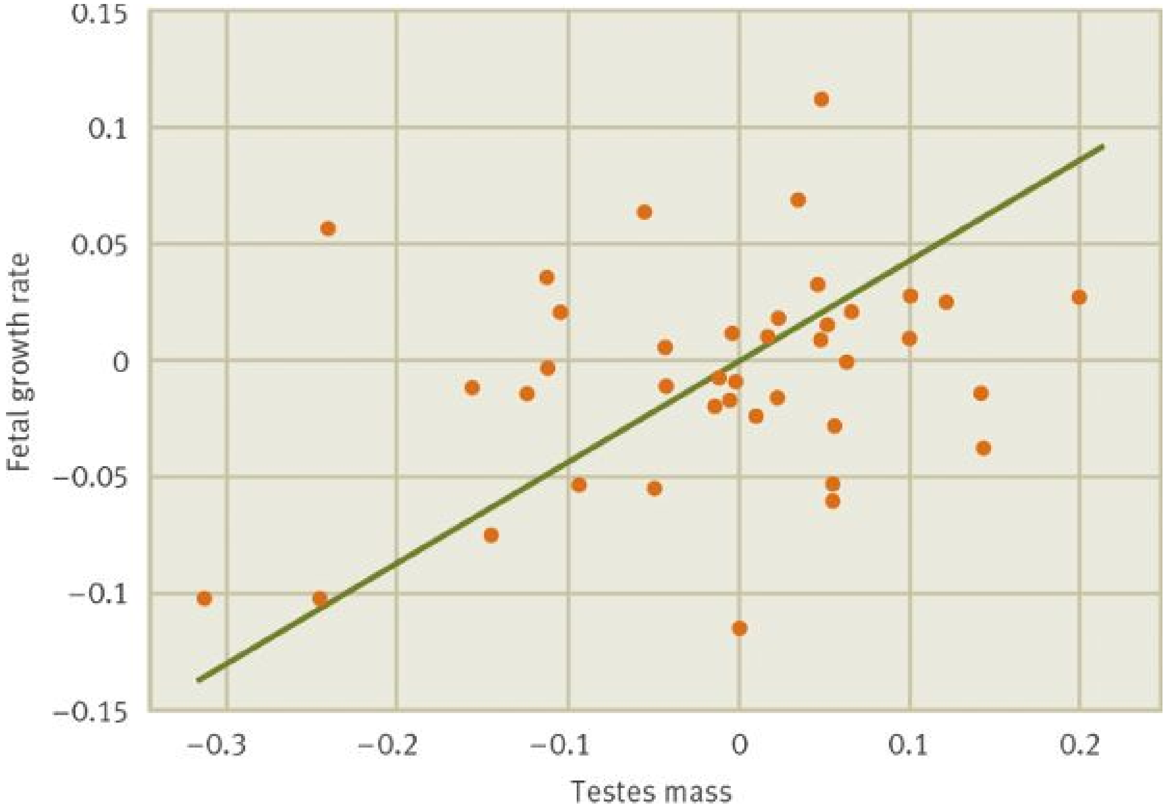


Figure 9.26. Parental investment and testes size. Testes size tends to be larger in males from polyandrous versus monogamous species. The relationship between testes size (a proxy measure of polyandry) and parent-offspring conflict (measured by fetal growth rate) was positive in this analysis of primates. The *x*- and *y*-axes measure residual log values of testes size and fetal growth rate, respectively. *(Based on Long, 2005)*

In Utero Conflicts in Humans

Parent-offspring conflict in pregnant women occurs because mother and fetus do not have identical interests in terms of how to maximize inclusive fitness (Geary, 2000; Haig, 1993; Schlomer et al., 2011; Figure 9.27). Using published medical literature, David Haig found that, in humans, fetal cells invade the maternal endometrium—the membrane lining the mother’s uterus—during implantation, and that such cells manipulate maternal spiral arteries in such a way as to make constriction of the arteries, which would make fewer resources available to the fetus, much more difficult. Such an action benefits the fetus in two ways: (1) by providing the fetus with direct access to maternal arterial blood and allowing the fetus to release hormones and other substances directly into the maternal bloodstream; and (2) by putting the volume of blood—and the nutrients it contains—under fetal, rather than maternal, control.

Figure 9.27. Mothers and babies. While the parent-offspring relationship is usually cooperative (A), parent-offspring conflict can occur, even in utero (B).

Haig suggests that placentally produced hormones, such as human placental lactogen and human chorionic gonadotropin, change the in utero environment in a manner that benefits the fetus at the cost of the mother. For example, a fetus may use human placental lactogen to manipulate insulin in such a manner that sugar would remain in the blood a longer time than normal. This manipulation would provide the fetus with more time to access such sugar for itself. The maternal counter response is to increase the production of insulin. If this countermeasure is unsuccessful, the fetus obtains extra sugar, but the mother suffers from gestational diabetes (Wells, 2007).

Gestational diabetes may be an outcome of parent-offspring conflict, and so the parent-offspring conflict explanation can have implications for the treatment of pregnancy-related medical conditions. If, for example, medical doctors viewed gestational diabetes as a “disease” that needs to be cured, they might act differently than if they viewed gestational diabetes as an evolutionary measure selected by fetal genes to increase sugar flow to the fetus (T. Moore, 2012). These sorts of issues are being studied by researchers in the field of evolutionary medicine (Ewald, 2000; Nesse and Williams, 1995; Nesse et al., 2010, Stearns et al., 2010; Haig, 2015).

SIBLING RIVALRY

Most readers are probably familiar with **sibling rivalry** from psychology classes, but animal behaviorists have been fascinated with such rivalries as well, and they have developed a substantial empirical and theoretical literature on this subject (Mock and Parker, 1997). The logic underlying the models of sibling rivalry is similar to that of parent-offspring conflict.

Mathematical models of sibling rivalry often consider sibling rivalry among many siblings, but for ease of explanation, let’s start by looking at the evolution of this sort of behavior when only pairs of siblings are involved. Consider two full siblings—sib 1 and sib 2—who share an *r* of 0.5. Such genetic relatedness means that what is good for sib 1 is *usually* good for sib 2, but because every individual has an *r* of 1 to itself, it also means that in a situation in which resources are limited and the siblings must compete for these resources, each individual will act as if it is more important to receive resources for itself than to have the same resources go to its sibling (Figure 9.28). We have already used this sort of logic in our discussion of parent-offspring conflict, but in sibling rivalry the competition is directly between siblings in a clutch of offspring, rather than between parent and offspring per se.

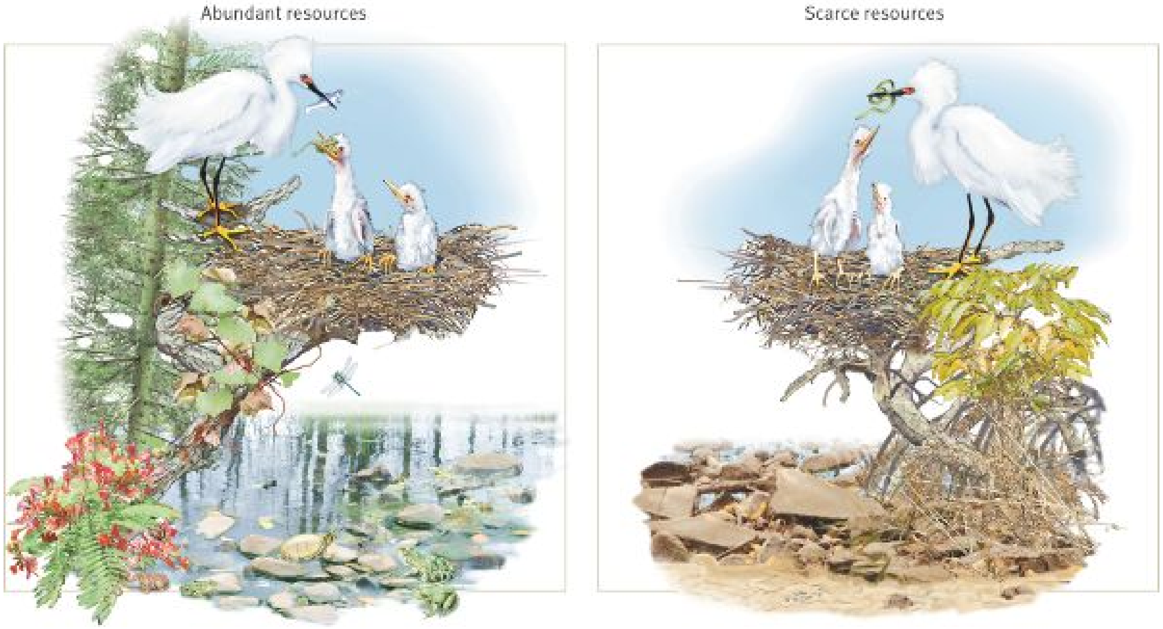


Figure 9.28. Sibling-sibling conflict. Kin selection theory predicts that individuals should not be very aggressive toward kin such as siblings, especially when there are abundant resources. But if there are limited resources, conflict over the resources will increase, because each individual is more related to itself ($r = 1$) than to its sibling ($r = 0.5$).

Imagine an extreme environment in which there is only enough food for one sibling to survive. Because of their genetic relatedness to one another, each sibling values the other at a level that is half of that at which it values itself. In such a resource-poor environment, we would expect intense, perhaps even lethal, competition to emerge among siblings. In a less harsh environment, we would expect sib-sib interactions to be less competitive, but because each values itself more than the other, some level of competition should still be the norm, rather than the exception. We simply expect the rivalry to emerge in less lethal ways when resources are not as limited.

Douglas Mock and his colleagues have studied sibling rivalry in egrets, including cattle egrets (*Bubulcus ibis*) and great egrets (*Ardea alba*) (Mock, 2004; Mock and Parker, 1997). As idyllic as downy chicks in a bird nest may seem to the casual observer, the interactions among egret chicks actually resemble prizefights more closely than some picturesque scene of nature taken from a Disney film (Figure 9.29). Consider Mock and Parker's description of such sib-sib interactions in cattle egrets and great egrets:

Sibling fights take many forms, depending mainly on how the loser concedes and how quickly it does so. The simplest fights, which usually occur while the participating dyad has had a series of increasingly one-sided battles, are those in which the attack inspires no retaliation. At the next level, return fire is brief until the loser is tagged with several unanswered shots and crouches low. From there, the severity of the beating is left largely to the victor's discretion. Sometimes it continues to jab at its opponent, causing the latter to screech and hide its face. As an alternative to jabbing, a dominant chick may seize the cowering victim by its head or neck, lift that part a few centimeters and then slam it down forcefully against the nest cup. If the attack persists for more than a few extra blows, the loser is likely to flee, sometimes squawking loudly and racing about the nest dodging behind the other nest occupants while being hit. During such chases, the primary target is the back of the head. Frequently bullied chicks soon develop a characteristic baldness, dotted with fresh and crusted blood, where the nape feathers have been plucked forcibly during fights. (Mock and Parker, 1997, pp. 103–104)

Figure 9.29. Sib-sib competition in birds. In nests of egrets, sib-sib competition can be intense and can result in the death of smaller, less dominant chicks. Sibling rivalry can be seen in the fights between siblings in the nest, as shown here, where the chick on the left is preparing to bite its sibling. *(Photo credit: Millard H. Sharp/Photo Researchers, Inc.)*

When egret chicks first hatch, parents bring back enough food to fill all the chicks' guts, minimizing sib-sib aggressive interactions. As the chicks grow, however, at some point the food brought to the nest is insufficient to feed all chicks to satiation, and intense competition among siblings emerges when a parent returns to the nest with food and regurgitates it in the nest. The key to obtaining the food is positioning within the nest, and specifically vertical positioning (the higher the better when mom returns). Even a chick tilting its head up, above horizontal is a cue likely to spark aggression in egrets' nests.

Egrets, like many birds, hatch eggs asynchronously, laying their eggs in sequence, rather than all at one time, so that hatching order produces chicks that differ in age by many days. Chicks that hatch first start to feed sooner and hence receive more food, which leads to a weight advantage over chicks that hatch later, and a very clear age-related dominance hierarchy exists among chicks. First-hatched chicks are often much larger than second-hatched chicks, who are often much larger than chicks hatched still later (Figure 9.30A). In sib-sib interactions, large size means better fighting ability, which translates into significantly more food (Figure 9.30B).

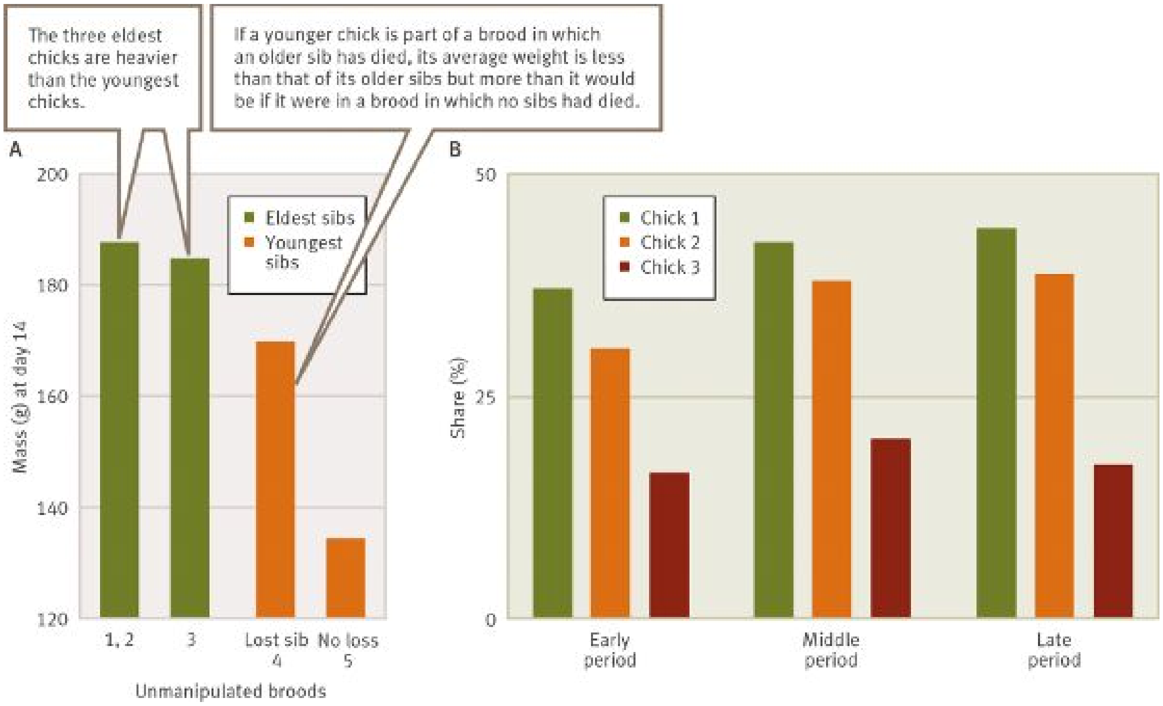


Figure 9.30. Birth order and food intake. (A) Normal broods of little blue herons include four to five chicks that are hatched asynchronously. (B) In egret broods, the oldest, dominant chick (1) receives more food than the middle chick (2), who in turn gets more than the youngest chick (3). This holds for the early period after hatching (1–13 days), the middle period (14–21 days), and the late period (22–30 days). *(Based on Mock and Parker, 1997)*

Kin Recognition

Because genetic kinship affects social interactions, ethologists and behavioral ecologists have a long-standing interest in how kin recognize one another (Fletcher and Michener, 1987; Hepper, 1991; Holmes, 2004; Pfennig and Sherman, 1995; Breed, 2014). Early in this chapter, we went through a general procedure to show how to calculate relatedness (*r*) (for discussions of kin recognition in humans, see Bressan and Zucchi, 2009; Kaminski et al., 2009; Lieberman et al., 2007; Lundstrom et al., 2009). Of course, animal behaviorists don't assume that nonhumans are able to calculate genetic relatedness in that manner. We need only assume that natural selection favors individuals that act in a manner that makes it appear as though they are making such calculations.

Kin recognition in animals has often been studied in situations in which there are important fitness benefits for recognizing kin, but in which the task of kin recognition is difficult—for example, when individuals live in very large groups. Consider the remarkable kin recognition abilities seen in some species of penguins. Parents travel long distances to the sea to obtain food to take back to the inland areas where their chicks have hatched. When parents return from their journey, they need to find their young among scores—sometimes thousands—of screaming, hungry chicks in a colony (Aubin and Jouventin, 2002; Brumm and Slabbekoorn, 2005). How do they do it? For species like the emperor penguin (*Aptenodytes forsteri*) and the king penguin (*Aptenodytes patagonicus*) (Figure 9.31), the answer appears to center on complex vocal cues that allow for kin recognition via "vocal signatures" emitted by the young (Aubin, 2004; Aubin and Jouventin, 1998, 2002; Aubin et al., 2000; Jouventin et al., 1999; Lengagne et al., 2000).

Figure 9.31. Kin recognition in penguins. Kin recognition via vocal signatures has been examined in (A) the emperor penguin (*Aptenodytes forsteri*) and (B) the king penguin (*Aptenodytes patagonicus*). Both species of penguins live in large colonies, and parents returning from foraging with food for their chicks use vocal cues to find their offspring in the middle of many other chicks. *(Credits: © BMJ / Shutterstock; © reisegraf.ch / Shutterstock)*

Not all penguins are as proficient as the king and emperor penguins at recognizing the vocal signatures of their offspring. Studies indicate that penguins that build nests are not as adept at recognizing the vocal calls of their young as are individuals that live in dense colonies and do not nest (Jouventin and Aubin, 2002; Searby et al., 2004). Why might that be? Parents in nest-building species can find their offspring by remembering the location of their nests, presumably because any chick in their nest is their offspring (see below), and hence natural selection to recognize offspring by vocal cues in these species is weak. When the problem of kin recognition is more difficult—in dense colonies with no nests—natural selection favors the evolution of more complex vocal recognition systems.

MATCHING MODELS

Many models of kin recognition hypothesize that individuals have an “internal template” against which they match others and gauge relatedness (Reeve, 1989). These **kin recognition matching models** differ in their specifics, but the basic idea is that individual 1 attempts to assess whether individual 2 is kin or nonkin, depending on how closely individual 2 matches the internal template of individual 1. The internal template may be generated genetically, via learning, or via social learning, but in all cases, the animal estimates the degree of kinship as some function of the extent to which others match its own template (Alexander, 1979, 1991; Boyse et al., 1991; Crozier, 1987; S. Robinson and Smotherman, 1991). Templates can range from dichotomous “kin/nonkin” classification systems to more graded systems of kinship, in which individuals can distinguish among kin at a finer level (sibling, cousin, and so on).

Template Matching in Tadpoles

David Pfennig and his colleagues have studied template matching in the behavior of spadefoot toad tadpoles (*Scaphiopus bombifrons*; Elgar and Crespi, 1992; Pfennig, 1999; Pfennig et al., 1993, 1999; Figure 9.32). Two feeding morphs of spadefoot toads exist: Juveniles that feed on detritus typically develop into herbivorous omnivores, while those that feed on shrimp tend to mature into carnivorous cannibals.

Figure 9.32. Tadpole cannibals. A tiger salamander (*Ambystoma tigrinum*) cannibal morph (right) is eating an omnivore morph (left). *(Photo credit: David Pfennig)*

Pfennig and his team examined kin recognition abilities in the herbivore and cannibal spadefoot morphs by testing both morphs in the presence of either *unfamiliar* siblings or *unfamiliar* nonrelatives. When visual cues (behavior and morphology, for example) and chemical cues (odors, for example) were both present, herbivores preferred associating with their siblings over unrelated individuals, receiving any inclusive fitness benefits associated with interactions with genetic kin. Carnivorous individuals that cannibalize other tadpoles were taken from the same sibship as the herbivores that were being tested. When these cannibals were tested by Pfennig and his colleagues, they spent more time near unrelated individuals, presumably to avoid the costs of killing their genetic kin (Figure 9.33).

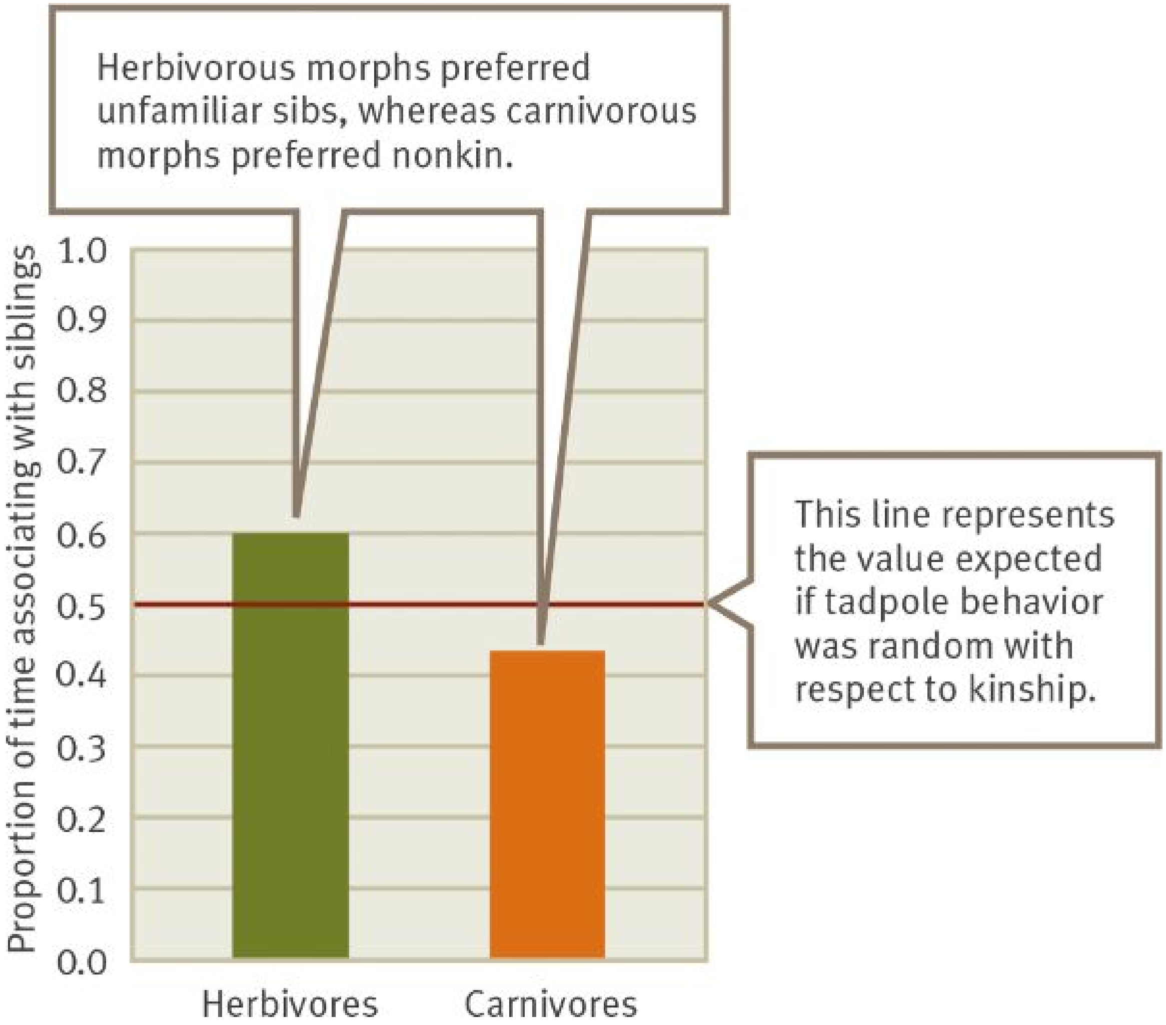


Figure 9.33. Kin recognition in spadefoot toads. Spadefoot toad tadpoles come in two morphs: carnivorous and herbivorous. Individuals from each tadpole morph were placed between two groups of tadpoles, one of which contained sixteen unfamiliar siblings, the other of which was composed of unfamiliar nonsiblings. *(Based on Pfennig et al., 1993)*

Pfennig and his colleagues also offered carnivores a choice between unfamiliar siblings and unfamiliar nonrelatives in a protocol that allowed carnivores to actually eat other tadpoles. Carnivores were not only more likely to eat unrelated individuals, but they were able to distinguish between relatives and nonrelatives by taste cues—carnivores were equally likely to suck relatives and nonrelatives into their mouths, but they released their relatives much more frequently than they released unrelated individuals. But as the costs and benefits of eating kin change, Pfennig and his team predicted that tadpoles' behavior would change. And indeed, the researchers found that cannibalistic toads were much less picky when they had been starved for twenty-four hours or more—when they were very hungry, they would occasionally eat even genetic kin (Figure 9.34).

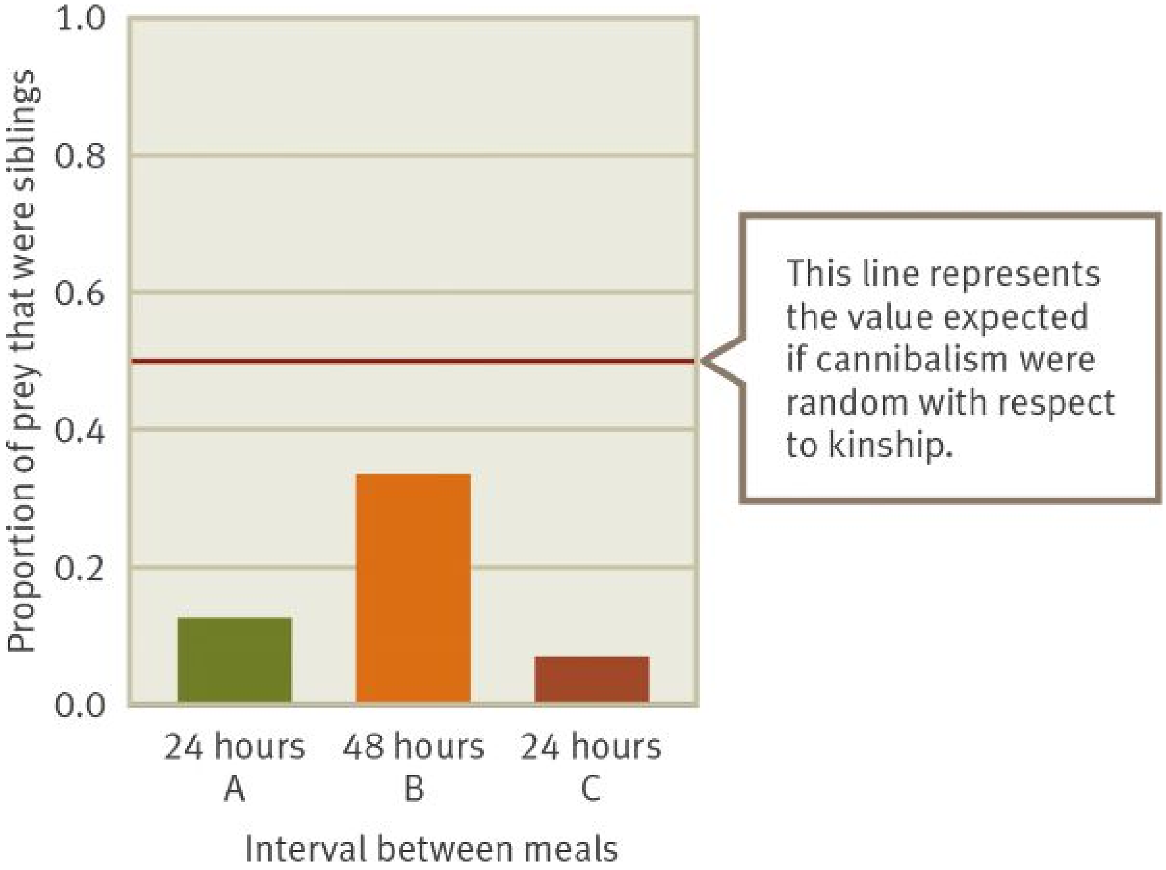


Figure 9.34. Hunger and carnivorous toads. The carnivorous morph of spadefoot toads prefers to eat nonkin over kin. When carnivorous morphs were starved for 24 hours (A), only a little more than 10 percent of individuals eaten were kin. If they were starved for 48 hours, this figure rose. As a control, toads were again starved for 24 hours (C), and results were similar to the original 24-hour deprivation treatment (A). *(Based on Pfennig et al., 1993)*

Recent work in a closely related species, the New Mexican spadefoot toad (*Spea multiplicata*), has found that cannibalistic tadpoles not only distinguish between relatives and nonrelatives, but that they are especially unlikely to consume relatives with phenotypic traits that suggest they possess relatively high future reproductive success (Dugas et al., 2016).

MHC, Kinship, and Templates

Recall from chapter 7 that animals sometimes use potential partners' major histocompatibility complex (MHC) genes, which they identify by odor, to determine which mate to choose. MHC also plays a role in kin recognition (J. L. Brown and Eklund, 1994; Frommen et al., 2007; Manning et al., 1992). Jo Manning and her colleagues examined MHC in house mice (*Mus musculus domesticus*), where females nest together and nurse all offspring at their nest (Manning et al., 1992). When female mice nest together, they all receive a benefit—protection from infanticidal males that sometimes attack and kill offspring that are not their own (Manning et al., 1995). At the same time, communal nesting creates a situation in which females can be "cheated"—this occurs when other females at their nest are protected from danger but do not nurse all pups present. One way to minimize the cheater problem and to maximize inclusive fitness benefits would be for females to form communal nests with their genetic relatives. And because MHC differences are correlated with differences in odor, one way that females may discriminate among kin and nonkin is through odors associated with the MHC (Brennan and Kendrick, 2006; Packer et al., 1992).

Manning and her colleagues worked with six wild populations of house mice, individually marking each mouse and determining its MHC type. They observed pregnant females and examined whether females that had just given birth opted to nest alone or in a communal nest. Ninety percent of the females chose to nest communally. With respect to kin recognition, when females selected which communal nests to join, they chose nests with individuals that had an MHC similar to their own. While these results do not definitively show that females use MHC as a cue for kinship, they are consistent with such a hypothesis.

The study of animal behavior was revolutionized by the introduction of inclusive fitness models. Since W. D. Hamilton introduced these models in the early 1960s, almost every animal behaviorist who has studied social behavior has at one time or another thought about whether kinship plays a role in the system that he or she is studying. As we have seen, kinship theory not only allows researchers to make predictions about when animals should be cooperative and altruistic toward their kin, but also makes predictions about when they should not be so (as in parent-offspring conflict, sibling rivalry). Work on inclusive fitness continues to be one of the most active in areas in ethology. Modern work employs molecular genetic and phylogenetic analyses to expand the frontiers of research in this area.

Box 9.4. COGNITIVE CONNECTION

Social Learning, Kinship, and Antipredator Behavior

In our discussions of cultural transmission, we have learned that although limited work has been done on teaching in nonhumans, it appears to be most common when teacher and pupil are also parent and offspring. Recent work in Siberian jays (*Perisoreus infautus*; Figure 9.35) suggests that the parent-offspring relationship may also be important with respect to social learning in general, not just teaching per se (Griesser, 2003; Greisser and Ekamn, 2005; Greisser and Suzuki, 2016).

Figure 9.35. **A Siberian jay.** The role of social learning and kinship has been studied in Siberian jays (*Perisoreus infautus*). *(Photo credit: Hans Bister)*

Siberian jays live in groups made up of adults and their offspring, plus unrelated young migrants who join the group. Griesser and Suzuki (2016) examined social learning, kinship, and antipredator behavior in a population of these birds living near Swedish Lapland. Predation by hawks and owls is the main cause of mortality in this population, and when a perched predator is spotted, adult males move higher in the trees and often emit mobbing calls (Griesser and Ekman, 2005). Because all young, both those related to adults in the group and the immigrant young, stand to gain by paying attention to the mobbing behavior of adults, and because other studies have documented social learning in Siberian jays, Griesser and Suzuki (2016) hypothesized that all young would copy the antipredator behavior of adults; that is, that kinship would not affect the role that social learning might have on antipredator behavior in young Siberian jays. They tested this idea by exposing groups of Siberian jays to stuffed model predators—either a Ural owl (*Strix uralensis*) or a sparrowhawk (*Accipiter nisus*).

The model predator was covered by black plastic and placed on a pole close to a feeding station where the jays fed. When a breeding adult and a young bird were together at the feeder, the plastic was removed and the pair was exposed to the model predator, and their behavior and vocalizations were recorded. Contrary to their prediction, Griesser and Suzuki found that kinship played a significant role with respect to social learning and mobbing behavior. When exposed to a model predator, all twenty of the adult breeding birds reduced their feeding, flew higher into the tree canopy, moving from tree to tree above the model while emitting mobbing calls, and sometimes swooping down in the direction of the model. Before the model was exposed, related and unrelated young moved independently of other group members. Once the model was exposed, related young followed their parents higher into the trees, often copying their mobbing calls, and rarely returning to forage at the feeding site. Unrelated individuals behaved very differently. They tended not to fly into the same tree as the adult they were with, and were less likely to give alarm calls than related young. They were also much more likely than related young to begin foraging again at the feeding site (Figure 9.36).

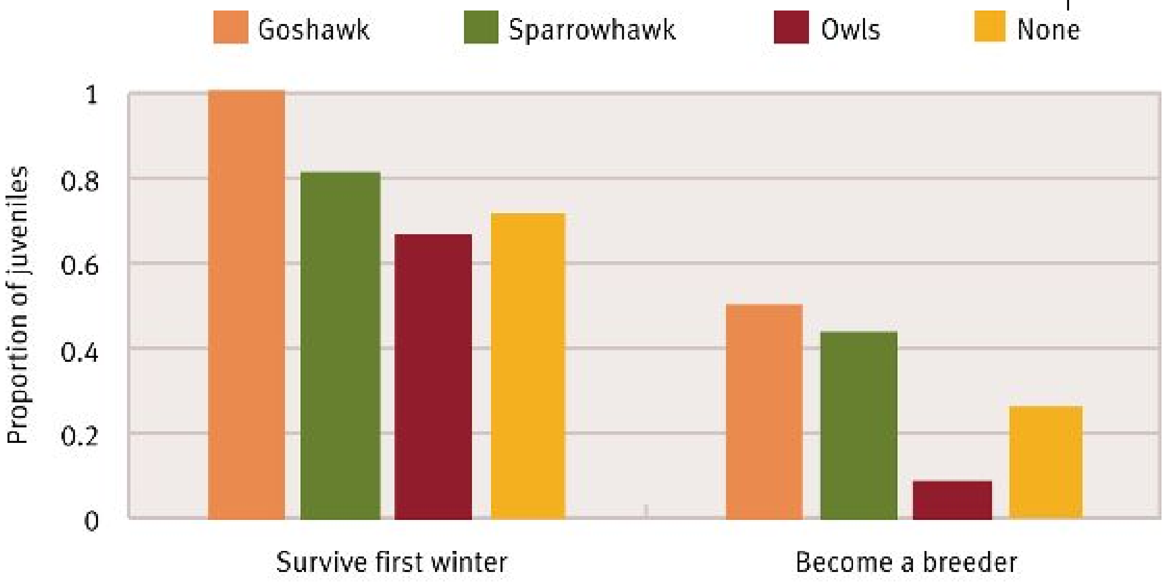


Figure 9.36. **Kinship affects social learning about predators and foraging.** When a model predator was present, a greater proportion of related vs. unrelated Siberian jay young behaved like the adults they were with, emitting alarm calls and reducing their foraging. Reprinted with permission from Elsevier. © 2016. *(From Griesser and Suzuki, 2016)*

Griesser and Suzuki (2016) suggest the differences they uncovered are due to the parent/offspring bond formed in Siberian jays. Birds are fed by their parents early in development and consequently have incentive to pay attention to where their parents are and what they do. Young jays in the study were already independent foragers, but the bond that formed between related young and their parents early on may have led to their being more likely to acquire new behaviors via social learning from parents later in life.

Interview with Dr. Francis Ratnieks

Why has so much work on animal behavior and kinship been done in the social insects? How did you decide to work with this group?

Becoming a social insect biologist was literally plan B. On completing my BSc in Ecology at the University of Ulster in Northern Ireland, I decided to study pest management. I felt this would be useful and would combine my interests in insects and ecology. I applied to do a PhD in the Department of Entomology at Cornell University, as this seemed the best place for studying insects. The professor of apiculture, the late Roger Morse, offered me a grant for university study. Although studying honeybees was something I had never thought of, I accepted. I quickly became enthusiastic about honeybees and beekeeping. More gradually, I developed interests and ideas about social evolution and behavior, and taught myself how to model social evolution. I also expanded into wasps and ants.

Social insects have been the most important group of organisms for testing predictions arising from William Hamilton's inclusive fitness theory. It has been a two-way street. Social insects have played a key role in validating the theory, and the theory has revolutionized our understanding of social insects, especially how eusociality evolved and the reproductive behavior of insect societies.

Social insects can be used to study practically any question. They are literally a gateway to biology. An immense number of important discoveries have been made with the honeybee alone, which is only one of 20,000 social insect species. Social insects have been very useful for testing Hamilton's theory because relatedness, the theory's central parameter, varies both within and between species because queens can be mated to one or more males, because there can be different numbers of queens per colony, and because haplodiploidy (in ants, bees, and wasps) causes relatedness to differ between the sexes. Insect colonies are also very practical to study. A colony of ants can be kept in a plastic box. A colony of honeybees can be kept in a hive. Honeybees are easy to study once you know how. Some honeybee studies are even based on decoding waggle dances by viewing the dancing bees through the glass walls of an observation hive. This is the only case in animal behavior where the animals "talk to" the researchers.

I often tell students that Hamilton's inclusive fitness theory is as important to the field of evolution and behavior as Einstein's $e = mc^2$ is to physicists. Is that an overstatement?

It is not an overstatement. Both are elegant and concise mathematical representations of a fundamental underlying relationship. Hamilton's Rule tells us the condition under which any behavior or trait that affects other individuals of the same species will be favored or disfavored by natural selection. Einstein's equation tells us the relationship between mass and energy. The relationship in Einstein's equation is inviolable. Technically speaking, Hamilton's Rule is not inviolable because gene frequencies, and therefore the traits they code for, can also be affected by genetic drift as well as by natural selection. Does that make Einstein's equation more important? I don't think so. It just reflects a difference between physics and biology.

How is it that a simple mathematical rule can be so important? The reason is simple. Many biological processes can be represented mathematically. For example, population growth can be represented by multiplication. The relatedness term in Hamilton's Rule comes from the simple fact that each gene in an organism has a precise probability of being passed on to an offspring. The probability is usually 0.5, but can be 1, for example, from a haploid male bee to his daughter.

Hamilton's Rule is also a good example of the importance of mathematics in biology. The mathematics is not hard. High school algebra is enough to understand it. The hard part for the student is combining the mathematics with the biology. The best way is to jump in and have a go!

Kinship isn't the only factor that promotes social behavior and altruism in animals—is it?

Kinship is very important. Consider the evolution of eusociality. The problem is to explain altruism—how can natural selection select for individuals to forgo reproduction to help others? Eusociality evolved within families, with offspring helping their parents rear more brothers and sisters. Helpers are as closely related to the individuals reared (brothers and sisters) as to their own sons and daughters. (Although many queen bees, wasps, and ants mate to several males, which diminishes relatedness, this evolved after eusociality.)

But if all that is needed for eusociality to evolve is high relatedness, why is eusociality not more common? Two other things are needed. First, a nest or some way of keeping the family together, so that help is directed to kin. Second, some way of helping, such as by providing food or by defending. Eusociality arose many times in the Hymenoptera because many species have nests to which the mother brings food for her offspring. Helpers can help simply by bringing more food. In termites food was not needed as the family was living inside its food—a log. Here, defense was the key.

In many modern-day insect societies, worker altruism is also caused by social pressure. Workers in most bee, wasp, and ant species have ovaries and can lay eggs. But in many such species, worker reproduction is rare. In the honeybee, fewer than 0.1 percent of the workers lay eggs. Egg laying by workers is deterred by an effective policing system that kills worker-laid eggs. This means that worker honeybees are better off working rather than laying eggs, given that almost all their eggs will be killed if they lay any.

Do the terms *kinship* and *family* differ in meaning when discussed in ethology as opposed to when they are used by nonscientists in the course of normal conversation? How so?

I don’t think there is much difference. Sometimes people will refer to other individuals as a brother or sister when they are not true relatives. But the people using these words probably know the difference. Referring to someone unrelated to you as brother or sister is often a way of showing that you have a common interest because you belong to the same group within society. The fact that we humans have what seems like a keen natural understanding of kinship suggests that it is important to us and is a human universal. That is, it is something innate in being human, rather than something that is purely cultural. Given the importance of relatedness in social behavior, this is not surprising.

Can you envision a day when sociologists and animal behaviorists will be using a common framework for studying kinship and behavior? What might such a framework look like?

A common interdisciplinary framework is something that is possible. However, even if this is established, the subjects and goals of the different disciplines may be sufficiently different that they may be using very different parts of a large and unwieldy framework. This is especially true when studying humans, given the vast number of disciplines involved, including history, economics, anthropology, sociology, political science, criminology, psychology, and biology. What insights would a historian studying the Tudors take from evolutionary biology, for example?

The value of a common framework can be seen when some important insight from one discipline is ignored in another discipline. For example, studies by evolutionary biologists Martin Daly and Margo Wilson have shown that kinship may influence abuse of children by parents and stepparents. This idea, which comes from Hamilton's theory (and is also part of common knowledge, given well-known stories like *Cinderella*), ran counter to the way that sociologists were trained. The question then is: Why were sociologists not trained to consider this and are they now doing so?

The debate triggered by the publication of the book *Sociobiology* by E. O. Wilson in 1975 is a good example of the friction that can be caused when disciplines and ideologies collide. It is easy for more heat than light to be generated. The value of ideas or theories originating in one discipline and exported to another can be gauged by the new insights they give and the degree that they unify previously disparate fields when tested with real data. Interdisciplinary cross-pollination is not just one way, from biology to social science. The study of animal behavior has greatly benefited from insights from game theory, which was originally developed within the social sciences.

Dr. Francis Ratnieks is a professor at Sussex University, England. His seminal work on social behavior has focused on the role of genetic relatedness in shaping insect societies.

SUMMARY

1. Inclusive fitness theory has revolutionized the way that scientists understand the evolution of behavior.
2. In evolutionary terms, relatedness centers on the probability that individuals share alleles that they have inherited from some common ancestor—parents, grandparents, and so on. The essence of inclusive fitness models is that they add on to classical models of natural selection by considering the effect of an allele not only on the individual that bears it but also on those sharing alleles that are identical by descent (that is, genetic kin).
3. The decision to aid family members is a function of how related individuals are, and the costs and benefits associated with the trait: when individuals are highly related and an allele codes for an action that provides a benefit to relatives at a relatively small cost, selection strongly favors this trait.
4. Parents should be willing to go to great lengths to help their offspring. But a zone of parent-offspring conflict is also predicted under basic kinship theory.
5. Inclusive fitness theory defines the conditions under which sibling rivalry should be favored.
6. Many models of kin recognition center on individuals having some "internal template" against which they match others and gauge relatedness.

7. In a species in which kin groups are spatially segregated from one another over relatively long periods of time, a second, simpler, form of kin recognition may evolve. In such scenarios, natural selection favors a kin recognition rule of the form “if it lives in your nest/cave/territory, then treat it like kin.”

DISCUSSION QUESTIONS

1. What might be some of the benefits to gauging very small differences in genetic kinship relationships? Why, for example, might it be better to be able to distinguish relatives at the level of cousin ($r = 0.125$) rather than simply sibling ($r = 0.5$)? What sorts of benefits might be possible when small differences in relatedness could be gauged?
2. Build a family tree and use it to calculate the genetic relatedness between paternal first cousins. Then expand the tree to the case of paternal second cousins.
3. Based on the parent-offspring conflict model, what differences in weaning behavior would you expect to see between younger and older mammalian mothers?
4. How might both kin selection and kin recognition rules be useful in understanding cases of adoption in animals?
5. How does a phylogenetic comparison of mating systems in primates shed light on kinship and parent-offspring conflict?

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10

Cooperation

Cooperation manifests itself in a myriad of ways in animals, and ethologists have devised many methods to study this behavior, both in the field and under more controlled laboratory settings. One method involves an experimental procedure in which two animals must each take on clear distinct roles to solve a problem, which, if solved, provides them both with a reward. Alicia Melis and Michael Tomasello used this method to examine cooperation in chimpanzees (*Pan troglodytes*) (Melis and Tomasello, 2013).

The experimental apparatus used is shown in Figure 10.1. To solve the problem and obtain a reward (grapes), a thin stick had to be inserted in the *top* part of the apparatus and grapes had to be raked from the left to the right. This could only be done from the *back side* of the apparatus. Then, a thick, long stick had to be inserted into the bottom of the apparatus and pushed until it caused the platform to be tilted (the thin stick would not cause the lever to tilt). This could only be accomplished from the *front side* of the experimental apparatus. If both tasks were done, grapes would drop down and be available from both the front and back sides of the apparatus.

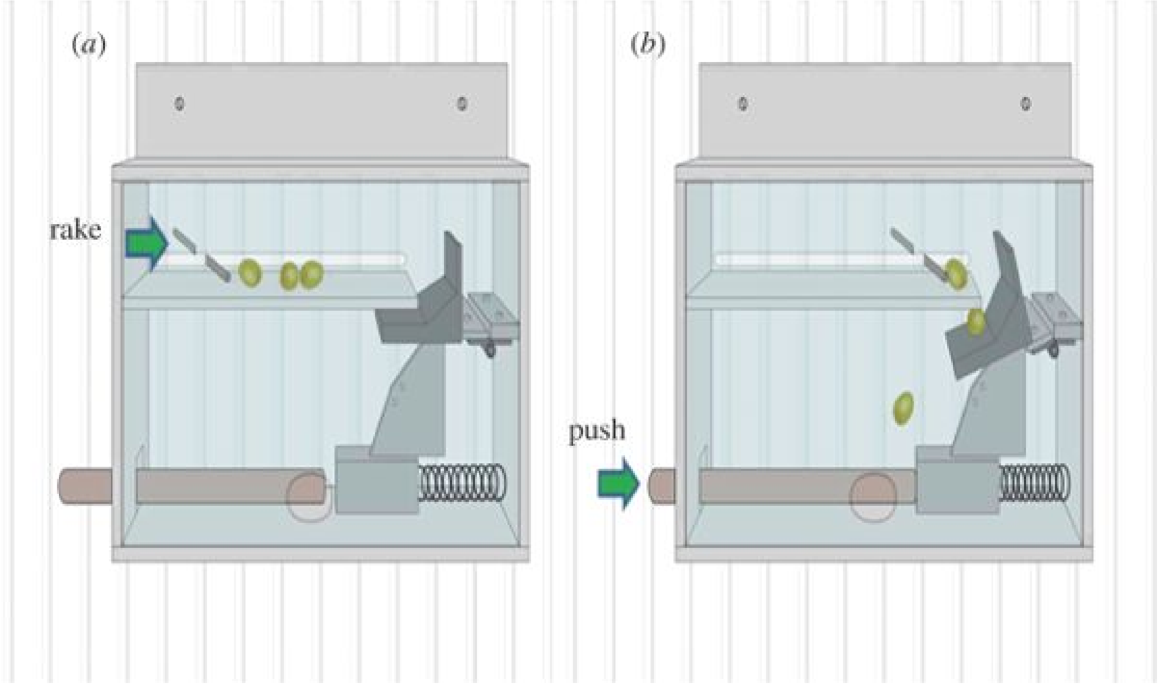


Figure 10.1. **An experimental apparatus for testing chimpanzee cooperation.** (A) The back side of the box: a chimp had to insert a thin stick and push ("rake") the grapes from left to right. (B) The back side of the box: another chimp had to insert a thick, long stick and then push to make the platform tilt. If both tasks were done, grapes fell to the front and back side of the box, and both chimps obtained food. By permission of the Royal Society. *(From Melis and Tomasello, 2013)*

Before trials began, twelve individual chimps were given the opportunity to learn about the apparatus and what needed to be done for grapes to become available to eat. Then pairs of chimps were tested. One chimp had access to the back side of the apparatus, and one had access to the front side, but the animals could see each other and they could see both sides of the apparatus. The experimenter then handed one of the two chimps *both* the short, thin stick *and* the long, thick stick. The question was then whether that chimp handed the other individual the correct tool, so that the two of them could solve the problem and both obtain some grapes. What Melis and Tomasello found was that regardless of whether the chimp handed both tools was facing the back or front side of the apparatus, they gave their partner the correct tool more often than expected by chance.

This same general testing paradigm has been modified to look at cooperation in dolphins (Kuczaj et al., 2015) and elephants. Joshua Plotnik and his colleagues (2011) taught an elephant to pull a rope that was attached to a table that was otherwise outside of its reach.

Between the table and the elephant was a bowl of food. When the rope was pulled, it moved the table toward the elephant, and the table in turn moved the bowl of food within the elephant's reach. Twelve elephants learned this task, and this group was then split into six pairs. Each pair was then given a new task to learn. Now the pair had to work in a coordinated way and simultaneously pull on a rope to move the table and food toward them. If they succeeded, they could reach the food (Figure 10.2).

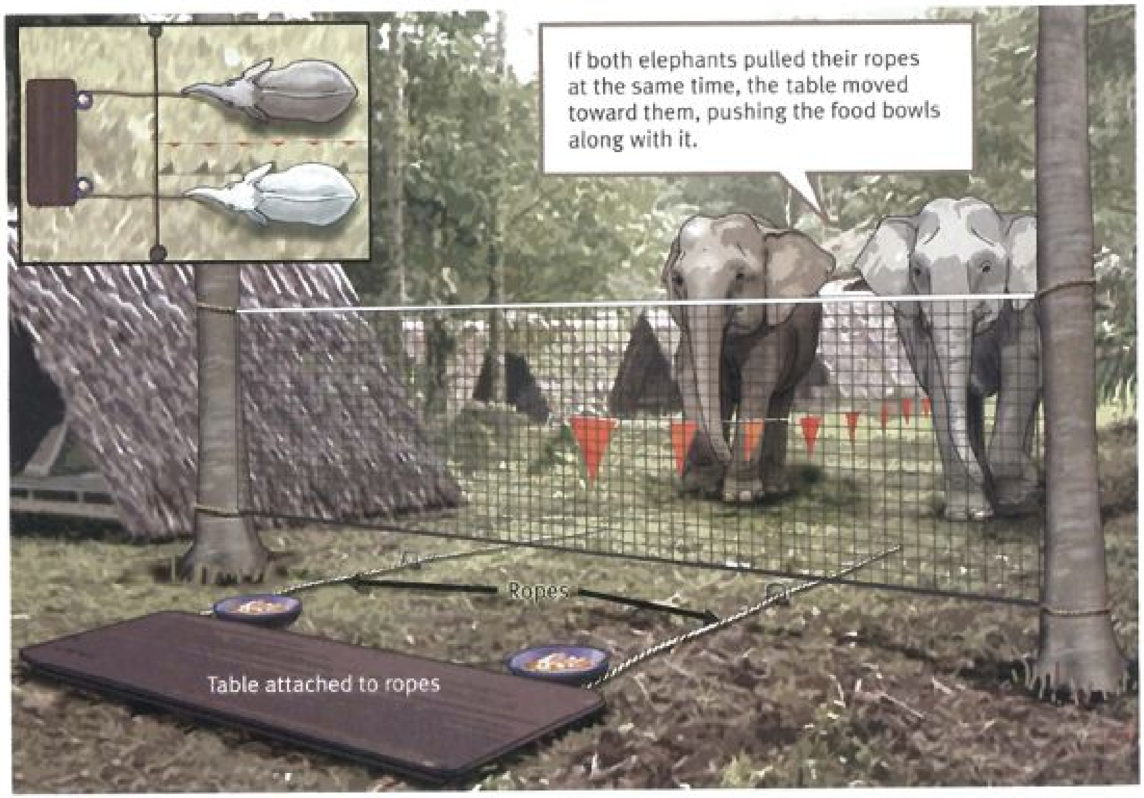


Figure 10.2. Elephant cooperation. A multiview perspective of the apparatus used in elephant cooperation. The inset shows the setup from above. *(Adapted from Plotnik et. al., 2011)*

In one treatment of this experiment, the two elephants were released at the same time and allowed to move toward the rope. Elephants in this treatment quickly learned how to pull the rope simultaneously and obtain the food as a reward. But this coordinated action may not represent cooperation at all. An elephant might have been using a very simple rule: "Pull the rope, and food comes."

In a second treatment, the release time of elephants in a pair was staggered. To obtain food, each elephant released into the experimental setup now had to wait until its partner was allowed in, and then the pair could simultaneously pull on the rope. Elephants learned this social coordination task—that is, they learned to wait for their partner and then simultaneously pull on a rope with that partner to obtain food. This finding *suggests* that the elephants were cooperating with one another to get food. At the very least, this treatment shows elephants were not just using a “pull the rope” rule; if they were, they would not have waited for their partners.

A third treatment provides more evidence that rope pulling was cooperative. In this treatment, a pair was released simultaneously, but one end of the rope was tied up so that the elephant near it could not pull on the rope. This elephant often remained idle, and its partner was much less likely to pull on the rope than in the first treatment (in which both partners had the rope available). When the partner’s inaction made it apparent that pulling on the rope would have been futile in terms of getting food, an elephant did not expend time and energy pulling on its end of the rope. When cooperation would have yielded no reward, elephants did not cooperate.

* * *

The previous chapter focused on the strong role that genetic relatedness plays in promoting prosocial behavior. Animals that are not genetic relatives, however, cooperate with each other in many contexts. Here we shall examine such cooperation among unrelated individuals.

Defining Cooperation

The word **cooperation** typically refers to an *outcome* in which two or more interacting individuals each receives a net benefit from their joint actions, despite the costs they may have to pay for undertaking such actions. For example, jointly hunting prey may provide each of two hunters with food, even though there are costs (possible injury, energy expended) associated with hunting. In addition to looking at outcomes (that is, successfully capturing prey), it is also important to examine cooperation in terms of individual action. Suppose, for example, that to successfully hunt prey, a pair of hunters needs to both (1) flush the prey into an open area and (2) pounce on the prey when it is flushed into the open. A successful hunting strategy might be for hunter 1 to flush out the prey, and for hunter 2 to follow up by pouncing on the prey. Regardless of what hunter 2 does, and regardless of whether prey is captured, if hunter 1 flushes the prey into the open, then it acted cooperatively, in that its behavior made a successful capture possible.

An *individual* can cooperate by acting in a way that makes cooperation (an outcome) possible. As such, *to cooperate* means to behave in such a way as to make the benefits that could be obtained from joint action possible, even though they may not necessarily be achieved (Dugatkin et al., 1992; Mesterton-Gibbons and Dugatkin, 1992).

Cooperation occurs in many species and in a wide variety of behavioral contexts. To better understand the origins and the costs and benefits of cooperation among unrelated individuals, in this chapter we will examine:

- What paths leading to cooperation have been identified by ethologists? What theory lies behind each? What empirical evidence supports each of these paths?
- What do we know about both the ultimate and proximate underpinnings of cooperation?
- What role does phylogeny play in explaining the distribution of animal cooperation?
- What role does cooperation play in coalition formation?
- How can we explain *interspecific* cooperation—that is, cooperation among animals from different species?

Paths to Cooperation

Work on the evolution of cooperation can be traced back at least as far as Charles Darwin (Darwin, 1859, 1871). Darwin was well aware that social insects displayed an array of cooperative behaviors. Although he was unable to completely explain why, Darwin did come close to explaining part of the “riddle” of such behavior via kinship. After Darwin, the study of cooperation was primarily (but not exclusively) kept alive first by Petr Kropotkin, a Russian prince and naturalist, and later by such researchers as W. C. Allee, A. E. Emerson, and others who were part of what was called the Chicago School of Animal Behavior (Dugatkin, 2006, 2012; Mitman, 1992). Although these natural historians, ethologists, and population biologists amassed a good deal of data that documented cooperation among animals, they did less in the way of advancing any theory on why cooperation evolved (Allee, 1951).

A theoretical foundation for studying the evolution of cooperation has emerged over the last forty years (reviewed in B'shary and Bergmueller, 2008; Clutton-Brock, 2009; Dugatkin, 1997a; Lehmann and Keller, 2006; Nowak, 2006b; Sachs et al., 2004; S. West et al., 2011). From Hamilton's innovative work in 1963 (see chapter 9) to the present, four paths to the evolution and maintenance of cooperation in animals have been developed—kin-selected cooperation, reciprocity, byproduct mutualism, and group selection (Axelrod, 1984; J. L. Brown, 1983; Hamilton, 1964; D. S. Wilson, 1980; Figure 10.3). There is now empirical evidence available to put some of the models underlying these paths to the test. Since kin selection was discussed in chapter 9, here we consider the remaining three paths to cooperation.

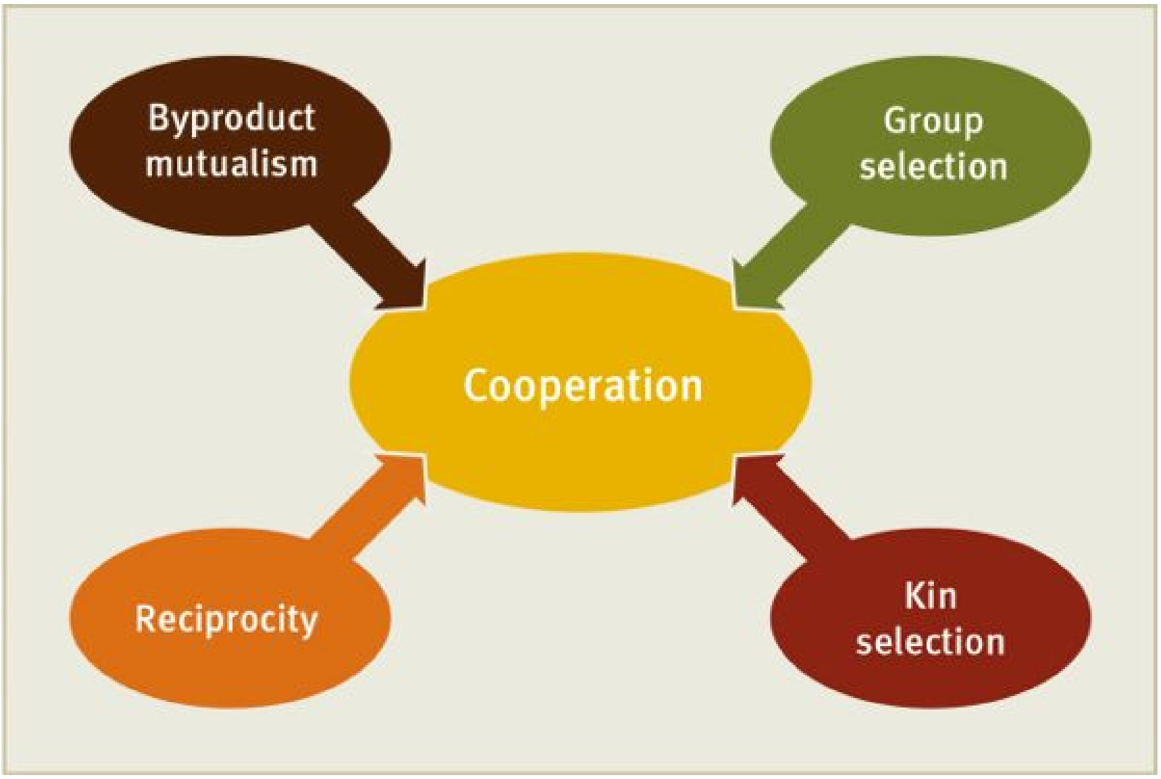


Figure 10.3. Four paths to cooperation. Reciprocity, byproduct mutualism, kin selection, and group selection can all lead to cooperative behavior.

PATH 1: RECIPROCITY

In his 1971 paper, "The Evolution of Reciprocal Altruism," Robert Trivers hypothesized that if individuals benefited from exchanging acts of cooperative and altruistic behavior—what he referred to as

reciprocal altruism—then this sort of exchange system might be favored by natural selection (Trivers, 1971). If individual A pays some cost to help individual B, but this cost is made up for at some point in the future, when B helps A, then natural selection might favor behaviors that lead to reciprocity. Trivers predicted that natural selection will more strongly favor reciprocal altruism when individuals that live in groups interact with the same partners, as well as when individuals have the ability to recognize in the future those that had helped them in the past, as both facilitate long-term partnerships.

Trivers modeled how reciprocal altruism evolves using a theoretical framework called **game theory**. Game theory is a mathematical tool that is used when the payoff—some resource such as food, mating opportunities, and so on—that an individual receives for undertaking an action depends on what behavior others adopt. In the evolutionary game theory literature, payoffs are used as indirect proxies for fitness. Trivers, with some help from W. D. Hamilton (see chapter 9), suggested that the evolution of cooperation could best be understood using a mathematical game called the **prisoner's dilemma**.

To understand how the prisoner's dilemma game works, let's begin with a human example and then examine this game in terms of nonhuman behavior. Imagine the following scenario: While in separate rooms, two criminal suspects are interrogated by the police in the hope of getting a confession from one or both of them. The options available to both suspects are cooperate or defect (don't cooperate). Cooperation and defection (also called "cheating") are defined from the perspective of the suspects. To defect means to tell the authorities that the other suspect is guilty, and to cooperate is to stay quiet and not betray the other suspect. Imagine that even without a confession from either, the police have enough circumstantial evidence to put both suspects in jail for one year. Further suppose that if each suspect informs on the other, both go to jail for three years. Finally, if only one suspect informs on the other suspect, such behavior allows the defector to walk away free, but results in the cooperator going to jail for five years.

Table 10.1 depicts the payoffs to each suspect as a function of how s/he behaves and how the other suspect behaves. If both suspects cooperate, they both receive a payoff of R (R is short for the reward for mutual cooperation; in Table 10.1, R = 1 year in jail), and if they both defect, each one receives P (the punishment for mutual defection; 3 years in jail). If suspect 1 defects, but suspect 2 cooperates, the former receives a payoff of T (the temptation to cheat payoff; 0 years in jail), and the latter receives S (the sucker’s payoff; 5 years in jail). If we order the payoffs in this matrix from high to low, we see that T > R > P > S. It is these inequalities that define our game as a prisoner’s dilemma. That is, for a game to be a prisoner’s dilemma, the payoff structure of the matrix must be T > R > P > S (a second more technical requirement is sometimes added to the model).

Table 10.1. The prisoner’s dilemma game. In this game, each player can either cooperate or defect. In the matrix, T = “Temptation to cheat” payoff, R = “Reward for mutual cooperation” payoff, P = “Punishment for mutual defection” payoff, and S = “Suckers” payoff. For the matrix to qualify as a prisoner’s dilemma game, it must be true that T > R > P > S. Each cell shows the payoff to suspect 1 (in the top left corner) and the payoff to suspect 2 (in the bottom right corner). For example, in the lower left cell, when suspect 1 defects and suspect 2 cooperates, the former gets 0 years in jail, while the latter gets 5 years in jail.

		Suspect 2	
		Cooperate	**Defect/Cheat**
Suspect 1	Cooperate	R = 1 year in jail R = 1 year in jail	S = 5 years in jail T = 0 years in jail
	Defect/Cheat	T = 0 years in jail S = 5 years in jail	P = 3 years in jail P = 3 years in jail

Examining Table 10.1 we see that suspect 1 will receive a better payoff individually if he defects, regardless of what suspect 2 does. If suspect 2 defects, suspect 1 does better to defect (3 versus 5 years in prison), and if suspect 2 cooperates suspect 2 does better to defect (0 versus 1 year in prison). Suspect 1 should always defect. The same holds true individually for suspect 2—she always receives a higher payoff for defecting, regardless of what suspect 1 does—and suspect 2 should also always defect. As such, both suspects should defect. The *dilemma* in the prisoner’s dilemma is that while each suspect receives

P (3 years in prison) when they both defect, both suspects would receive a higher payoff (R, 1 year in prison) if they had both cooperated (Poundstone, 1992): mutual cooperation provides all parties with a higher payoff than mutual defection.

If each individual does better defecting regardless of the action of the other player, but both do better when there is mutual cooperation rather than mutual defection, the prisoner's dilemma game can be used to model animal cooperation. Before we look at animal examples, let us explore the prisoner's dilemma in more depth and examine what sort of predictions about behavior emerge from this model.

Using both analytical mathematics and computer simulations, Robert Axelrod and W. D. Hamilton modeled what sorts of behavioral strategies fared well—obtained high payoffs—when individuals were playing the prisoner's dilemma game. They looked at the success of an array of behavioral strategies in the *iterated*, or repeated, prisoner's dilemma game (Axelrod and Hamilton, 1981). In one version of the iterated prisoner's dilemma game, two individuals play the game with one another many times, but the endpoint for such interactions is not known to the players with certainty. This type of game mimics certain natural situations, since social, group-living animals generally encounter each other more than once, but the number of possible future encounters is uncertain. In the iterated prisoner's dilemma game complex rules, including "if-then" rules of the form "if the other individual does X, then I will do Y," can be used—for example, "if she cooperates, I will cooperate; otherwise I will defect."

Axelrod and Hamilton searched for the **evolutionarily stable strategy (ESS)** to the iterated prisoner's dilemma game (Maynard Smith, 1982; see Box 10.1 for an explanation of ESS). They demonstrated that if the probability of meeting a given partner in the future was sufficiently high, and the exact endpoint of interactions was not known by individuals, then in addition to the success of a simple strategy of "always be noncooperative" (labeled "always defect" or ALLD), a *reciprocity-based* strategy called **tit for tat (TFT)** was one solution to the iterated prisoner's dilemma (see Box 10.2).

Box 10.1. MATH

Evolutionarily Stable Strategies (ESS)

An *evolutionarily stable strategy* is defined as “a strategy such that, if all the members of a population adopt it, no mutant strategy can invade” (Maynard Smith, 1982). In this definition *mutant* refers to a new strategy introduced into a population, and successful invasions center on the relative fitness of strategies already present versus mutant strategies. For a strategy to be evolutionarily stable, its payoff must be greater than the payoff to any mutant strategy. More formally, consider two strategies, I and J, and denote the expected payoff of strategy I against strategy J as E(I, J), the payoff of J against I as E(J, I), the payoff of I against I as E(I, I), and the payoff of J against J as E(J, J).

Strategy I is an ESS if the following two conditions are met:

Either

$$E(I, I) > E(J, I) \quad (1)$$

or

$$E(I, I) = E(J, I), \text{ but } E(I, J) > E(J, J) \quad (2)$$

If condition (1) holds, then I does better against other I’s than J does against I. Since we start with a population full of I’s (except for one, or a very small number of J mutants), this means that I is an ESS.

Condition (2) addresses what happens when I and J have the same fitness when interacting with I. If this is the case, then J may reach higher frequencies by chance, since when J occurs as a mutant, it does just as well as I. I is then an ESS if it does better than J when each is paired up against J; when E(I, J) > E(J, J).

Box 10.2. MATH

An ESS Analysis of TFT and the Prisoner's Dilemma Game

Axelrod and Hamilton (1981) examined whether tit for tat (TFT) and the strategy "always defect" (ALLD) were evolutionarily stable: whether they could resist invasion from mutants if they themselves were at a frequency close to 1. They began by demonstrating that if the strategy ALLD or a strategy that alternates D and C (ALTDC) could not invade TFT, then no single pure strategy (a strategy that specifies a specific behavior in every situation) could invade. They then considered whether ALLD or ALTDC could invade TFT.

Let w equal the probability of interacting with the same player on the next move of a game. Then the moves of the game can be represented as a geometric series, and the expected number of interactions with a given individual is equal to $1/(1 - w)$. For example, if $w = 0.9$, the expected number of interactions with a given partner is 10 $[1/(1 - 0.9)]$.

When TFT is close to a frequency of 1, virtually all TFT players meet other TFT players, and their payoff is:

$$\mathrm{R} + w\mathrm{R} + w^2\mathrm{R} + w^3\mathrm{R} + \ldots, \text{ which sums to } \mathrm{R}/(1 - w) \qquad (1)$$

A single ALLD mutant would have all its interactions with TFT, and its payoff would be:

$$\mathrm{T} + w\mathrm{P} + w^2\mathrm{P} + w^3\mathrm{P} + \ldots, \text{ which sums to } \mathrm{T} + w\mathrm{P}/(1 - w) \qquad (2)$$

so TFT can resist invasion from ALLD when:

$$\mathrm{R}/(1 - w) > \mathrm{T} + w\mathrm{P}/(1 - w) \qquad (3)$$

Solving the inequality for w, ALLD fails to invade TFT when:

$$w > (\mathrm{T} - \mathrm{R})/(\mathrm{T} - \mathrm{P}) \qquad (4)$$

When playing TFT, ALTDC gets a payoff of:

$$T + wS + w^2T + w^3T \ldots \text{, which sums to } (T + wS)/(1 - w^2) \qquad (5)$$

TFT can resist invasion from ALTDC when:

$$R/(1 - w) > (T + wS)/(1 - w^2) \qquad (6)$$

Solving the inequality for *w*, ALTDC fails to invade TFT when:

$$w > (T - R)/(R - S) \qquad (7)$$

TFT is resistant to *any* invasion when:

$$w > \text{maximum of these two values: } (T - R)/(T - P) \text{ and } (T - R)/(R - S) \qquad (8)$$

When an individual uses the TFT strategy, she cooperates on the initial encounter with a partner and subsequently copies her partner’s previous move. Thus, after the first move, she operates under an if-then rule: if my partner cooperates, then cooperate; if my partner defects, then defect. TFT reciprocates acts of cooperation, as well as acts of defection. This behavioral rule also nicely ties together work on cooperation and work on social learning (see chapter 6), as individuals copy what their partners do, and such behavior can potentially ripple through an entire population.

Axelrod hypothesized that the TFT strategy’s success is attributable to three characteristics: (1) “niceness”—a player using TFT is never the first to defect, as she initially cooperates with a new partner, and then cooperates as long as her partner cooperates; (2) swift “retaliation”—an individual playing TFT immediately defects on a defecting partner since she copies her partner's previous move, so if her partner defects, she defects; and (3) "forgiving"—because TFT instructs players to do what their partner did on the last move, those using a TFT strategy have a memory window that is *only one move back in time* (Axelrod, 1984). As such, the player using TFT forgives prior defection if a partner is currently cooperating—those using a TFT strategy do not hold grudges (Figure 10.4). Since the original models of TFT have appeared, dozens of variants of this strategy have been examined, but most share the essential characteristics we have just discussed (Dugatkin, 1997a).

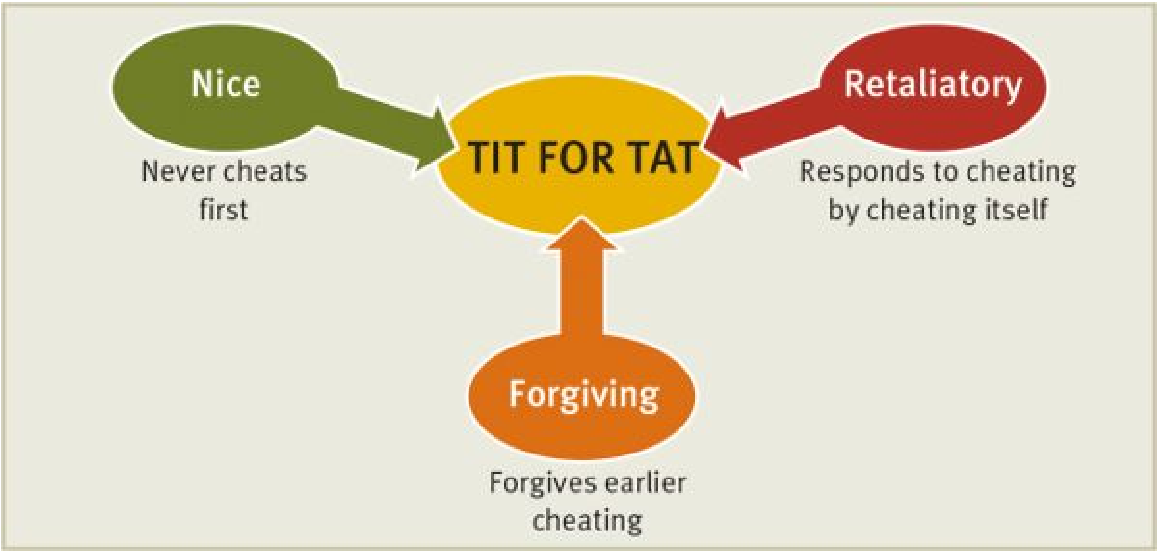


Figure 10.4. Tit for tat. The tit-for-tat strategy has three basic characteristics. The individual using TFT is (1) nice—she never cheats first; (2) retaliatory—she always responds to a partner that is cheating by cheating herself; and (3) forgiving—she only remembers one move back in time, and hence "forgives" cheating that is done more than one move back in time.

Numerous studies have examined reciprocity in animals; here we will focus on three of these. The first examines the prisoner's dilemma and the use of TFT during antipredator behavior in guppies, the second addresses reciprocity and vampire bat food sharing, and the third looks at the proximate underpinnings of human reciprocity.

Predator Inspection and Tft in Guppies

In many streams of the Northern Mountains of Trinidad, the water is clear, and during the dry season, the behavior of guppies (*Poecilia reticulata*) can be seen from the riverbank. Pairs of guppies sometimes break away from their group and approach a potentially dangerous predator, such as a pike cichlid (*Crenicichla alta*). This behavior is called predator inspection (see chapter 2). These guppies are typically not genetic relatives, and they could just as easily have headed for cover (many do). Instead, inspectors approach the predator and do so in what looks like a coordinated fashion (Pitcher et al., 1986; Figure 10.5).

Figure 10.5. Risk taking and cooperation in guppies. Two male guppies (lower left and lower center of photo) inspect a pike cichlid predator. Experimental work has examined whether guppies cooperate during such risky endeavors. *(Photo credit: Michael Alfieri)*

Guppy 1 is better off if guppy 2 takes all the risks and passes the information it receives onto guppy 1. But the same holds true for guppy 2, as its highest payoff comes when guppy 1 approaches the predator alone, and then passes the information it receives to guppy 2. But if both fish opt to wait for the other to inspect the predator, each may be worse off than if they had inspected the predator as a pair. In this scenario, inspecting a predator would be acting cooperatively, while failing to inspect, or just lagging behind during inspection, would be a form of cheating. Before addressing whether guppies use TFT while inspecting a predator, we first need to examine whether a pair of fish inspecting a predator are playing the prisoner’s dilemma game

(Dugatkin, 1997a). Recall that for a payoff matrix to be a prisoner’s dilemma, it must be true that T > R > P > S. What evidence is there that these inequalities hold true for guppies inspecting a predator?

- Is T > R? Milinski has argued that a fish that trailed behind its partner while inspecting a possible predator would do better than its co-inspector, as it could assess how dangerous the predator was by observing whether the lead fish was attacked (Milinski, 1987). The trailing fish would receive a payoff of T if it stayed behind, but a payoff of R if it swam beside its partner (Table 10.2). Two pieces of evidence suggest that the temptation payoff T is greater than the R payoff associated with mutual inspection. First, inspectors are more likely to get eaten the closer they approach a predator (Figure 10.6): it is more dangerous to be leading an inspection than lagging behind. Second, inspectors transfer the information that they receive during an inspection, so that any fish lagging behind would still receive the benefits associated with inspection (Dugatkin, 1992c; Magurran and Higham, 1988; Milinski et al., 1997; Figure 10.7).
- Is R > P? If P is greater than R—if the payoff for inspecting in a group (R) is less than the payoff when no one inspects (P)—it would not pay for any individual to inspect, so predator inspection should be rare and maladaptive when it occurred. Given that inspection occurs in many species, this seems unlikely, and so R, the payoff for mutual cooperation, is probably greater than P, the payoff for mutual defection (Dugatkin and Godin, 1992; Pitcher, 1992; Figure 10.8).
- Is P > S? For the payoffs of predator inspection to qualify as a prisoner’s dilemma, it must also be true that the payoff to mutual cheating (P) is greater than the payoff to inspecting alone (S). While it appears to be the case that having no inspectors in a shoal is dangerous for all group members, as no one obtains information on danger levels, the most dangerous situation for a single fish is to be the lone inspector in a group. Evidence from a number of experiments indicates that single fish suffer very high rates of predation, suggesting, though not definitively demonstrating, that P > S (Milinski, 1977).

Table 10.2. The payoffs for predator inspection. When T > R > P > S, the payoffs for predator inspection qualify as a prisoner’s dilemma. Fish 1’s payoff is shown in the top left corner of each cell, and fish 2’s payoff is shown in the bottom right corner of each cell.

		Fish 2	
		Inspect	**Don’t inspect/lag behind**
	Inspect	R	S
Fish 1		R	T
	Don’t inspect/lag behind	T	P
		S	P

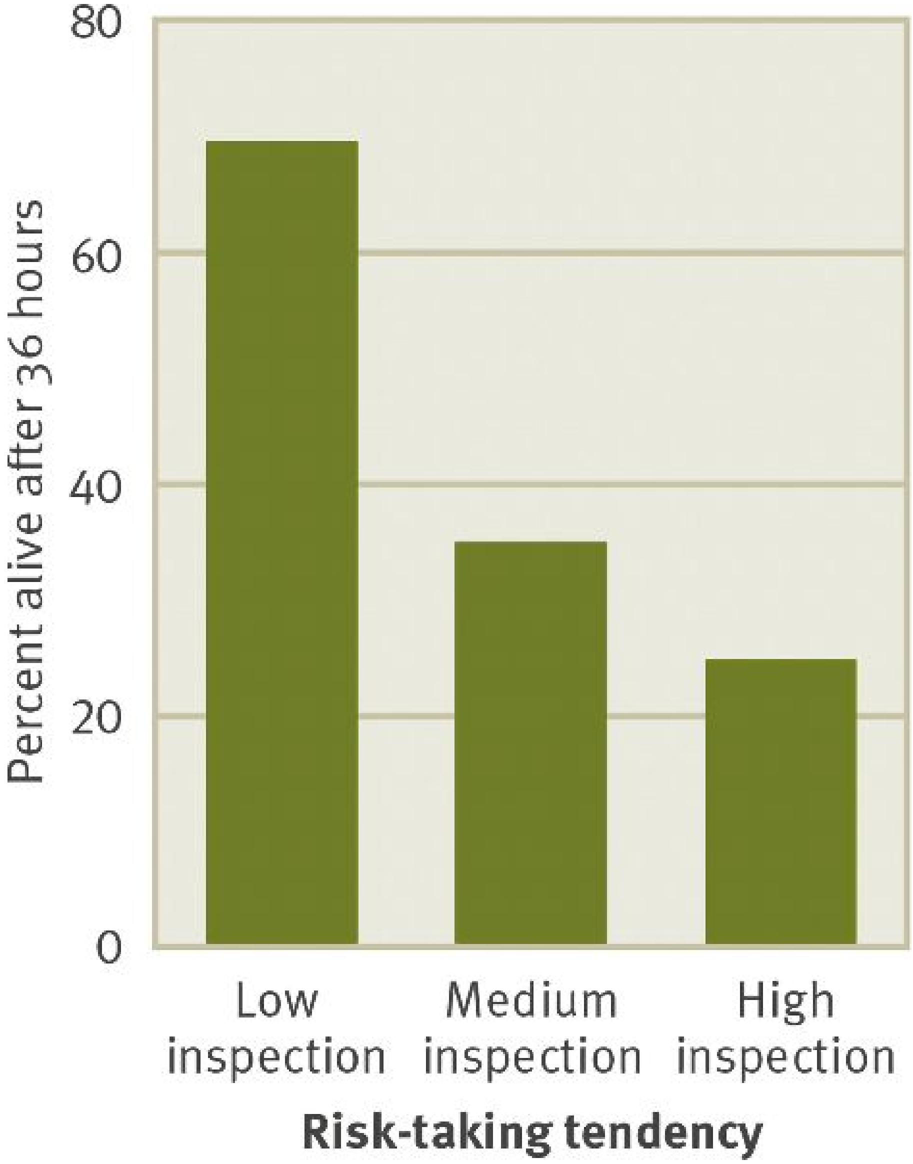
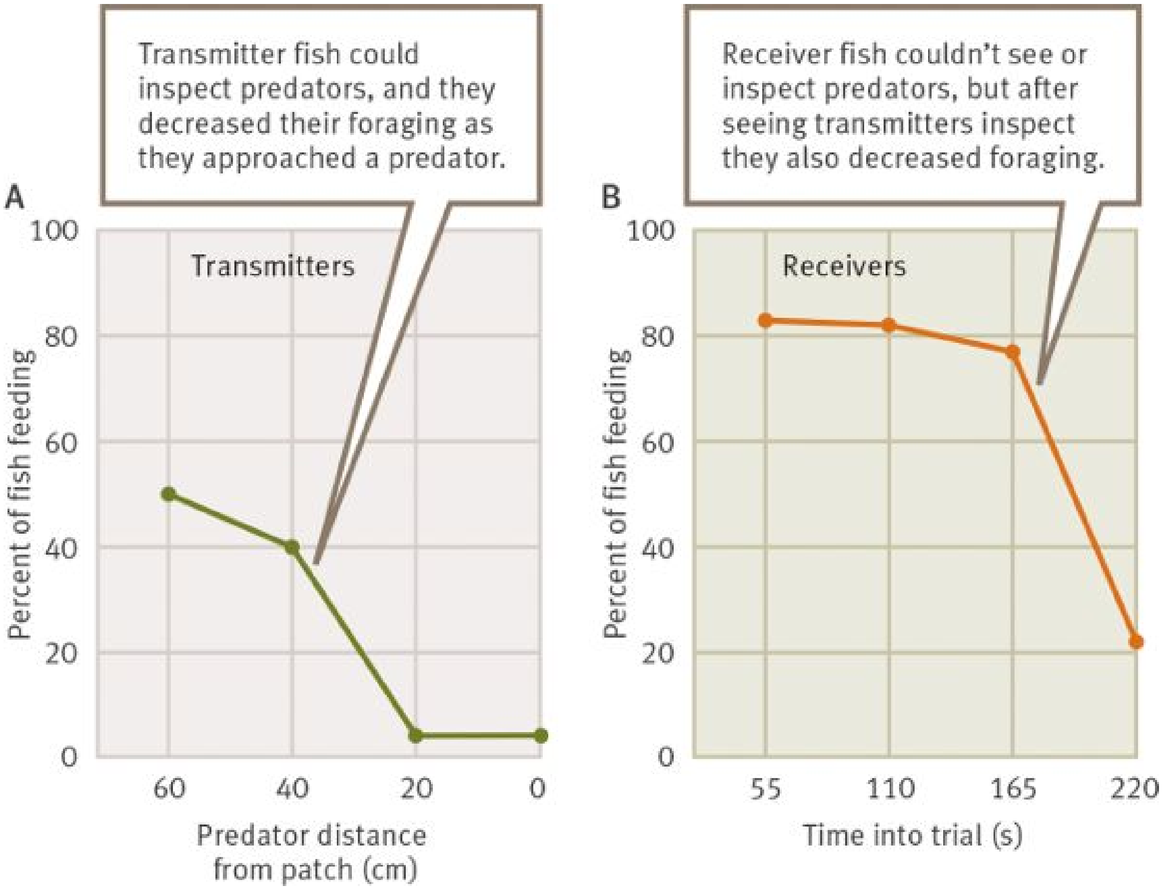


Figure 10.6. The risk of inspecting predators. Ten groups of six guppies each—two low inspectors, two medium inspectors, and two high inspectors—were placed with a predator in a pool that was one meter in diameter. The probability of surviving thirty-six hours was a function of inspection tendencies, with those inspecting most often suffering the highest mortality. *(From Dugatkin, 1992b)*



Transmitter fish could inspect predators, and they decreased their foraging as they approached a predator.

Receiver fish couldn't see or inspect predators, but after seeing transmitters inspect they also decreased foraging.

Figure 10.7. Information transfer in minnows. Information obtained by inspectors is transferred to individuals that do not inspect. *(Based on Magurran and Higham, 1988, p. 157)*

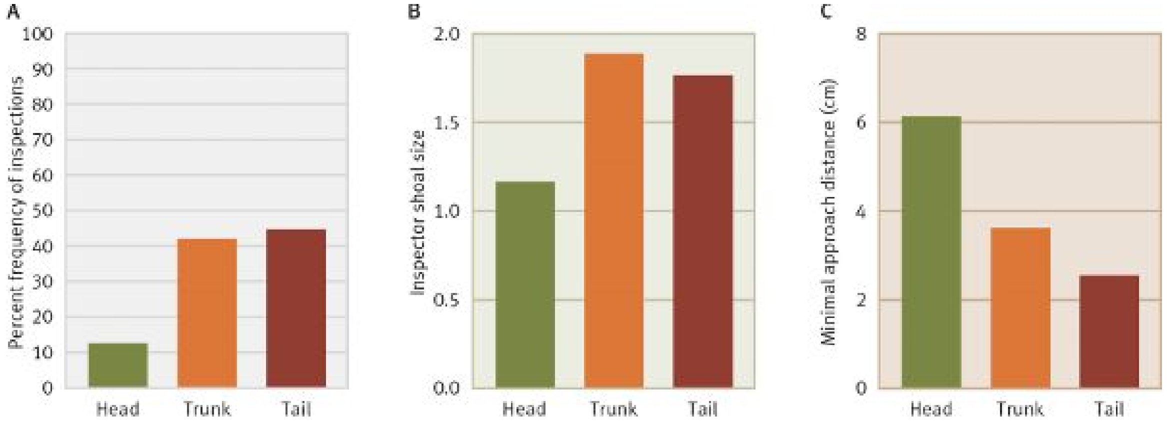


Figure 10.8. Inspection behavior in the wild. A model predator was placed into a tributary of a river in Trinidad, and the predator inspection behavior of guppies was recorded. Inspectors recognize the head region of a predator as most dangerous. (A) There were fewer inspections of the predator's head than of its trunk and tail. (B) Inspector group size was smallest when inspecting the head region of a predator. (C) Approach distance was a function of the part of the predator's body that was being inspected; inspectors stayed farthest away when they were inspecting the predator's head. *(Based on Dugatkin and Godin, 1992)*

Measuring T, R, P, and S precisely in controlled experiments is difficult, but assuming that the payoff matrix associated with inspection meets the prisoner's dilemma requirement that T > R > P > S, theory suggests that fish inspecting a predator should use the TFT strategy. Do they? (Dugatkin, 1997a).

The dynamic nature of inspection behavior in guppies and sticklebacks, but not mosquitofish, support the prediction that inspectors do, in fact, use the TFT strategy when inspecting potential predators (Dugatkin, 1997a; Stephens et al., 1997). Fish that inspect predators appear to use a strategy that is:

- "nice," as each starts off inspecting at about the same point in time,
- "retaliatory," as an inspector ceases inspection if her partner stops (Figure 10.9),
- "forgiving"—if inspector A's partner has cheated on it in the past, but resumes inspection, A then resumes inspection as well (Dugatkin, 1991).

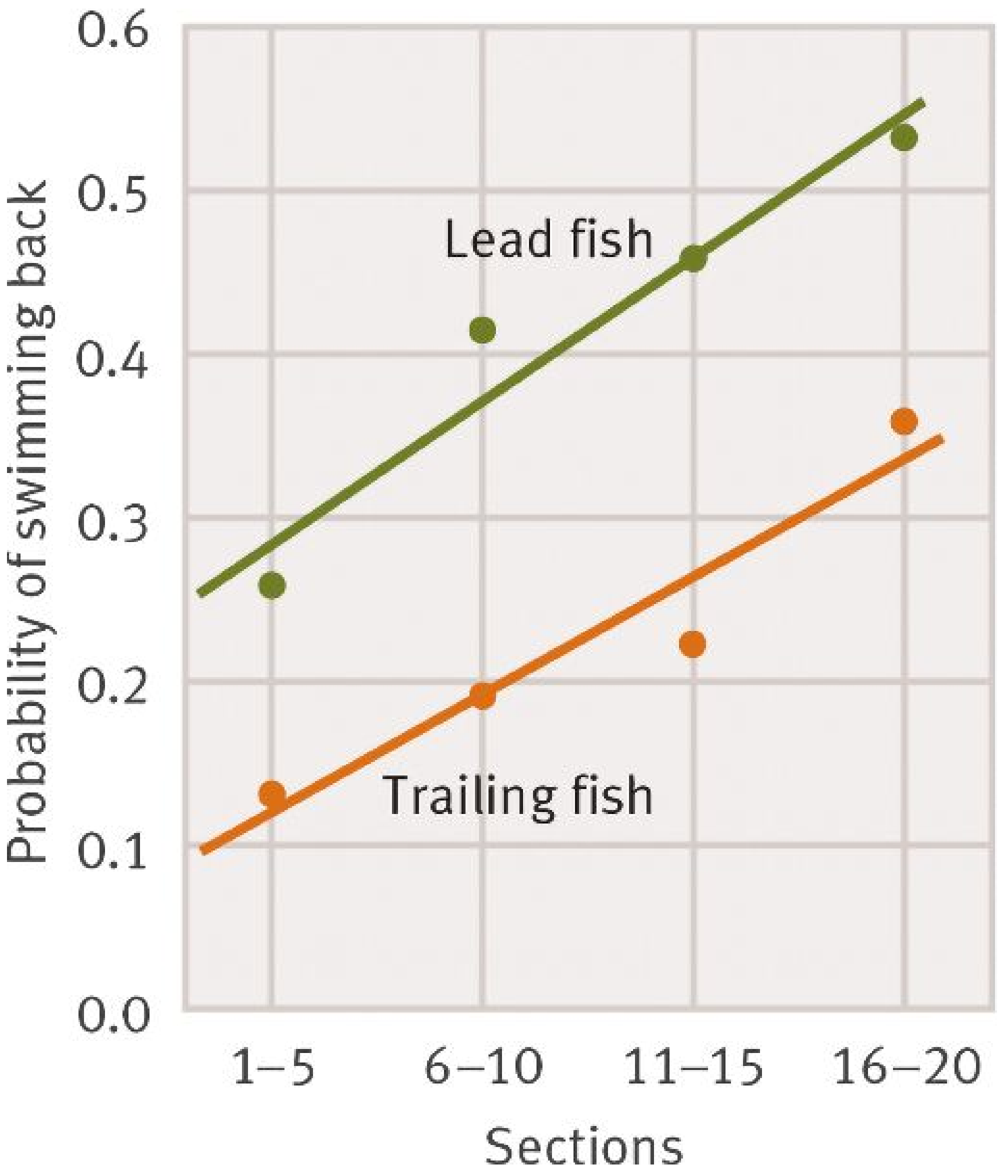


Figure 10.9. **Retaliation in guppies?** Pairs of guppies were given the opportunity to inspect a predator. Lead fish in a given section of an aquarium were more likely to turn back and swim to safety than were trailing fish in the same section of the aquarium. This could be interpreted as lead fish retaliating against trailing fish, who fail to stay by their side. *(Based on Dugatkin, 1991, p. 130)*

If the payoffs for inspection match those of the prisoner's dilemma, then the payoffs shown in Table 10.2 suggest that each individual should prefer to associate with cooperators. This is because cooperators do better when paired with other cooperators, and defectors also do better when paired with cooperators, so whenever possible, all individuals should prefer to associate with cooperators. Evidence exists that inspectors remember the identity and behavior of their co-inspectors. When an individual fish is given the choice between associating with a fish that has been cooperative during prior encounters versus a fish that has not been cooperative, she prefers to associate with cooperators over defectors, at least when group size is small (Dugatkin and Alfieri, 1991a, 1992; Dugatkin and Wilson, 2000; Milinski et al., 1990).

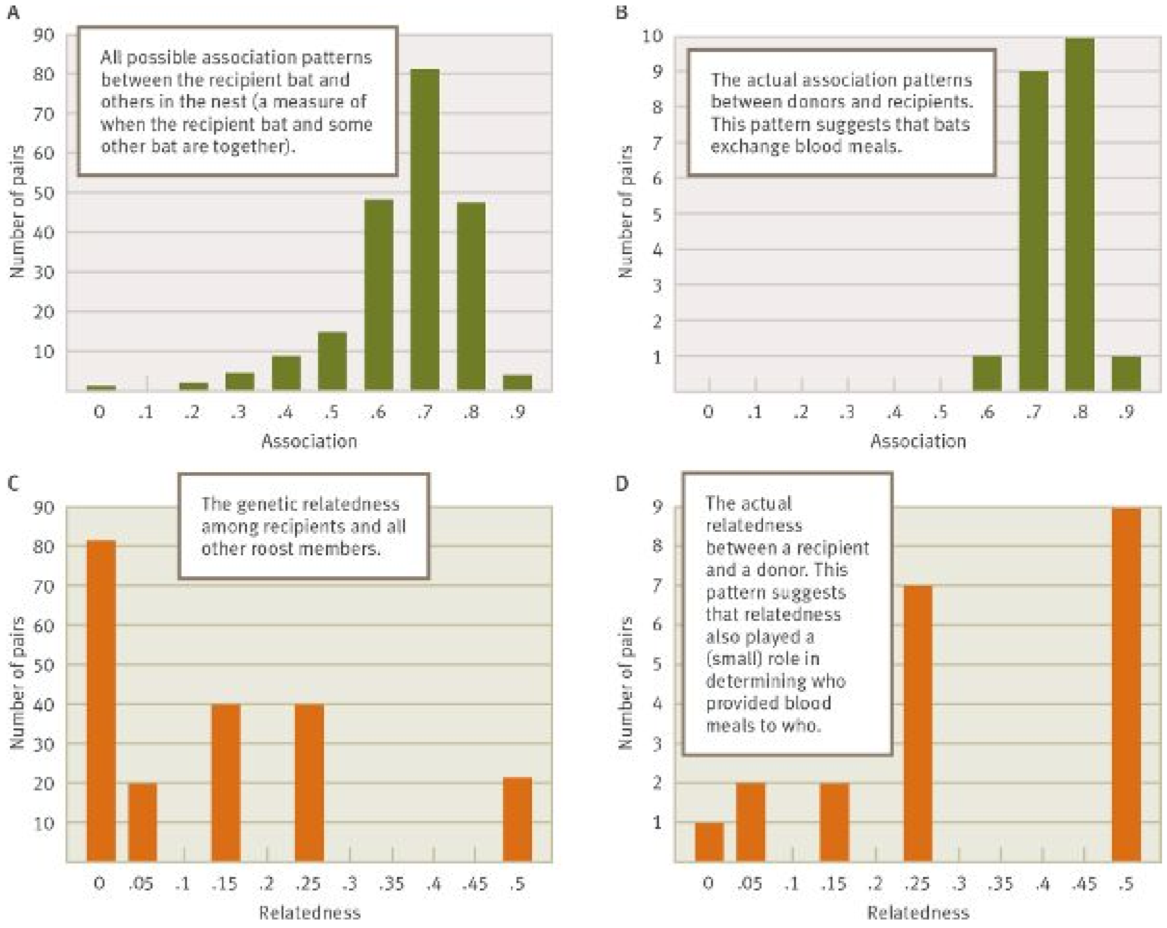
Reciprocity and Food Sharing in Vampire Bats

One of the first studies of reciprocity was that of food-sharing behavior in vampire bats (*Desmodus rotundus*). Roosts of vampire bats are composed largely of females, with a low average coefficient of relatedness (between 0.02 and 0.11; Wilkinson, 1984, 1990; Figures 10.10 and 10.11). Females in a roost sometimes regurgitate blood meals to other bats that have failed to obtain food in the recent past (Wilkinson, 1984, 1985). This sort of food sharing can be a matter of life or death, as individuals may starve to death if they don’t receive a blood meal approximately every sixty hours (McNab, 1973). Jerry Wilkinson examined whether relatedness, reciprocity, or some combination of the two best explained the evolution and maintenance of sharing blood meals in vampires.

Figure 10.10. Vampire bat blood meals. Female vampire bats need frequent blood meals. Individuals often regurgitate part of their blood meals to others, but they are more likely to do so for those that have shared a meal with them in the past. *(Photo credit: Jerry Wilkinson)*

Figure 10.11. Vampire bat cooperation. If a hungry bat approaches a satiated bat, she is much likely to get a regurgitated blood meal if she has fed the satiated bat in the past. *(Licensed under Creative Commons by Gerald Carter)*

Although the average relatedness in groups was low, Wilkinson found that genetic relatives were still more likely to swap blood meals with one another than with other individuals (Figure 10.12). To examine whether reciprocity per se was also important, Wilkinson created an "index of opportunity for reciprocity." When analyzing the data with this index, Wilkinson found three lines of evidence that reciprocity may be important in sharing blood meals in vampire bats: (1) the probability of future interaction between group members in a nest of vampire bats is high, as required by TFT models; (2) blood meals provide a large, potentially life-saving benefit for recipients, while the cost of giving up some blood is relatively low to the donor; and (3) vampire bats are able to recognize one another, allowing for the possibility of reciprocal exchange. In addition, there is some data that vampire bats are more likely to give blood to those that have donated blood to them in the past. While vampire bats don't necessarily use the TFT strategy, they appear to be using some sort of reciprocal altruistic strategy (Box 10.3).



All possible association patterns between the recipient bat and others in the nest (a measure of when the recipient bat and some other bat are together).

The actual association patterns between donors and recipients. This pattern suggests that bats exchange blood meals.

The genetic relatedness among recipients and all other roost members.

The actual relatedness between a recipient and a donor. This pattern suggests that relatedness also played a (small) role in determining who provided blood meals to who.

Figure 10.12. Relatedness, reciprocity, and sharing blood meals. Twenty-one regurgitation events not involving mothers and their offspring were used to examine the role of relatedness and reciprocity in sharing blood meals. Bats were much more likely to regurgitate a meal to close kin and to those with which they associated more often. Follow-up laboratory work found that bats were capable of keeping track of those that fed them in the past and those that didn't. *(From Wilkinson, 1984)*

Box 10.3. SCIENCE AT WORK

What is the research question? Do vampire bats reciprocate acts of costly food sharing?

Why is this an important question? Reciprocal altruism is one of the paths to cooperation identified by animal behaviorists, but at the time of the vampire bat study, little work had been done to test the models developed.

What approach was taken to address the research question? After controlling for levels of genetic relatedness among members of a vampire bat roost, researchers created an index of reciprocity between potential donor and recipient bats.

What was discovered? Vampire bat association patterns favor reciprocal interactions, and some evidence that bats exchange costly blood meals was uncovered.

What do the results mean? When the conditions favorable to reciprocal altruism are in place, animals are capable of using such a strategy.

Neurobiological and Endocrinological Underpinnings of Human Reciprocity

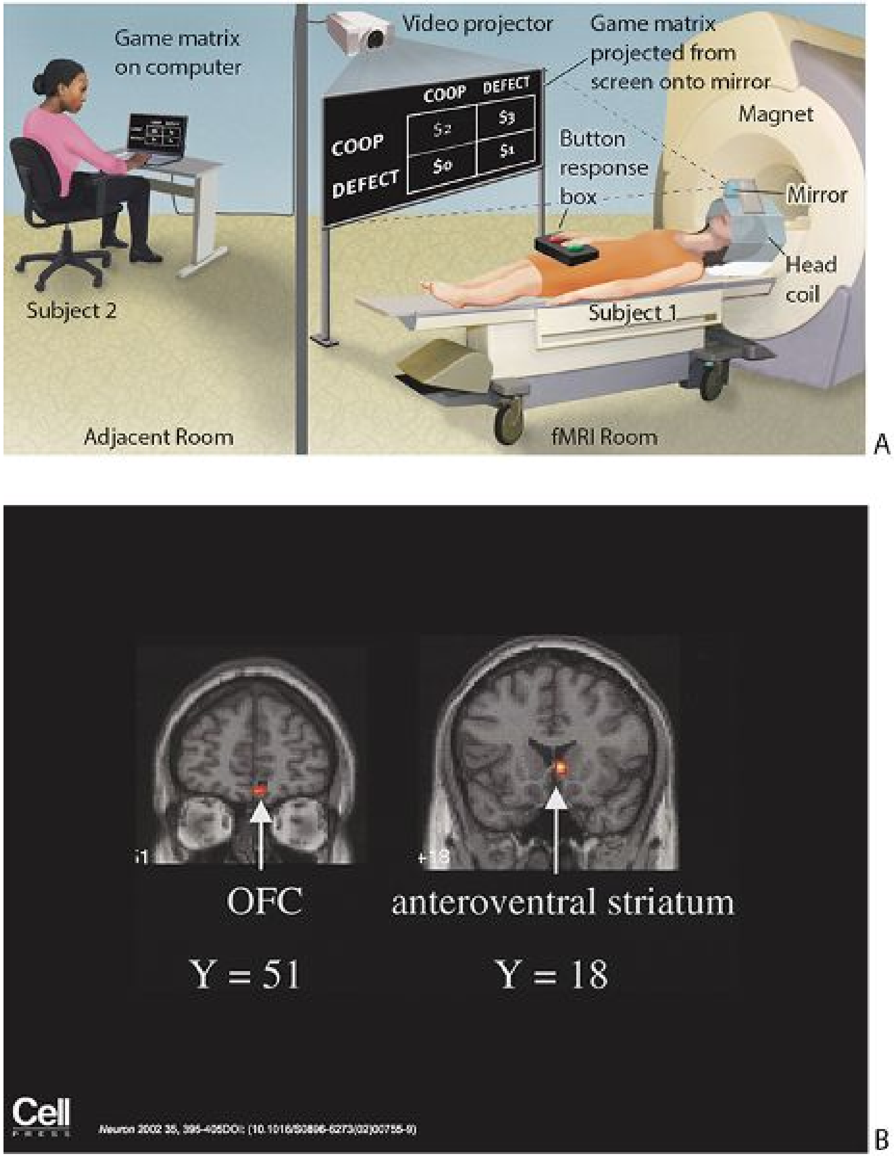
In this section we look at work on the neurobiological and endocrinological underpinnings of reciprocity and trust in humans.

Much of this proximate work on the neurobiology of human cooperation has been undertaken by researchers in **neuroeconomics**—a collaborative research effort between economists and neurobiologists who specialize in brain science (Glimcher, 2004, 2010; Glimcher and Rustichini, 2004; Montague, 2006; Sanfey et al., 2006; Zak, 2004; Glimcher and Fehr, 2013; Reuter and Montag, 2016).

Experiments in neuroeconomics involve subjects making an economic decision—in our case, one centering on reciprocal altruism—while their brain activity patterns are monitored by a magnetic resonance imaging machine (fMRI), or a positron emission tomography (PET) or some similar device. For example, Rilling and his team had women subjects play the prisoner's dilemma depicted in Table 10.3 (Rilling et al., 2002). Subjects were in an fMRI machine and played the iterated prisoner's dilemma game over a networked computer with another subject who was in a different room (Figure 10.13).

Table 10.3. The monetary prisoner's dilemma game. The payoff matrix for the game played by women who were either cooperating or cheating (defecting) in an economic cooperation experiment. Subject 1's payoff in top left corner of each cell. Subject 2's payoff in bottom right corner of each cell.

		Subject 2	
		Cooperate	**Defect/Cheat**
Subject 1	Cooperate	R = $2 R = $2	S = $0 T = $3
	Defect/Cheat	T = $3 S = $0	P = $1 P = $1



Neuron 2002 35, 395-405DOI: (10.1016/S0896-6273(02)00755-9)

Figure 10.13. The prisoner's dilemma game and social cooperation. To study the neurobiological basis of reciprocal altruism, researchers had subjects play an iterated prisoner's dilemma game. (A) One of the subjects played from inside an fMRI machine that monitored her brain activity as she played, while the other subject played the game on a computer in a different room. Each subject saw the payoff matrix that represented her own payoffs. (B) The fMRI scans showed that, when both subjects cooperated, brain areas associated with reward processing—the ventromedial/orbitofrontal cortex (OFC), the rostral anterior cingulate cortex (rACC), the anteroventral striatum (including the caudate nucleus and the nucleus accumbens), and the subgenual anterior cingulate cortex (ACC)—were activated. *Reprinted by permission of Cell Press. (Based on Rilling et al., 2002; photo credit: James Rilling)*

Rilling and his team found that even though the highest monetary reward in their experimental game ($3) was received by individuals who cheated when their partner cooperated, players said they felt best about receiving the $2 reward from mutual cooperation and they often cooperated. What's more, fMRI scans found that it was the mutual cooperation payoff of $2 that caused the greatest activation in areas of the brain associated with reward processing in humans, the ventromedial/orbitofrontal cortex (OFC), the anterior cingulate cortex (ACC), and the nucleus accumbens.

Work in neuroeconomics has also examined what sections of the brain are active when we punish those who fail to act cooperatively during economic interactions (Izuma, 2012; Rilling and Sanfey, 2011). Such behaviors often entail a *cost* to those who dispense the punishment, and a *benefit* to others not even involved in the interaction. Punishing those who violate social norms is of particular interest to those behaviorists, including animal behaviorists, who wish to understand how social norms evolved before modern legal codes came into place. Dominique de Quervain and his colleagues hypothesized that one proximate mechanism involved in maintaining punishment lies in the pleasure that we derive from enforcing social norms (de Quervain et al., 2004), and that this pleasure can be measured, indirectly, through neurobiological scans of the brain.

De Quervain had pairs of subjects play what is known as the trust game. In this game, two players—who are not allowed to communicate with each other—each begin with 10 units of money (called monetary units, or MUs, in this experiment). Player A is attached to a PET scanner and starts the game by deciding whether to give his 10 MUs to player B or to keep them for himself. A is told that, if he gives his money to B, the investigator will quadruple the gift to 40 MUs, so that B now has 50 MUs, and A has 0. Then player B is given a choice. He can send half his MUs back to player A, or he can keep everything for himself. So if A "trusts" B to send the money back, and B does send back the money, A and B each end up with 25 MUs; while if A opts to give B nothing, they both end up with 10 MUs.

If A does trust B to play fairly and gives him the money, but B then decides to keep all the MUs, A should view this as a violation of trust and social norms. De Quervain et al. hypothesized that, in such a case, A should then punish B. To allow for this possibility, one minute after B makes his decision, A can opt to "punish" B by revoking some of the MUs that he initially gave B. In one treatment of the experiment, A paid a cost in MUs for doing so, and in other treatments, punishing player B did not have any cost associated with it.

If A trusts B, but B violates that trust, A does punish B, even if it is costly to do so. Not only did subjects say that they enjoyed punishing those who violated their trust, PET scans of their brains demonstrated that one section of the brain associated with *reward* (the dorsal striatum, which includes the caudate nucleus) is most active when A undertakes the act of retribution. Individuals appear to derive *pleasure* from punishing cheaters. Indeed, results suggest that the more intense the punishment doled out to cheaters was, the more active was the dorsal striatum of the individual exacting retribution (Figure 10.14). In an interesting twist to the original experiment, A was sometimes told that B’s decision was determined by the equivalent of an electronic coin toss, so it was out of B’s hands. In that condition, when B did not send money back to A, A did not view this as a violation of trust and did not respond by punishing B, nor did the researchers see the increased activity in the dorsal striatum that was observed when A was punishing B.

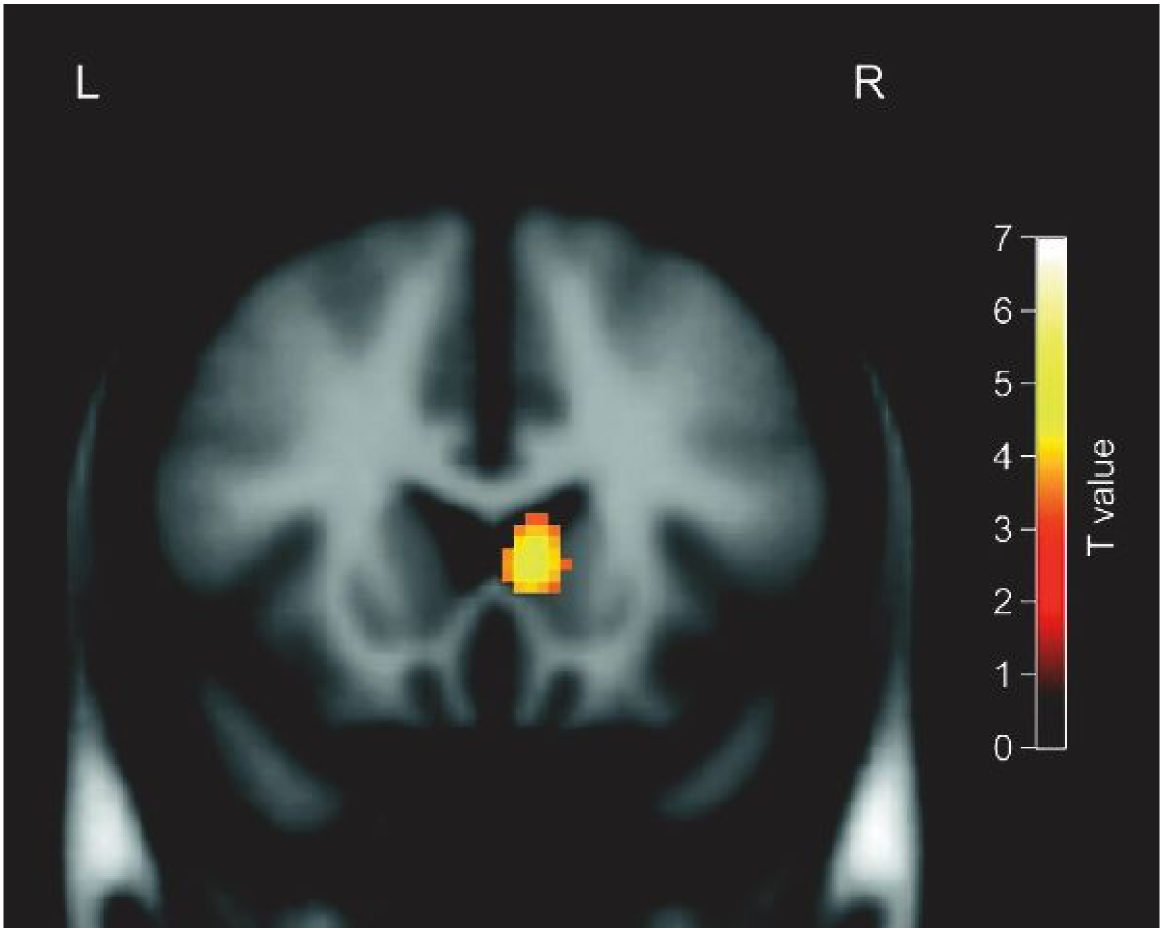
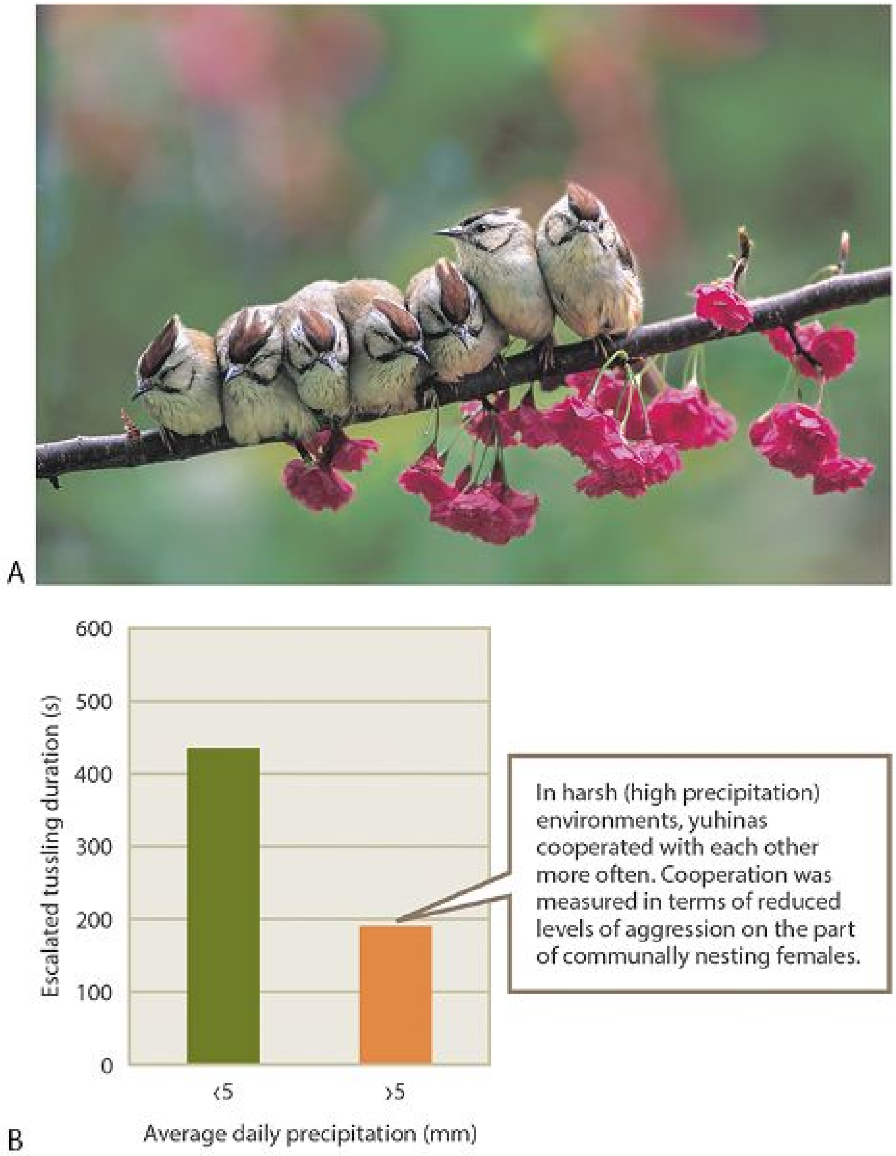


Figure 10.14. The trust game and punishment. Two subjects played the trust game while one of them (player A) was hooked up to a PET scanner that monitored his brain activity. The caudate nucleus, which is part of the dorsal striatum of the brain—depicted in yellow—was very active when player A punished player B for failing to return some of the money that A had provided to B. *Reprinted by permission from AAAS. (From de Quervain et al., 2004)*

PATH 2: BYPRODUCT MUTUALISM

A second path to the evolution of cooperation is **byproduct mutualism** (J. L. Brown, 1983; Connor, 1995; Rothstein and Pirotti, 1987; West-Eberhard, 1975). Cooperation here is a “byproduct” of the immediate cost or penalty an individual would incur if it did *not* act cooperatively. The immediate net benefits of byproduct mutualism outweigh the costs. There is no temptation to cheat, so individuals should cooperate.

Mathematical models predict that byproduct mutualism is more likely to evolve in “harsh” versus “mild” environments. What constitutes harsh and mild will depend on the system being studied (Dugatkin et al., 1992; Shen et al., 2011). For example, in Taiwanese yuhina (*Yuhina* *brunneiceps*), harsh environments are characterized as those with excessively high levels of rainfall, which is correlated with lower foraging success and lower hatching success in yuhinas. When Sheng-Feng Shen and his colleagues studied these communal nestings, they found significantly more cooperation in harsh than in mild environments (Shen et al., 2011; Figure 10.16). Harsh environments have also been found to favor cooperative behaviors in packs of feral dogs (Bonanni et al., 2010).



In harsh (high precipitation) environments, yuhinas cooperated with each other more often. Cooperation was measured in terms of reduced levels of aggression on the part of communally nesting females.

Figure 10.16. Harsh environments favor cooperation. (A) A group of yuhinas (*Yuhina brunneiceps*). (B) During the breeding season, females cooperate with one another more when in harsh than in mild environments. Reprinted by permission of Macmillan Publishers Ltd. © 2012, rights managed by Nature Publishing Group. *(Adapted from Shen et al., 2011)*

Byproduct mutualism differs from reciprocity in two ways. First, there is no temptation to cheat under byproduct mutualism, but the temptation to cheat (because of the increased payoff) always exists in systems involving reciprocity. In addition, while most (but not all) forms of reciprocity require some form of scorekeeping, with byproduct mutualism, individuals need not keep track of the past behavior of partners because in such situations it is always in the best interest of all parties to cooperate.

Blue Jays and Byproduct Mutualism

Kevin Clements and David Stephens used Skinner boxes, which allow precise control over the payoffs that animals encounter in the lab, to study byproduct mutualism in blue jays (*Cyanocitta cristata*) (Clements and Stephens, 1995).

Clements and Stephens tested pairs of blue jays: each bird could peck one of two keys—a cooperate key or a defect key. After the birds made their decisions, they were given food, the amount of which depended on what action they took (cooperate or defect), what action the other bird took, and which of two different payoff matrices the researchers had set up. The first matrix had payoffs that matched a prisoner's dilemma matrix (P matrix), while the second had the payoffs with byproduct mutualism (M matrix), where there was no temptation to cheat, because the birds always received more food for cooperating. In all trials, bird 1 would begin a trial by pecking one of the keys and bird 2 would end the trial (again by pecking either the cooperate or defect key). For example, if a pair was in the P matrix part of the game and bird 1 cooperated when bird 2 defected, bird 2 obtained five food items, while bird 1 received no food items (Table 10.4).

Table 10.4. The P matrix and the M matrix. The two payoff matrices used to examine the relative importance of reciprocity (a possible outcome of the P matrix) and byproduct mutualism (a possible outcome of the M matrix) in blue jays. In the M matrix, there was no temptation to defect, as cooperating jays always fared better than defecting jays (that is, 4 > 1, 1 > 0). Bird 1's payoff is shown in the top left corner of each cell and Bird 2's payoff is shown in the bottom right corner of each cell. (*Data from Clements and Stephens, 1995*)

P MATRIX		**Bird 2**	
		Cooperate	**Defect**
Bird 1	Cooperate	3 3	0 5
	Defect	5 0	1 1

M MATRIX		**Bird 2**	
		Cooperate	**Defect**
Bird 1	Cooperate	4 4	1 1
	Defect	1 1	0 0

Box 10.4. COGNITIVE CONNECTION

Empathy

Empathy is usually defined as the ability to share the feelings of another individual. In his 1759 book, *The Theory of Moral Sentiments*, economist Adam Smith proposed that empathy was one key to human goodness:

> How selfish soever man may be supposed there are evidently some principles in his nature, which interest him in the fortune of others . . . of this kind is pity or compassion, the emotion which we feel for the misery of others, when we either see it, or are made to conceive it in a very lively manner. The greatest ruffian, the most hardened violator of the laws of society, is not altogether without it.

More than a hundred years later, evolutionary biologist Petr Kropotkin argued that Smith was right, but that this same set of emotions was present in nonhumans: “Adam Smith’s only mistake,” Kropotkin wrote, “was not to have understood that this same feeling . . . in its habitual stage exists among animals as well as among men” (Kropotkin, 1890). Was Kropotkin right? Is there evidence for empathy in nonhumans? The jury is still out, but some recent works suggests there is.

Ethologists have found that some animals are capable of judging the “desire state” of others. Male Eurasian jays (*Garrulus glandarius*), for example, can assess the food preferences of their mates, independent of their own food preferences, and feed their mates accordingly (Ostojic et al., 2013). Desire state is not the same thing as empathy, but it may be a prerequisite for empathy.

Some experimental work suggests that rodents display empathy under certain conditions. Early studies by Church found that rats that had been trained to get food by pushing a lever dramatically reduced their lever pushing when it was also associated with shocking another rat (Church, 1959). More recently, Peggy Mason and her colleagues placed two rats that had lived together beforehand into an experimental enclosure. One of the rats—labeled the “free rat”—could move about the enclosure, but the other rat was placed inside a small clear plastic canister with a door that was locked, and could only be opened from the outside. The trapped rat emitted ultrasonic distress calls. What Mason and her team tested was whether the free rat would attempt to release the trapped rat. What they found was that once the free rat figured out how to open the door, it released the trapped rat and did so over many trials (Figure 10.15).

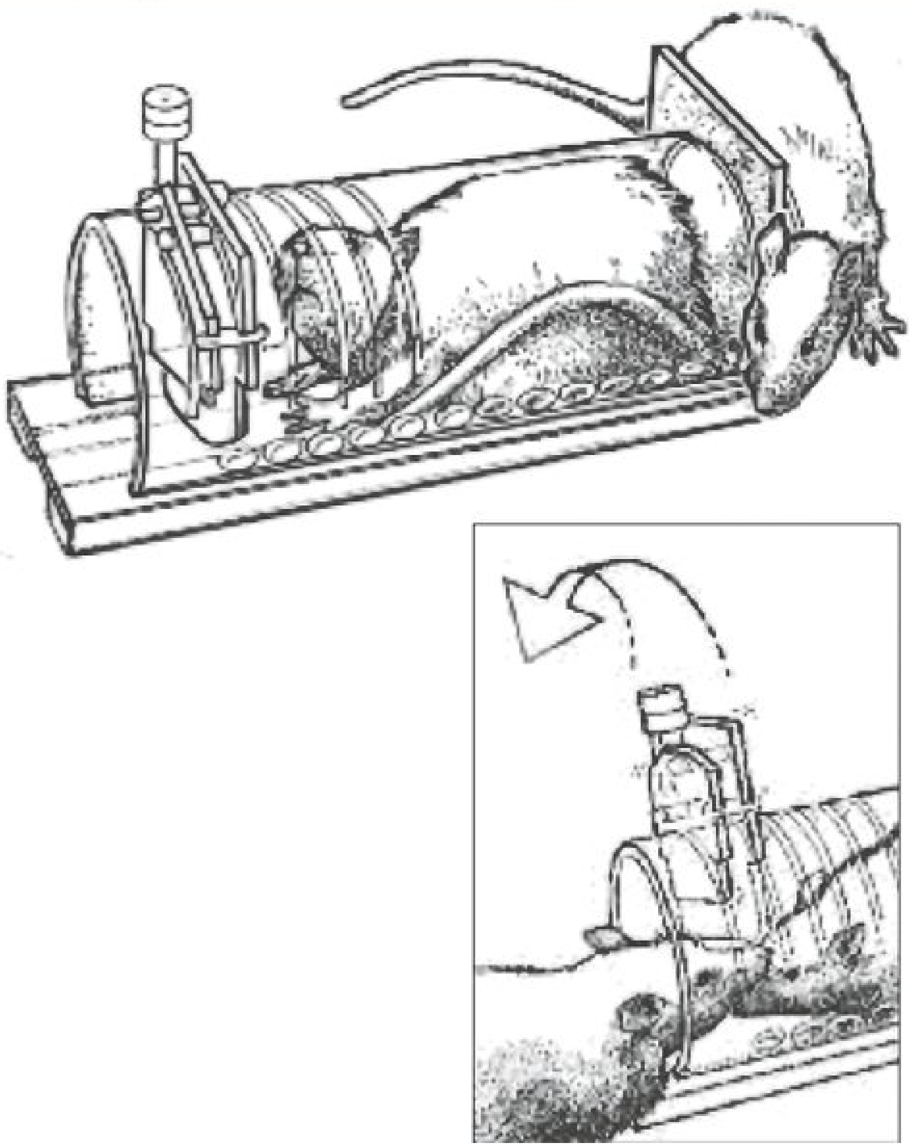


Figure 10.15. **Freeing a trapped partner.** The experimental setup for the experiment on empathy in rats. Top: one rat was trapped in a canister with a door that was locked and could only be opened from the outside. Bottom: the other rat opened the door, releasing the trapped individual.

Control trials found that the free rat did not open up the door if the canister was empty, nor when the canister contained a model (toy) rat (no distress calls). If the experimental setup is slightly modified and a second canister containing chocolate placed behind a locked door is added, the free rat often opens the door to the canister with the trapped rat first, before opening the door to the chocolate. Once the door to the canister with the chocolate is then opened, the rats typically share the food (Bartal et al., 2011).

The proximate underpinnings of empathy have been examined in the monogamous prairie voles (*Microtus ochrogaster*) that we have discussed in numerous earlier chapters. Larry Young and team looked at consolation behavior in this species, which they described as “a common empathetic response seen in humans . . . an increase in affiliative contact in response to and directed toward a distressed individual, such as a victim of aggression, by an uninvolved bystander, which produces a calming effect" (Burkett et al., 2016). At the time of their experiment, consolation behavior had been documented in groups described as having "advanced cognitive abilities"—for example, primates, canids, elephants, and corvids, but not in rodents.

Pairs of prairie voles were tested: each pair had lived together before trials, and each pair contained a "demonstrator" and an "observer." At the start of a trial the demonstrator was placed into a cage and was either exposed to a stressor—five tones paired with foot shocks—or not exposed to the stressor. The observer was in a separate cage and had no direct knowledge of which treatment the demonstrator had been exposed to. When the demonstrator and observer were reunited, the observer groomed the stressed demonstrator significantly more than it groomed a nonstressed demonstrator (this was the case both when pairs were males and when they were females). This grooming calmed the demonstrator: demonstrators that were groomed had reduced levels of anxiety-related behaviors compared to a separate control in which stressed demonstrators were not exposed to observers after being stressed. When these same experiments were repeated using polygymous meadow voles, who display much less prosocial behavior than the meadow voles, no consolation behavior was found.

In an interesting follow-up experiment, Young and his team found that when a demonstrator prairie vole had been stressed and then reunited with an observer, but a see-through partition separated the two voles so that no contact was allowed, demonstrators had higher levels of plasma corticosterone than when the partition was absent. In addition, observers who could not console demonstrators when the partition was present also had higher levels of plasma corticosterone, suggesting an empathetic response to being unable to help the demonstrator.

In humans, empathy is sometimes linked to activity associated with oxytocin, and Young and team examined whether this might also be the case for the prairie voles (Andari et al., 2010; Domes et al., 2007). They did this a number of ways, including injecting observer voles with an oxytocin antagonist before their interactions with stressed demonstrators. After such injections, demonstrator rats failed to display consolation behavior, suggesting that oxytocin is one of the underlying proximate factors linked to empathy in prairie voles.

Birds were exposed to the P matrix, then to the M matrix, and then again to the P matrix, and on any given day a pair of birds would play these games with each other more than 200 times. Clements and Stephens found that, regardless of whether the jays could see each other or not, birds defected in the first P matrix, cooperated in the M matrix, and reverted to defection the second time they encountered the P matrix (see Figure 10.17). Blue jays appeared to cooperate via byproduct mutualism and not reciprocity, even when a payoff matrix (the prisoner’s dilemma) that, in theory, should promote reciprocity was presented.

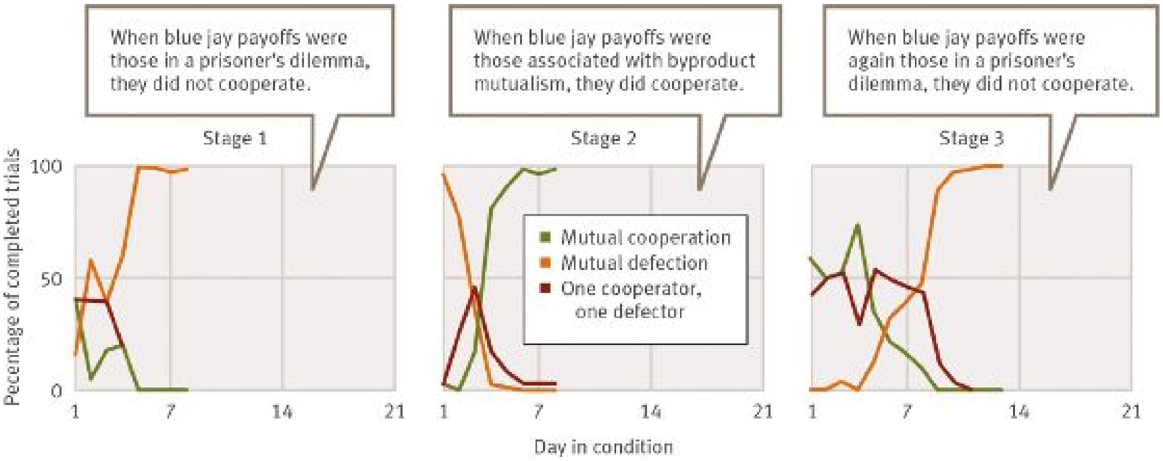


Figure 10.17. Byproduct mutualism and blue jays. Blue jays were tested in a three-stage experiment: stage 1 = prisoner’s dilemma, stage 2 = byproduct mutualism, and stage 3 = prisoner’s dilemma. Jays cooperated when the payoff matrix matched byproduct mutualism, but not when it matched the prisoner’s dilemma. *(Based on Clements and Stephens, 1995)*

Byproduct Mutualism and House Sparrow Food Calls

House sparrows (*Passer domesticus*) produce a “chirrup” call when they discover a food resource (Summers-Smith, 1963). This call attracts other birds to a newly discovered bounty, and may involve cooperative signaling. To examine just what type of cooperation, Marc Elgar examined whether the chirrup vocalization brought conspecifics to a newly discovered food source, and if so, under what conditions (Elgar, 1986).

Elgar recorded chirrup calls at artificial feeders containing bread that was either divisible among sparrows or that was just enough food for a single bird. He uncovered some evidence that those sparrows arriving at a patch of food first (labeled as “pioneers”) were more likely to produce chirrup calls than other sparrows. Elgar hypothesized that if the food items were small enough that sparrows could pick them up and fly away, they would do so without producing chirrup calls—and sparrows did just that. Chirrup call rates were higher when the food resource was large and divisible (Figure 10.18). It may be that since sparrows needed to remain at a feeder with large food items, and it is safer to do so in the company of other sparrows, the benefits associated with predator detection outweighed the costs of inviting other foragers to share food at the site. If that is the case, the payoffs associated with chirrup calls would match those of byproduct mutualism.

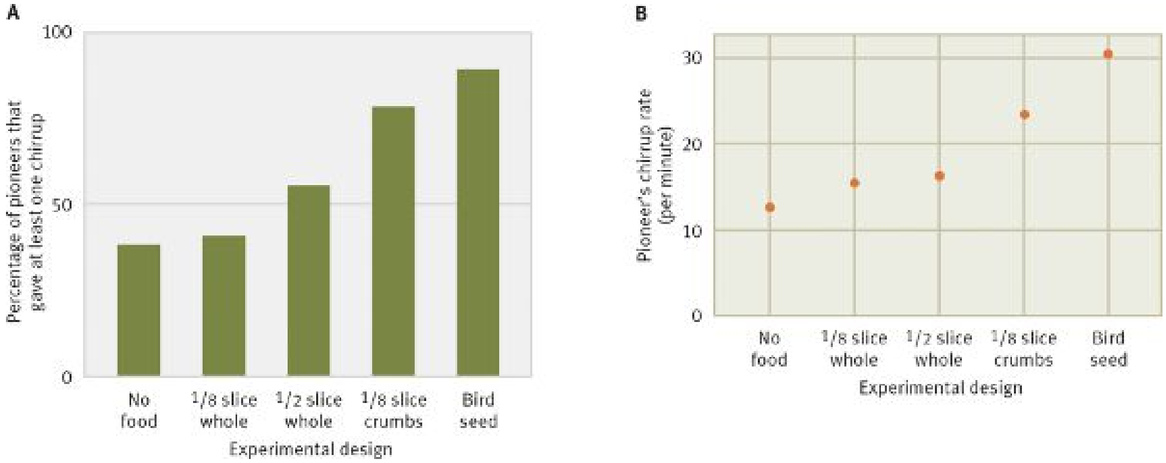


Figure 10.18. Food size and food calls in sparrows. (A) When resources were more divisible the first bird to arrive at a food patch (labeled the pioneer) was more likely to give "chirrup calls" that attracted other birds. (B) Pioneers also called more often when food was easily divisible. *(Based on Elgar, 1986, p. 171)*

PATH 3: GROUP SELECTION

A third path to cooperation is trait-**group selection**, where a trait group is defined as a group in which all individuals affect one another's fitness (Sober and Wilson, 1998; D. Wilson, 1980; D. Wilson and Wilson, 2007).

The crux of modern trait-group selection models is that natural selection operates at two levels: within-groups and between-groups. Within-group selection acts *against* cooperators and altruists, because such individuals, by definition, pay some cost that others do not. Selfish types—those that do not cooperate—are always favored by within-group selection, since they receive any benefits that accrue because of the actions of cooperators and altruists, but they pay none of the costs.

Between-group selection favors cooperation when groups with more cooperators outproduce other groups—for example, by producing more total offspring or being able to colonize new areas faster. Consider the case of alarm calls. Alarm callers pay a cost within groups, as they may be the most obvious target of a predator homing in on such a call. But their sacrifice may benefit the group overall, as other individuals—

including other alarm callers, as well as those that don't call—are able to evade predators because of the alarm calls, and groups with many alarm callers may outproduce groups with fewer cooperators. For such group-level benefits to be manifest, groups must differ in the frequency of cooperators within them, and groups must be able to "export" the productivity associated with cooperation (for example, more total offspring, faster colonization of newer areas, and so on).

Group selection models remain controversial. Many animal behaviorists argue that all group selection models can be mathematically translated into selfish gene models. They posit that group selection models simply partition the effect of a trait into within- and between-group components, but that if you sum up the effects over all groups you get the same solution as a selfish gene model would produce (Dawkins, 1979; Queller, 1992). This is correct. One can always take a group selection model and translate the mathematics into a classic natural selection model that operates at the level of only the gene. Such mathematical equivalence, however, does not necessarily mean that group selection models do not sometimes shed new light on animal behavior, as trait-group selection models necessarily focus attention on what is happening within and between groups, whereas selfish gene models do not do so as readily (Dugatkin and Reeve, 1994): under certain conditions, group selection models may spur investigators to construct experiments that would not be obvious if they were using selfish gene models.

Within- and Between-Group Selection in Ants

Cooperative colony foundation occurs in a number of species of ants where cooperating co-foundresses are *not* closely related (Bernasconi and Strassmann, 1999; Holldobler and Wilson, 1990). Cooperative colony foundation has been studied in the desert seed harvester ant *Messor pergandei*. Let's partition the costs and benefits associated with such colony foundation into between-group and within-group components. With respect to between-group factors, adult *M. pergandei* are very territorial, and "brood raiding"—in which brood captured by ants from nearby colonies are raised within the victorious nests, and colonies that lose their brood in such interactions die—is seen among starting colonies in the laboratory (Ryti and Case, 1984; Wheeler and Rissing, 1975). Within groups, all co-founding queens in a nest assist in excavating their living quarters, and each produces approximately the same number of offspring, so there is a positive correlation between the number of cooperating foundresses in a nest and the number of initial workers (brood raiders) produced by that colony (Rissing and Pollock, 1986, 1991; Table 10.5). Nests with more cooperating foundresses and so more workers, are more likely to win brood raids (Rissing and Pollock, 1987).

Table 10.5. Cooperating co-foundresses. In the ant *Messor pergandei*, unrelated queens (here W, Y, B, and O) co-found nests. The reproductive output of queens within a nest tends to be approximately equal. Differences in all three measures across the four queens were not statistically significant. *(From Rissing and Pollack, 1986)*

		Percentage laid by			
Nest no.	**No. of eggs**	W	Y	B	O
1	22	—	32	41	27
2	24	38	25	38	—
4	32	41	28	25	6
5	11	45	—	55	—
8	29	28	34	38	—
9	44	34	16	27	23
10	36	31	19	50	—
11	21	43	—	24	33
15	29	38	—	21	41

Until workers emerge, queens within a nest do not fight, and no dominance hierarchy exists (Figure 10.19). But, after workers emerge and the between-group benefits of having multiple foundresses are already set in place with the presence of brood raiders, all that remains is within-group selection, which favors being noncooperative. It is at this point in colony development that queens within a nest often fight to the death.

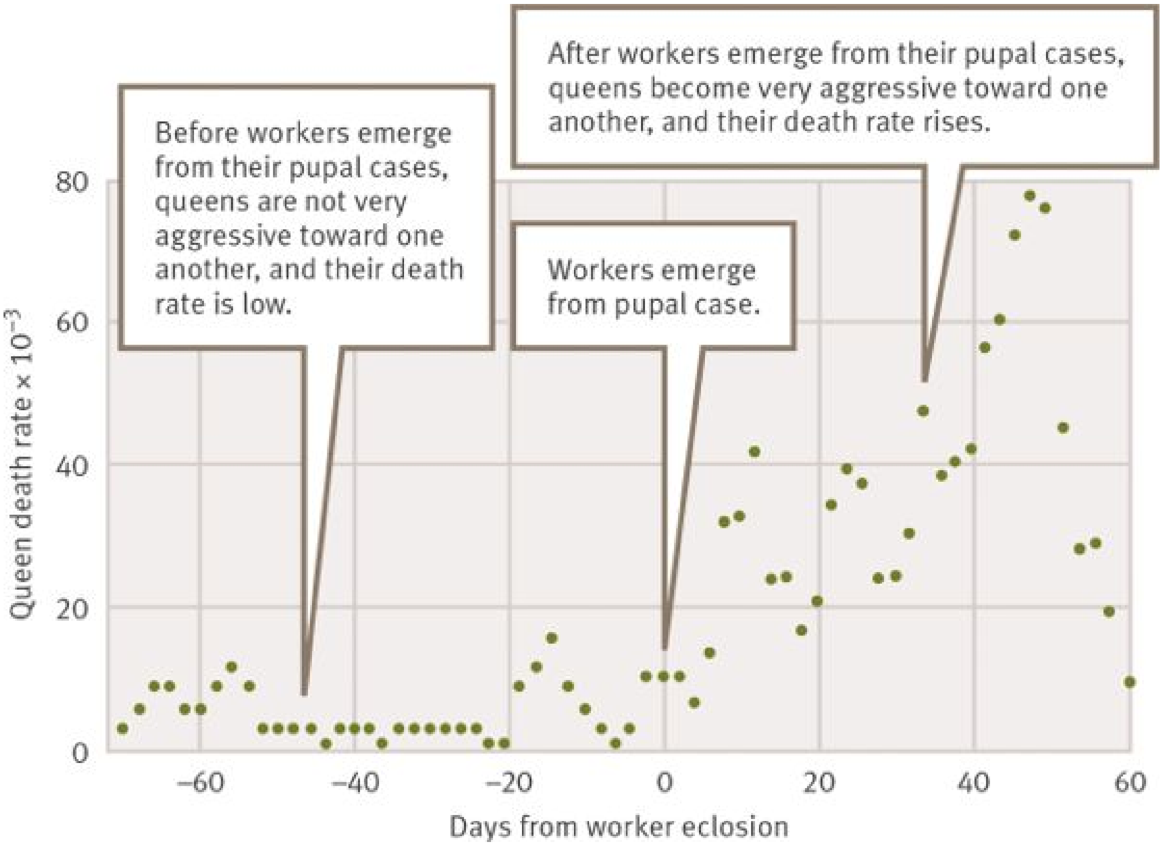


Figure 10.19. From cooperation to aggression in *Messor pergandei*. Queen-queen aggression and queen death rate rise as colonies move to the stage of colony development at which workers emerge from pupae and then begin helping. *(From Rissing and Pollock, 1987)*

The scenario depicted above is ideal for studying group selection models of cooperation, as group selection requires the differential productivity of groups based on some trait. In the case of *M. pergandei*, the trait is queen-queen cooperation. Such cooperation is selected against *within* groups because cooperators pay a cost—the energy to excavate the nest—not paid by noncooperators. But cooperation may be selected for between groups, because groups with many cooperators differentially survive brood raiding—the between-group component of group selection (also see Shaffer et al., 2016, for more on this).

One problem with the *M. pergandei* studies we have discussed is that field experiments contrasting single and double foundress associations in *M. pergandei* found that double foundress nests do not outlive single foundress nests, and no brood raiding at all was observed, calling into question all of the elements necessary for group selection to operate in the wild (Pfennig, 1995).

One of the stronger cases of group selected cooperation comes from Steve Rissing's work on the ant, *Acromyrmex versicolor* (Rissing et al., 1989). As with *M. pergandei*, in *A. versicolor*, nests are founded by multiple unrelated queens, there is no dominance hierarchy among queens, all queens produce workers, brood raiding among starting nests appears to be common, and the probability of the nest surviving the brood-raiding period is a function of the numbers of workers produced. *A. versicolor* differs from *M. pergandei*, however, in that *A. versicolor* queens forage after colony foundation (Figure 10.20).

Figure 10.20. Extreme cooperation by foraging queen. In the ant *Acromyrmex versicolor*, a single queen (shown in the blowup circle) is the forager for a nest. Such foraging is very dangerous, but all food collected is shared among (unrelated) queens.

Foraging involves bringing back materials that increase the productivity of the nest's fungus garden, the food source for the colony. Increased predation and parasitization make foraging a dangerous activity for a queen. Once a queen takes on the role of forager, she remains in that role.

After a queen becomes the sole forager for her nest, all queens share equally in the food produced by the fungus garden—the forager assumes both the risks and the benefits of foraging, while the other queens in her nest receive the benefits but do not pay the costs (Table 10.6). But cooperation—in this case, cooperation on the part of the forager—within nests appears to lead to more workers. The number of workers affects the probability that a given nest will be the one to survive the period of brood raiding, providing the between-group component necessary for cooperation to evolve (Cahan and Julian, 1999; Rissing et al., 1989; Seger, 1989). Indeed, when Rissing and his team experimentally blocked the foraging queen's opportunity to leave the nest and gather food, none of the remaining queens became the new forager, causing failure of the fungus garden and a decrease in the number of workers produced by the remaining queens (Pollock et al., 2004; Rissing et al., 1996).

Table 10.6. Cooperation among *Acromyrmex versicolor* queens. In *A. versicolor*, unrelated queens co-found nests, and a single queen takes on the dangerous role of forager for everyone in the nest. Reproductive success within nests is approximately equal in foragers and nonforagers. *(Based on Rissing et al., 1989)*

	Forager	**Nonforager**
Mean number of primary eggs	8.6	8.5
Mean primary egg length	0.52	0.54
Mean number of total eggs	20.37	18.94

We could, of course, analyze the cooperation described in both ant examples without using group selection models, and instead rely on classic models that do not decompose selection into within- and between-group selection, and we would come to the same conclusions we arrived at from the trait-group perspective. That said, in both *M. pergandei* and *A. versicolor*, we see systems in which population biology and demographics may match those that are postulated in trait-group models. The multiple nests, intense competition between nests, and multiple unrelated foundresses in these species make them ideal for an analysis at both the within-group and between-group levels (Box 10.5).

Box 10.5. SCIENCE AT WORK

What is the research question? Do group selection models of cooperation explain foraging behavior in the desert leafcutter ant, *Acromyrmex versicolor*?

Why is this an important question? Group selection models of cooperation have been a matter of heated debate in animal behavior circles for decades.

What approach was taken to address the research question? The within-colony costs of foraging behavior for a single queen forager in an *A. versicolor* starting colony was examined in relation to potential colony-level benefits associated with brood raiding behavior.

What was discovered? The costs and benefits associated with a single queen forager were consistent with predictions from a group selection model of cooperation in *A. versicolor*.

What do the results mean? Although the results of this study could be recast in a more traditional individual selection framework, they suggest that analyzing costs and benefits within and between groups can, in some circumstances, be fruitful.

Coalitions

Many examples of cooperative behavior involve dyadic, or pairwise, interactions. In these **dyadic interactions**, two individuals interact in such a way that the fitness of each is affected by both its own action and the action of its partner. Cooperation also occurs in **polyadic interactions**—interactions that involve more than two individuals (see Box 10.6). One example of such polyadic cooperative interactions is **coalition** behavior, defined as a cooperative action taken by at least two individuals or groups against another individual or group. When coalitions exist for long periods of time, they are often referred to as **alliances** (A. Harcourt and de Waal, 1992).

Box 10.6. CONSERVATION CONNECTION

Cooperation, the Tragedy of the Commons, and Overharvesting

Work in fisheries conservation and management has the dual goal of protecting species and providing an economic good (food) to the public. Rules are often put into place about how much a person, a company, or even a country can fish in a given area. These rules are, in effect, attempts to make people act cooperatively and reduce the threat of overharvesting. Yet despite such attempts, overharvesting fish populations remains a serious problem, to the extent that many species are threatened to the level of extinction. Why is this overharvesting occurring, and what can be done to solve the problem (Kraak, 2011)?

To understand why people, companies, and countries don't abide by the rules regarding harvesting fish populations, consider what Garret Hardin has famously referred to as the "tragedy of the commons." Hardin asked his reader to consider: "a pasture open to all. . . . As a rational being, each herdsman seeks to maximize his gain. Explicitly or implicitly, more or less consciously, he asks, 'What is the utility to me of adding one more animal to my herd?'" (Hardin, 1968; Figure 10.22).

Figure 10.22. The tragedy of the commons in grazing animals. The tragedy of the commons focuses on the decisions that people have to make about how often they should allow their herd animals (here sheep) to feed on a “commons” pasture that is shared by all in the community. (*Photo credit: Dennis Frates / Alamy Stock Photo*)

Adding one additional animal—let’s say a goat—to his own herd grazing on communal land gives the herdsman one more animal that he can use or sell. The herdsman’s net benefit is one goat. But there is a cost: the overgrazing of the commons that is caused by the herdsman’s extra animal. This cost is shared by everyone who grazes a herd on the commons, so even if the cost is quite large, the part that the individual herdsman pays is only a small fraction of one goat. As a result, Hardin postulates: “The rational herdsman concludes that the only sensible course for him to pursue is to add another animal to his herd. And another. . . . But this is the conclusion reached by each and every rational herdsman sharing a commons. Therein is the tragedy. Each man is locked into a system that compels him to increase his herd without limit—in a world that is limited.”

In the case of harvesting fish, the commons area is the ocean, rather than the grazing pasture, and being altruistic means not overharvesting fish rather than not adding another grazing animal to the field. But the problem is the same as Hardin described, as is the potential end state—the tragedy when the commons falls. How to prevent this outcome is something that economists, biologists, psychologists, and many other researchers have been trying to achieve for decades. But they have done so with only moderate success, as the commons problem exists in many forms today.

Sarah Kraak has suggested that future work minimizing the tragedy of the commons in fish populations should focus on (1) eliminating the options for users (people who use commons) to “buy out” of being altruistic—that is, eliminating the possibility of buying the part of the commons allocated to some other person or institution; (2) eliminating anonymity in the commons, so that fishermen are known to one another and the general community, thereby allowing for reputations to emerge; (3) providing those in the commons with detailed information about the state of the resource (in this case, fish population size); and (4) face-to-face communication among those in the commons and those managing the commons (Kraak, 2011; Kraak et al., 2013)

Coalitions have been documented in many species (Harcourt and de Waal, 1992; Mesterton-Gibbons et al., 2011; Silk, 2007; Bissonnette et al., 2015; Figure 10.21). In most instances, coalitions involve an animal intervening in a dyadic, usually aggressive, interaction between other group members (Harcourt and de Waal, 1992; Bissonette et al., 2015). Often, the intervening individual is dominant to others involved in the interaction. In primates, interventions often take the form of the intervener coming to the aid of one of the two other individuals involved in an interaction (A. Harcourt and de Waal, 1992). This need not be the case, however, as intervening animals may break up an interaction between two others, without favoring either combatant (Dugatkin, 1998a,b; R. Johnstone and Dugatkin, 2000). This type of intervention has been found in various primate species (A. Harcourt and de Waal, 1992), as well as in the cichlid fish, *Melanochromis auratus* (Nelissen, 1985).

Figure 10.21. Coalitions. (A) Three male dolphins swim together, forming a long-term coalition (or alliance). Such male coalitions “herd” females. A female is seen to the left of the three males. Occasionally different alliances join together to form superalliances that compete against other such superalliances. (B) Pairs of male chimps often form coalitions to act against larger, more dominant, individuals. *(Photo credits: Richard Connor; Sergey Uryadnikov / Alamy Stock Photo)*

We will examine two examples of coalitions, one in primates and one in dolphins. In each of these cases, coalitions form among males to gain access to reproductively active females.

COALITIONS IN BABOONS

In baboons (*Papio anubis*), a male solicits coalition partners by rapidly turning his head between the solicited animal—the individual from which he is requesting aid—and his opponent, while at the same time threatening his opponent (Packer, 1977; Figure 10.23). Craig Packer documented ninety-seven solicitations that resulted in coalitions being formed. On twenty of these occasions, the opponent was consorting with an estrous female, and this increased the probability of a coalition being formed between the other two individuals (the enlisting male and the solicited male). On six of these twenty occasions, the estrous female deserted the opponent and went to the enlisting male, suggesting a benefit to coalition formation, at least for the enlisting individual.

Figure 10.23. Baboon coalitions. A male baboon (middle) involved in an aggressive interaction (with male on left) will often solicit others to aid him by turning his head in the direction of a potential coalition partner (male on right).

What are the costs and benefits to the animal that is solicited into a coalition? Joining a coalition can be costly to solicited individuals, who rarely obtain access to the estrous female but who risk being attacked by the opponent. Packer's results suggest that solicited males may overcome such costs by having the individual that enlisted them respond when they themselves need help (reciprocal coalitions). He found that baboons had favorite partners, and that favorite partners solicited each other more often than they solicited other group members, suggesting alliance formation.

Other studies of coalitions and their effect on access to reproductive opportunities in baboons have reported results similar to Packer's findings (Noe, 1986; Smuts, 1985), although in olive baboons (*Papio cyanocephalus anubis*), males that enlisted others in coalitions were no more likely than solicited males to obtain mating opportunities with females, and baboons that declined to join a coalition were again solicited in the future (Bercovitch, 1988).

ALLIANCES AND "HERDING" BEHAVIOR IN CETACEANS

Richard Connor and his colleagues have been studying alliance formation in bottlenose dolphins (*Tursiops truncatus*; Connor, 1992; Connor et al., 1992, 2001, 2011; Krutzen et al., 2003). Dolphins are notoriously difficult to track for long periods of time, and so while ethologists have generally thought dolphins had complex social networks in the wild, these have been very challenging to document. Connor and his colleagues examined pairs and trios of males forming close associations in the bottlenose dolphin population of Shark Bay, in Western Australia. He and his team found not one, but two types of alliances between male dolphins, both of which involved males "herding" reproductive females to keep them close (Connor et al., 2011).

"First-order" alliances among males involved pairs or trios acting in a coordinated fashion to keep females by their side, presumably as potential mates. Males in first-order alliances stay very close to one another, and alliances remain stable for many years. When females herded by an alliance of male dolphins try to swim away, as they often do, the males act in a very coordinated, aggressive manner to prevent the females from leaving (Connor et al., 1992).

What makes alliance formation in male dolphins unique is that different first-order alliances also join together in second-order superalliances and aggressively attack and bring females from other alliances into their alliance. Connor found that on two occasions, a defending alliance was assisted by another alliance in its attempts to maintain the female it was herding, creating a battle of second-order alliances. Second-order alliances have been documented in only one other species—humans—and Connor argues that the complex social interactions inherent in such superalliances, may, in part, help explain the evolution of large brain size in dolphins (Connor, 1992).

A Phylogenetic Approach to Cooperation

In conjunction with inclusive fitness theory (see chapter 9), the work we have examined so far provides the conceptual foundations for predicting when natural selection favors cooperation. We can now examine other aspects of cooperative behavior, including a phylogenetic component.

A phylogenetic analysis allows us to test whether cooperation is common in a taxa as a result of common ancestry and/or as a result of an independent selection regime in species in that taxa: such an analysis lets us ask whether one reason that cooperation is common within a taxa is that members of that taxa share a common ancestor that possessed this trait. Phylogenetic and adaptationist analyses of cooperation are not mutually exclusive. They can complement one another: phylogenetic history may help us understand whether cooperation *originated* in a common ancestor, while natural selection may be crucial in *maintaining* such cooperation.

PHYLOGENY AND COOPERATIVE BREEDING IN BIRDS

Edwards and Naeem examined cooperative breeding in birds from a phylogenetic perspective (S. Edwards and Naeem, 1993). Using 166 species of cooperatively breeding passerine birds in ninety-seven genera, they began by testing whether the distribution of cooperatively breeding species was random within the genera of passerine birds on which they focused. They built a computer simulation to predict what the distribution of cooperative breeding species would be if they distributed into genera simply based on the number of species in that genera. They found that the distribution of cooperative breeding species in nature differed significantly from the random distributions generated by computer simulations, with some genera having more than the expected number of cooperatively breeding species, and others less than the expected number (Figure 10.24).

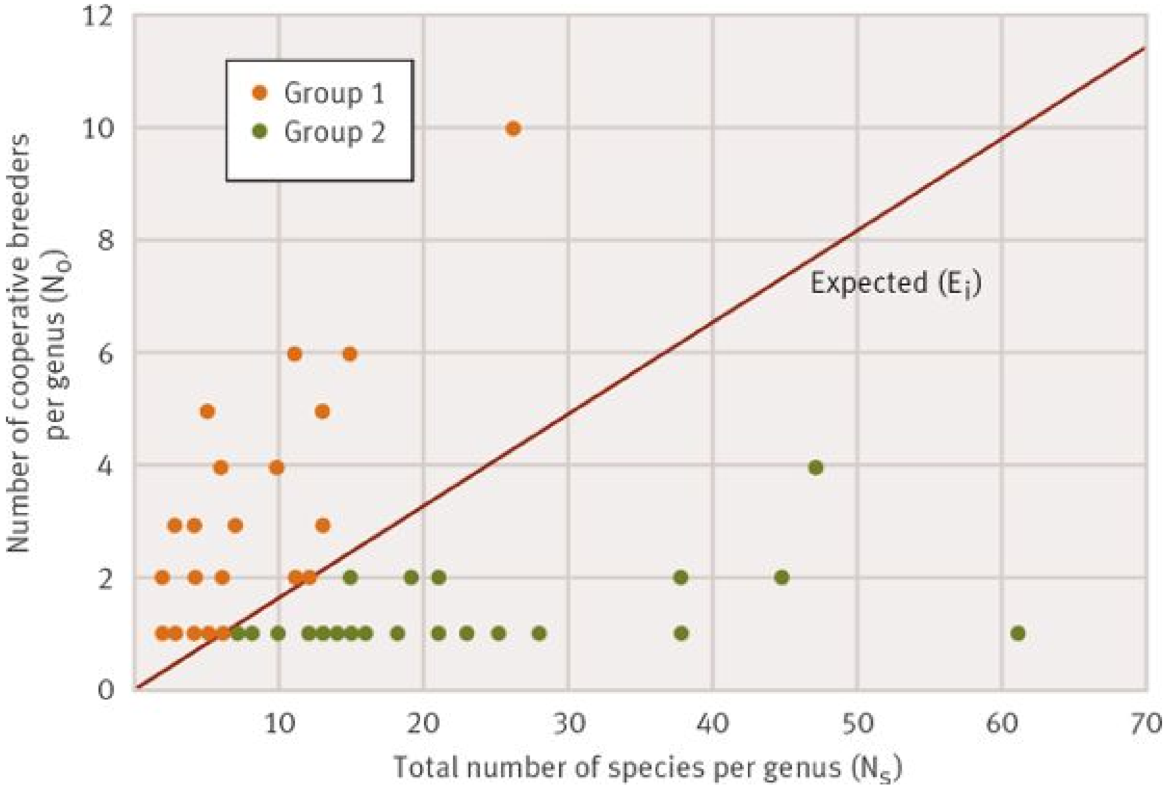


Figure 10.24. Phylogeny and cooperative breeding. The solid line represents the slope expected if the number of species with cooperative breeders per passerine genus (seventy-one) was proportional to genus size. In group 1, cooperative breeding was overrepresented; in group 2, cooperative breeding was underrepresented. *(Based on S. Edwards and Naeem, 1993, p. 761)*

Edwards and Naeem followed this analysis by using already published phylogenetic trees to examine the distribution of cooperative breeding. For example, their phylogenetic analysis of jays, Australian songbirds, Australian treecreepers, and New World wrens suggests that cooperative breeding may have arisen a very limited number of times in common ancestor(s) of modern-day species. Phylogenetic analysis suggests that in these groups of birds, modern species displaying cooperative breeding had a common ancestor that had this type of mating system, and modern species that do not display cooperative breeding had a common ancestor in which cooperative breeding was absent.

PHYLOGENY AND COOPERATION IN SHRIMP

Closely related species of *Synalpheus* shrimp, which live in sponge hosts, vary in the extent of cooperative behavior when defending their sponge hosts. In some species, “sentinel” shrimp respond to intruder danger by recruiting others to help defend their sponge host. The sentinel and recruits display an antipredator behavior called “snapping.” Phylogenetic analysis of thirteen species found three independent origins of cooperative defense in these shrimp (J. E. Duffy and MacDonald, 2010; Duffy et al., 2000; Hultgren and Duffy, 2011; Figure 10.25).

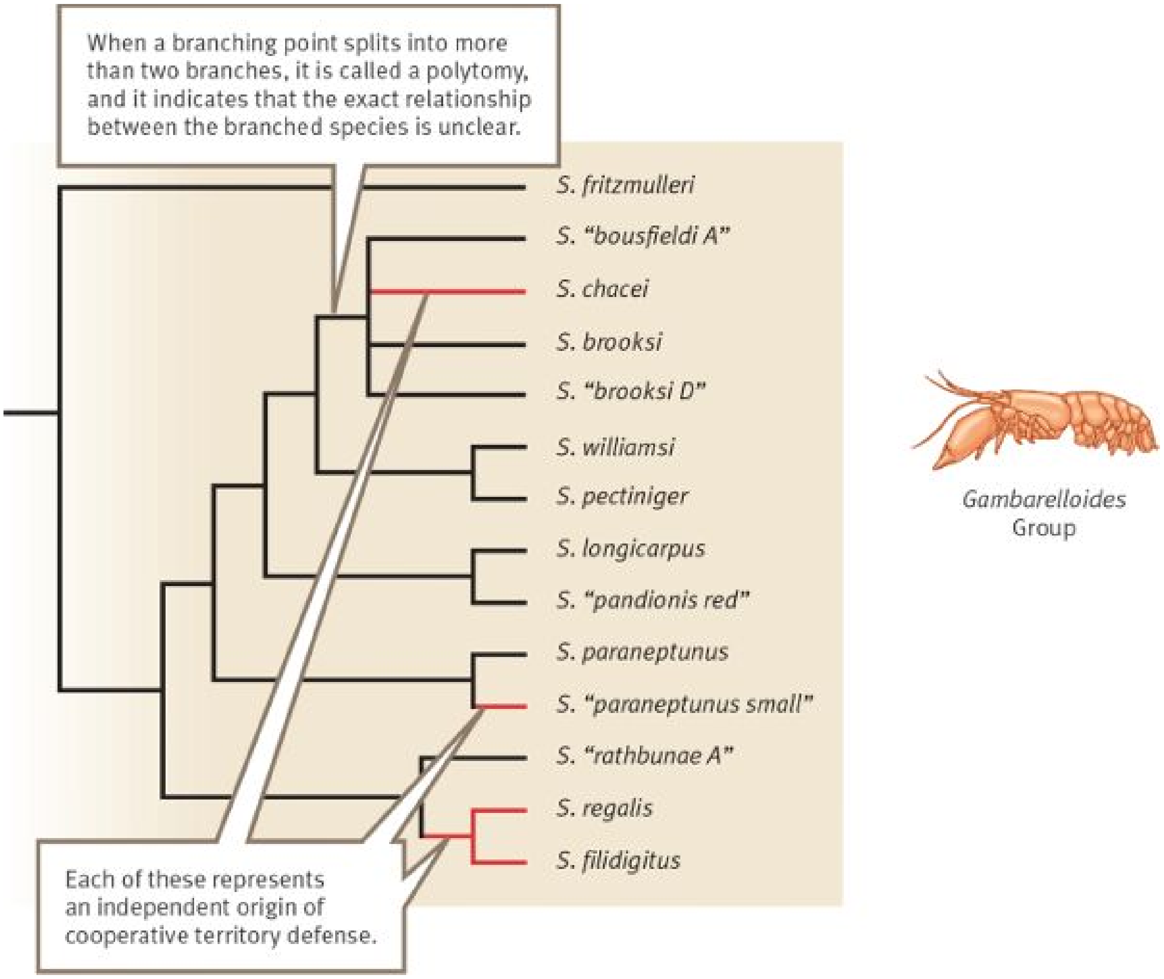


Figure 10.25. Multiple origins of cooperative behavior in shrimp. A phylogenetic analysis of closely related species of *Synalpheus* shrimp found three independent origins of cooperative territory defense (shown in red). The analysis was based on both morphological and molecular genetic data. *(From Duffy et al., 2000)*

PHYLOGENY AND COOPERATION IN SOCIAL SPIDERS

Most spiders build individual webs and hunt alone. But, there are a few species of social spiders—23 out of about 39,000 species—in which individuals display extreme levels of cooperation (Agnarsson et al., 2006). In these species, individuals build very large communal webs, jointly maintain these webs, cooperatively hunt for prey, and cooperate in raising brood born in their colonies (Figure 10.26).

Figure 10.26. Communal webs. A giant web built by a communal spider group. *(Photo credit: Bill Gozansky / Alamy Stock Photo)*

Ingi Agnarsson and his colleagues examined the phylogenetic history of sociality in spiders to estimate the number of times sociality had independently evolved in this group: of the twenty-three species in which sociality has been recorded, how many of these represented independent evolutionary events (Agnarsson et al., 2006, 2013; Blackledge et al., 2011)? Their analysis found that sociality had evolved either eighteen or nineteen different times in spiders—this was evident because, except for one instance, sociality was scattered across the spider phylogenetic tree, and not clustered in species with a common ancestor that displayed sociality. Eighteen or nineteen is a remarkably high number of evolutionary origins for cooperation. And, indeed, the twenty-three social species that have been documented today appear to represent only a small fraction of the number of social spider species that have existed through evolutionary time, as Agnarrson and his colleagues estimate that most of the spider species that evolved sociality have gone extinct.

This phylogenetic analysis of spider sociality has implications for other evolutionary/ behavioral questions. For example, it seems that cooperative nest maintenance, cooperative foraging, and other components of social spider life may be “evolutionary dead ends” in the sense that they are associated with high rates of extinction. Why might this be so? Agnarrson and his colleagues propose that although the short-term benefits of sociality in spiders—increased foraging success and so on—may allow for social spider species to initially prosper, sociality has a long-term cost, and data on *Anelosimus* spiders suggests this to be the case (Agnarrson et al., 2013). Social spiders are very inbred, and display very skewed sex ratios, with females dramatically outnumbering males, sometimes in a 10:1 ratio (Aviles and Maddison, 1991; Aviles et al., 1999, 2000; Johannesen et al., 2002; Lubin and Crozier, 1985; Roeloffs and Riechert, 1988; D. R. Smith and Hagen, 1996). In the long run, as inbreeding and skewed sex ratios become more and more pronounced, the probability of extinction may increase.

Interspecific Mutualisms

We have been focusing on cooperation among individuals from the same species. In this section we will examine evidence that *interspecific* cooperation (cooperation between individuals from different species) is important in shaping animal social behavior as well (Boucher, 1985; Bronstein, 1994; B’shary and Bronstein, 2004; Connor, 1995, 2010; Kawanabe et al., 1993; Leigh, 2010; J. Thompson, 1982). Such cooperation *between species* is usually referred to as **mutualism**.

ANTS AND BUTTERFLIES—MUTUALISM WITH COMMUNICATION?

In some species of butterflies and ants, a mutualistic relationship has evolved in which butterfly pupae and larvae produce a sugary secretion that ants readily consume, and ants protect the larvae from fly and wasp predators (Pierce et al., 2002; Quek et al., 2007). In such mutualistic relationships, individuals in both species are better off than they would be otherwise (Eastwood et al., 2006).

Naomi Pierce has been studying the mutualistic relationship between the imperial blue butterfly (*Jalmenus evagoras*) and the ant *Iridomyrmex anceps* (Figure 10.27). The benefits to both parties in this mutualism are substantial. Pierce and her colleagues found that when ants are experimentally removed from their environment butterflies have reduced rates of survival (Figure 10.28). While ants can survive in the absence of the nectar they consume from larvae and pupae, they obtain a significant portion of their nutrients from their butterfly larvae partners (Fiedler and Maschwitz, 1988; Pierce et al., 1987, 2002).

Figure 10.27. Butterflies and ants in a mutualistic relationship. In the mutualism between the butterfly *Jalmenus evagoras* and the ant *Iridomyrmex anceps*, butterfly larvae cannot survive in the absence of ants, and ants receive some of their food from the nectar produced by the butterfly larvae. *(Photo credit: © Mark Ridgway)*

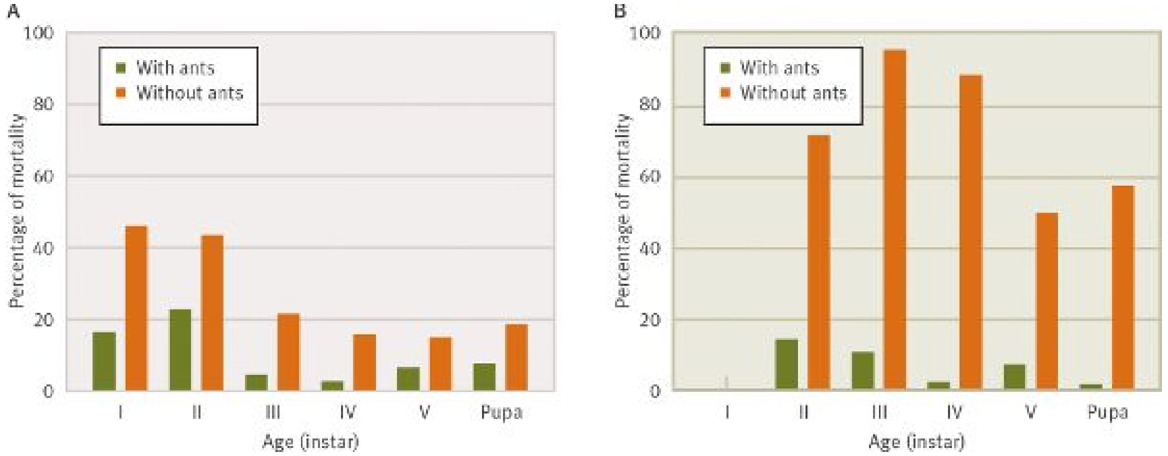


Figure 10.28. Butterflies need their ant partners. The probability of survival of *Jalmenus evagoras* larvae and pupae when predators were present was much higher when ants were present than when they were experimentally excluded at two Australian field sites: (A) Mt. Nebo and (B) Canberra. *(From Pierce et al., 1987, p. 242)*

This ant-butterfly mutualism involves costly investment in the other by both parties. Larvae raised in a predator-free and ant-free laboratory environment pupate later at a much larger size (Pierce et al., 1987), as they are able to modify the amount of nectar they secrete and use the nutrients normally distributed to ants for their own development. Size in both male and female *J. evagoras* is correlated with reproductive success. Pupating early represents a significant cost because smaller body size as a result of earlier pupating leads to reduced reproductive success in the butterflies (Elgar and Pierce, 1988; G. Hill and Pierce, 1989; L. Hughes et al., 2000). Although the costs to ants for protecting butterfly larvae have not been quantified, it is likely an increased risk of detection by their own predators and parasitoids, as well the metabolic costs associated with defense (Pierce et al., 1987).

Travasso and Pierce examined whether there was interspecific communication in the *J. evagoras*/ *I. anceps* system. Ants are almost deaf when it comes to airborne sounds, but they are sensitive to vibrational cues and Travasso and Pierce hypothesized that vibrational cues may play a role in communication between these species (Travasso and Pierce, 2000). They found that sound production (stridulation) in larval *J. evagoras* was higher when ants were in the vicinity, suggesting that vibrational cues were used as a way to communicate with ant guards.

In a follow-up experiment, pairs of butterfly pupae were tested together: one of the pair was muted when the experimenters applied nail polish to its stridulatory organs. Then, using a preference testing device that included two bridges on which the ants could move about, Travasso and Pierce examined whether ants were more attracted to the muted individual in a pair or the individual that was free to produce vibrational communication. They found that ants demonstrated a preference for associating with the pupae that could (and did) produce vibrations, providing further evidence that vibrational communication plays a real role in this ant-butterfly mutualistic relationship (Figure 10.29).

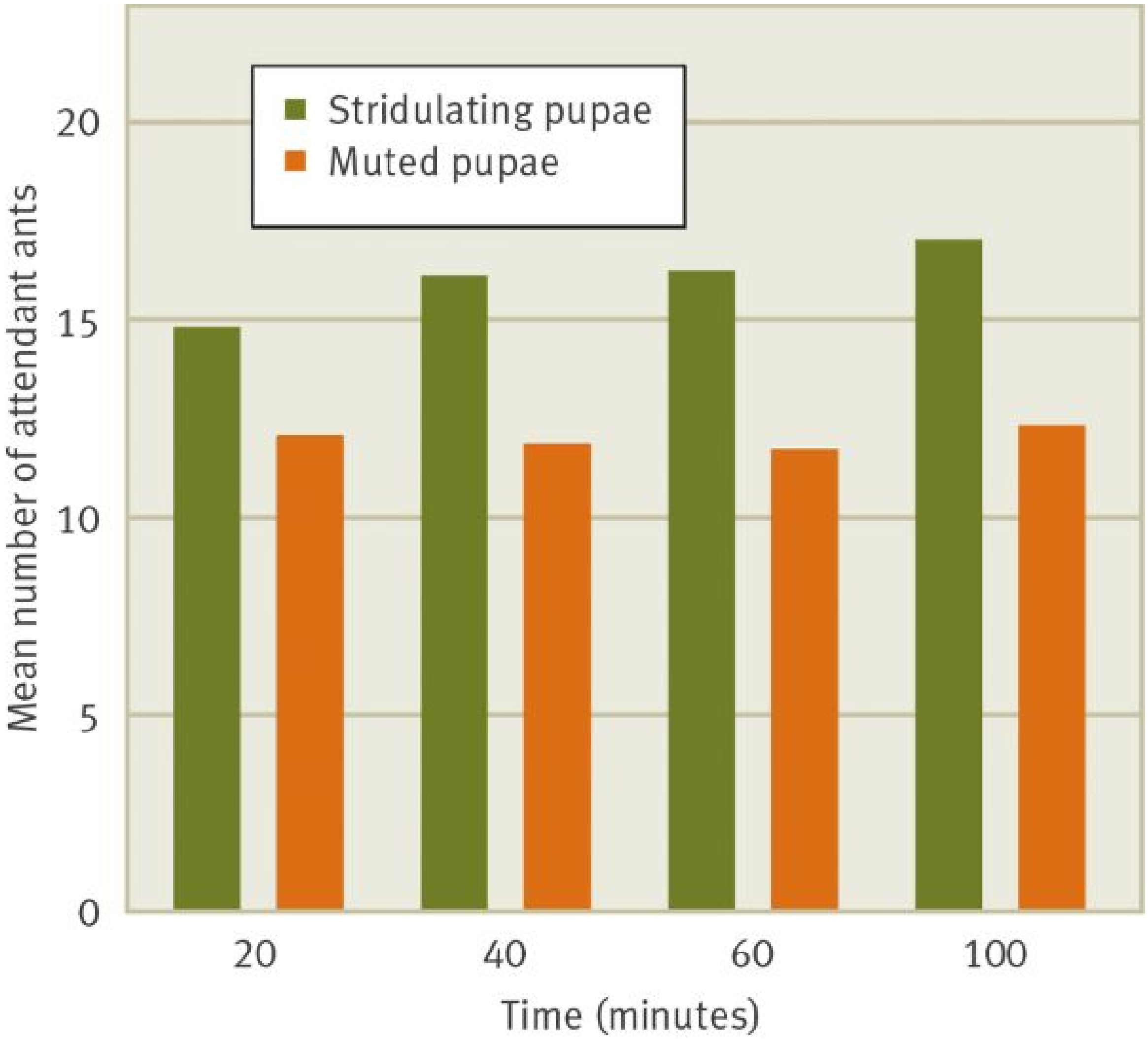


Figure 10.29. Stridulating attracts ants. Stridulating *J. evagoras* pupae attracted more ants than pupae that had been experimentally muted. *(Based on Travasso and Pierce, 2000)*

CORAL AND CORAL REEF FISH

A second mutualism in which communication plays an important role is that between the coral *Acropora nasuta* and *Gobiodon histrio*, a goby fish that lives in coral reefs. *Acropora nasuta* is a fast-growing coral species, whose branching topography lays the foundation for other coral species in reefs. Many coral reef fish species, including *G. histrio*, swim in the relative safety of reefs that include *Acropora nasuta*. When coral species go into decline, part of the decline is often the result of competition from seaweed species that secrete chemicals that inhibit coral growth. Because *G. histrio* consumes some of the seaweed species that outcompete corals, Danielle Dixon and Mark Hay examined whether *A. nasuta* recruits *G. histrio* when seaweed competitors (*Chlorodesmis fastigiata*) are close by (Dixson and Hay, 2012) (Figure 10.30).

Figure 10.30. **Coral-goby mutualism.** The coral *Acropora nasuta* (A) secretes a chemical that recruits gobies (*Gobidon histrio*) (B), who then forage on a seeweed (*Chlorodesmis fastigiata*) (C) that is a dangerous competitor to *Acropora nasuta*. *(Photo credit: Goby fish © Danielle L. Dixon)*

In a series of controlled field experiments, researchers found that compared to controls, *C. fastigiata* seeweed abundance declined by 30% when *G. histrio* was present, and damage caused by seaweed decreased by 70% as a result of predation by *G. histrio*. The researchers found that *G. histrio* were recruited to the vicinity of *A. nasuta* by a chemical signal secreted by *A. nasuta* when seaweed competitors were present, but not when they were absent. Through an experimental manipulation in which they could separate chemical cues from the *A. nasuta* and *C. fastigiata* species, they were able to determine that it was the chemical secreted by the coral, not the seaweed, that recruited the gobies to their vicinity.

The benefits to *A. nasuta* for recruiting *G. histrio* are clear, but what are the immediate benefits to the gobies foraging on the seaweed? Part of the answer is nutrients per se, but there are other food items in the environment, and to provide any help to *A. nasuta*, *G. histrio* need to pay the travel cost of moving from wherever they were before they were recruited. What other compensating benefits do they receive? The answer appears to be protection from their own predators. Even when they are not feeding on *A. nasuta*, *G. histrio* produce a mucus that contains some chemicals that are toxic to their predators (such chemicals are known as **allelopaths**). But the toxic effect of this mucus on *G. histrio* predators is magnified *after* they consume *C. fastigiata* (Box 10.7).

Box 10.7. SCIENCE AT WORK

What is the research question? Do corals recruit coral reef fish to inhibit growth of their competitors?

Why is this an important question? How mutualisms are maintained in nature, particularly the role that communication plays in such maintenance, is important to our understanding of the evolution of cooperation.

What approach was taken to address the research question? The costs and benefits of a potential mutualism between the coral *Acropora nasuta* and the coral reef goby *Gobiodon histrio* were examined in the field.

What was discovered? Gobies were recruited to the vicinity of the *coral* by a chemical signal secreted by the coral. The gobies reduced the prevalence of a seaweed competitor of the coral. By consuming the seaweed, the gobies not only obtained food, but as a result of incorporating allelopathic chemicals produced by the seaweed, the gobies were better protected from their own predators.

What do the results mean? A complex, communication-based mutualism exists between some corals and the coral reef fish that swim amongst them.

Interview with Dr. Hudson Kern Reeve

You've worked on cooperation in both wasps and naked mole rats. Isn't that a strange combination? How did you settle on these species?

Superficially, it is indeed a very strange combination—social paper wasps are aerial insects and naked mole rats are subterranean mammals! But there is a deep evolutionary connection between them that has stimulated my interest in both: I think that both manifest common principles of social evolution. The ways that the societies are organized are actually quite similar, with high reproductive skews (near reproductive monopoly by one or a few individuals) occurring among cooperating relatives. In both, the highest-ranking reproductive female behaviorally enforces her reproductive dominance.

I know you spend a good chunk of time engaged in fieldwork each year. Do you find that long hours of behavioral observation and tracking lead you toward new work on cooperation? Could you provide an example?

Yes, I think ultimately that all of the best evolutionary theories are rooted in field observation. For example, Bill Hamilton, the architect of kin selection theory, was a superb naturalist. My own view that social organisms, including social insects, engage in reproductive transactions (as embodied in "transactional skew theory") grew out of repeated observations of resource exchanges and *restraint* of aggression in social wasp colonies. Social wasps are constantly exchanging food and water and are curiously nonaggressive when each is laying an egg, as if they had the equivalent of a "social contract" over the division of resources, and, ultimately, reproduction. I don't think that I ever would have seriously considered the idea that social wasps are reproductively paying each other to cooperate, had I not watched nearly a thousand hours of videotapes of field colonies.

Perhaps more theory is devoted to the evolution of cooperation than to any other issue in ethology. Why do you think that is?

I think that it has attracted a great deal of theoretical interest because it represents an evolutionary puzzle that even had Darwin fretting: How could an organism ever achieve a reproductive advantage by enhancing the reproductive output of another organism at the expense of its own? Hamilton provided one important answer to this puzzle through his kin selection theory. But this solution left unanswered the question of how cooperation could evolve between unrelated organisms—the latter, of course, has been the focus of intense theoretical activity. No doubt, we humans are especially interested in cooperation among nonrelatives, because each of us observes and experiences it regularly (to a varying degree!) every day.

Do you ever encounter the sense that some in the scientific community simply believe animals are not cognitively sophisticated enough to undertake acts of cooperation and altruism?

Yes, unfortunately, this is still a pervasive view. I think that this view is highly questionable. An organism needn't have a huge brain in order to engage in high-order social interactions. (I refer back to the notion that social wasps can have "social contracts" over reproduction!) I think that many behavioral biologists currently underestimate the cognitive complexity of their organisms, and the situation isn't helped by the fact that most theorists find it easiest to model simply behaving organisms!

In fact, there is now a major push to think of social organisms (especially social insects) as self-organizing robots whose rules of social interaction are very simple. I think that the latter view is headed in the wrong direction, because it ignores the evidence that organisms are highly conditional (context-specific) in their social behavior. I think that the evidence will eventually reveal that most social organisms are best viewed as proactive inclusive fitness maximizers; that is, they behave according to their cognitive *projections* of the inclusive fitness consequences of alternative social actions—and are not anything like toasters with a few settings determining simple input-output (stimulus-response) relationships. An inclusive fitness projector will always win evolutionarily over a self-organizing robot, provided that the neural machinery costs are not too great, and it is precisely the latter that I think has been systematically overestimated. Another way to put this is that the difference between a large brain and a small brain is not that the latter results in less sophisticated behavior; rather, the smaller brain still enables very sophisticated behavior, but over a somewhat narrower range of conditions (the ones regularly encountered by its bearers).

How have the fields of mathematical economics and political science contributed to our understanding of the evolution of cooperation?

The influence of economics and political science on evolutionary biology is immense, in large part because the theoretical apparatus of game theory was developed and refined in these two disciplines by people such as von Neumann and Nash and many others. Now, game theory is *the* central theoretical tool in understanding the evolution of social behavior.

Ironically, I think that evolutionary biology, now enriched by game theory, eventually will absorb human economics and political science as part of itself, because the latter two disciplines are just two subfields of the study of human social behavior, and we evolutionary biologists believe that the only satisfying theory of any organism's social behavior ultimately must be evolutionary! I am sometimes criticized for thinking that social wasps have reproductive transactions on a human economic analogy—surely that is too anthropomorphic! But this criticism gets things backward: If human economic behavior and wasp social behavior are evolved responses to similar selection pressures, then the connection between them is much deeper than a simple analogy; that is, if they really are manifestations of the same evolutionary principles, then anthropomorphism is the correct stance!

Do you think that the rules governing cooperative behavior are sometimes transmitted culturally in nonhuman primates?

There is growing evidence that this is so, and the important consequence is that, for such primates (and certainly for humans), we need to understand how cultural and biological evolution will interact. Do they proceed independently of each other, as some believe, or does one somehow entrain the other? This will be a hugely important focus for theoretical and empirical research in the years ahead.

How close are we to having a comprehensive understanding of animal cooperation? What, if anything, remains to be done?

My view is that we are still very far away. There is no shortage of theories, but I suspect the best ones have yet to be developed. What is most limiting are the data that cleanly discriminate among alternative theories. The latter is true in part because theorists have not always been clear about which predictions separate alternative theories and in part because empiricists have not always been good at deriving the right theoretical predictions for their study organisms (or for the contexts in which the latter are studied). This is not to sound pessimistic. On the contrary, it is an extremely exciting time to be a sociobiologist, as we are on the brink of beginning to solve many, many puzzles! In my view, what we cannot afford to lose is the conviction that these puzzles have general, elegant solutions.

Dr. Hudson Kern Reeve is a professor at Cornell University. His work integrates theoretical, empirical, and conceptual approaches to ethology to understand cooperation, kinship, aggression, and the distribution of reproductive opportunities within nonhuman and human groups.

SUMMARY

1. Cooperation typically refers to an *outcome* in which two or more interacting individuals each receives a net benefit from their joint actions, despite the potential

costs they may have to pay for undertaking such actions.

2. In addition to kin-selected cooperation, which we discussed in chapter 9, three paths to the evolution and maintenance of cooperation in animals have been identified: reciprocity, byproduct mutualism, and group selection. Game theory, as well as other, analyses have been used to model these three paths.
3. Work on cooperation via reciprocity has centered on what is known as the prisoner’s dilemma game and a strategy called tit for tat. Recent work in neuroeconomics has shed light on some proximate aspects of human reciprocity by examining which areas of the brain are associated with trust and how individuals respond to cheating by their partners in some economic games.
5. Cooperation via byproduct mutualism occurs when an individual would incur an immediate cost or penalty if it did not act cooperatively, such that the immediate net benefit of cooperating outweighs that of cheating.
6. Group selection models of cooperation have both a within- and between-group component. Within-group selection favors cheating, whereas between-group selection favors cooperation. Every group selection model can be recast as a classic model that averages over different groups, but produces exactly the same result as the corresponding group selection model.
7. Cooperation can also occur in interactions that involve more than two individuals. One example of this type of cooperation is coalition behavior, which is defined as a cooperative action taken by at least two individuals or groups against another individual or group.
8. Phylogenetic analyses can be used to help better understand the distribution of cooperation among related species.
9. In addition to cooperation between members of the same species, there is a great deal of evidence that *interspecific* cooperation—cooperation between members of different species—is also important in shaping animal social behavior.

DISCUSSION QUESTIONS

1. Read G. Wilkinson’s (1984) article “Reciprocal Food Sharing in Vampire Bats,” in *Nature* (vol. 308, pp. 181–184). Outline how Wilkinson was able to separate the effects of kinship and reciprocity in his study of vampire bats.
2. Run a small prisoner’s dilemma experiment with a few other students. In one group, using coins as payoffs, test pairs of subjects (who cannot communicate with each other in any manner) and tell them beforehand that they will play this game only once. In a second treatment, use pairs of subjects (who cannot communicate with each other), but inform them that they will play this game many, many times together, but do not tell them exactly how many times. In a third and fourth treatment, repeat treatments 1 and 2, but allow the subjects to communicate with each other before the game starts. What sorts of differences and similarities do you predict across treatments? What do the data suggest?
3. Respond to the following statement: Animals aren’t capable of human-like thought processes, and therefore they cannot be cooperating.
4. Why do you suppose that work on animal behavior and cooperation draws more attention from other disciplines, such as mathematics, political science, and psychology, than any other area in ethology? What might we learn about human cooperation from studies of animal cooperation? What sorts of things would be difficult to glean about human cooperation by studying animal cooperation?
5. Work from neuroeconomics has shed light on the neurobiology of cooperation in humans. What sorts of evolutionary questions come to mind when you read about these proximate studies in neuroeconomics?

SUGGESTED READING

Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*, 1390–1396. A classic paper that introduced many ethologists to using game theory to address cooperative behavior.

B'shary, R., & Bergmueller, R. (2008). Distinguishing four fundamental approaches to the evolution of helping. *Journal of Evolutionary Biology*, *21*, 405–420. A review of hypotheses about the evolution of helping behavior.

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Dugatkin, L. A. (1997a). *Cooperation among animals: An evolutionary perspective*. New York: Oxford University Press. A review of theoretical and empirical work on cooperation.

Packer, C. (1977). Reciprocal altruism in *Papio anubis*. *Nature*, *265*, 441–443. A highly cited study that was one of the first to experimentally study alliances and cooperation.

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11

Foraging

- CONSERVATION CONNECTION: Behavioral Traditions, Foraging, and Conservation in Killer Whales
- Foraging Innovation and Diversification in *Emberizoidea*
- Social Learning and Foraging

Interview with Dr. John Krebs

There's a famous dilemma in economics known as the traveling salesman's problem. If a salesman has to visit many cities on her route, and visit each one only once, what is the optimal path to take? Foraging animals face a dilemma. Suppose an animal has information on a series of unique and separate prey items in its environment: what is the optimal path to obtain as many of these items as possible? Are animals capable of fine-tuning the foraging strategies that lead them on such paths? Fujioka and colleagues set out to answer these questions by studying bat foraging behavior (Fujioka et al., 2016).

Because the solution to the traveling salesman problem gets very complicated if more than just a handful of prey items (or cities, in the more classic version of the model) are on the list, Fujioka's team simplified the question to this: suppose that two prey items are available to a foraging bat. Does the bat fly in a manner that is best suited to capture the first of these items, or do its foraging sorties take into account the best path to obtain both items? The researchers began by building a mathematical model that predicted what path a bat would take in each of these cases. They then allowed bats to forage in a large outdoor arena that had 32 microphones stationed around it, so that the echolocation clicks bats use to home in on prey could be recorded (Figure 11.1).

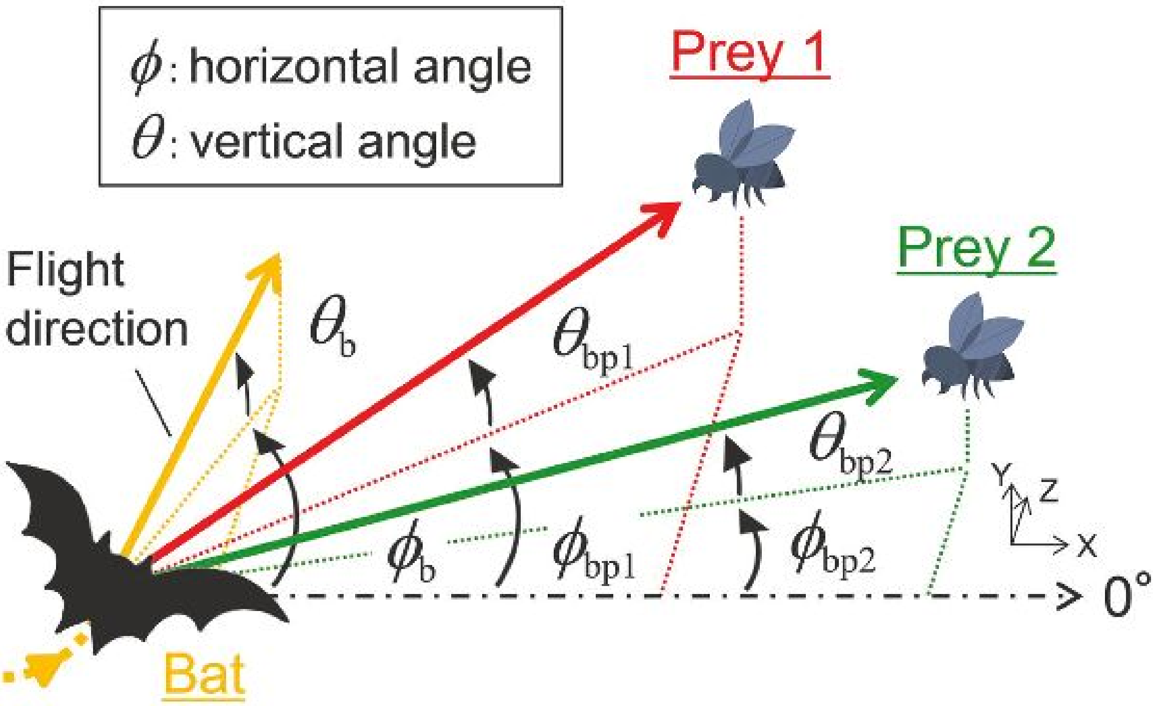


Figure 11.1. **Modeling flight paths in bats.** Researchers built a mathematical simulation that allowed them to predict how a foraging bat would behave if it flew along the optimal path to obtain prey item 1 versus the optimal path to obtain both prey items. ϕ and θ show horizontal and vertical angles, respectively. Here, we see the simple case of the flight path a bat would take if it was considering only prey 1 (ϕ_{bp1} and θ_{bp1}, the red arrow) or only prey 2 (ϕ_{bp2} and θ_{bp2}, the green arrow). *(From Fujioka et al., 2016)*

What Fujioka et al. found was that the bats tended to fly along paths that took into account how best to obtain both food items, not just the first item they targeted (Figure 11.2). This strategy seems to pay off, as bats that flew along a trajectory that was best suited to capture the first prey item, not both prey items, rarely were successful in obtaining that second prey item, while bats that foraged more like a traveling salesman planning ahead often obtained both prey items.

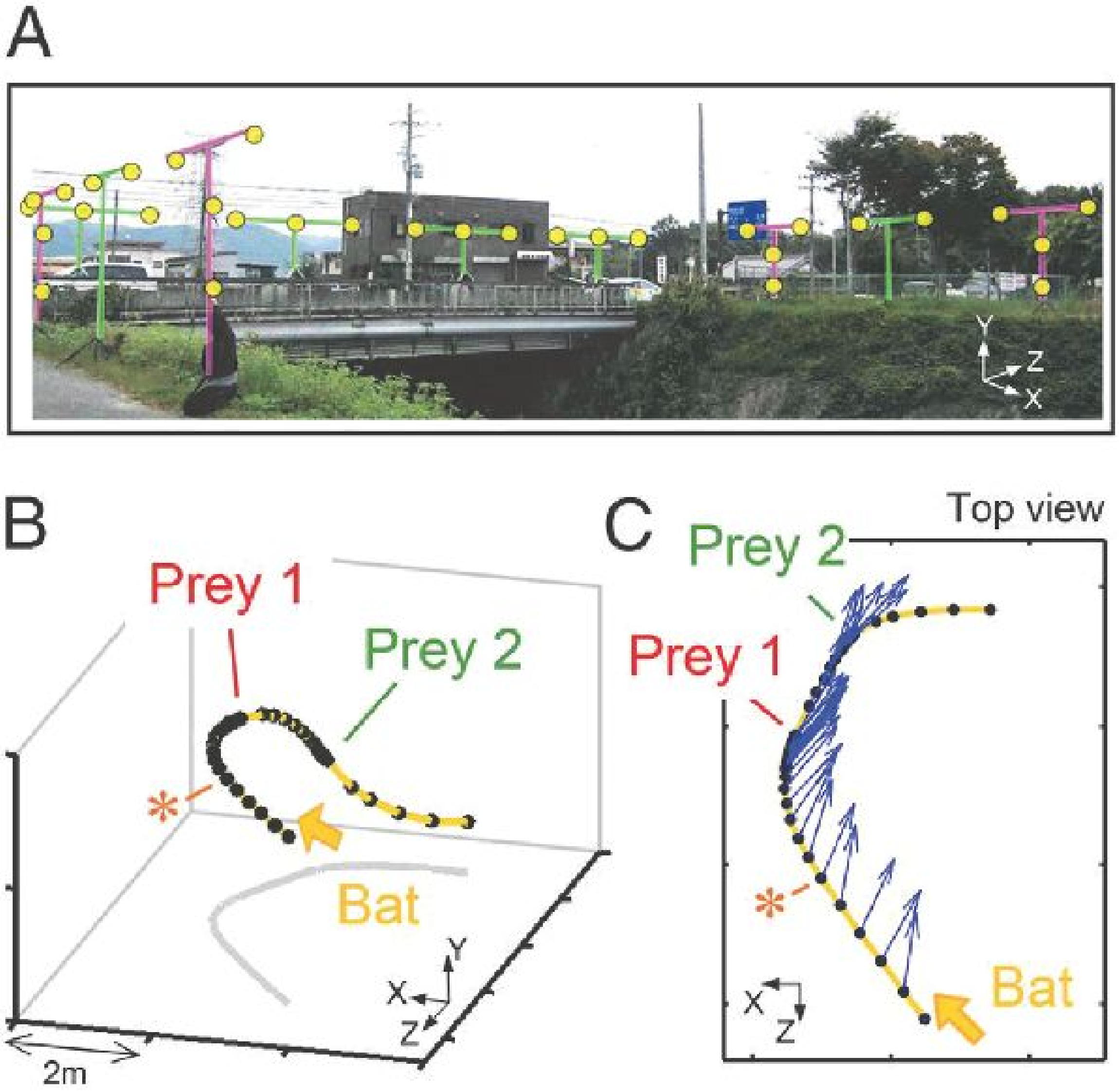


Figure 11.2. **Flight paths of bats.** (A) The outdoor enclosure used to test bat foraging behavior had 32 microphones (yellow circles) that allowed the researchers to track the echolocation behavior of the bats. (B, C) An example of the flight path of a bat attacking both prey items. Black dots (the yellow curve) represent locations where an echolocation click was recorded. *(From Fujioka et al., 2016)*

* * *

Searching for and consuming food—**foraging behavior**—makes up a large part of the time budget of many animals. Animals spend much of their time foraging, whether their food is seeds, nuts, and berries (as in granivores); plants (as in herbivores); living animals (as in carnivores); or dead animals (as in scavengers; Figure 11.3).

Figure 11.3. Foraging. Many animals spend much of their waking hours foraging. Here (A) a black bear and (B) a Richardson's ground squirrel are foraging. *(Photo credits: © Jacki Dickert www.lightdance.org; © Yvann KRUPA/Krupa-photo.fr)*

In this chapter, we will touch on the following foraging-related questions:

- How do animals know what food items look like?
- How does foraging theory predict where animals will forage and what they will eat?
- How do group social dynamics affect foraging?
- How are neurobiology, molecular biology, and endocrinology incorporated into the study of animal foraging behavior?
- What role does learning play in foraging decisions?

Finding Food and the Search Image

How do animals determine what a particular type of food looks (and smells, and feels) like? Although there are many ways we could answer that question, we will focus on what is called **search image** theory. First proposed by Luke Tinbergen in 1960, the idea behind a search image is that when animals encounter a prey type more and more, they form a representation of that target—the prey—and this representation or image becomes more and more detailed with experience, so that the forager becomes more successful at finding that type of prey (L. Tinbergen, 1960; White and Gowan, 2014).

Some researchers argue that foragers are keying in on one or two salient attributes of the prey (color, movement, pattern), while others argue that the search image formed is closer to some sort of representation of the entire prey item (Langley, 1996; Pietrewicz and Kamil, 1979; Reid and Shettleworth, 1992; Van Leeuwen and Jansen, 2010). In either case, animals are learning something relevant about their prey, and most animal behaviorists think that the use of the search image likely evolved as a response to the difficulty of finding cryptic prey, and assessing what is prey and what is not (Balda et al., 1998; Kamil and Balda, 1990; Zentall, 2005).

Optimal Foraging Theory

In this section, we will examine a class of mathematical models that are collectively known as **optimal foraging theory** (**OFT**; Kamil et al., 1987; Sih and Christensen, 2001; Stephens and Krebs, 1986; Stephens et al., 2007). These models often employ a mathematical technique known as optimization theory to predict various aspects of animal foraging behavior within a given set of constraints. Optimal foraging theory can be traced back to 1966 with back-to-back papers in the *American Naturalist*, one of which was written by Robert MacArthur and the other by John Emlen (J. M. Emlen, 1966; MacArthur and Pianka, 1966). These papers set the stage for ethological and behavioral ecological models that followed in abundance, especially during the 1970s (see Stephens and Krebs, 1986, for a review of these models).

Although there are many optimal foraging models in the animal behavior literature, we will examine three models, which address the following questions:

- What food items should a forager eat?
- How long should a forager stay in a certain food patch?
- How does variance in food supply affect a forager's decision about what food types to eat?

WHAT TO EAT

There are a large number of different items an animal could *potentially* consume, and so one of the most basic foraging problems faced by an animal is deciding which type of food items should be in its diet and which should be excluded (Charnov and Orians, 1973; Stephens and Krebs, 1986). For example, imagine that a forager can search for, and potentially consume, food types 1, 2, 3 . . . N. Should the forager eat all N types? Only one type? Two? and so on. To tackle this question, animal behaviorists have developed optimality models of prey choice. We will now examine the underpinnings of such an optimal foraging model and then review a test of it.

Let's consider the simplest possible case—a forager choosing between two different types of food (Figure 11.4). For carnivores, this might be a choice between two prey species; for granivores, the choice could be between two different types of seeds. Indeed, the choice a forager might have to make could even be between two different size classes (small or large) of the same food type.

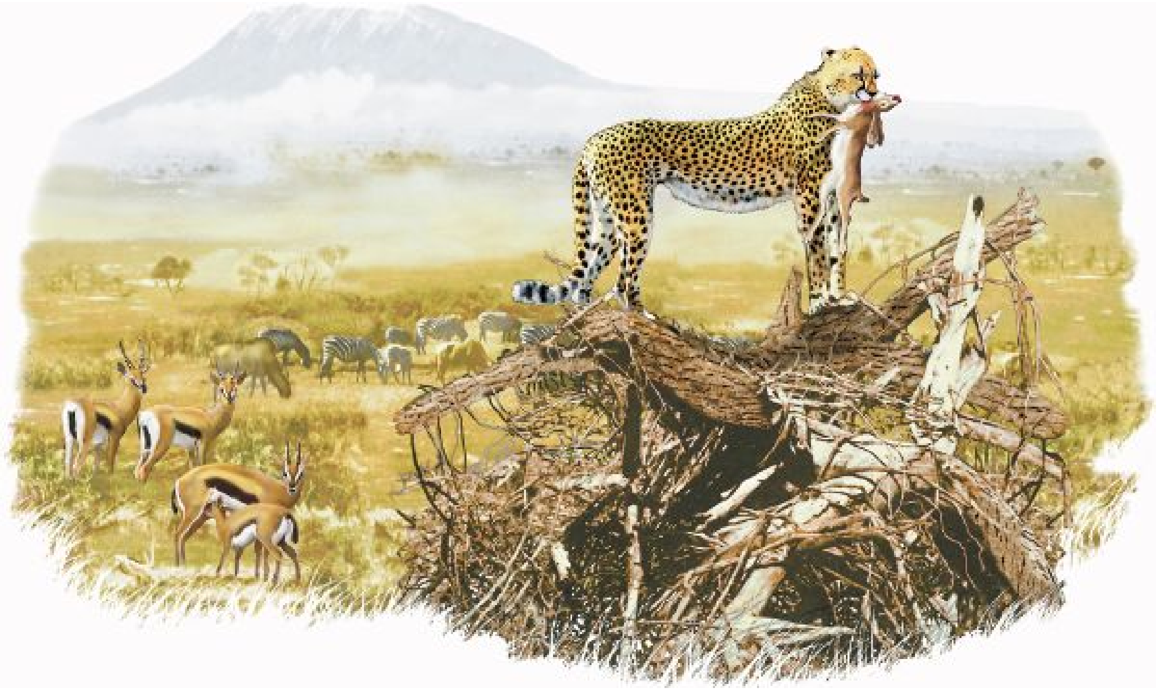


Figure 11.4. Foraging decision. A female cheetah (the forager) has killed a hare (the prey). In making the decision whether to take hares rather than some other prey into the diet, models of animal foraging behavior assume that foragers will compare the energy value (the amount of calories provided to the forager by consuming this prey), encounter rate (how often the prey is encountered by the forager), and handling time (time for the forager to kill and ingest the prey) for each putative prey. *(Based on Caro, 1994a)*

In the model, each prey item will have an energy value, encounter rate, and handling time associated with it. For example, one prey type might be encountered every three minutes (encounter rate); once encountered, it might take two minutes to kill and ingest (handling time) and provides the forager with 300 calories (energy value). The profitability of a prey item is defined as its energy/handling time. The greater the energy/handling ratio, the greater the profitability of a prey type.

We will assume that the prey type with the highest profitability—denoted as prey type 1—is always taken by a forager. If we only have two prey items, this means that the optimal diet problem boils down to two questions—should prey type 2 also be taken, and if it should, under what conditions? We begin by examining the assumptions that are made in the basic optimal prey choice model (Charnov and Orians, 1973; Krebs and McCleery, 1984).

The model assumes:

- Energy intake from prey can be measured in some standard currency (for example, calories).
- Foragers can’t simultaneously handle one prey item and search for another.
- Prey are recognized instantly and accurately.
- Prey are encountered sequentially.
- Natural selection favors foragers that maximize their rate of energy intake.

With these assumptions in place, a bit of mathematical analysis (Box 11.1) produces a fascinating, and somewhat counterintuitive, prediction. Recall that we are asking whether a forager that consumes prey 1 should add prey type 2 to its diet. What the model predicts is that the encounter rate with prey type 2—that is, how often a predator encounters this less profitable item—does *not* affect whether *that* item should be added to the diet. Instead, the model predicts that there exists a critical encounter rate with the *other*, more profitable, item (prey type 1)—if the encounter rate the predator experiences for prey 1 is above this critical value, only prey type 1 is taken and, if it isn’t, then both prey type 1 and prey type 2 are taken. The decision of whether to add prey type 2 to the diet is not dependent on the forager’s encounter rate with prey type 2; rather, it is related to its encounter rate with prey type 1. This basic prediction of optimal diet choice has been tested many times.

Box 11.1. MATH

The Optimal Diet Model

Consider a forager that consumes only two prey types. The forager must eat one of these prey items (or it will starve), so the question becomes: Which item does a forager always take, and under what conditions does a forager take both types of prey?

Let:

e_i = energy provided by prey type i

h_i = handling associated with prey type i

λ_i = encounter rate with prey type i

T_s = amount of time devoted to searching for prey

T = total time = time searching + handling time

We will assume that an animal always takes the prey type that has a higher e_i/h_i value (called the profitability of a prey type), and we will label this prey type as prey 1. The question is then whether a forager should take prey 1 alone, or should it take both prey 1 and prey 2 upon encountering them?

We begin by calculating the total energy (E) associated with prey 1 divided by the total time associated with prey 1.

For prey type 1:

$$\frac{\mathrm{E}}{\mathrm{T}}=\frac{T_s \lambda_1 e_1}{T_s + T_s \lambda_1 h_1} \tag{1}$$

The numerator is the total number of prey type 1 captured ($T_s\ \lambda_1$) multiplied by the energy value (e_1) of each prey, which totals to the energy associated with foraging for prey 1. The denominator sums the total search time (T_s) and the total handling time ($T_s\lambda_1 h_1$) associated with prey 1. This simplifies to:

$$\frac{\mathrm{E}}{\mathrm{T}}=\frac{\lambda_1 e_1}{1 + \lambda_1 h_1} \tag{2}$$

Now we can ask whether this value is greater than the E/T associated with taking both prey types. To find the E/T of taking both prey type 1 and prey type 2, we calculate the following:

$$\frac{\mathrm{E}}{\mathrm{T}}=\frac{T_s \lambda_1 e_1 + T_s \lambda_2 e_2}{T_s + T_s \lambda_1 h_1 + T_s \lambda_2 h_2} \tag{3}$$

The numerator represents the total energy obtained from prey 1 and 2, while the denominator adds together the total search time (T_s) and the total handling time for prey 1 and 2. This simplifies to:

$$\frac{\mathrm{E}}{\mathrm{T}}=\frac{\lambda_1 e_1 + \lambda_2 e_2}{1 + \lambda_1 h_1 + T_s \lambda_2 h_2} \tag{4}$$

Our question then boils down to when the following inequality is true:

$$\frac{\lambda_1 e_1}{1 + \lambda_1 h_1} > \frac{\lambda_1 e_1 + \lambda_2 e_2}{1 + \lambda_1 h_1 + \lambda_2 h_2} \tag{5}$$

When this inequality holds true, the predator should take only prey type 1. Otherwise the predator should take prey type 1 and prey type 2. Solving Equation 5 for λ_1:

$$\lambda_1 > \frac{e_2}{e_1 h_2 - e_2 h_1} \qquad (6)$$

From Equation 6 we can derive two predictions:

1. Once a critical encounter rate with prey type 1 is reached, it alone should be taken.
2. The decision about whether to take prey 2 does *not* depend on how common prey 2 is (that is, on prey 2's encounter rate). This can be seen in equation 6 by the absence of λ_2 from our inequality.

John Krebs and his colleagues tested the prediction of this optimal prey choice model in the great tit, *Parus major* (Krebs, 1978; Krebs et al., 1978). In a laboratory experiment, birds were placed in front of a moving conveyor belt (Figure 11.5). Krebs and his team used two different-sized pieces of mealworm as the two different prey item types, and they controlled: 1) the rate at which these two prey types were encountered by the birds, 2) the energy provided by both types of prey, and 3) the handling time associated with each size of mealworm. With knowledge of these parameters in hand, it was possible to use the model to predict when the birds should take only the most profitable prey types, and when they should take both types of prey.

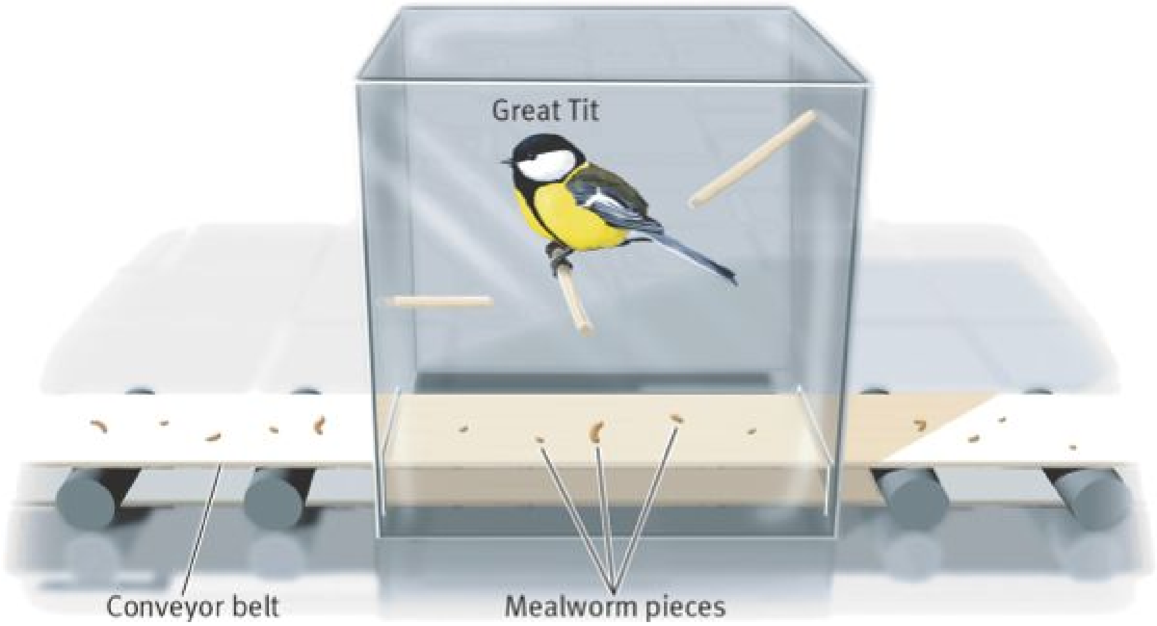


Figure 11.5. Great tit foraging. One early experiment testing optimal foraging theory had mealworms of different sizes presented on a conveyor belt to great tits.

Krebs and his team found support for one important prediction the model makes: it was the encounter rate of the most profitable prey, not the least profitable prey, that determined whether tits took the least profitable items (Figure 11.6). Similar results have been found in foraging experiments with bluegill sunfish (Werner and Hall, 1974).

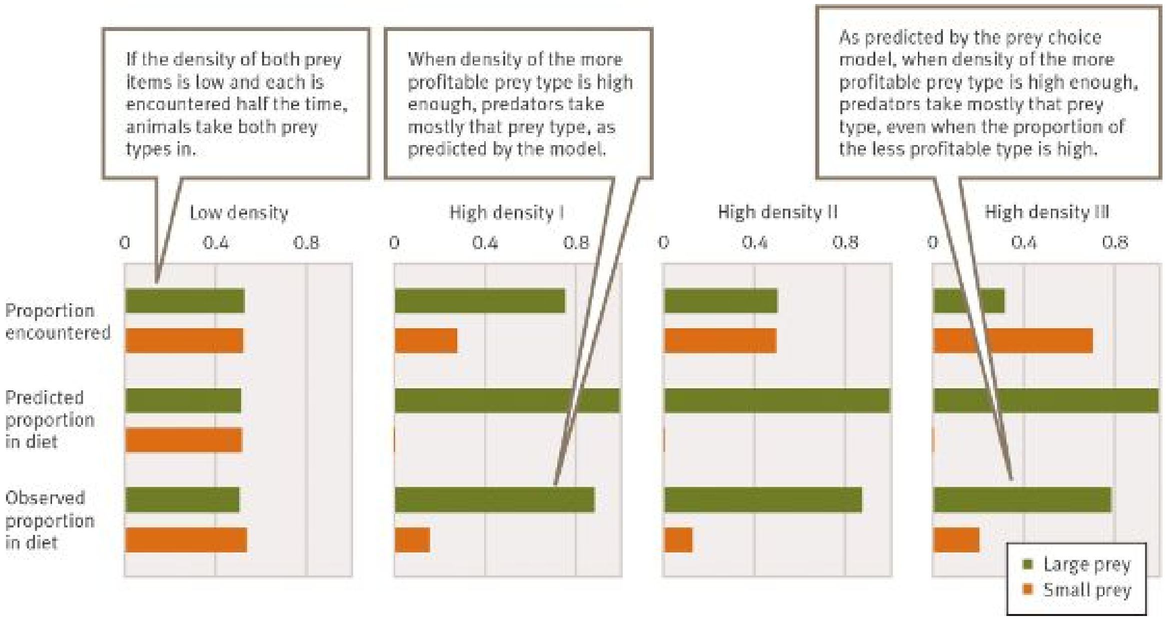


Figure 11.6. Optimal choice of diet. Optimal foraging in great tits was examined by Krebs and his colleagues in four density conditions. With a knowledge of encounter rates, handling times, and energy values, the researchers were able to predict the birds' optimal diet of larger, more profitable and smaller, less profitable prey. *(Based on Krebs, 1978, p. 31)*

This same optimality model could be used for any type of forager deciding between two prey types—for example, the case of a carnivore predator choosing between two herbivore prey species. This model has also been applied to foraging behavior in humans. For example, Kim Hill has studied foraging in the Aché people, an indigenous tribe of Indians in Paraguay. When Hill examined the prey choices made by Aché foragers, he found that their choices generally matched those of the prey choice model (Hawkes et al., 1982; K. Hill, 2002; K. Hill and Hurtado, 1996; K. Hill et al., 1987; Figure 11.7).

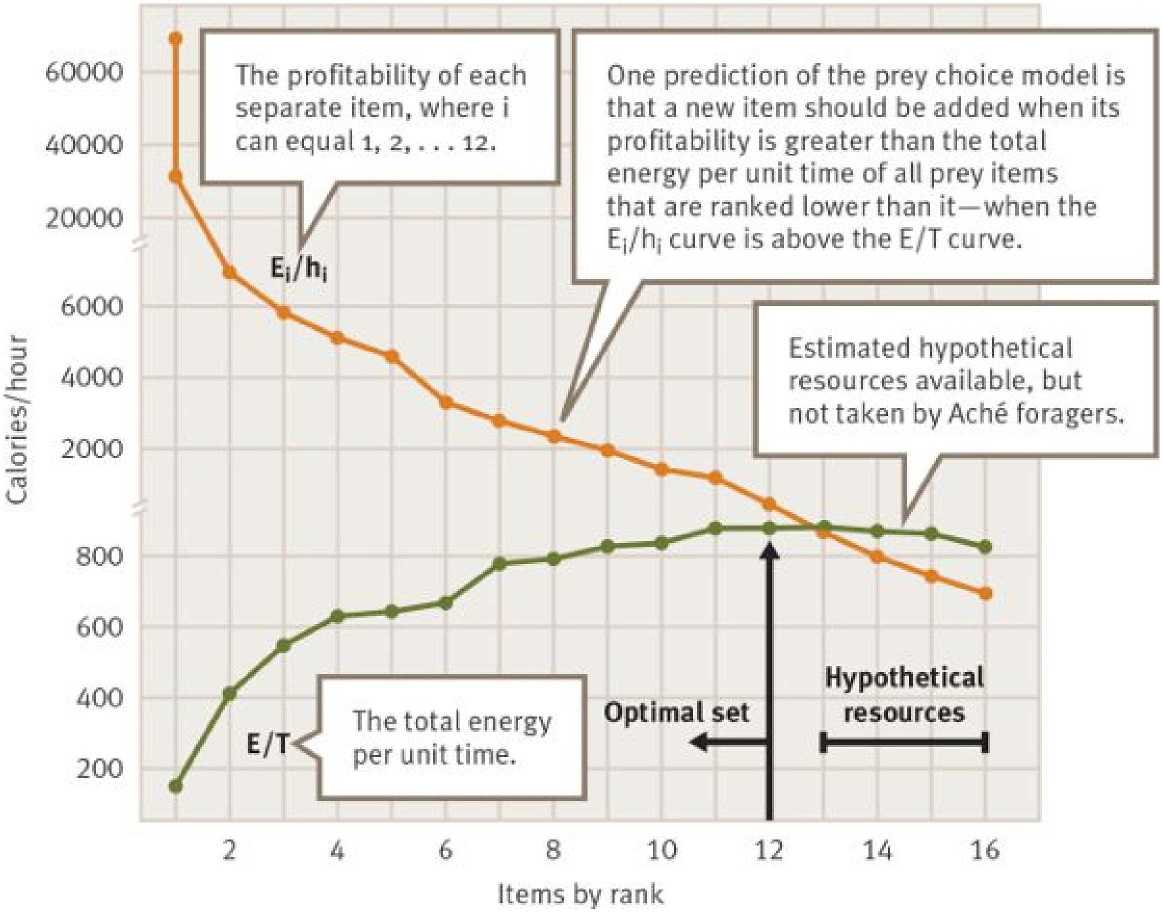


Figure 11.7. Optimal prey choice in Aché foragers. Aché foragers select prey items as predicted by the prey choice model. For items ranked 1 through 12, the profitability of a new item is greater than the total energy per unit time for all lower-ranked items. The prey choice model predicts that Aché foragers should take prey items 1 through 12, but not others. The data support this prediction. *(From Hawkes et al., 1982)*

WHERE TO EAT

In addition to deciding which prey items to consume, foragers often have to make decisions about how long to stay in a patch of food. For example, how long should a hummingbird spend sucking nectar from one flower, given that there are other flowers available, or how long should a bee spend extracting pollen from one flower before moving on to the next flower or the next patches of flowers? To address such questions, Eric Charnov developed an optimality model (Charnov, 1976; G. Parker and Stuart, 1976).

Imagine a forager feeding in an area that contains different patches of a single type of food. A patch of food for a chimp could be a tree full of fruit; for a bee it might be a flower or cluster of flowers (Figure 11.8).

More generally, a patch is defined as a clump of food that can be depleted by a forager. Once a forager begins feeding in a patch, the *rate* at which it takes in food slows down, as the more the forager eats, the less food remains in the patch. Other less depleted patches will then have relatively large amounts of food available, but in order to get to these patches, the forager must pay some cost—energy associated with travel, time lost while traveling, increased rate of predation, and so forth—associated with traveling between patches. The question then becomes how long a forager should stay in a patch that it is depleting before moving on to another patch.

Figure 11.8. Patch choice. For a bee, different clusters of flowers in a field of flowering plants might represent different patches.

Assuming that we know the rate of food intake, Charnov's **marginal value theorem** makes a series of testable predictions regarding patch residence time.

- A forager should stay in a patch until the marginal rate of food intake—that is, the rate of food intake associated with the next food item in its patch—is equal to that of the average rate of food intake across all patches available. That is, a forager should stay in a patch T time units, where T is that point in time when its marginal rate of food intake in that patch is equal to the average amount of food it could get in other patches, given that it has to pay a cost to get to such other patches.
- The greater the time between patches, the longer a forager should stay in a patch. Increased travel time leads to an increase in the costs associated with such travel, and such costs need to be compensated—remaining in a patch longer is one means by which such compensation can be achieved.
- A forger should remain longer in patches if patch quality in the environment is poor versus rich. In order to make up for the travel costs associated with a move from a

patch, a forager has to stay longer in a poor patch than in a good patch to obtain a fixed amount of energy (Figure 11.9).

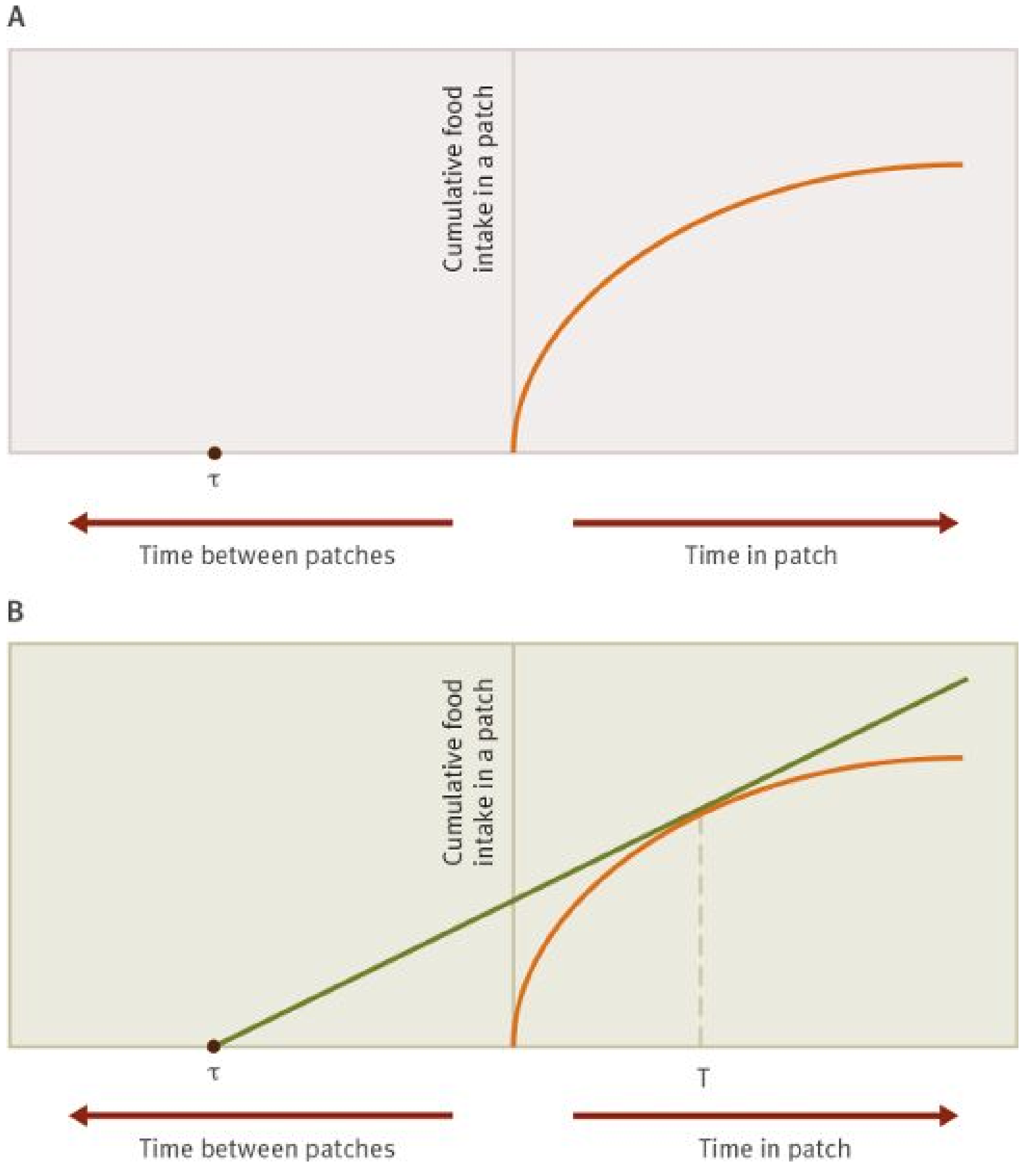


Figure 11.9. Graphical solution to marginal value problem. (A) To calculate the optimal time for a forager to remain in a patch, draw a curve that represents the cumulative food gain in an average patch in the environment. Then, going west on the *x*-axis find the average travel time between patches (τ). (B) Draw a straight line from τ that is tangent to the food gain curve. From the point of tangency, drop a perpendicular (dashed) line to the *x*-axis, and this gives the optimal time (T) for the forager to stay in the patch.

Cowie tested one of the predictions of the marginal value theorem in great tits. Inside a large aviary he built a series of artificial trees, each of which contained numerous branches (Cowie, 1977). Attached to the branches were sawdust-filled potting baskets and under the sawdust were mealworms (prey for the birds; Figure 11.10A). Cowie was able to calculate the rate of intake gain in different types of sawdust-filled patches. In addition, he could manipulate the travel time between patches, because each pot had a lid, and the lids could be made to be easily dislodged—creating a short travel time between leaving one patch and starting to forage at another—or the lids could be constructed so as to be very difficult to open, simulating a long travel time. Based on this, Cowie calculated the optimal time to stay in a patch as a function of travel time between patches. The amount of time birds spent in a patch matched the optimal time predicted by the marginal value theorem (Figure 11.10B).

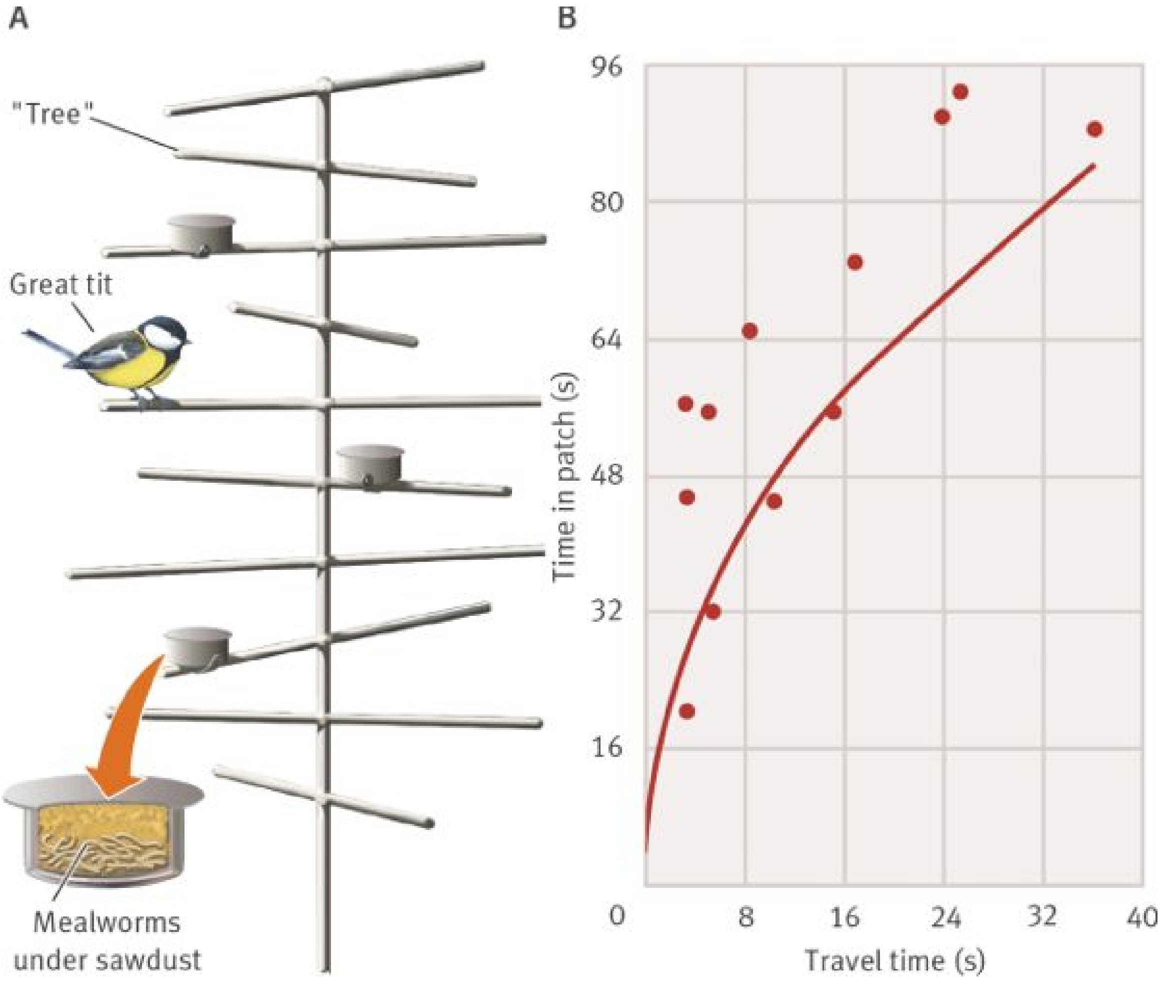


Figure 11.10. Optimal time in patch and travel time. A test of the marginal value theorem. (A) An artificial tree allows control of both patch quality and travel time. (B) The red curve is the predicted optimal time in a patch plotted against the travel time, which was calculated based on the marginal value theorem, while the data points are the observed times great tits stayed in the patch plotted as a function of travel time between patches. *(Based on Krebs, 1978, p. 44)*

Any time a resource depletes as a function of use, and costs associated with traveling between patches of that resource are present, one can use the marginal value theorem to solve for optimal patch time (Hills et al., 2015). This approach has, for example, been used to calculate how long a male should search for and mate with a female (where the female is now the “patch”; G. Parker and Stuart, 1976) and how long a “cheater” should remain in a patch to exploit cooperators (Dugatkin and Wilson, 1991; Dugatkin, 1992a).

RISK-SENSITIVE FORAGING

Suppose an animal can choose to forage in one of two patches, both patches have the same type of food item, and the animal has learned what to expect in each patch. In patch 1, each forager will always receive eight prey items. In patch 2, there is a 50 percent chance a forager will receive sixteen food items and a 50 percent chance it will get nothing. The mean number of food items that the forager can expect in both patches is identical (eight), but the variance (risk) in food intake is greater in patch 2. Should our forager take the differences in the variability into account when deciding between patches?

In the language of statistics, this variance in food intake is referred to as *risk*—the term was first used in economics, where more variance implied a greater chance of loss (or gain). The word *risk*, when used in foraging models, is sometimes confused with risk in the sense of danger—but one type of risk need not have anything to do with the other, and it is important to keep them separate in your thinking. Here, as we work through what are known as **risk-sensitive optimal foraging models**, *risk* is used in the economic sense (Caraco, 1980; McNamara and Houston, 1992; Real and Caraco, 1986; Smallwood, 1996; Stephens et al., 2007).

Hunger state and how it relates to the value (utility: Bernoulli, 1738) associated with food items plays a key role in many risk-sensitive foraging models. There are three basic value or utility functions that a forger can have:

1) A linear utility function, where every additional food item is valued equally.
2) A convex utility function, where every additional food item has less value. This sort of utility function would be one that we might expect a fairly satiated forager to have. (Think about the value to you of a slice of cake after you have just had two

ice cream cones. It might be worth something, but not what it would have been worth before consuming the ice cream.)

3) A concave utility function, where every additional food item is worth more and more (to a limit), as might be the case for a very hungry forager (Figure 11.11).

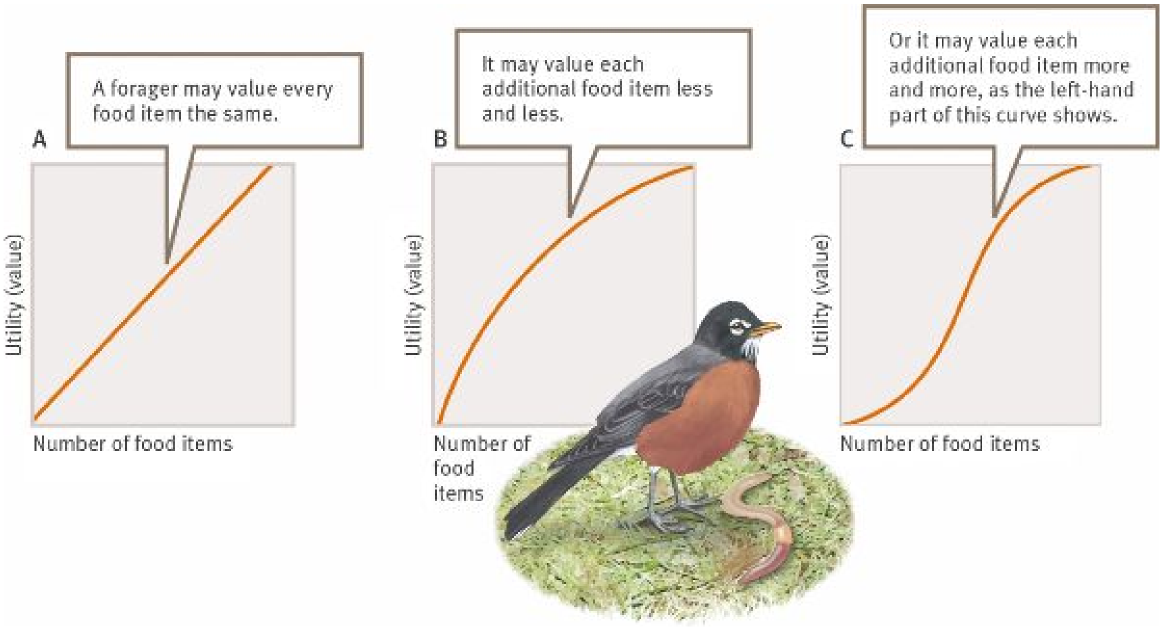


Figure 11.11. Utility of food. The bird in (A) is predicted to be risk insensitive, the bird in (B) is predicted to be risk averse, and the bird in (C) is predicted to be risk prone.

Risk-sensitive foraging models can be mathematically complex, but they make a straightforward prediction. Because of a mathematical theorem called Jensen's inequality (Jensen, 1906), fairly satiated foragers have a convex utility function and they are predicted to be *risk averse*—they should prefer to forage in patches with low variance. Very hungry foragers, with their concave utility function, should be *risk prone*, and prefer high variance patches. Foragers with a linear utility function should be indifferent to foraging related variance.

To see why foraging environments with high variance are favored by hungry animals but avoided by relatively satiated animals, let's return to the two hypothetical patches we discussed above. For the forager that is not all that hungry, each additional piece of food isn't worth that much more; thus, it should opt for a consistent food source, because sixteen pieces of food isn't worth all that much more than eight food items when a forager is not especially hungry. For our very hungry animal, though, eight pieces of food may not be enough to provide it with enough energy to survive the night, but sixteen food items may. In that case, it is worth taking the chance of getting no food at all (one possible outcome in our risky patch) in exchange for the chance of getting sixteen items.

As with all the mathematical models we have discussed, there is no assumption that animals make the mental calculations that we just went through, only that natural selection favors any “rule of thumb” behavior that allows the animals to solve the problem at hand. In this case, the favored rule of thumb might be “When very hungry, use patches of food where variance in food intake is high.”

Caraco et al. examined foraging behavior in yellow-eyed juncos. They presented birds with two trays containing birdseed, and once a bird made the choice to go to one tray, the other was immediately removed (Caraco et al., 1980; Figure 11.12). The trays had the same mean amount of food, but one tray had a “fixed” amount—for example always had five seeds—while the other tray had a “variable” amount for example, no seeds half the time, and ten seeds half the time. Caraco and his team calculated utility function both for hungry birds (concave utility functions) and for less hungry birds (conxex utility functions) (Figure 11.13).

Figure 11.12. Optimality models have been tested in juncos. Junco foraging behavior has been used to test numerous optimal foraging models. *(Photo credit: © Jeff Maw)*

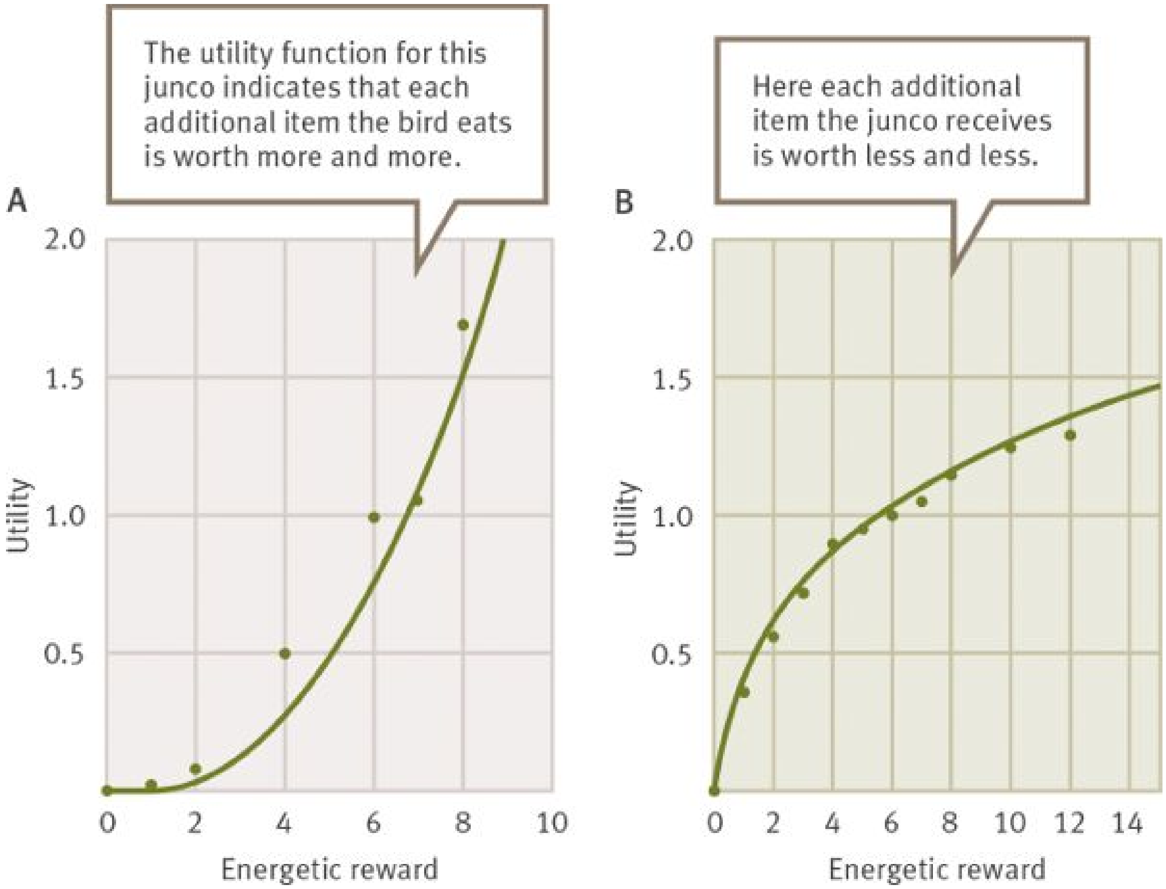


Figure 11.13. Utility functions and risk sensitivity. (A) Juncos with a concave utility function were risk-prone foragers. (B) Juncos with a convex utility function were risk-averse foragers. *(From Caraco et al., 1980)*

When choosing between trays, risk-sensitive foraging models predict that birds with convex utility functions should choose the fixed trays, while birds with concave utility functions should select the variable trays. The juncos in Caraco's study behaved in a fashion very similar to that predicted from theory. Yellow-eyed junco foraging is risk-sensitive, shifting between risk-averse foraging and risk-prone foraging according to energy budgets. Following this study, similar results on risk-sensitive foraging were uncovered in other birds, as well as in mammals and in invertebrates such as honeybees and crayfish. However, in a review of risk-sensitive foraging, Kacelnik and El Mouden note that while early studies like the one described above support some basic predictions of some risk-sensitive models of foraging, an analysis of all experiments since Caraco's seminal paper indicates much weaker support (Kacelnik and El Mouden, 2013). They suggest revising early models of risk sensitivity with more realistic assumptions and then constructing a new round of experimental work to test these revised models.

Growing Food

Approximately fifty million years ago, individuals in some species of ants began cultivating their own food by entering into a symbiotic (mutually beneficial) relationship with certain species of fungi (Caldera et al., 2009; Poulsen and Currie, 2009; Figure 11.14). The ants promote the growth of the fungi (good for the fungi), while also eating the vegetative shoots produced by their fungal partners (good for the ants). Aside from humans, ants are one of the few species on the planet that grow their own food.

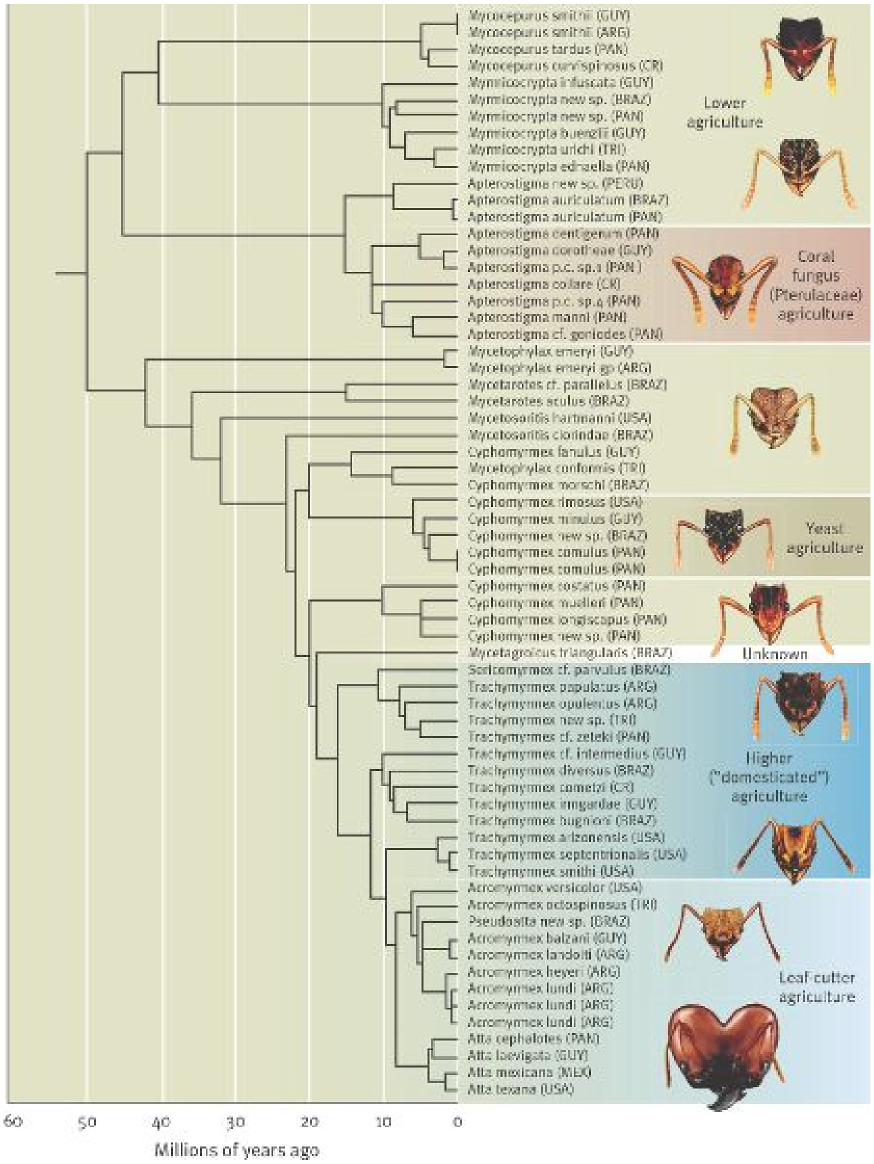


Figure 11.14. A phylogeny of fungus-growing ants. The phylogenetic history of five ant "agriculture" systems. *(Adapted from Schultz and Brady, 2008)*

Scientists who study fungus-growing ants have long known of a whitish-gray crust found on and around many ants with fungus food gardens. Research has shown that this is a mass of *Streptomyces* bacteria—a type of bacteria that produces many antibiotics that kill other bacteria. Currie and his colleagues hypothesized that ants use antibiotics produced by the *Streptomyces* to kill parasites that grow in their fungal gardens (Cafaro and Currie, 2005; Currie, Mueller, et al., 1999; Currie, Scott, et al., 1999; Figure 11.15). They proposed that not only have ants evolved a complex relationship with their food source (fungi), but a means to protect their food source from destruction has also evolved in this system.

Figure 11.15. Tending the garden. A worker of the leaf-cutter ant (*Acromyrmex octospinosus*) tending a fungus garden. The thick whitish-gray coating on the worker is the mutualistic bacterium (*Actinomycetous*) that produces the antibiotics that suppress the growth of parasites in the fungus garden. *(Photo credit: Alex Wild/alexanderwild.com)*

Four lines of evidence support this hypothesis. First, all twenty species of the fungus-growing ants Currie and his team examined had *Streptomyces* bacteria associated with them. Second, ants transmit the *Streptomyces* across generations, as parents pass the bacteria on to offspring. Third, when male and female reproductive ants are examined (before their mating flights), only females possess *Streptomyces*. This is critical, as only females start new nests that will rely on the *Streptomyces* to produce antibiotics, and only females are involved in “cultivating” fungus gardens. Fourth, and most important, the bacteria found on fungus-growing ants produce antibiotics that wipe out only *certain* parasitic diseases. When Currie’s team tested the antibiotics produced by *Streptomyces*, they found that they were effective only against *Escovopsis*, a serious parasitic threat to the ants' fungus garden. Other species—those not a danger to fungus-growing ants—were unaffected by *Streptomyces* antibiotics. Recent work has explored the use of such "natural fungicides" for use by humans as biocontrol agents (Folgarait et al., 2011).

In addition to directly using the antibiotics produced by *Streptomyces* to clean their fungal gardens, the ants meticulously clean these gardens and remove fungus infected with *Escovopsis*. Ants pick up parasitic *Escovopsis* spores and hyphae and place them in areas of their body called infrabuccal pockets. Inside these pockets, the spores and hyphae are killed by chemicals that are also present in the infrabuccal pockets. The ants then take the dead spores and hyphae and deposit them in a separate pile away from the fungus garden (Little et al., 2003, 2006). Indeed, within nests, different castes of ant workers specialize on different tasks associated with defending the fungal garden against parasites (Abramowski et al., 2011).

Currie and his team predicted that because fungal gardens break down plant matter that becomes available to the ants, leaf-cutter ants might have lost some genes associated with nutrient acquisition and normal digestion. When the genome of one fungal-growing, leaf-cutter species (*Atta cephalotes*) was sequenced, researchers found some evidence supporting this prediction, including reduction in the production of enzymes (serine proteases) often used during digestion (Suen et al., 2011).

Foraging and Group Life

The dynamics of group life can affect both how animals forage and foraging success. In this section we explore the following questions:

- How does group size affect animal foraging behavior?
- What role does cooperation within groups play in foraging?
- How does work on the public information available in some groups shed light on animal foraging?

GROUP SIZE

In group-living species, increasing the number of foragers in a group can increase the amount of food *each* forager receives (Krause and

Ruxton, 2002). This may occur because more foragers flush out more prey, or because cooperative hunting creates a division of labor between different group members and increases the success rate of the cooperator. Below, we examine an example of each of these possibilities.

Foraging in Bluegills

Bluegill sunfish feed on small aquatic insects that live in dense vegetation. These items need to be flushed from substrate, and increasing the size of foraging groups may flush more prey out of the vegetation (Bertram, 1978; Mock, 1980; Morse, 1970). Some prey flushed from the vegetation may not be eaten by the specific bluegill chasing them, but by other bluegill group members, and this could increase the mean number of prey obtained per group member. Mittlebach examined whether this was occuring by manipulating the foraging group size of bluegills in a controlled laboratory setting (Mittlebach, 1984).

Mittlebach placed 300 small amphipods (aquatic prey for bluegills) into a large aquarium containing juvenile bluegill sunfish and measured the success of fish that were foraging alone, in pairs, and in groups (ranging from three to six bluegills). He found a positive relationship between foraging group size and individual foraging success up to a group size of four fish (Figure 11.16). The increased feeding rate per individual was due to two factors. First, more prey were flushed when group size rose. Second, prey clumped together, so when one group member found amphipods, others swam over to this area and then often found food themselves (Figure 11.17).

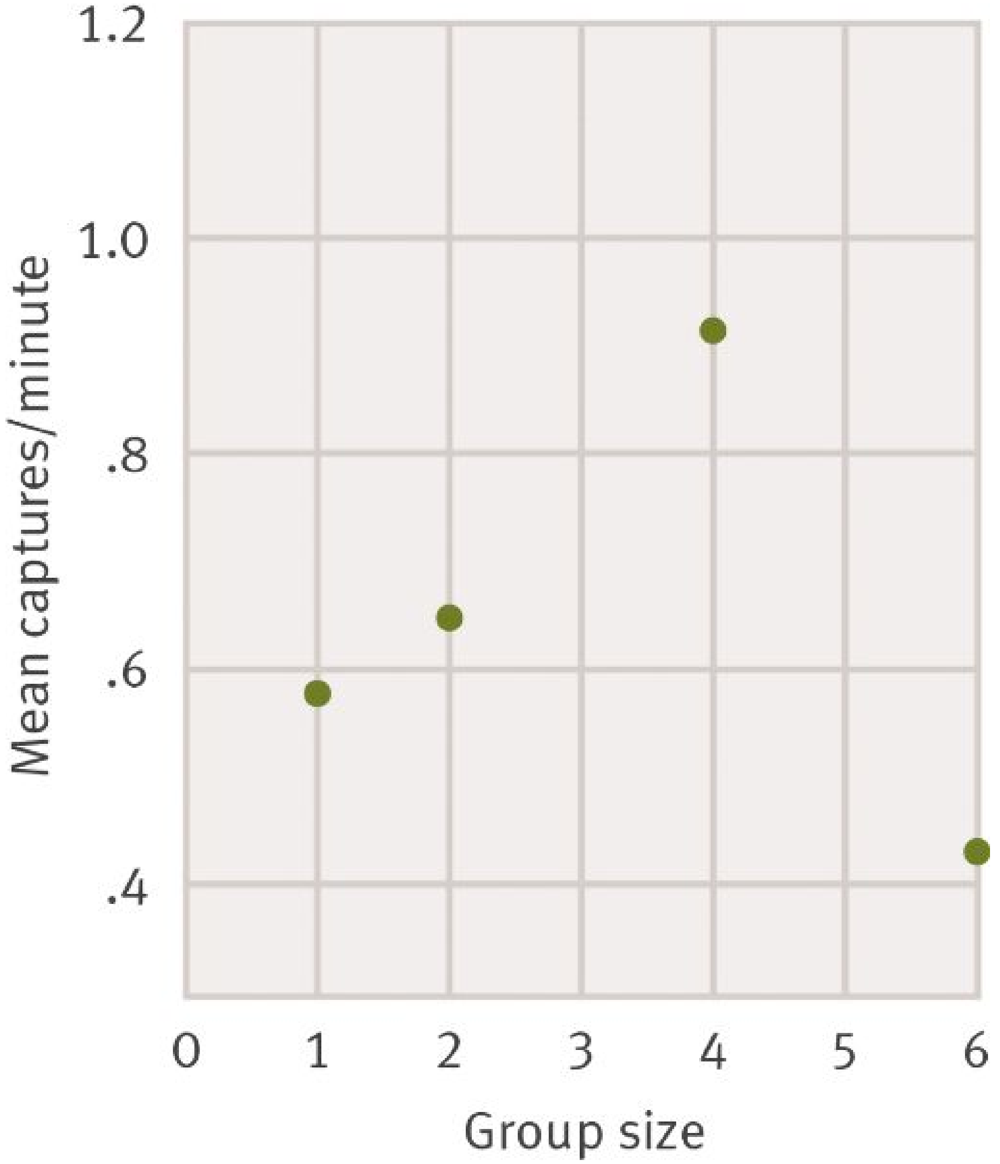


Figure 11.16. Group size and foraging success. In bluegill sunfish, the mean rate of prey captured increases with group size until group size reaches about four individuals. *(Based on Mittlebach, 1984, p. 999)*

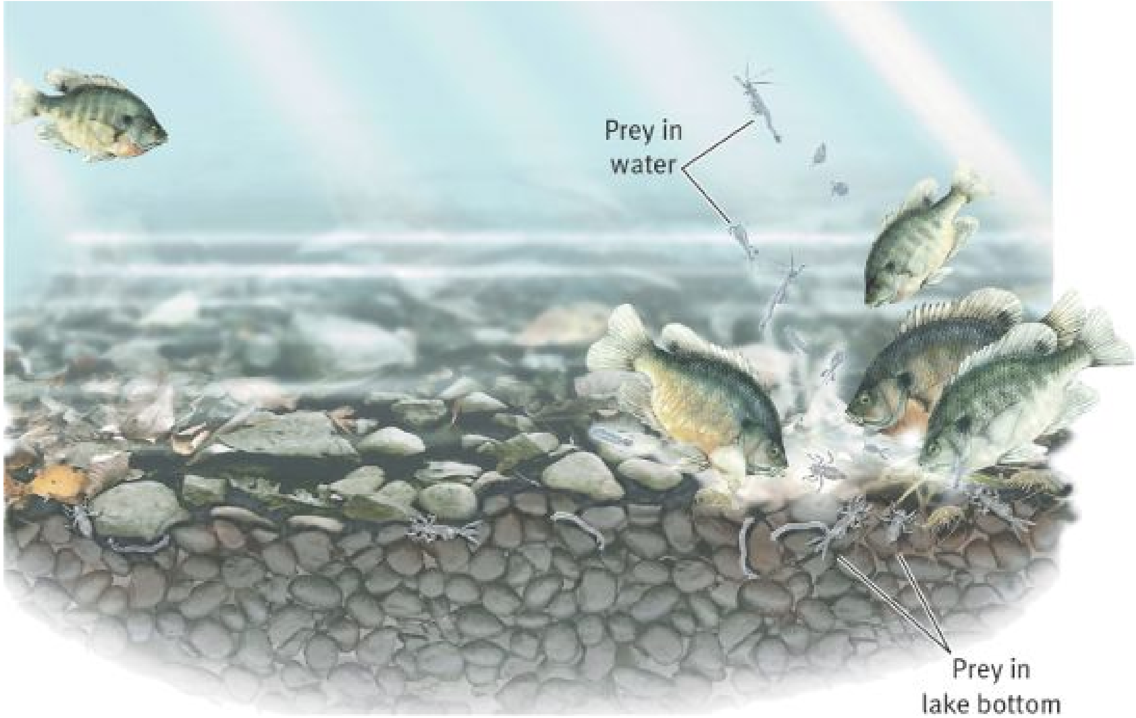


Figure 11.17. Bluegill group foraging. When bluegills forage in groups, they flush out more prey and attract other fish to the foraging site.

While increased group size in bluegills benefits each individual forager in its intake of food (its per capita foraging success), there is no evidence to suggest that bluegill foragers searched for prey in any coordinated fashion—the effect is merely a byproduct of having more individuals searching for food.

The general relationship between group size and foraging success uncovered by Mittlebach has been found in many animal studies, although the mechanism varies across studies. When Scott Creel ran an analysis on foraging success and group size in seven species that hunt in groups, he found a strong positive relationship between per capita foraging success and group size (Creel, 2001). Increased group size reduces the amount of time that any given individual needs to devote to antipredator activities—often, but not always, increasing per capita foraging success (Caraco, 1979; Ens and Goss-Custard, 1984; K. Sullivan, 1984).

Disentangling the Effect of Group Size and Cooperation on Foraging Success

Individuals sometimes cooperate with one another when hunting in groups: when wild dogs hunt down a prey item, for example, it is a coordinated effort (Creel, 2001; see chapter 2). Different members of the hunting pack play different roles in the hunt—flushing the prey, making the initial attack, disemboweling the prey, and so forth. In such cases, it is useful to separate the effects of cooperation from that of group size per se. To see how animal behaviorists disentangle these effects, let us examine hunting behavior in chimps.

Cooperative hunting or the lack of it has been examined in chimp populations in (1) the Gombe Preserve in Tanzania (Boesch, 1994b; Busse, 1978; Lawick-Goodall, 1968; Telecki, 1973), (2) the Mahale Mountains in Tanzania (Nishida et al., 1983; S. Uehara et al., 1992), and (3) the Tai National Park in the Ivory Coast (Boesch, 2002; Boesch and Boesch, 1989; Gomes and Boesch, 2009, 2011; Normand and Boesch, 2009). In Christophe and Hedwige Boesch's comparison of hunting patterns across Gombe and Tai chimp populations, they uncovered differences in hunting strategies between these populations.

In Tai chimps, hunting success was positively correlated with group size in a nonadditive fashion: adding more hunters to a group did not simply increase the amount of food by a fixed amount for each new hunter added. Instead, with each new hunter, all group members receive more additional food than they did when the last new hunter was added to the group (up to a limit). In addition to these group-size effects, Christophe Boesch found evidence of cooperation in Tai chimp hunting behavior (Boesch, 1994a; Gomes and Boesch, 2009, 2011; Figure 11.18). Very complex, subtle, social rules exist that regulate access to fresh kills and assure hunters who cooperated greater foraging success than those that fail to join a hunt.

Figure 11.18. Cooperative chimps. Chimps, though primarily vegetarian, readily add meat, when it is available, to their diet. In the Tai Forest (Ivory Coast), chimps cooperate in both capturing and consuming prey. Once a prey is caught, complex rules for food distribution are invoked. *(Photo credit: Cristina Gomes)*

No correlation between group size and hunting success was found in chimps from Gombe. In addition, unlike in the Tai population, behavioral rules limiting a nonhunter's access to prey were absent, and nonhunters received as much food as those that hunted cooperatively (Boesch, 1994a; Goodall, 1986). Part of the difference in hunting behavior in Tai and Gombe chimps may be because the success rate for Gombe solo hunters was quite high compared with the individual success rate for chimps in the Tai population, relaxing selection pressure for cooperative hunting in the Gombe population.

GROUPS, PUBLIC INFORMATION, AND FORAGING

One way for a forager to assess a whole host of environmental variables—food availability, predators, and so on—is to use **public information**, that is, information based on the actions of others, as a cue to changes in environmental conditions (Beauchamp et al., 2012; Danchin et al., 2004; Valone, 1989; Valone and Templeton, 2002).

Public information differs from the sort of information acquired during social learning. In social learning, individuals learn something specific (a new behavior, the preference of others). In public information models, individuals use the actions of others as a means of assessing the condition of the environment, and as such, public information allows group members to reduce environmental uncertainty (Valone and Giraldeau, 1993). While public information models are general and can apply to numerous environmental parameters, here we will focus on how these models have been tested in the context of foraging behavior.

Public information models predict that social foragers in poor patches should leave such patches earlier than solitary individuals, because social foragers can use the failed foraging attempts of their groupmates as additional information about when they themselves should leave a patch of food. Jennifer Templeton and Luc-Alain Giraldeau tested this prediction in starlings (*Sturnus vulgaris*). Starlings fed at an artificial feeder that had thirty cups that were either empty or contained a few seeds (Templeton and Giraldeau, 1996; Figure 11.19). A given bird (B1) fed from such a feeder either alone or paired with a second bird (B2). Before being paired with B1 partners, B2 birds had been given the chance either to sample a few cups in this feeder or to sample all such cups. Two results support the predictions of public information models. First, when tested on completely empty feeding patches, B1 birds left such patches earlier when paired with any B2 bird than when foraging alone. Second, B1 birds left patches earliest of all when paired with B2 birds that had complete information about the patches (as compared with those B2 birds with only partial information).

Figure 11.19. Public information. Social foragers such as starlings have been used to test public information models of foraging behavior. Starlings in this public information experiment were tested using an array of food placed into cups. *(Photo credit: Jennifer Templeton)*

Natural Selection, Phylogeny, and Seed Caching

Some birds and mammals can remember where they have stored thousands of different food items (Raby and Clayton, 2010; Gibson and Kamil, 2009; Smulders et al., 2010). Watching a squirrel find the nuts it has stored for winter all over a garden often inspires a sense of awe in the observer. And it isn't only squirrels; for example, many bird species in the families *Corvidae* and *Paridae* have such abilities—individuals in some species cache (store) tens of thousands of items per year, and others an astonishing hundreds of thousands of items each year (Balda and Kamil, 1992; Pravosudov and Clayton, 2002). How is that possible? How can an animal find scores of food items, often hidden, that are scattered across its environment over the course of months?

HIPPOCAMPAL SIZE AND CACHING ABILITY

Sue Healey and John Krebs examined memory, hippocampal volume, and food caching in seven species of corvid birds (Healey and Krebs, 1992). The hippocampal region in birds is known to be associated with food retrieval and corvids are ideal for examining the relationship between hippocampal volume and food storage in more detail, because so much variation in food-storing behavior exists within this group (Balda and Kamil, 1989; de Kort and Clayton, 2006; Emery, 2006; D. Goodwin, 1986; Krebs et al., 1989; Sherry, 2006; Sherry and Vaccarino, 1989; Pravosudov and Roth, 2013). Some corvids store no food, while others rely on the food they have stored over the course of nine months.

Healey and Krebs studied two species—jackdaws (*Corvus monedula*) and Alpine choughs (*Pyrrhocorax graculus*)—that rarely if ever cache food; four species—rooks (*Corvus frugilegus*), European crows (*Corvis corone*), European magpies (*Pica pica*), and Asian red-billed blue magpies (*Cissa erythrorhyncha*)—in which food caching plays some role; and one species—the European jay (*Garrulus glandarius*)—in which not only does food caching play an important role, but the location of 6,000 to 11,000 seeds must be remembered for nine months. When food-caching behavior was examined in relation to hippocampal volume in these seven species, a strong positive relationship was uncovered (Figure 11.20). Though correlational studies like this cannot tease apart cause and effect, this much is known—the more food-storing behavior seen in a species, the greater the hippocampal volume.

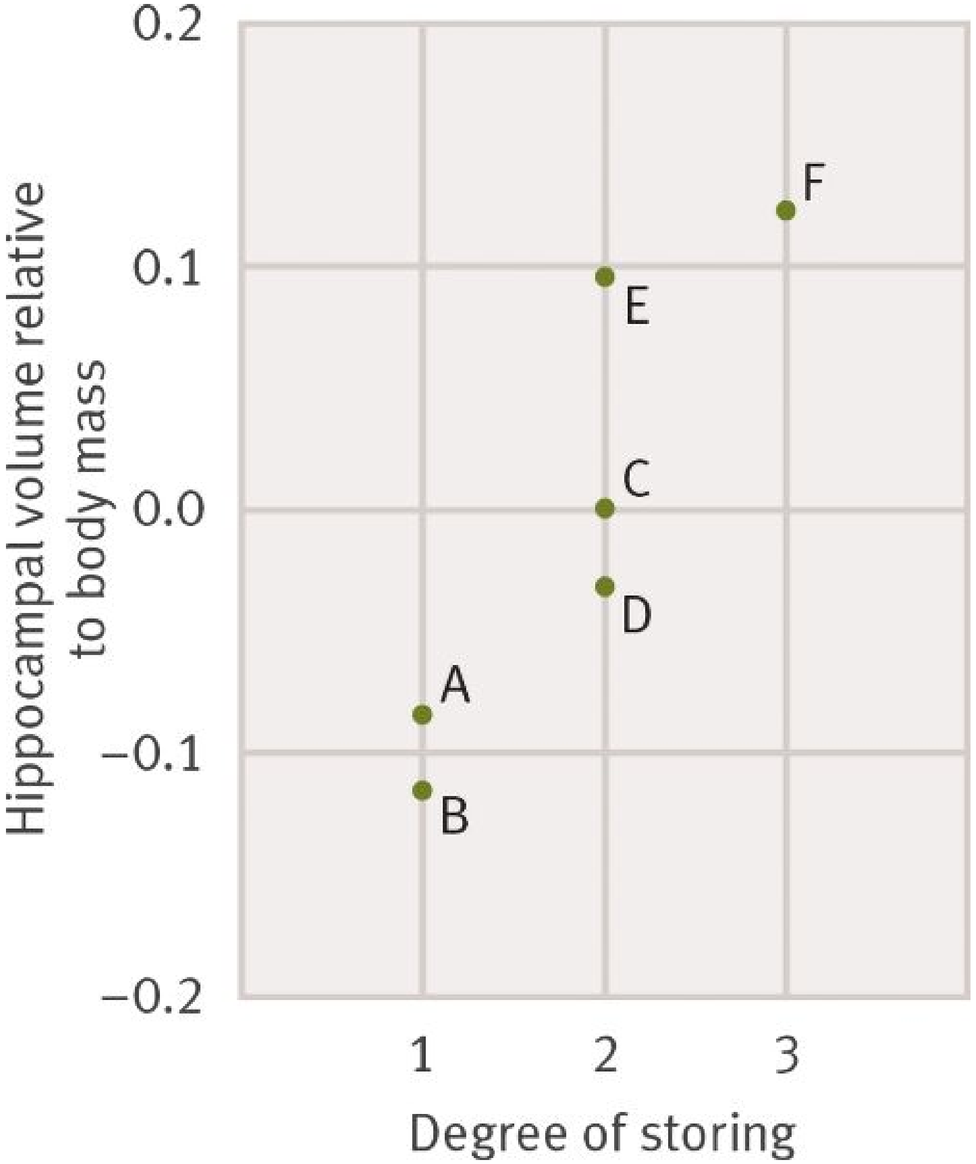


Figure 11.20. Foraging and brain size. The volume of the hippocampal region relative to body mass was positively correlated with the extent of food storing in six species of birds: (A) alpine chough, (B) jackdaw, (C) rook and crow combined, (D) red-billed blue magpie, (E) magpie, and (F) European jay. *(Based on Healey and Krebs, 1992)*

Animal behaviorists have also examined the relationship between hippocampal size and caching ability within a single species. Researchers have hypothesized that within a given species, individuals from populations where food resources are relatively scarce would be better at caching and recovering food and would possess a larger hippocampus than individuals from food-rich environments (Pravosudov and Grubb, 1997; Pravosudov et al., 2001). Natural selection should favor better caching and retrieval abilities when individuals live in harsh foraging environments, where caching and retrieval is at a premium, and selection should favor larger hippocampal areas and more hippocampal neurons under such conditions. Vladimir Pravosudov and Nicky Clayton tested this idea using black-capped chickadees (*Poecile atricapilla*) from two populations—Colorado, which is a food-rich environment, and Alaska, which is a food-poor environment (Pravosudov and Clayton, 2002; Kozlovsky et al., 2014).

They captured fifteen chickadees from a site in Anchorage, Alaska, and twelve birds from a population near Windsor, Colorado, and brought them back to their laboratory. Forty-five days after being brought into the lab, the birds were tested on their ability to retrieve seeds they had cached. When provided with seeds that could be cached, the birds from Alaska (food-scarce population) cached a greater percentage of seeds than the birds from Colorado (food-rich population). The Alaskan birds also found a greater proportion of their cached seeds than did the Colorado birds, and their searches were more efficient in that they made fewer errors (Figure 11.21).

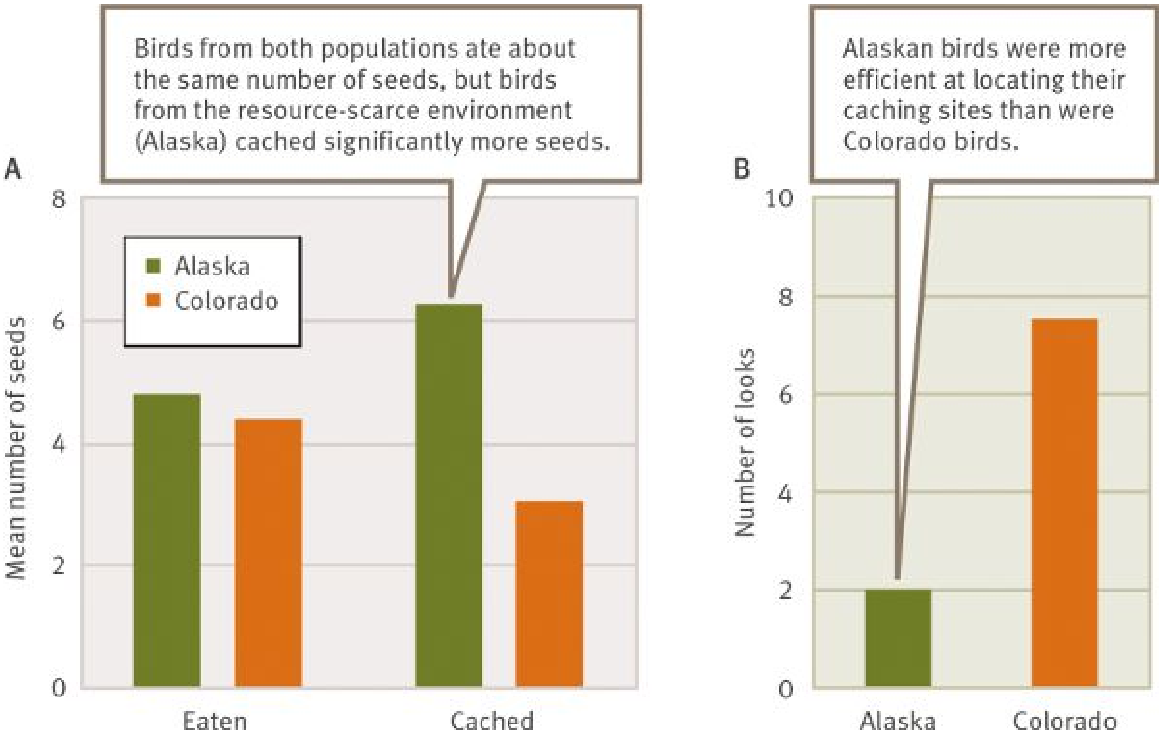


Figure 11.21. Population differences in food storing in black-capped chickadees. (A) Mean number of sunflower seeds eaten and cached. (B) Mean number of sites inspected. *(Based on Pravosudov and Clayton, 2002, p. 519)*

Even though the birds from Alaska had a hippocampus that weighed less than the Colorado birds, the hippocampal volumes of the Alaskan birds were greater and their hippocampuses contained more neurons than those of the Colorado birds. What's more, when Pravosudov and Clayton compared birds from Colorado and Alaska that were *not* given the chance to cache seeds, the same hippocampal differences were found, suggesting that the caching experience per se did not increase hippocampus size.

A PHYLOGENETIC APPROACH TO STUDYING CACHING ABILITY

To better understand the evolutionary history of caching behavior in corvids, Selvino de Kort and Nicky Clayton constructed a phylogeny of forty-six species from this family of birds (de Kort and Clayton, 2006). Each species was then categorized on its tendency to cache seeds. Based on a combination of published laboratory and field studies, each of the species was placed into one of three categories. Non-cachers were defined as species that virtually never cache food. Moderate cachers were those that cached food throughout the course of a year and cached many different types of food, but were never entirely dependent on cached food sources for survival. Finally, specialized cachers were defined as species in which individuals cached a large number of items, the cached items were typically one food type, caching was seasonal, and cachers often recovered their items after long periods of time had passed. Information about caching ability was then mapped onto the phylogeny of the group (Figure 11.22).

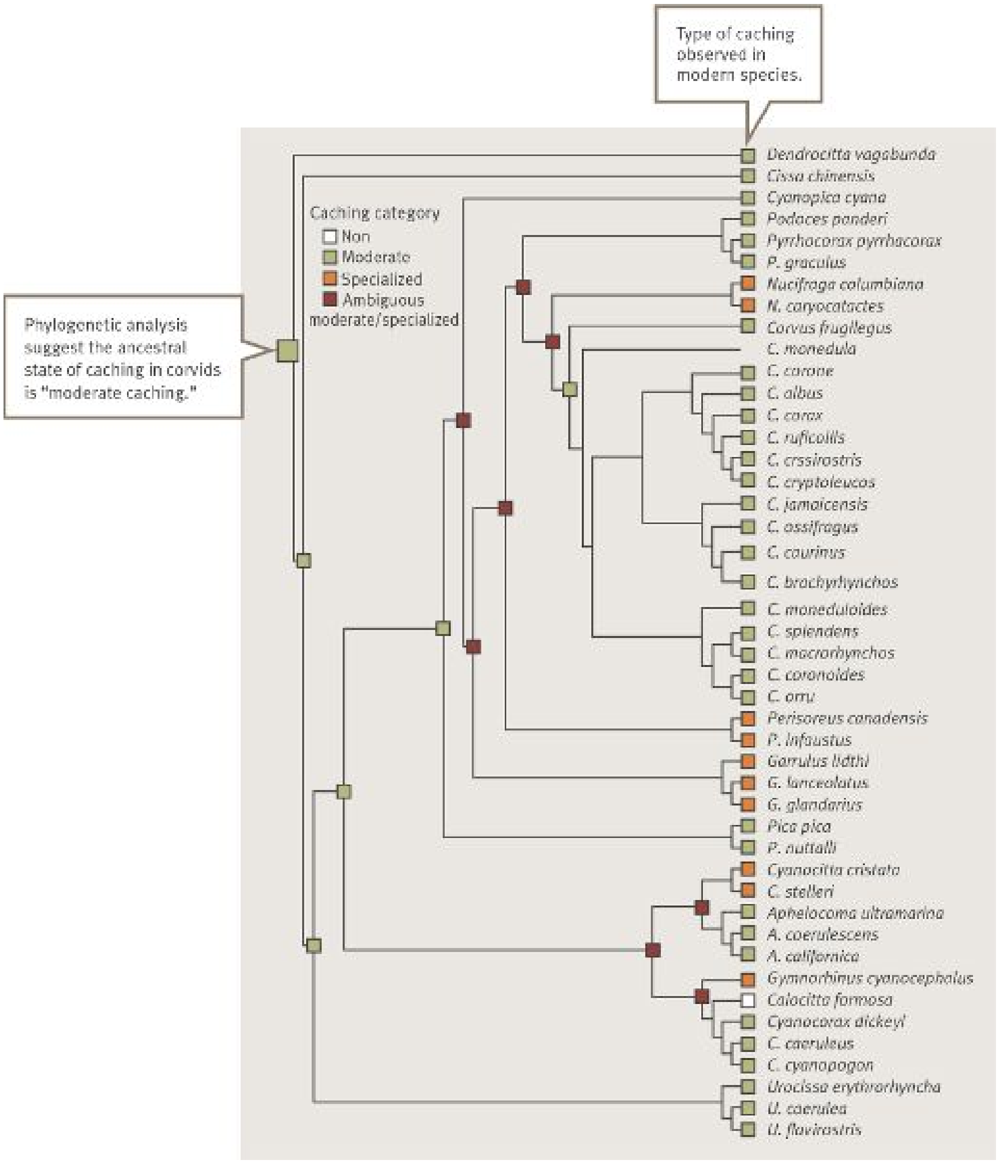


Figure 11.22. Phylogenic history of caching in corvids. Boxes on the far right indicate observed caching behavior for modern species. All boxes to the left of modern species represent hypothesized ancestors and their inferred caching states. *(From de Kort and Clayton, 2006)*

A phylogenetic analysis suggests that the most likely ancestral state of caching in corvids is moderate caching. This result was somewhat surprising. Many animal behaviorists assumed that the ancestral state in corvids was non-caching. De Kort and Clayton's findings that the ancestral state was moderate caching suggest that some corvid species evolved into specialized cachers, while others lost the caching trait altogether. Indeed, de Kort and Clayton found that evolution toward highly specialized cachers occurred independently at least twice, and perhaps as many as five times. Conversely, over evolutionary time, at least two lineages completely lost the ability to cache seeds, perhaps because the benefits of caching did not make up for the metabolic costs of maintaining a relatively large hippocampus (Attwell and Laughlin, 2001; Laughlin et al., 1998; Box 11.2).

Box 11.2. SCIENCE AT WORK

What is the research question? Does phylogenetic history explain variation in caching ability?

Why is this an important question? While much work has been done on the evolution of foraging behavior, most of this work has taken an explicitly adaptationist approach, and much less is known about how phylogenetic history affects this behavior.

What approach was taken to address the research question? Researchers mapped variation in caching abilities (noncachers, moderate cachers, and specialized cachers) in corvids onto a phylogenetic tree of this family of birds.

What was discovered? A phylogenetic analysis found that moderate caching is the most likely ancestral trait in corvids.

What do the results mean? Since moderate caching was the most likely ancestral caching trait among corvids, this phylogenetic analysis suggests that the simplest variety of a trait—in this case caching behavior—is not always the most ancestral variety of that trait.

Box 11.3. COGNITIVE CONNECTION

Proximate Factors in Foraging-Related Learning

Honeybees, *Apis mellifera*, forage in a complex landscape and they learn about their environment over time using sophisticated strategies to optimize colony food intake. Forager bees, for example, can learn to pair color, odor, shape, and flower topography with sugar (sucrose) rewards. From a cognitive perspective, one interesting finding from prior work is the individual variation seen among foraging bees—some foragers learn to pair much more quickly than others. What leads to such differences? This sort of question can be answered at both the proximate and ultimate level: here we will focus on the underlying proximate factors that may help to explain these individual differences in foraging-related learning.

The birth weight of honeybees—their weight when they emerge from their brood cells—ranges from about 80 to 150 mg (Jay, 1963), and is affected by the amount of care dispensed by nurse bees, the amount of food present at the hive, and the time of year (Lee and Winston, 1985). Because low birth weight has been linked to poor cognitive skills in other species, including humans, Ricarda Scheiner examined whether variation in birth weight mapped onto between-individual differences in learning abilities in three-week old bees (the age at which many honeybees become foragers) (Scheiner, 2012).

Scheiner weighed bees soon after they emerged from their brood cells. Immediately after that, he tested how quickly each individual extended its proboscis when it was exposed to a sugary liquid. When these bees turned three weeks old, he tested them in controlled trials where foragers needed to pair an odor (citral) with a reward (a sucrose solution). Scheiner found a positive correlation between birth weight and foraging-related learning at age three weeks, with bees that were heavier at birth developing into foragers that learned better than their lighter counterparts (Figure 11.23). There was, however, significant variation in learning abilities even among individuals that were heaviest at emergence from the brood cell. Much of this variation was correlated with how quickly an individual extended its proboscis when exposed to a sugary liquid right after emergence. Bees that did this quickly on emergence tended to be the best learners when subsequently tested at three weeks old.

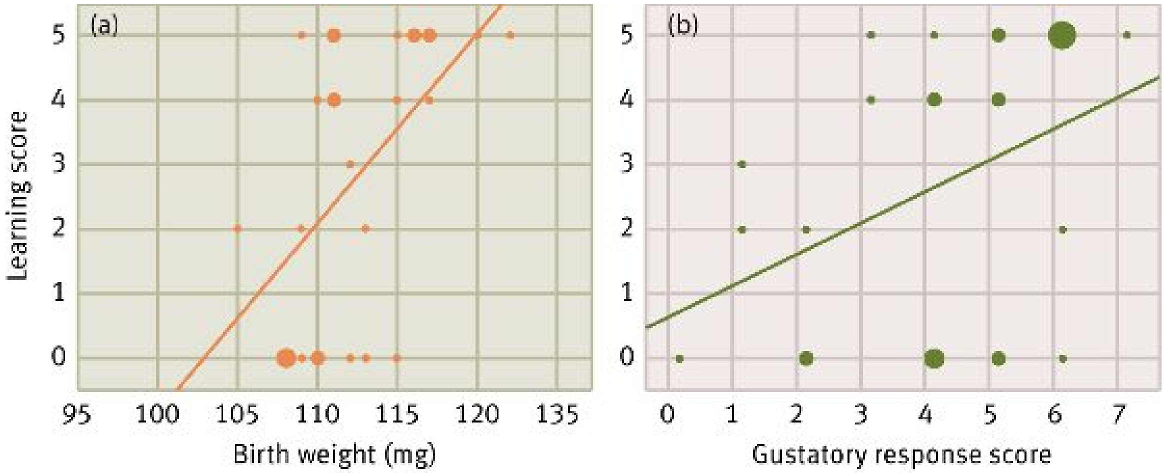


Figure 11.23. **Birth weight and foraging-related learning.** Bees that were heavier on emergence from brood cells were better learners when tested on a foraging task at three weeks old. Reprinted with permission of Elsevier. © 2012. *(From Scheiner, 2012)*

Learning and Foraging

While the studies described so far often involve animals learning something about their foraging environment, they were not explicitly designed as studies on foraging and learning per se (see Box 11.4 and Box 11.5).

Box 11.4. SCIENCE AT WORK

What is the research question? How does developmental variation in honeybees map onto subsequent variation in their ability to learn about food sources?

Why is this an important question? The proximate underpinnings of variation in the ability to learn are of interest to both behavioral ecologists and psychologists.

What approach was taken to address the research question? Honeybees were weighed on emergence from brood cells and immediately tested on their response to a sucrose solution. These same bees were then tested on a foraging-related learning task when they three weeks old.

What was discovered? A positive correlation between birth weight and foraging-related learning at age three weeks was found. Variation in learning among the bees was also positively correlated with how quickly an individual responded to the sucrose solution after emergence.

What do the results mean? The underlying proximate factors that affect learning while foraging can be studied experimentally. This is will help shed light on why we see individual variation in learning.

Box 11.5. CONSERVATION CONNECTION

Behavioral Traditions, Foraging, and Conservation in Killer Whales

As a general rule, conservation biologists assume that individuals in populations they are trying to protect will have similar diet preferences, especially if populations are geographically close to one another. But when diet choice is affected by social learning and foraging traditions that differ across populations emerge this may not be true (Whitehead, 2010). The food choices made by only a few individuals in a group—often older, more experienced individuals—can ripple through a population, creating variation in foraging preferences across groups (recall the case of Imo the Japanese macaque monkey and her potato washing, discussed in chapter 6).

Killer whales (*Orcinus orca*) are a species found on the US Endangered Species List and are considered endangered in many places around the world. A survey of the foraging behavior of killer whale populations from around the world showed that they feed on at least 120 species of fishes, as well as cephalopods, sea turtles, sea birds, pinnipeds, and cetaceans (J. Ford and Ellis, 2006). But at the level of the individual population, there is often specialization on one or just a few species of prey, and this prey choice is, in part, determined by social learning within a population (J. Ford et al., 1998; Guinet and Bouvier, 1995; Saulitis et al., 2000; Ford et al., 2016).

One population of killer whales near British Columbia, Canada, shows a pronounced foraging tradition for specializing on chinook salmon (*Oncorhynchus tshawytscha*; Figure 11.24). This socially learned preference for chinook prey has been maintained for numerous generations, even though other species of salmon—some of which are readily taken as prey in other populations of killer whales—are present.

Figure 11.24. Foraging in killer whales. The variance in foraging behavior seen across killer whale populations may be in part due to differences in socially learned food preferences. *(© Tory Kallman / Shutterstock)*

Any attempt at protecting the British Columbian killer whale population needs to consider their foraging tradition for chinook salmon. Even though there are many *potentially* edible salmon species available for these whales to consume, behavioral traditions limit what the animals will eat. An understanding of the role that social learning plays in the foraging behavior of these whales suggests that researchers pay special attention to ensuring that a sufficient number of chinook salmon are available for individuals in this population.

FORAGING, LEARNING, AND BRAIN SIZE IN BIRDS

Because the forebrain appears to be involved in behavioral plasticity, ethologists have hypothesized that larger forebrains might be associated with superior learning abilities (R. Byrne, 1993; Clutton-Brock and Harvey, 1980; Dunbar, 1992; T. Johnstone, 1982; Jolicoeur et al., 1984; Mace et al., 1981; Wyles et al., 1983). In one test of this hypothesis, Louis Lefebvre and his colleagues examined whether there was a relationship between foraging innovations and forebrain size in

North American and British Isle bird groups (Lefebvre, 2011; Lefebvre et al., 1997a,b; Overington, Griffin, et al., 2011).

Lefebvre and his colleagues defined a *foraging innovation* as “either the ingestion of a new food type or the use of a new foraging technique.” Here, we will focus on the latter types of innovations, which include some examples of social learning. They used descriptions of avian foraging innovations found in nine ornithology journals to gather data on 322 foraging innovations—126 in British Isle birds and 192 in North American birds (Table 11.1). Innovations included behaviors ranging from herring gulls “catching small rabbits and killing them by dropping them on rocks or drowning them” to common crows “using cars as nutcrackers for palm nuts” (Grobecker and Pietsch, 1978; H. Young, 1987). Lefebvre and his colleagues then examined how these innovations were distributed across different orders of birds, at the same time taking into account how common or rare a particular bird order was in Britain or North America.

Table 11.1. Examples of foraging innovations in birds. Lefebvre and his colleagues gathered data on 322 foraging innovations, including those on this list. (*Based on Lefebvre et al., 1997b, pp. 552–553*). Many other examples of avian foraging innovation have been found since this study was published.

Species	Innovation
Cardinal (Florida subspecies)	Nipping off nectar-filled capsule on flower and eating it
Herring gull	Catching small rabbits and killing them by dropping them on rocks or drowning them
Ferruginous hawk	Attracted to gunshot, preys on human-killed prairie dog
Magpie	Digging up potatoes
Storm petrel	Feeding on decaying whale fat
Great skua	Scavenging on roadkill
House sparrow	Using an automatic sensor to open bus station door; systematic searching and entering of car radiator grilles for insects
Galápagos mockingbird	Pecking food from sea lion’s mouth
Common crow	Using cars as nutcrackers for palm nuts
Osprey	Opening conch shells by dropping them on concrete-filled drum

Species	Innovation
Turnstone	Raiding gastric cavities of sea anemones
Red-winged blackbirds and Brewer's blackbirds	Following a tractor and eating frogs, voles, and insects flushed by it
Sparrowhawk	Drowning blackbird prey
Carrion crow	Landing on floating sheep corpse and feeding from it
Downy woodpecker	Using swaying caused by wind to catch meat hung from a branch

Once they had the data about foraging innovations, Lefebvre's team obtained information about relative forebrain size in the bird species of interest (Holden and Sharrock, 1988; Portmann, 1947; S. Scott, 1987). In both North American and British Isle birds, relative forebrain size correlated with foraging innovation. Bird orders that contained individuals with relatively larger forebrains were more likely to have high incidences of foraging innovation (Figure 11.25).

Lefebvre's group ran an analysis on Australasian birds and found similar results on foraging innovation and forebrain size (Lefebvre et al., 1998). In a series of follow-up studies, Daniel Sol, Lefebvre, and their colleagues examined the potential fitness benefits associated with being a large-brained bird (Sol, Duncan, et al., 2005; Sol and Lefebvre, 2006; Sol, Lefebvre, et al., 2005; Sol et al., 2006; Sol et al., 2007). One long-held, but largely untested, hypothesis for the fitness advantage associated with large brains (relative to body size) was that large brains would be particularly beneficial when a population was introduced into novel or altered environments, where innovation might be especially important (Allman, 1998; Reader, 2004; Reader and Laland, 2002). Sol and his colleagues tested this hypothesis by examining the 646 introductions (involving 196 species) in which humans had placed a population of birds in a novel environment, most often an island or a park outside its native range (Cassey et al., 2004; Cauchard, Overingtton et al., 2011; Sol, Duncan, et al., 2005). They collected data on brain size from 156 of the 196 species, and in the 40 remaining species in which there were no direct measures, they estimated brain size by using the brain size found in the closest phylogenetic relative for which data were available. Because larger-brained birds are generally larger than smaller-brained birds, Sol and his team corrected for this potential bias by using brain size relative to body size as their key parameter.

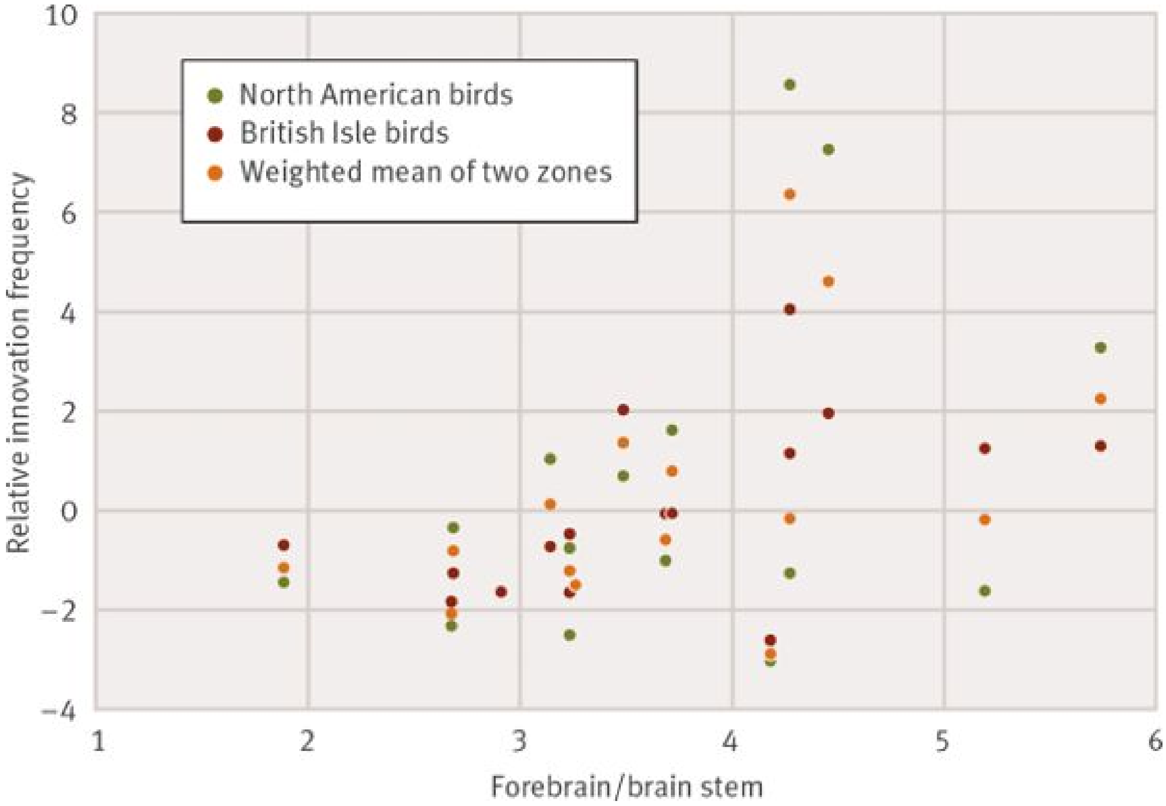


Figure 11.25. Brain size and foraging innovation in birds. In North American and British Isle birds, and in the weighted mean of North American and British samples, the relative frequency of foraging innovation is positively correlated with the ratio of forebrain mass to brain stem mass. *(Based on Lefebvre et al., 1997b)*

As discussed in chapter 6, Sol and his team found a positive relationship between relative brain size and the birds' success in novel environments. What's more, after correcting for potential confounding factors, they found evidence that the success of large-brained species was, at least in part, due to their relatively high use of innovative new foraging techniques, which increased their rate of food intake (Figure 11.26). These findings suggest that there is a fitness correlate with relatively large brains and the innovative abilities associated with them.

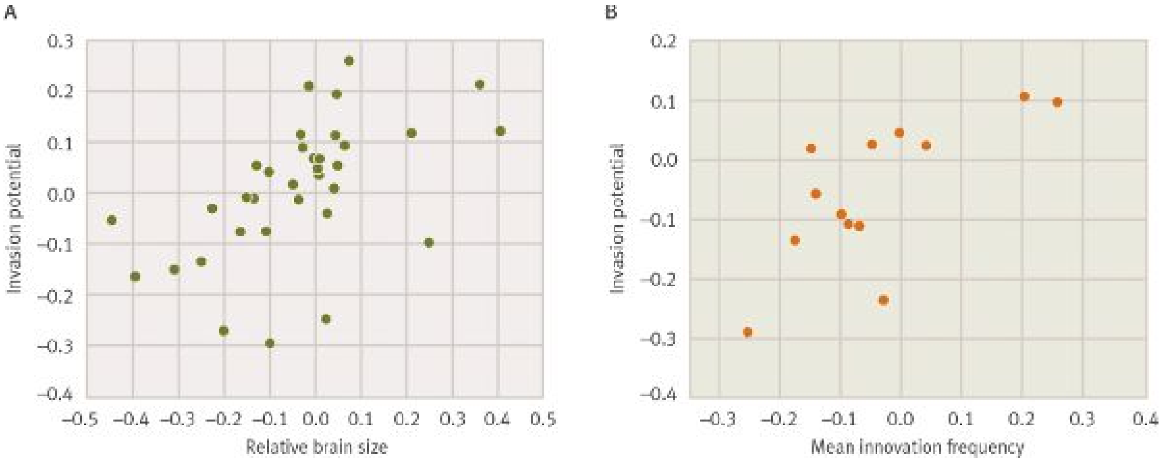


Figure 11.26. Brain size, innovation, and survival in birds. (A) The relationship between mean relative brain size and invasion potential (survival in a new environment) across avian families. (B) The relationship between mean foraging innovations and invasion potential across avian families. *(From Sol, Duncan, et al., 2005)*

FORAGING INNOVATION AND DIVERSIFICATION IN *EMBERIZOIDEA*

Chances are that you have learned about Darwin's finches and the exquisite fit between the shape of the bill and the type of food eaten in these fifteen species (Lack, 1947) (Figure 11.27). But Darwin's finches, along with their relatives, have recently shed light on the phylogeny of flexible foraging strategies and rates of evolutionary diversification, defined as an increase in species composition over evolutionary time.

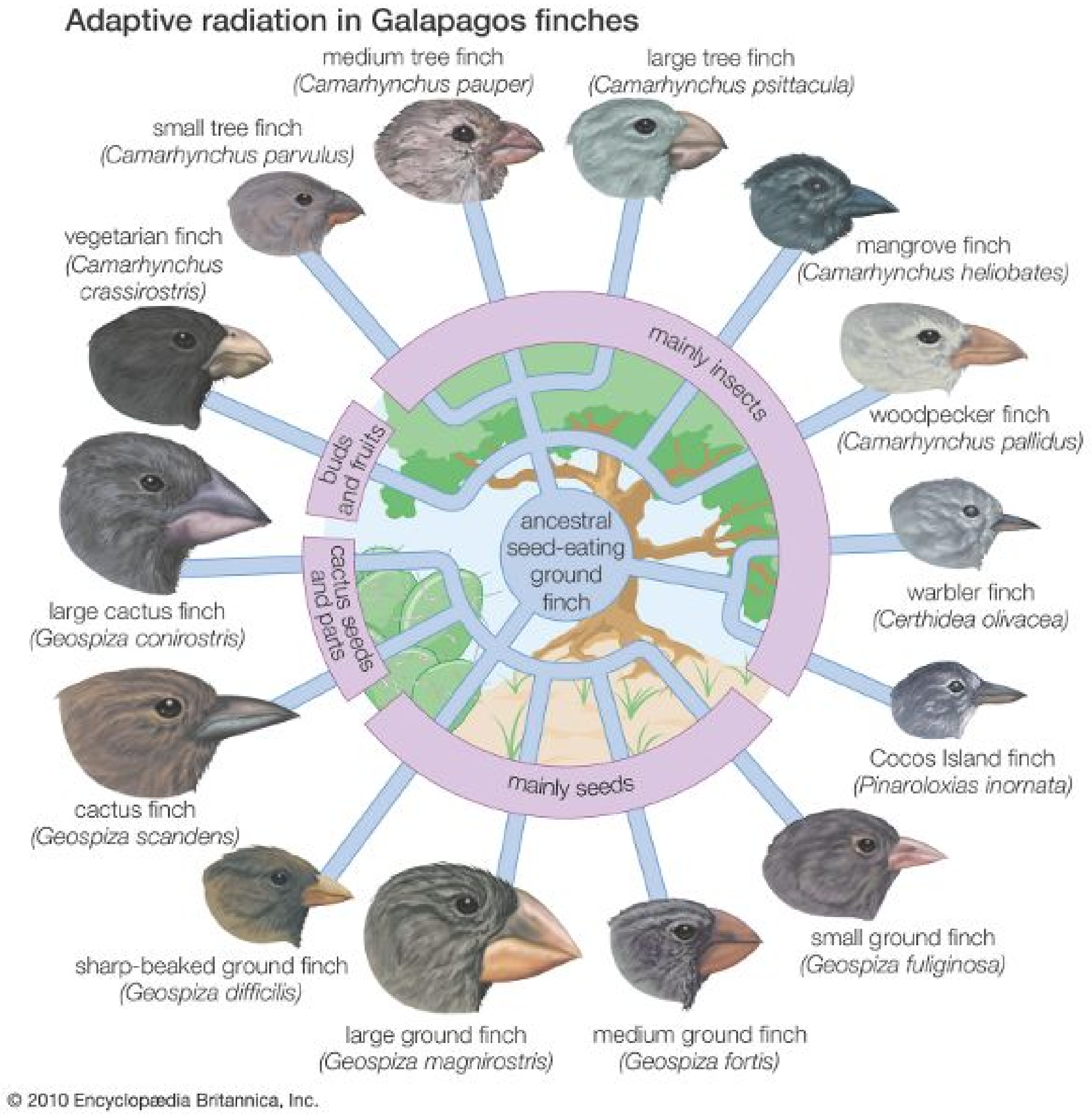


Figure 11.27. **Adaptation in Darwin's finches.** Beak size is well matched to the type of food individuals in different species consume. *(Credit: Universal Images Group North America LLC / Alamy Stock Photo)*

Taxonomically, Darwin's finches are part of the avian family *Thraupidae*, which is embedded within the superfamily *Emberizoidea*. Both this family and superfamily have an extremely high diversification rate (Barker et al., 2013). *Thraupidae* has diversification rates five times higher than avian means and ten times greater than that in vertebrate families. Some researchers have suggested that species in *Thraupidae* and *Emberizoidea* possess an intrinsic evolvability—defined as a propensity for dispersal, an ability to colonize, and high levels of phenotypic variation—which allows them to occupy new, diverse niches

(Burns et al., 2014). A related idea, Mary Jane West-Eberhard’s “flexible stem hypothesis,” proposes that such evolvability is especially likely when members of a clade possess flexible *behavioral* strategies (West-Eberhard, 2003). Lefebvre used phylogenetic analyses of innovative foraging behavior (one measure of behavior flexibility) to examine whether the clade to which Darwin’s finches belong show high rates of innovation, in part explaining the high diversification rates in these clades (Lefebvre et al., 2016).

Lefebvre and his colleagues used 352 published instances of foraging innovations, including drinking blood from a wounded mammal, opening sugar packets using a tool, and baiting fish with bread, to test this hypothesis. Using the comparative approach we discussed in earlier chapters, the researchers found strong support for West-Eberhard’s hypothesis: after correcting for research effort on each of the superfamilies in their analysis, the *Emberizoidea* superfamily had a higher frequency of innovations that any of the other 31 avian superfamilies analyzed (similar results were found at the family level) (Figure 11.28; Box 11.6).

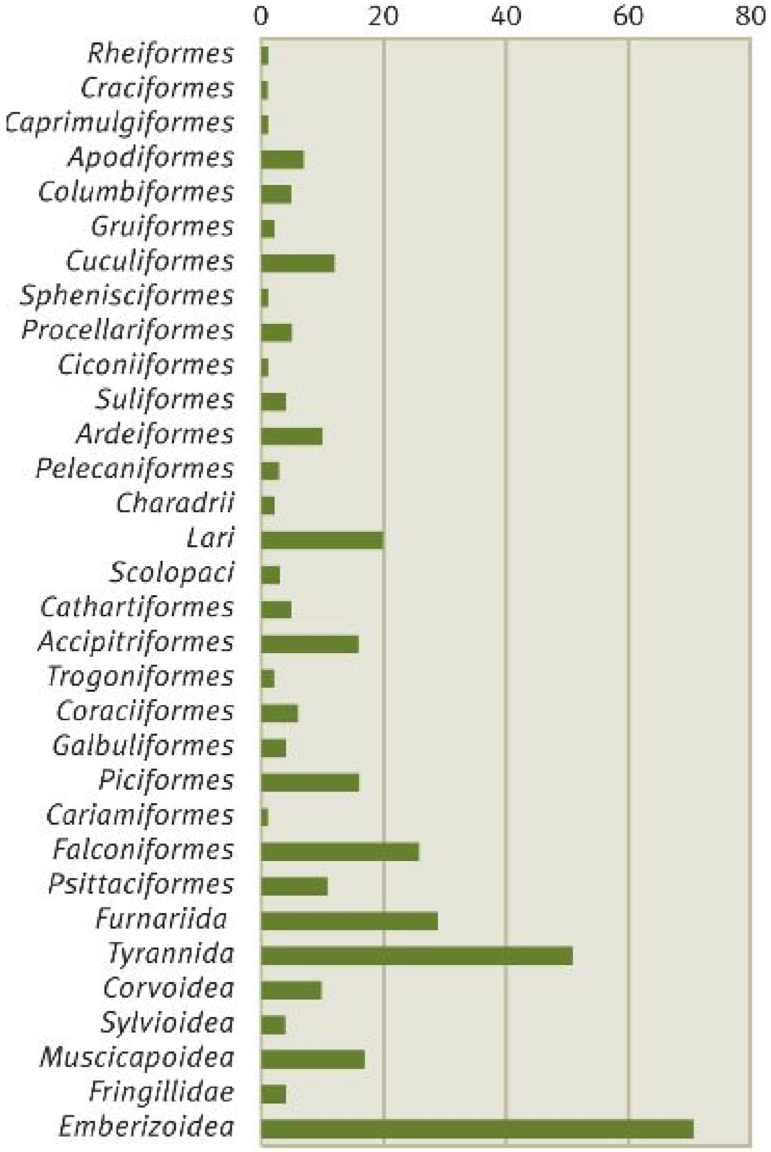


Figure 11.28. **Foraging innovations.** Innovation frequency in 32 avian subfamilies. By permission of the Royal Society. *(From Lefebvre et al., 2016)*

Box 11.6. SCIENCE AT WORK

What is the research question? Are high rates of foraging innovation associated with high rates of diversification rates in *Emberizoidea*, the superfamily of birds that include Darwin's finches?

Why is this an important question? Adaptive radiations—bursts of diversification in a clade—have long been of interest to evolutionary biologists.

What approach was taken to address the research question? A comparative analysis using already published data on 31 superfamilies of birds.

What was discovered? Compared to other avian supefamilies, *Emberizoidea* shows very high rates of both foraging innovation and diversification.

What do the results mean? In addition to such things as a propensity for dispersal and a general ability to successfully colonize new niches, one behavioral factor that may be linked to rates of high evolutionary diversification is a propensity to use new foraging techniques.

SOCIAL LEARNING AND FORAGING

Pigeons (*Columbia livia*) are an ideal species in which to examine cultural transmission associated with foraging (Figure 11.29). Being primarily scavengers feeding on human garbage, pigeons face a foraging dilemma: Which new food items are safe, and which are dangerous? Louis Lefebvre and his colleagues Luc-Alain Giraldeau and Boris Palemeta ran a series of experiments to examine whether cultural transmission plays a role in pigeon foraging behavior. This work focused on three related issues: (1) what type of information do pigeons transfer about food? (2) how does such information spread or fail to spread through a population of pigeons? and (3) what factors favor the cultural transmission of information over alternative means of acquiring information?

Figure 11.29. Scavenging pigeons. Pigeons are scavengers and are ideal for studying foraging and cultural transmission. *(© kmint stock / Shutterstock)*

The task that observer pigeons needed to learn was piercing the red half of a half-red/half-black piece of paper covering a box. Under the paper were seeds for the bird. Four groups were tested and in each an observer pigeon was placed in an arena with such a food box with a half-red/half-black paper cover. In the first group, observer birds saw no model on the other side of a clear partition. None of the pigeons in this group learned how to get at the hidden food, suggesting that it was a difficult task to master through individual learning. In a second group, observers saw a model that was eating from a hole in the paper. The hole was made by the researchers; although observers did see a model eating, they did not they did not see the model pierce the red half of the cover. Pigeons in this group did learn how to get food from the multicolored box, but the time lag until they began feeding from the box was long. In the final two groups in the experiment, birds either saw a model pierce the red side of the paper but get no food, or they saw a model both pierce the paper and eat. Birds in the former did not learn to solve the food-finding dilemma. Birds in the latter learned this task and learned fairly quickly (Figure 11.30), suggesting an important role for cultural transmission in the foraging behavior of pigeons (Palameta and Lefebvre, 1985).

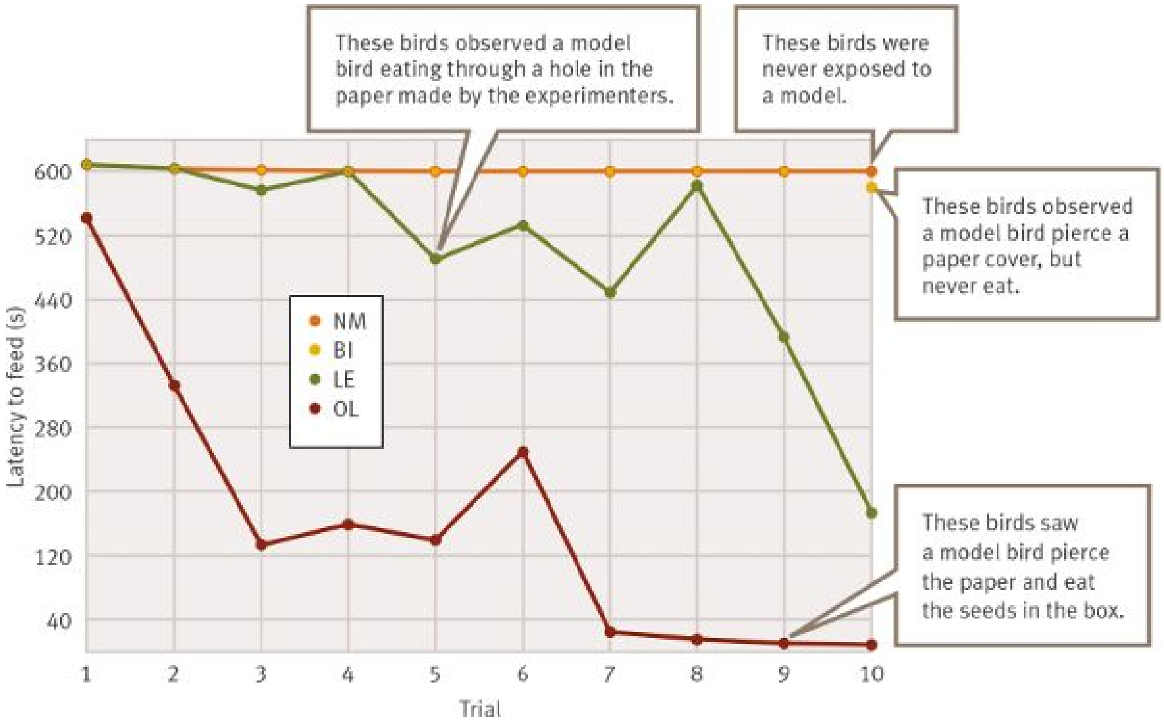


Figure 11.30. Social learning and foraging in pigeons. Pigeons needed to learn to pierce the red half of a paper covering a box of seeds. The graph shows average latency to eating for four groups: NM (no model), BI ("blind" imitation), LE (local enhancement), and OL (observational learning). Pigeons in the NM and BI treatments never learned to feed in the experimental apparatus. The quickest learning occurred in the OL treatment. *(Based on Palameta and Lefebvre, 1985)*

Pigeon groups contain both producers and scroungers. **Producers** find food, while **scroungers** follow producers and eat the food that producers have uncovered (Barnard, 1984; Giraldeau and Caraco, 2000; Giraldean and Lefebvre, 1986). And it is the unusual way that producing and scrounging interact with social learning that makes the pigeon studies particularly useful in furthering our understanding of cultural transmission and foraging.

Despite the above work demonstrating social learning in pigeons, when birds are tested in groups only a few birds seem to learn new feeding behaviors. Giraldeau and Lefebvre examined whether scrounging behavior somehow inhibited cultural transmission (Giraldeau and Lefebvre, 1987).

Flocks of pigeons were allowed to feed together. Forty-eight small test tubes were placed in a row and five of these tubes had food. Which five had food was unknown to the birds. To open a tube, an individual had to learn to peck at a stick in a rubber stopper at the top of the tube. When this task was done correctly, it caused the test tube to open and the contents to spread over the floor below. Once the food was out, any bird in the vicinity, not just the one that opened the tube, could eat it (Figure 11.31).

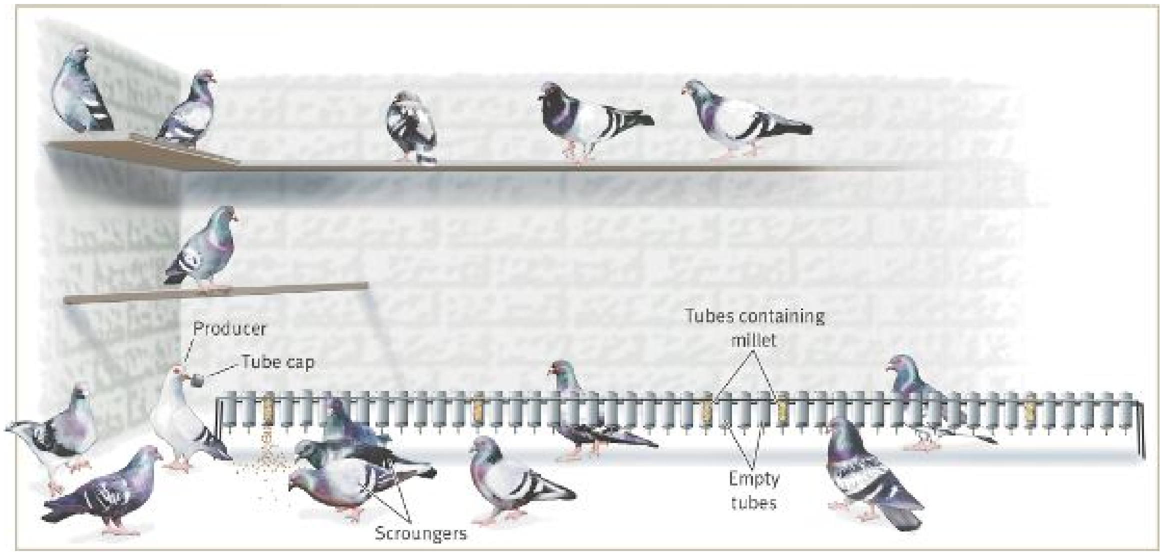


Figure 11.31. Producing and scrounging. When a group member finally opens a tube with food in it, the food spills on the floor and is accessible to all. Out of sixteen pigeons, only two learned to open tubes (these were the producers), while fourteen acted as scroungers. Labels show where millet was hidden, but the birds were not privy to this information.

As predicted based on earlier work, only two of the sixteen pigeons in the group learned to open tubes—the flock was composed of two producers and fourteen scroungers. Two findings suggest that scrounging inhibited an individual from learning how to open tubes via observation. First, scroungers followed producers and seemed more interested in *where* producers were than in *what* producers did to get food; the scroungers' attention was not directed at the actions taken by the producers to open the tubes. Second, by removing the two producers from the group, Giraldeau and Lefebvre discovered that scroungers not only didn't *display* the tube-opening trait, but they also didn't know how to open these tubes: it was not as if scroungers could open the tubes but opted not to, they seem never to have learned to do so from observing the producers.

In order to better understand how scrounging blocked cultural transmission of foraging skills, Giraldeau and Lefebvre ran a second set of experiments. Now they paired a single observer with a single demonstrator that already knew how to obtain food. If an observer had the chance to view a demonstrator open tubes and obtain food, over time the observer learned how to open tubes. All birds were capable of learning the foraging task. Giraldeau and Lefebvre then set up the experimental cages so that every time the demonstrator opened a tube, the food in that tube slid over to the observer's side of the cage. In these treatments, the observers rarely learned how to open the tubes themselves (Figure 11.32). Their scrounging on the food that was found by others interfered with learning about how to get the food themselves.

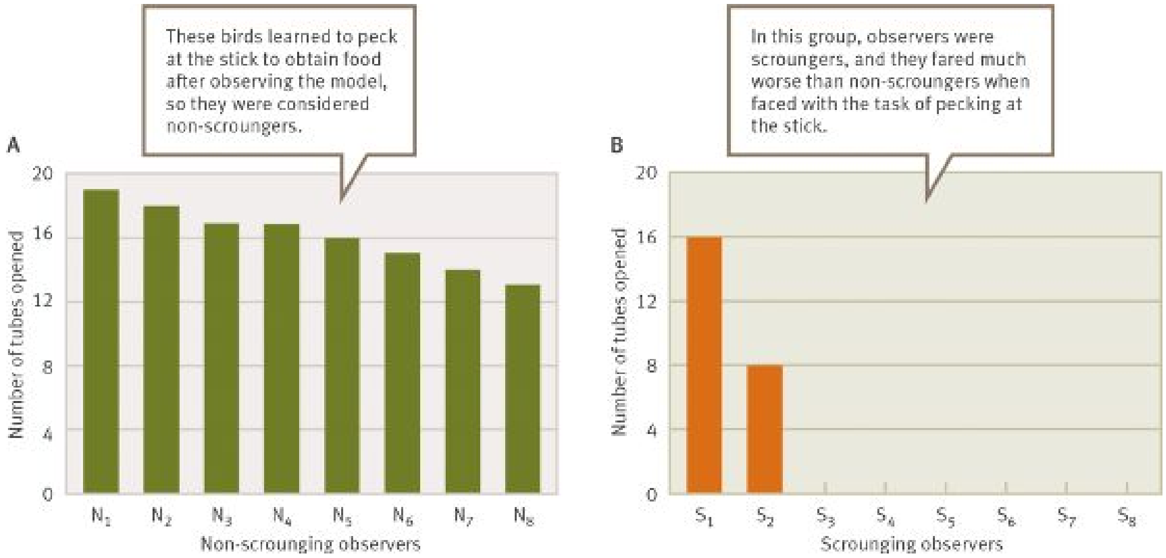


Figure 11.32. Scrounging prevents social learning. Two groups of pigeons were trained: (A) One group of birds saw a model bird peck at a stick in a rubber stopper at the end of the tube. This behavior provided food to the model. (B) In the second group of birds, when the model pecked at the stick, food was released, but to the observer. *(Based on Giraldeau and Lefebvre, 1987)*

Current work on foraging behavior continues in most of the areas we have covered in this chapter—prey choice, patch-leaving rules, risk sensitivity, group effects, and the role of phylogeny in shaping behavior, as well as in the role that both individual and social learning play in making foraging decisions.

Interview with Dr. John Krebs

How did it come to be that someone whose father won a Nobel Prize for coming up with the Krebs cycle made his initial mark in science by studying animal behavior?

No single factor, but a concatenation of many events led me to a career in animal behavior. I came to zoology as a bird-watcher; as a high school pupil I spent two summers working in the laboratory of the famous ethologist Konrad Lorenz; and as an undergraduate at Oxford, I was lucky enough to be taught by two giants of their generation, David Lack and Niko Tinbergen. Having said all this, my father dissuaded me from my first choice of a university course, namely archaeology, and I ended up as a zoologist, having failed to get in to study medicine! My PhD at Oxford was unusual in that I studied population ecology in Niko Tinbergen's animal behavior group. This meant that right from the start I saw the linkages between ecology and behavior that led to the emergence of "behavioral ecology."

One of the most innovative aspects of your work on foraging in great tits was the use of a conveyer belt to present food to the birds. How did you come up with that idea? What did this allow you to do that otherwise would have been impossible?

Throughout my career I have been extraordinarily fortunate in the exceptional colleagues, students, and coworkers I have had. The “conveyor belt” was not my idea. A graduate student in the animal behavior group at Oxford, Jon Erichsen, had devised it for psychophysical studies of reaction times in birds. Together we saw its potential for foraging studies. It would enable us to control encounter rates very accurately by having the prey move past the bird, rather than vice versa. I remember vividly posting to (no email in those days) Ric Charnov the first results from the conveyor belt. These showed that the inclusion or exclusion of the less profitable prey type depended exclusively on the encounter rate with the more profitable prey. The theory actually worked!

Psychologists have been studying the feeding behavior of animals for more than fifty years. Why the lag in ethological studies in this area? Why did they start up in earnest in the 1970s?

Ethologists had in fact been studying feeding behavior for many years. The important concept of “search image” was well established, and there were many studies of the cues used by animals for detecting food and the development of feeding skills during the life of an individual, as well as of predator avoidance strategies such as crypsis, mimicry, and warning colors. The new approach in the 1970s, known as “optimal foraging theory,” resulted from a confluence of ideas from ethology, ecology, evolution, psychology, and economics. As so often happens when new ideas are beginning to crystallize, more than one person independently came to similar conclusions. The seeds of foraging theory were more or less independently sown by J. T. Emlen, R. H. MacArthur and E. R. Pianka, J. D. Goss-Custard, and G. A. Parker. The attraction of foraging theory for me at the time, and I think for many others, was the juxtaposition of a broad theoretical framework, testable predictions from mathematical models, and both field and laboratory data.

How do classical psychologists and ethologists differ in the way they study animal foraging?

Traditionally, psychologists studied the mechanisms of behavior in the laboratory while ethologists and behavioral ecologists studied function or adaptation in the field. These boundaries have become blurred, to the benefit of both disciplines. For example, ethologists have adopted some of the experimental and theoretical tools of operant and classical conditioning as well as of cognitive psychology. Psychologists have increasingly taken on board the potential value of an evolutionary framework for understanding behavior.

Many optimal foraging models involve complex mathematics. Does that mean the animals have to know how to solve mathematical equations to forage efficiently?

Mathematical models of flight are complex, but birds do not need to be mathematicians in order to fly. Nor do they need to do sums in order to forage according to the predictions of optimal foraging models. Mathematics is the universal language used by a scientist to describe and analyze what goes on in nature. There is no implication that nature itself uses mathematics.

A number of foraging models focus on what are called “rules of thumb.” Could you explain the basic idea here?

Traditional foraging models were concerned with the end result (or adaptive significance) of foraging—for example, maximizing energy intake, rather than about the mechanisms that control feeding behavior. The notion of “rules of thumb” is that the end result, analyzed in a foraging model, might be achieved by a mechanism that approximates the “right” answer. If, for example, you were trying to find the best textbook of animal behavior, the rule of thumb “read if it is by Dugatkin” might bring you close enough to the optimal solution to be virtually indistinguishable from a more complex search strategy. If students following a different rule of thumb did better in exams, over time, the “Dugatkin rule” would be replaced by another rule that came closer to the optimal solution. In other words, rules of thumb are themselves subject to evolution by natural selection.

One potential critique of the foraging literature in ethology is that so many of the experiments undertaken are run in the laboratory and not in the field. In your estimation, how serious a problem is this?

If you are studying fundamental properties of animals—for example, decision-making rules—then they can be elucidated in the laboratory as well as in the field. A potential danger is that in the laboratory you may end up finding out more about the properties of your apparatus and experimental set-up than about the animal! This is a criticism that has sometimes been leveled at earlier studies of “schedules of reinforcement” by operant psychologists. Probably the ideal approach is to use a combination of field and laboratory work. Laboratory work certainly has the advantage that it is possible to control the variables more precisely. For laboratory work, intelligent design of the experimental set-up will help to ensure that the essence of the natural situation is captured.

What’s “the big question” to be tackled next in the study of animal foraging behavior?

Foraging theory, like any other branch of inquiry, will continue to evolve and change. I do not see a single “big question” on the horizon, but I see several potentially important ways in which the study of foraging behavior could develop. One of these is to apply ideas from foraging behavior to conservation. The pioneering work of J. D. Goss-Custard and W. J. Sutherland has shown how foraging models can be used to predict the effects of habitat loss and disturbance on threatened populations. The key has been to link the foraging of individuals to density-dependent influences on the population as a whole. Another area of recent, and likely continuing, growth consists of the links between behavioral economics, decision theory, and foraging behavior. This is a development of the links between animal psychology and foraging behavior that began decades ago. New insights are flowing in both directions. More generally, I do not think we should regard “foraging behavior” as an ineluctable, distinct field of inquiry. The basic ideas may be reconfigured, remolded, and reinvented so that the categories used to describe behavior today might seem outmoded in ten years’ time.

Dr. John Krebs is emeritus professor at Oxford University in England. Dr. Krebs's work on foraging behavior was seminal to the development of optimal foraging theory. Dr. Krebs (along with Dr. Nick Davies) is the editor of *Behavioural Ecology: An Evolutionary Approach*, 4th ed. (Blackwell Science, 1997).

SUMMARY

1. One way animals determine what sort of food to search for is through the development of a search image. A search image is formed when animals that encounter a prey type more and more form some sort of representation of the prey, and as this representation or image becomes more and more detailed with experience, the forager finds itself more successful at finding that type of prey.
2. Optimal foraging theory is a class of models that predicts what and where animals should eat, the effect of hunger state on risk-sensitive foraging, and much more.
3. Optimal foraging models of prey choice predict that the encounter rate with the less profitable of two prey items does not affect whether that item should be added to the diet or not. Instead, a critical encounter rate with the *most* profitable item is what determines which prey items should be added to a diet.
4. The marginal value theorem predicts how long a forager should stay in a given patch, given that it can leave and travel to feed in less depleted patches.
5. Theory predicts that hungry foragers will be risk prone—willing to assume greater variance (risk) in food intake than less hungry individuals.
6. Compared with solitary foraging, foraging while in groups often, but not always, increases the foraging success of individuals. Benefits of group life include the ability to learn about various aspects of the foraging environment from observing others.
7. Animals often learn how and on what to forage. Learning sometimes manifests itself in foraging innovations; brain size often correlates with the frequency of such foraging innovations.

DISCUSSION QUESTIONS

1. Read R. Pulliam's 1973 article "On the advantages of flocking," in the *Journal of Theoretical Biology* (vol. 38, pp. 419–422). Based on the article, outline the "many eyes" hypothesis, and discuss how it relates to foraging behavior.
2. Read E. L. Charnov's 1976 article, "Optimal foraging, the marginal value theorem," in *Theoretical and Population Biology* (vol. 9, pp. 129–136). How might you modify the model to examine other behaviors displayed by animals?
3. Using the model developed on p. 301 as a starting point, construct a foraging model with three prey types. Imagine that you already know that it pays for a forager to eat prey type 1 and prey type 2. What are the conditions under which the forager should add prey type 3?
4. Why do you suppose it took so long for ethologists and psychologists to recognize the larger literature on foraging behavior that exists in each other's field? What do you think were the biggest differences in the way foraging was studied in these two disciplines?
5. Using the graphs in Figure 11.9 as a starting point, examine what happens to the time an animal should spend in the patch as a function of how profitable that patch is. This will involve changing the shape of the curve that describes food intake as a function of patch residence time and examining what this change does to optimal time in a patch.

6. How does the corvid phylogeny paper discussed in this chapter show that the adaptationist and phylogenetic approaches to studying brain size and caching can complement one another?

SUGGESTED READING

Gibson, B., & Kamil, A. (2009). The synthetic approach to the study of spatial memory: Have we properly addressed Tinbergen's "four questions"? *Behavioural Processes*, *80*, 278–287. A thought-provoking piece on the different ways to study memory, with an emphasis on foraging behavior.

Giraldeau, L. A., & Caraco, T. (2000). *Social foraging theory*. Princeton, NJ: Princeton University Press. A comprehensive overview of social foraging theory, with many empirical examples to lead the reader through the math.

Hill, K. (2002). Altruistic cooperation during foraging by the Aché, and the evolved human predisposition to cooperate. *Human Nature–an Interdisciplinary Biosocial Perspective*, *13*, 105–128. Foraging behavior and its relation to cooperation in the Aché Indians of Paraguay.

Kacelnik, A., & El Mouden, C. (2013). Triumphs and trials of the risk paradigm. *Animal Behaviour*, *86*, 1117–1129. A review of risk-sensitive foraging and where the field should move in the future.

Stephens, D., Brown, J. S., & Ydenberg, R. C. (Eds.). (2007). *Foraging: Behavior and ecology*. Chicago: University of Chicago Press. An edited book on foraging theory and animal behavior.

12

Antipredator Behavior

In 2009, for example, Karen Osborn and her colleagues discovered seven new species of annelid worms—some of which were found swimming as deep as 3,793 meters (more than 12,000 feet) below the ocean surface. Osborn and her colleagues wondered how these species, living in a world with almost no light, defend themselves from the dangers around them. To their surprise, they found that these newly discovered worms startle or distract potential predators with "bombs" of green fluorescent light (Osborn et al., 2009).

Five of the seven species that Osborn and colleagues discovered produce small bioluminescent sacs (globules)—what the researchers termed *bombs*—that they likely release when encountering predators (Figure 12.1). These bombs light up for a few seconds after the worms release them and may startle a predator long enough to allow the worm to escape the danger. Much remains to be learned about exactly how the bioluminescent bomb system works (Haddock et al., 2010; Widder, 2010), but a phylogenetic analysis based on gene sequences from these worm species allowed researchers to estimate where in the evolutionary history of these worms bioluminescent sacs evolved (Figure 12.2). What's more, these bioluminescent sacs are homologous with other known anatomical structures (called segmented branchiae) in annelid worms that do not have bioluminescent sacs, so animal behaviorists have an idea what structure the bioluminescent sacs are derived from.

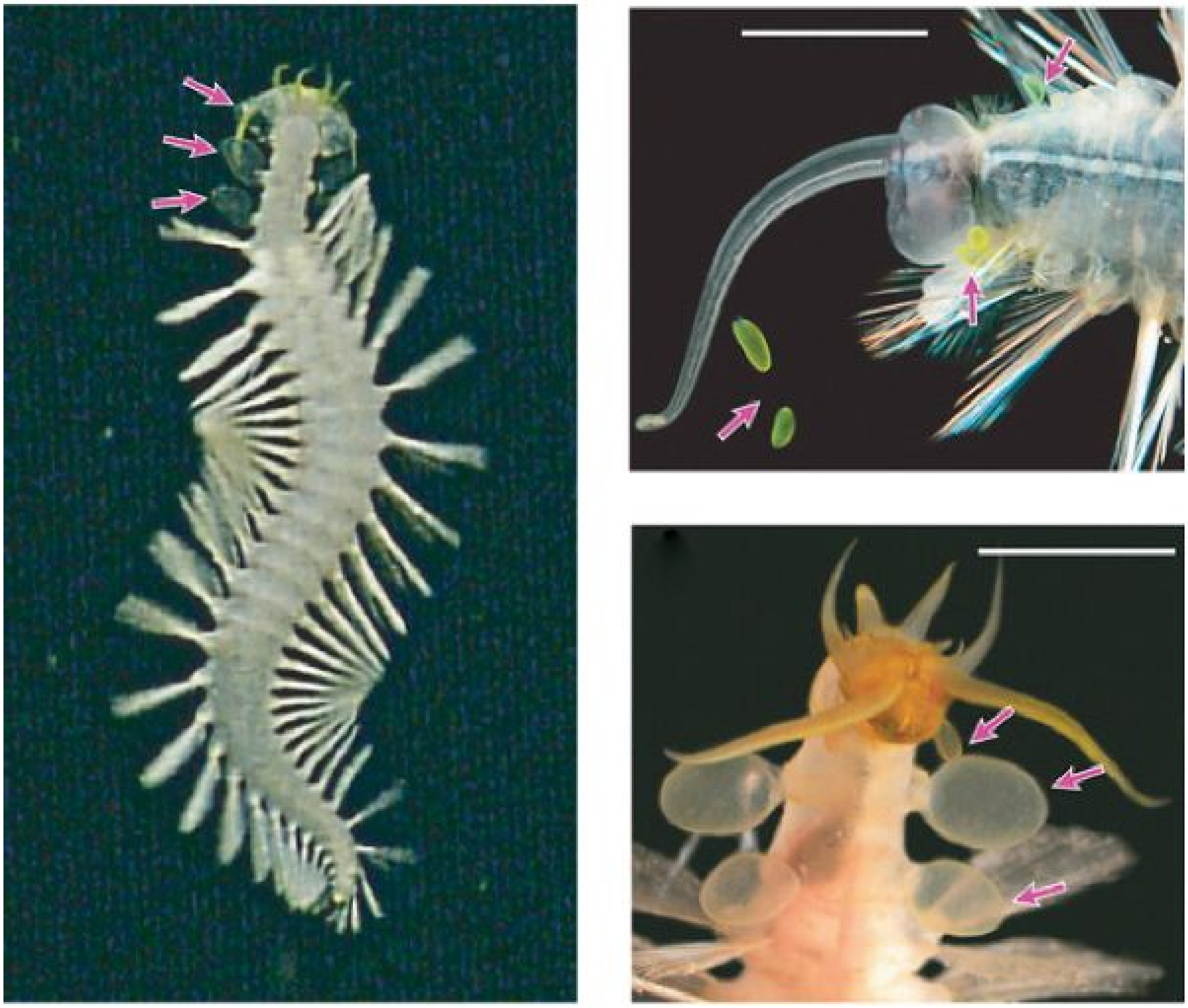


Figure 12.1. Luminescent bombs as an antipredator defense. (A) *Swima* sp. 3, with arrows indicating bombs. (B) *Swima* sp. 1 with three attached and two unattached bombs. Two bombs are shown at the bottom left and the center arrows. (C) *Swima* sp. 3 with three pairs of attached bombs. *Reprinted with permission from AAAS. © 2009. (From Osborn et al., 2009)*

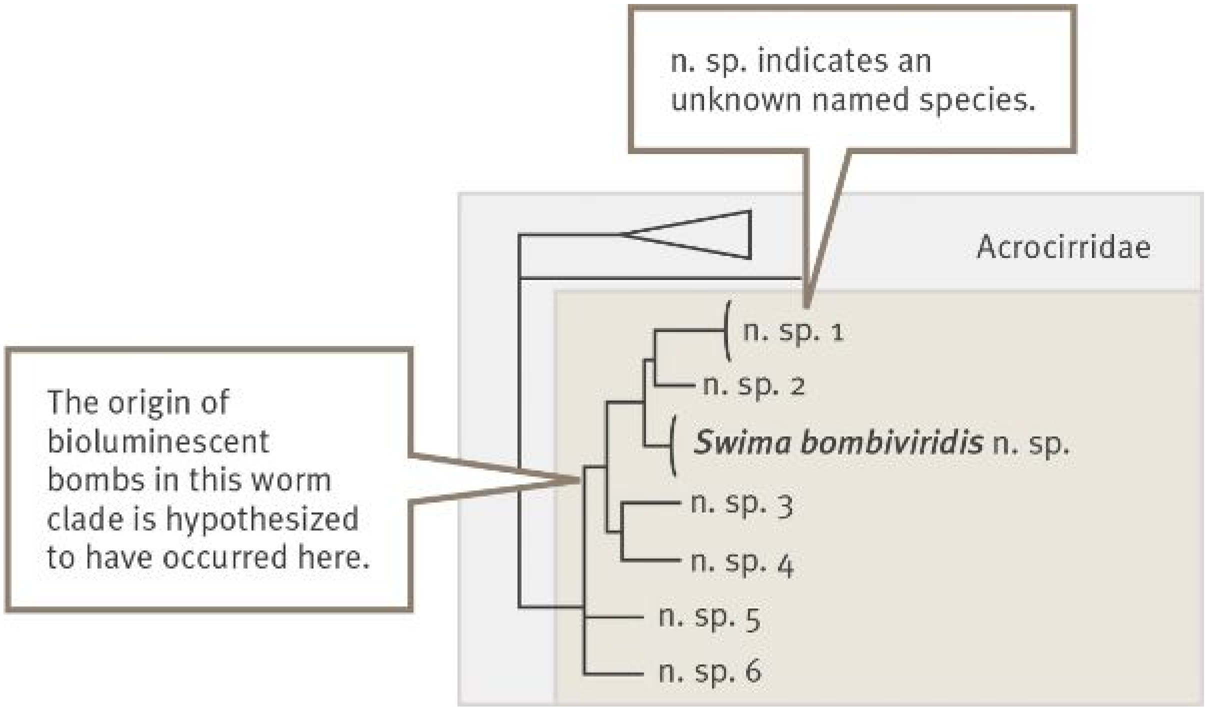


Figure 12.2. Phylogeny of bioluminescent bombs in annelid worms. A phylogeny of *Swima* species. *Swima bombiviridus* and unnamed species 1–4 produce “bombs.” Unnamed species 5 and 6 do not produce “bombs.” *(From Osborn et al., 2009)*

Scientists need not look 12,000 feet below the ocean surface to find defense compounds used against predators. Larval *Zygaena filipendulae* (Hymenoptera) secrete a viscous compound through segmentally arranged cavities on their cuticle when they encounter a potential predator (Pentzold et al., 2016). These droplets, composed of a mélange of proteases, protease inhibitors, oxidases, and other chemicals, essentially glue together the appendages of predators, sometimes killing them (Figure 12.3).

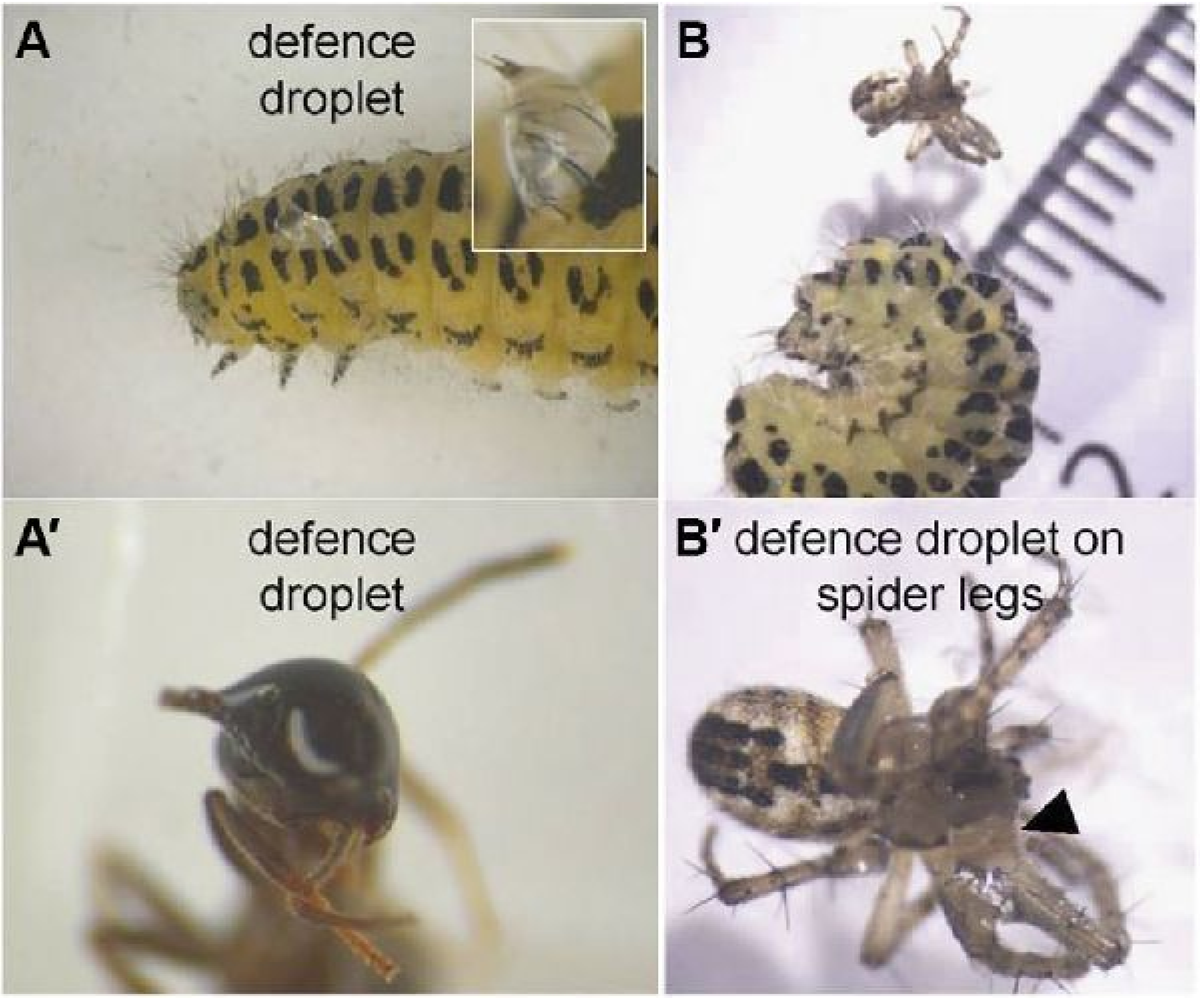


Figure 12.3. **Viscous droplets.** After contact with a predator larval *Zygaena filipendulae* secrete a viscous compound. (A) a defense droplet being produced by *Z. filipendulae*, A′) a defense droplet on an ant's head, B) a predatory spider, *Mangora acalypha*; and B′) the defensive droplet glues the legs of the spider together. *(From Pentzold et al., 2016)*

* * *

If an individual makes an error with respect to the antipredator tactics it uses, its future reproductive success may be zero. This obvious, but striking, fact suggests that natural selection should operate very strongly on antipredator behavior and that we might expect fine-tuned adaptations in this behavioral venue. Both because interactions between predators and their prey are often spectacular to observe, and because such interactions are so critical for understanding the process of natural selection, ethologists have a long history of studying antipredator behavior (Lind and Cresswell, 2005). Comparative psychologists have also long been interested in predator-prey interactions. But it was not until Robert Bolles developed an explicitly evolutionary approach to this subject that comparative psychologists conceptualized specific antipredator behaviors as specific adaptations (Bolles, 1970).

There are two basic types of antipredator behaviors: those that help prey avoid detection by predators, and those that function once a prey encounters a predator. In this chapter, we will explore these two forms of antipredator behavior from both a proximate and an ultimate perspective. Before proceeding, two caveats: (1) while these two categories encompass most antipredator behaviors, they are not meant to be exhaustive; and (2) only biotic (living) predators are considered in this chapter. Fire, for example, kills many animals, and there is evidence that reed frogs (*Hyperolius nitidulus*) respond to the sound of oncoming flames and flee (Grafe et al., 2002). We will not consider such instances here.

Avoiding Predators

If prey can avoid being detected by their predators, they decrease not only the probability of being captured and eaten but also the costs associated with fleeing or fighting back (Brilot et al., 2012; Ruxton et al., 2004; Stanford, 2002). We will examine three ways that animals can avoid their predators: (1) blending into the environment, (2) being quiet, and (3) choosing safe habitats.

BLENDING INTO THE ENVIRONMENT

One way for animals to avoid predators is through cryptic matching to the environment, making detection by predators less likely. This sort of background matching need not be behavioral per se. Francis Sumner, for example, found that populations of the mouse *Peromyscus polionotus* had fur coloration that matched the background of the beaches (or inlands) on which they lived (F. B. Sumner, 1929a,b). Mice were not behaving in any particular way that increased their crypsis; “beach mice” displayed light coat pigmentation that better matched the sand on which they lived, and coat pigmentation became darker in populations farther from the beach and closer to the inland areas (Figure 12.4). Subsequent work has found that a single mutation in the melanocortin-1 receptor (Mc1r) plays a role in this example of crypsis (Hoekstra, 2006).

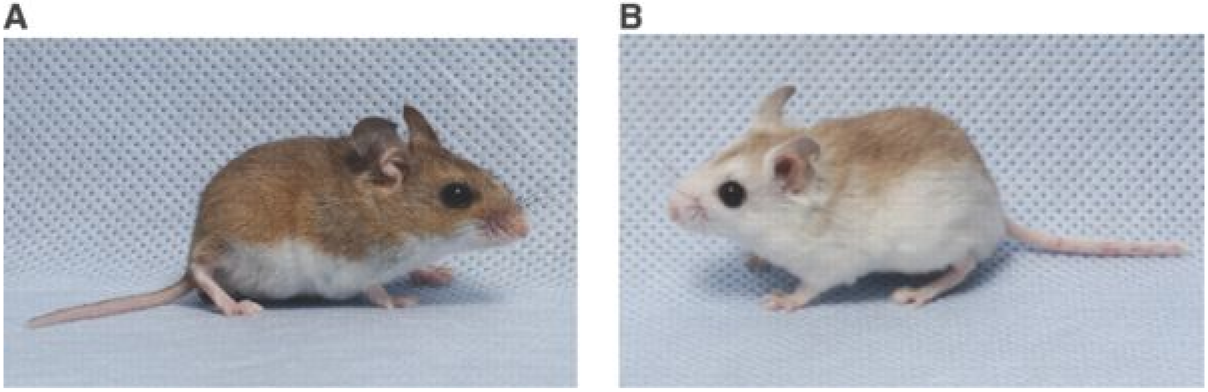


Figure 12.4. Coat color variation. In *Peromyscus polionotus*, mice on inland populations (A) tend to have darker coats than mice from beach populations, (B) where the sand is light in color. *Reprinted with permission from AAAS. © 2006. (From Hoekstra et al., 2006)*

Animals can also hide from their prey by behaviorally changing color to match their environment. Cephalopods—which include octopuses, squids, and cuttlefish—are especially adept at changing color quickly to blend into their background, decreasing their chances of being attacked by a predator (Hanlon and Messenger, 1988; Packard, 1972). While most work on camouflage from predators has been conducted during the day or at sunset, Roger Hanlon and his team have found that predation on cephalopods also occurs at night, as many predators of cephalopods have sharp night vision.

Hanlon and his colleagues used a noninvasive light source—one that relied on a red filter—to observe the nocturnal behavior of the giant Australian cuttlefish (*Sepia apama*), and, in particular, to test whether the cuttlefish used camouflage at night, to hide from predators with good night vision (fur seals, bottlenose dolphins, and some species of fish; Hanlon et al., 2007, 2013; Buresch et al., 2015). The researchers found that cuttlefish were camouflaged in seventy-one of eighty-three (86 percent) nocturnal observations, which is likely an underestimate, as some cuttlefish may have matched the environment so well that the underwater camera employed simply missed them. Hanlon found that cuttlefish could match their background in one of three ways, and they could change their color and pattern to match their background in a matter of seconds.

The first kind of crypsis involved a “uniform” camouflage pattern in which cuttlefish takes on a single skin color—a color that matched their background (Figure 12.5). Although this form of camouflage was rare, when it occurred it often involved a cuttlefish mimicking the rocks around them. The second kind of crypsis made up almost half of the instances of background matches and involved “mottled camouflage” patterns, where cuttlefish changed their appearance such that their skin had small dark and light splotches all over. The size and color of the splotches often mimicked the cuttlefish’s background. This patterning was observed most often when the background is composed of small rocks and dark algae.

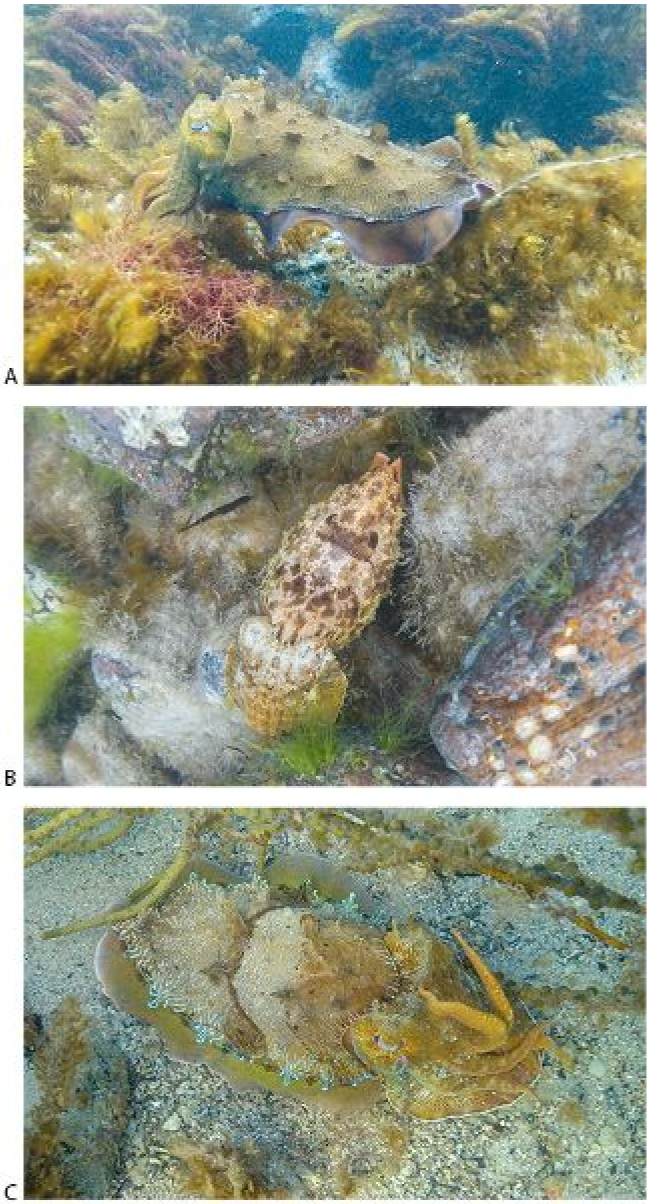


Figure 12.5. Cuttlefish camouflaging. (A) Cuttlefish using uniform color to camouflage itself against the rocks; (B) cuttlefish using a "mottled" camouflage pattern, with small dark splotches resembling the dark patches on rocks and sand; and (C) cuttlefish using a "disruptive" camouflage pattern, with large light and dark areas that enable it to blend in with the background. Arrows indicate where the cuttlefish are located. *(Photo credits: Roger Hanlon)*

The third form of crypsis employed by cuttlefish was "disruptive camouflage," in which a cuttlefish changed color and pattern, taking on large light and dark stripes. This had the effect of visually breaking up (disrupting) the animal's body so it did not look like a cuttlefish. On some occasions, though not often, the stripes actually mimicked the pattern of the cuttlefish background.

All of these different forms of camouflage techniques strongly suggest that for large, soft-bodied creatures such as the giant cuttlefish, blending into the environment is an important antipredator behavior (Hanlon and Messenger, 1988).

BEING QUIET

When predators use sounds made by their prey to detect them one thing that an animal can do to escape danger is to be quiet (M. Ryan, 1985). Luke Remage-Healey and his colleagues examined the role of sound suppression in the antipredator repertoire of the Gulf toadfish (*Opsanus beta*; Remage-Healey et al., 2006).

Gulf toadfish are preyed on by adult bottlenose dolphins (*Tursiops truncatus*), making up 13 percent of the dolphin’s diet (Barros, 1993). Prior work had shown that dolphins orient toward the “boat-whistle” sound produced by male toadfish during breeding season (Gannon et al., 2005). Once the dolphin locates a toadfish, it locks onto this prey and tracks it. The question Remage-Healey and his colleagues addressed was whether toadfish listen for sounds associated with bottlenose foraging behavior and then reduce the boat-whistle sounds they produce (Figure 12.6).

Figure 12.6. Gulf toadfish. Gulf toadfish are preyed on by bottlenose dolphins. Dolphins orient toward the "boat-whistle" sound produced by male toadfish during the breeding season. *(Photo credit: © Margaret Marchaterre)*

Bottlenose dolphins produce a variety of sounds, including high-frequency whistles used in dolphin-to-dolphin social communication (not foraging), as well as two sounds—"clicks" and low-frequency "pops"—that are associated with foraging (Janik et al., 2006; Nowacek, 2005; Tyack and Clark, 2000). Remage-Healey and his colleagues captured toadfish during the breeding season, and they kept individual males in tanks. When males began to emit boat-whistle sounds to attract females they were exposed to one of three sounds—the pops associated with dolphin foraging; the high-frequency whistles produced during dolphin social communication; and, as a control, the "snapping" sounds made by snapping shrimp. All sounds were broadcast using underwater speakers, and the activity of toadfish was recorded for the five minutes before sounds were emitted, the five minutes during which the experimental sounds were broadcast, and the five minutes after the sounds were played.

Remage-Healey found no differences between treatments in call rate between males *before* exposure to the experimental sounds (Figure 12.7). But males exposed to pop sounds reduced their call rates by 50 percent. In addition, males exposed to the pop sounds maintained their reduced calling rate for the five minutes following exposure to pops. Males in the other treatments showed no changes in boat-whistle call rate when they heard the recorded sounds.

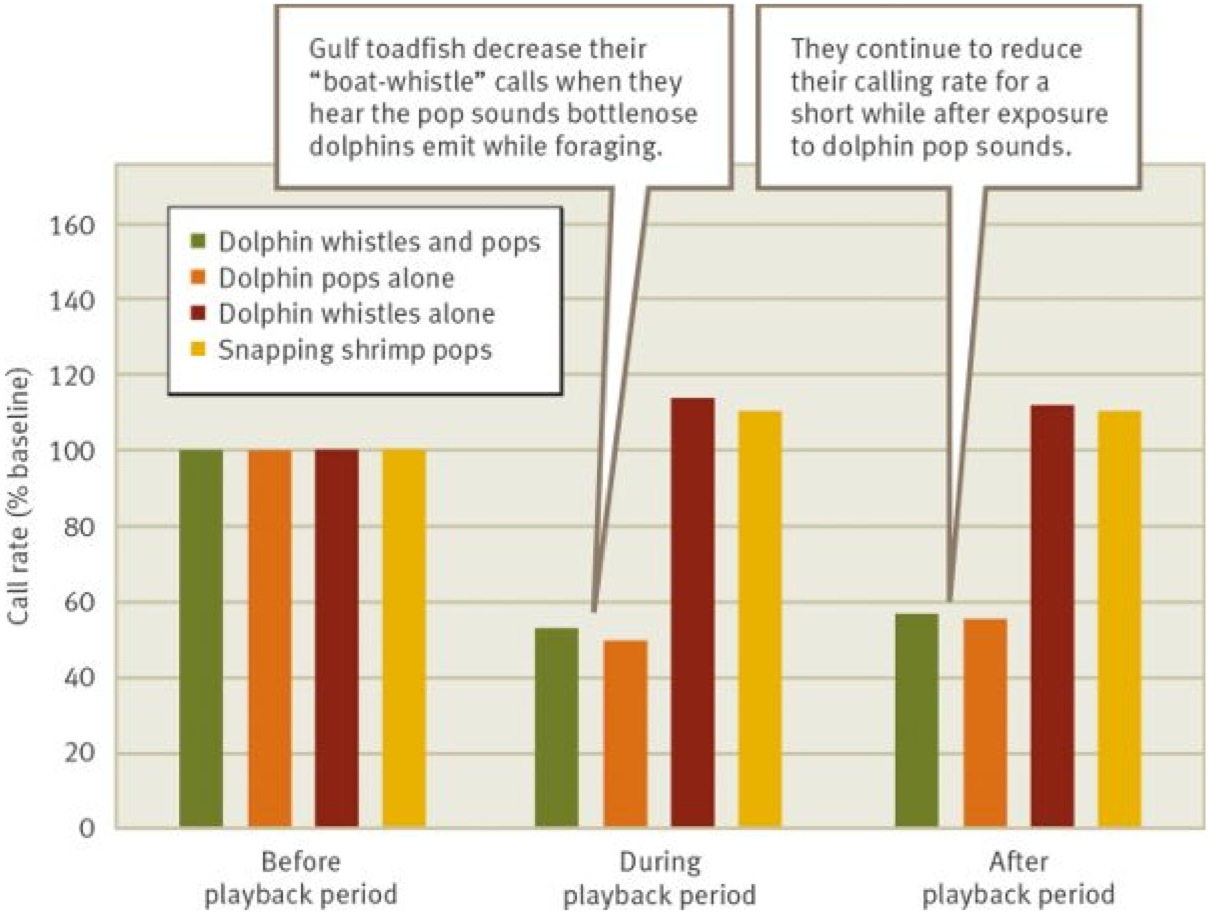


Figure 12.7. Gulf toadfish become silent. Gulf toadfish responses to four different calls, before, during, and after hearing these calls. The "before-playback-period" data were standardized to a baseline value of 100 for means of comparison. *(From Remage-Healey et al., 2006)*

Remage-Healey and his team followed up their behavioral work on call rates and exposure to predators with a hormonal analysis that examined whether dolphin pops produce a stress response in the toadfish. After experimentally exposing the male toadfish to pops or snapping shrimp sounds, they drew blood from the males and measured their cortisol levels. Males exposed to pops not only responded to the pops by reducing their own boat-whistle calls, but they also showed higher levels of cortisol than males exposed to the sound of snapping shrimp.

CHOOSING SAFE HABITATS

Another way that prey can avoid predators is by living in habitats that are relatively predator free (see also Box 12.1). Here we will look at a case study that involves a phylogenetic perspective on habitat selection and predator avoidance in parrots.

Box 12.1. CONSERVATION CONNECTION

Co-evolution, Naive Prey, and Introduction Programs

Conservation biologists sometimes use translocation programs—moving individuals from one natural habitat to another—to protect threatened or endangered species (Ewen et al., 2012, 2014; Germano et al., 2014). Researchers involved in such translocations are starting to take into account that the species they are moving originally evolved in an environment with a particular set of predators, and that **co-evolution** may have been occurring between these predators and prey. Co-evolution occurs when changes to traits in species 1 lead to changes to traits in species 2, which in turn feed back to affect traits in species 1, and so on. Predator-prey co-evolution can lead to an evolutionary **arms race** between predator and prey: The prey evolve behaviors that help them protect themselves against the predators, and the predators evolve detection systems that help them find prey. This co-evolutionary dynamic is important to understand for translocation programs, as such programs may inadvertently introduce the translocated species to predators with which they have had no evolutionary history and to which they are especially susceptible.

To understand how exposure to new predators in a new environment affects prey, Isabel Barrio and her colleagues studied the antipredator behavior of the wild rabbit (*Oryctolagus cunuculus*), which was introduced into Australia by European settlers (Barrio et al., 2010). Rabbits use odor cues to detect many of their predators. In Australia, rabbits are preyed upon by foxes, cats, and ferrets, which have also been introduced there. But rabbits and these other species have a long-shared evolutionary history, primarily on the Iberian peninsula (Jaksic and Soriguer, 1981). Wild rabbits are also preyed upon by predators that are native to Australia, such as the spotted-tail quoll (*Dasyurus maculatus*; Glen and Dickman, 2006).

When Barrio and her colleagues exposed the wild rabbits in Australia to the odor of foxes, cats, and ferrets, the rabbits responded by reducing their use of the area with the predator odor. No such response occurred when the rabbits were exposed to the odor of the spotted-tail quoll, with whom they shared no evolutionary history (Figure 12.9). The rabbits' usual first line of defense against predators, odor detection, was ineffective for this new predator, leaving the rabbits vulnerable to the quolls.

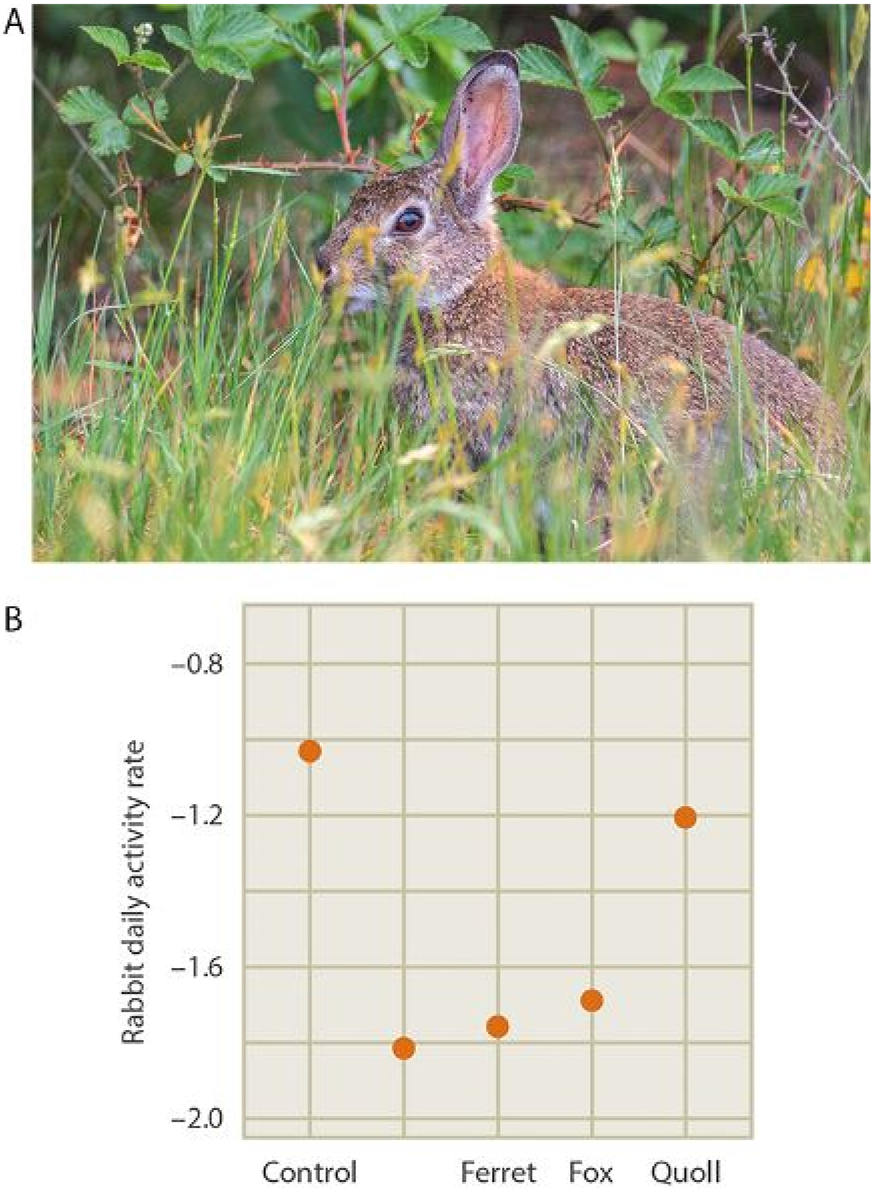


Figure 12.9. Rabbits’ antipredator behavior and co-evolutionary history. Compared with controls, rabbits decreased their use of areas that had the scent of three predators with which they had an evolutionary history (ferrets, cats, and foxes), but they did not decrease their use of areas that had the scent of the predator that was native to Australia, with which they shared no evolutionary history (the spotted-tail quoll). The *y*-axis data is given in negative numbers as a result of the way researchers transformed the data on activity rate. *(Photo credit: © Bernd Wolter / Shutterstock; From Barrio et al., 2010)*

This work suggests that to maximize success rates, introduction and relocation program managers need to consider whether the species they are trying to protect shares an evolutionary history with the predators in the new environment. The species may not possess evolved antipredator adaptations in either a specific or a general sense. In some cases, translocated species may be at serious risk because they have not evolved antipredator behaviors to a specific predator in their new environment, as in the case of the wild rabbits in Australia (though, fortunately, some recent work suggests that rabbits are starting to display an evolved recognition of the odors of two quoll species; Tortosa et al., 2015). In other cases, the translocated species may not have evolved antipredator behaviors to certain *types* of predators in their new environment (for example, ambush hunters, predators that detect prey by odor, and others). Detailed knowledge of these sorts of issues can help conservation biologists and managers design better programs.

Predation and Choice of Nesting Sites in Parrots

Many birds build their nests in tree cavities. Others nest in different kinds of cavities—old termite mounds, the sides of cliffs, etc. From a phylogenetic perspective, there are bird taxa that contain both species that nest in tree cavities (TC nesters) and species that nest in other sorts of cavities (OC “other cavity” nesters). This raises a number of questions: Within a clade, which of these behaviors—nesting in tree cavities or nesting in other sorts of cavities—is the ancestral variety of the state? In addition, once we know the ancestral state, what selective forces were responsible for the evolution of the other (derived) behavioral state? Did predation drive the choice of nesting area so as to minimize encounters with predators?

Donald Brightsmith addressed these questions in parrot species from both Australia and Amazonia, where many populations are at risk from manmade (anthropogenic) factors (Olah et al., 2016). He obtained molecular genetic-based phylogenies from six Australian parrot species and dozens of species of Amazon parrots (Brightsmith, 2005a,b; Ribas and Miyaki, 2004; Rowden, 1996; Russello and Amato, 2003). Brightsmith also collected published data on the nesting behavior (TC or OC) of as many of the species in the above-mentioned phylogenies that he could uncover. He then mapped the nesting data onto the phylogenies to examine ancestral and derived nesting behaviors. This analysis suggests that the ancestral state was tree cavity nesting, and that nesting in other cavities had evolved independently many times in both Australian and Amazonian parrot species (Figure 12.8).

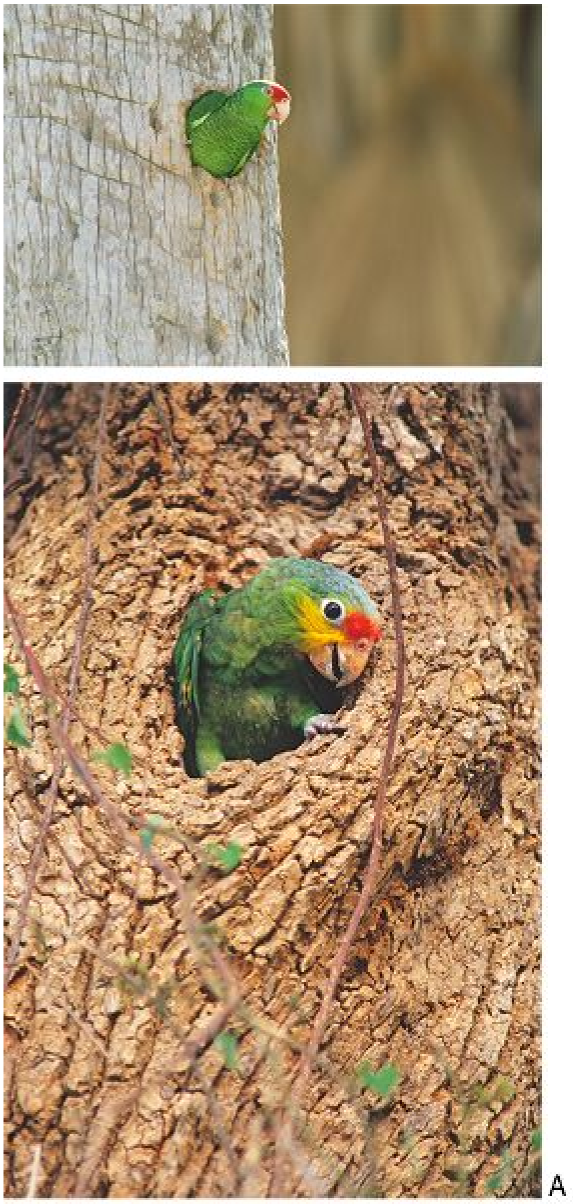


Figure 12.8. A phylogeny of nesting behavior in parrots. (A) Red-lored parrots (*Amazona autumnalis*: top) and red-crowned parrots (*Amazona viridigenalis*: bottom). (B) A (partial) phylogeny of the nesting behaviors of Amazon parrots. “?” denotes unknown nesting behavior. *(Photo credits: Claudio Contreras/ npl / Minden Pictures; Rolf Nussbaumer/ npl / Minden Pictures)*

Brightsmith next examined what selective forces, if any, were responsible for the evolutionary shift from tree cavity nesting to OC nesting. In particular, ecologists had suggested two possible selective forces driving OC nesting: (1) because competition for tree cavity nests is typically intense, selection in some species may have favored nesting in other sorts of cavities (Beissinger, 1996; T. E. Martin, 1993; Monkkonen and Orell, 1997; Wiebe, 2011); and (2) predation on eggs and chicks is very high during the nesting period, and shifting from tree cavities to nesting in such places as old termite mounds or the face of cliffs may have decreased predation pressure (Lack, 1968). Predation and competition, of course, are not mutually exclusive explanations here.

To test for the effects of competition and predation on the shift in nesting behavior, Brightsmith reasoned as follows: Prior work suggested that when birds were released from competition an increase in clutch size often occurred over evolutionary time. Having had limited opportunities to find nests in the evolutionary past should favor investing heavily in offspring production. They did not find any evidence for increased clutch size in OC nesters, providing no support for the competition hypothesis.

To examine whether predation was the key force selecting for the shift away from tree cavity nesting, Brightsmith turned to an idea first suggested by David Lack (Lack, 1968). Lack hypothesized an inverse correlation between nest predation rate and the length of nesting period, and a subsequent study of 101 North American species found such a correlation (T. E. Martin, 1995). Brightsmith hypothesized that if the shift away from tree cavities was due to predation pressure, then OC nesters should have longer nesting periods. The data on both Amazonian and Australian parrot species do show that those species that nest in cavities other than tree cavities have longer nesting periods.

With respect to the Amazonian parrots, Brightsmith estimates that almost all of the species that rely on cavities other than trees arose in the late Oligocene–early Miocene geological period, 20 to 30 million years ago (Miyaki et al., 1998). South American mammal communities were undergoing a large change at that time, with rapid increases in the number of nest predators, including both tree rats and primates from Africa (Poirier et al., 1994). These nest predators may have been responsible, in part, for the Amazonian parrots' evolutionary shift away from tree cavity nesting.

Box 12.2. SCIENCE AT WORK

What is the research question? Can knowledge of the co-evolutionary behavioral dynamics between a species involved in translocation programs and its potential predators increase the success rates of such programs?

Why is this an important question? Translocation programs are common in conservation biology. Some are successful, some are not. An ethologically informed approach may help rates of successful translocations.

What approach was taken to address the research question? Researchers studied the antipredator behaviors of rabbits, whose ancestors had been translocated to Australia hundreds of years ago by European settlers.

What was discovered? When exposed to olfactory cues from predators that were similar to predators in Europe that rabbits have evolved with, Australian rabbits responded with adaptive antipredator behaviors. When exposed to olfactory cues from quoll, an endemic Australian predator, rabbits did not display antipredator behaviors, leaving them susceptible to quoll predation.

What do the results mean? Even many generations after being introduced into Australia, rabbits do not yet respond adaptively to cues of quoll predatory danger, suggesting that knowledge of the evolutionary behavioral history of translocated species can facilitate successful translocations.

What Prey Do When They Encounter Predators

In this section, we will examine how animals respond when they encounter predators (Figure 12.10). Before we go into detail on specific behaviors, let's examine the sort of neuroendocrinological changes that occur when a predator is encountered. Work by David Smith and his colleagues on the proximate effect of predator odor on mice has shown that the frontal cortex area of the brain regulates the effect of stressors on behavior in rodents and humans, and that this area of the brain may alter neurological and endocrinological responses to stressors such as predators (Amat et al., 2005; Drevets, 2000; Osuch et al., 2000; D. G. Smith et al., 2006; Spencer et al., 2005). To examine this in more detail, Smith and his team exposed mice to two different stressors. One group of mice were exposed to the odor of a predator. A second group of mice was exposed to a physical stress—these individuals were immobilized in a device with the bizarre name of a Universal Mouse Restrainer (UMR). A third group of control animals was exposed to neither predator odor nor the UMR.

Figure 12.10. Encounter with a predator. A skua gull descends from the air in search of penguin eggs or unattended chicks, while two gentoo penguins attempt to fend it off. *(Photo credit: Seth Resnick / SuperStock)*

To measure the neuroendocrinological responses to predator stress (as well as UMR stress), the investigators anesthetized the mice prior to the experiment and implanted a device into their brains that allowed them to draw out a small amount of fluid from the mice's prefrontal cortex. The researchers then took fluid samples from the prefrontal cortex of the experimental mice throughout the course of the experiments. Smith and his group found that both predator odor and the UMR increased the circulation of the neurotransmitters acetylcholine, serotonin, and dopamine within the frontal cortex, but that the increase was greater in response to predator odor.

While it is always difficult to measure whether a predator induces anxiety in nonhumans, Smith and his team did find that when chlordiazepoxide, a drug that reduces anxiety in humans, was administered to mice before exposure to the odor of predators, the increases in acetylcholine, serotonin, and dopamine described above disappeared. This finding suggests that predators may indeed cause anxiety in nonhumans.

Just being exposed to the odor of a predator caused a significant change in the neurological and endocrinological states of the brain in mice—a greater change, in fact, than when they were being physically restrained. Such neuroendocrinological changes will, in turn, produce antipredator behavior such as reduced foraging, burying for safety, and so on (T. Campbell et al., 2003; Koolhaas et al., 1999).

Here we shall examine five behaviors that prey use once they encounter a predator: (1) fleeing, (2) approaching a predator to obtain information, (3) feigning death, (4) signaling to the predator, and (5) fighting back (see chapter 9 for a discussion of another example of antipredator behavior—alarm calling).

FLEEING

The most common response of prey that have spotted a predator is to flee for safety (Blumstein, 2003; Camp et al., 2012; Cooper and Blumstein, 2104; Lima, 1998; Lima and Dill, 1990; Stankowich and Blumstein, 2005; Ydenberg and Dill, 1986; Figure 12.11). Fleeing involves behaviors that range from a squirrel sprinting to its underground den, to a bird flying into the trees for safety, to a fish heading for cover in a coral reef or, as we shall see in a moment, to embryonic tadpoles falling from a branch into the relative safety of the water.

Figure 12.11. Fleeing. The most common response of prey that have spotted a predator is to flee for safety. *(Photo credits: imageBROKER / Alamy Stock Photo; © Mario Nonaka; © Prazis Images / Shutterstock; © Cathy Keifer / Shutterstock)*

A Meta-Analysis of Flight Initiation Behavior

Animal behaviorists have measured flight initiation distance—how close a predator can approach before prey flee—in many species. This is a fairly easy measure to obtain, both observationally and experimentally, in part because researchers can manipulate predator behavior by using trained animals or through the use of "model" predators (e.g., a stuffed hawk flown over an area with pigeons).

Ted Stankowich and Dan Blumstein used meta-analysis to study flight initiation distance. A meta-analysis employs data from *already* published papers and uses statistical tools to search for large scale *trends* across many different studies. Stankowich and Blumstein gathered published data from sixty-one studies of flight initiation in mammals, fish, birds, and reptiles. They analyzed data from a wide variety of taxa, searching for patterns in flight initiation behavior, and reviewed studies to see how characteristics of the predator, the physical condition of the prey itself, the prey’s environment, and the prey’s prior experience with predators affected the prey’s decision as to when to flee from a predator (Stankowich and Blumstein, 2005) (Figure 12.12).

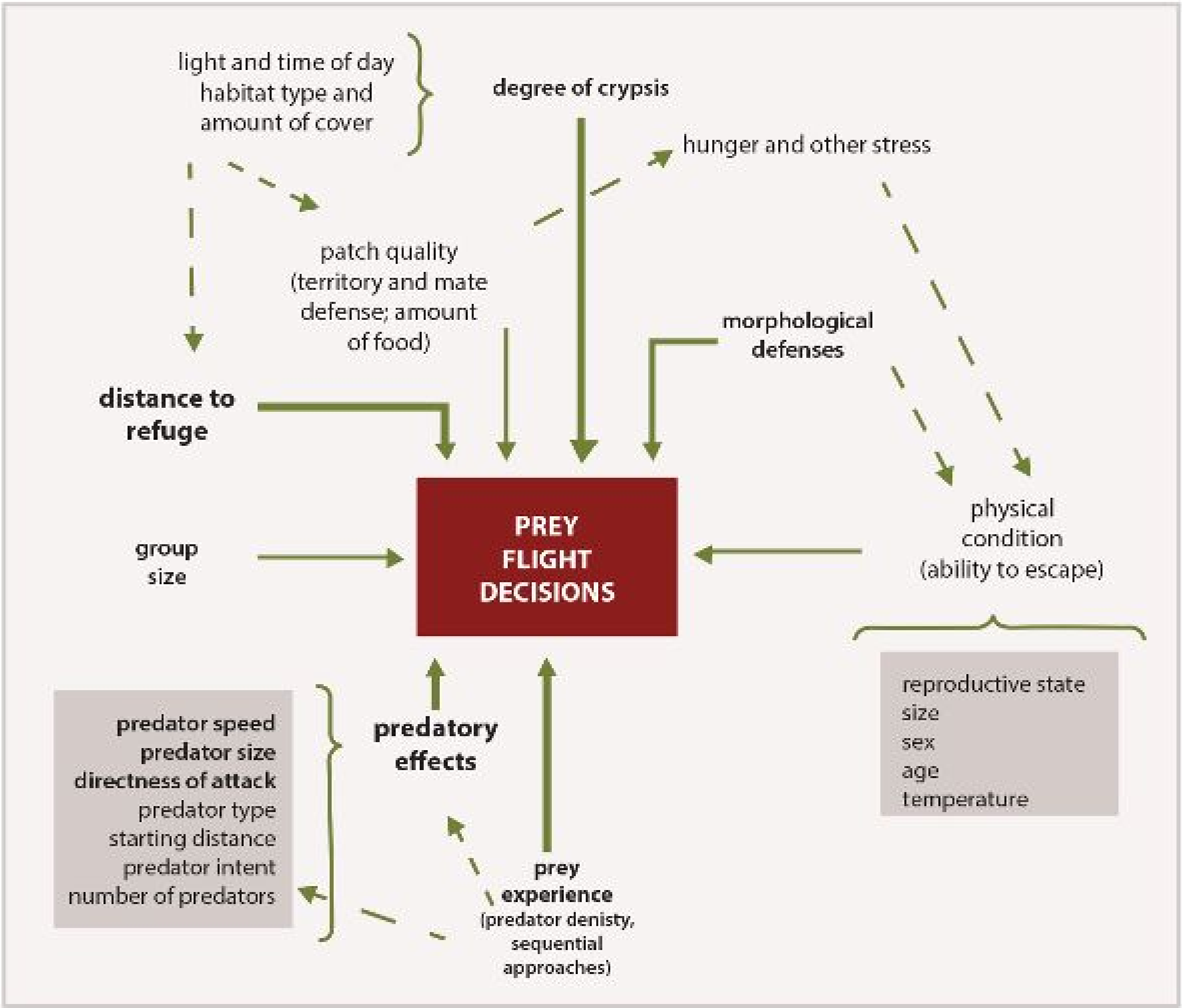


Figure 12.12. Flight initiation distance. The different factors that may influence when an animal decides to flee from a predator. Bolder and larger type and thicker arrows indicate more important factors. Dashed lines indicate factors that may have indirect effects on other factors. Reprinted by permission of the Royal Society. *(From Stankowich and Blumstein, 2005, p. 2630)*

What they discovered was that animals that were far from a refuge (their territory, for example) began fleeing from a predator sooner than animals closer to their refuge. In addition to the distance to safety, they found that animals involved in foraging, mating, or fighting were slower to flee from predators than animals that were not currently involved in such behaviors: when animals were distracted by other activities, they were less alert for predators. These sorts of trade-offs between antipredator behavior and foraging, mating, and so on are well documented in the literature (Lima and Dill, 1990).

Stankowich and Blumstein also found that the predator’s size and speed and the directness of its approach affected the prey’s perception of risk. Morphological traits of the prey affected its behavioral decision of when to flee from a predator. The presence of armor (spines, shells, etc.) reduced flight initiation distance—at a given distance, armored animals were not as likely to flee from a predator as prey without armor. The prey’s ability to camouflage itself affected its flight decision as well. Other factors affecting flight initiation distance included the quality of the habitat and the physical condition of the prey (how hungry it was, its size and age, whether it was pregnant, and whether it was defending young offspring).

Stankowich and Blumstein found that experience per se and learning played a strong role in when prey initiated flight—prey typically flee at a greater distance as a function of experience with predators, including human predators or intruders (Croes et al., 2007; Fa and Brown, 2009; Coetzee and Chown, 2016; Box 12.3).

Box 12.3. SCIENCE AT WORK

What is the research question? How can the use of meta-analyses help ethologists understand antipredator behaviors?

Why is this an important question? Tools for doing meta-analysis—a statistical approach that searches for broad scale trends across already published studies—are now available to ethologists.

What approach was taken to address the research question? Data from more than sixty published studies on flight initiation behavior across many taxa was used to examine which variables most strongly influenced this antipredator behavior.

What was discovered? The meta-analysis found that many variables, including the degree of crypsis, the distance to a refuge, and the prey's experience with a predator influenced decisions about flight initiation distance.

What do the results mean? Meta-analysis is a powerful technique for studying broad scale patterns with respect to antipredator behavior. This same approach can be employed for studying other animal behaviors as well.

The Genetics of Schooling Behavior in Fish

Schooling fish tend to flee from predators en masse (though there are exceptions), and so an understanding of schooling behavior can shed light on fleeing behavior. Marine sticklebacks (*Gasterosteus aculeatus*) from open-water (pelagic) habitats encounter more predators and school more tightly than sticklebacks from more vegetated, benthic environments. Fish from the open-water areas also position themselves at a particular angle with respect to others within schools, which facilitates efficient school movement (Figure 12.13) (Wark et al., 2011; Di-Poi et al., 2014).

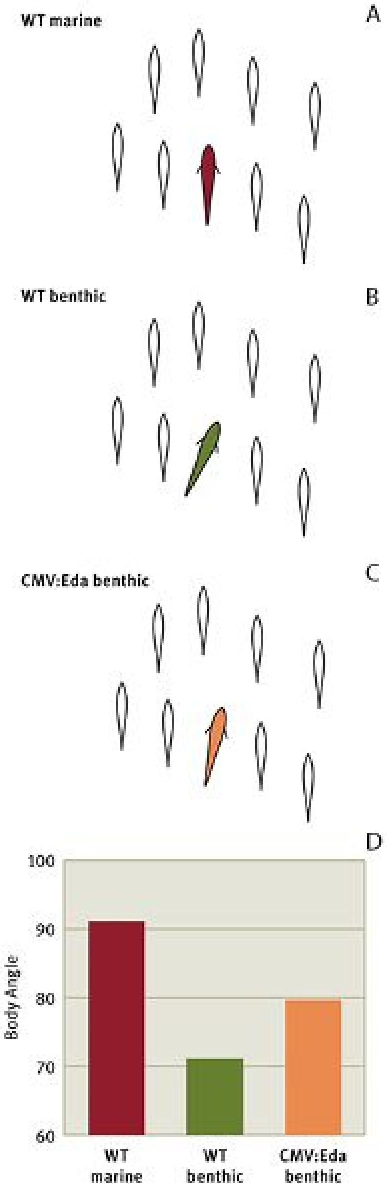


Figure 12.13. **The *Eda* gene and schooling behavior.** A stickleback was placed in a school of robotic fish that faced and swam in one direction. (A) A fish from a marine population (test fish in black). (B) A fish from a benthic population (test fish in light gray). (C) Offspring of benthic fish that expressed the pelagic version of the *Eda* gene (test fish in dark gray). (D) Average body angle of fish in A, B and C. *(From Greenwood et al., 2016)*

Using a combination of what are known as forward genetic mapping and transgenic experiments, Anna Greenwood and her colleagues examined whether genetic variation between fish in the pelagic versus benthic populations might help explain the observed phenotypic differences in schooling behavior across habitats (Greenwood et al., 2016). Earlier work by this group of researchers had found that variation in schooling and variation in the body armor of sticklebacks were linked to a region of chromosome 4 (Greenwood et al., 2013, 2015; Wark et al., 2012; Mills et al., 2015). Because the *Eda* gene is found in the same region of chromosome 4, Greenwood and her team examined whether variation in the *Eda* gene might be responsible, in part, for the variation in schooling behavior seen in pelagic versus benthic sticklebacks.

Using transgenic techniques, they inserted a genetic promoter of the pelagic *Eda* gene into fish from benthic populations: the insertion was at the single cell embryo stage as prior work had shown that this led to changes of expression of *Eda* throughout the adult fish. This promoter led to the expression of the pelagic version of *Eda* in benthic fish. They mated these fish to sticklebacks from natural benthic populations and the schooling behavior of offspring from these mating was then tested as they swam in schools with robotic fish (robotic fish were used to control the behavior of school mates). The genetically modified offspring of fish from benthic populations schooled more like those from the pelagic population than did their wild-type siblings (fish from benthic population), suggesting that variation in the *Eda* gene in part explains variation in stickleback schooling behavior (Box 12.4).

Box 12.4. SCIENCE AT WORK

What is the research question? Can transgenetic tools be used to determine whether genetic variation explains phenotypic variation in schooling behavior?

Why is this an important question? Molecular genetic techniques are changing at a rapid rate. When these techniques are used to study phenotypic variation, they are a very powerful tool for ethologists.

What approach was taken to address the research question? Using transgenetic tools, the promoter for a gene hypothesized to be associated with schooling behavior in sticklebacks living in an open water habitat was inserted into embryonic sticklebacks from the benthic population. When they matured, these individuals were then mated to wild fish from the benthic population and the schooling behavior of their offspring was recorded.

What was discovered? Offspring from benthic population parents with the inserted promoter schooled in a manner more similar to pelagic than wild-type benthic fish.

What do the results mean? Transgenic tools may speed the rate at which animal behaviorists can map genotype-phenotype associations.

Treefrog Embryos and Snakes

Though we think of the antipredator options available to embryos as limited, some research suggests embryos have evolved adaptations to flee from predators. As a case study, we will examine Karen Warkentin's work on the red-eyed treefrogs (*Agalychnis callidryas*) and their predators in Panama to see how natural selection can shape fleeing behavior on the part of embryos (Gomez-Mestre et al., 2010; Touchon et al., 2011; Warkentin, 2000).

Red-eyed treefrogs attach their eggs to the vegetation that hangs over water. When eggs hatch, the tadpoles that emerge drop down into their aquatic habitat. Both the terrestrial habitat of the egg/embryo and the aquatic habitat of the tadpole have a set of predators. But the predators are different in each of the habitats. If terrestrial predation from snakes and wasps is weak, eggs hatch late in the season (Warkentin, 1995, 1999; Figure 12.15). This serves two functions: First, it lengthens the time that the eggs/embryos are in a low-predator terrestrial habitat, and second, such late hatching allows the embryos to grow to a size that lowers the levels of fish predation once the eggs finally hatch and the tadpoles fall into the water.

Figure 12.15. Predators that feed on treefrogs. Red-eyed treefrogs have numerous predators that specialize in feeding on their eggs. (A) Here a wasp forages on treefrog eggs. (B) Snakes are another dangerous predator that feed on red-eyed treefrog eggs. *(Photo credits: Karen Warkentin)*

Warkentin predicted that treefrog eggs would hatch sooner if predation in the terrestrial environment increased, because natural selection should favor embryos that avoid terrestrial predators when such predators are at high frequencies (compared with the aquatic predators that feed on treefrogs; Warkentin, 2000). Both snakes and wasps are terrestrial predators on treefrog eggs—wasps feed on one egg at a time, while snakes can eat many eggs at a time. When predation from snakes and wasps is high, it might increase survival rates to mature early and drop into the water, away from heavy terrestrial predation.

Box 12.5. COGNITIVE CONNECTION

Heritability of Conditioned Fear Responses

For natural selection to act on a cognitive trait associated with antipredator behavior, there must be variation, fitness correlates, and heritability associated with the cognitive trait in question (Croston et al., 2015; Rowe and Healy, 2014; Thorton et al., 2014). In this box we will focus on the small, but growing, work on the heritability of cognitive traits associated with conditioned fear responses (Croston et al., 2015).

In chapter 4 we discussed the general experimental protocol used in conditional learning studies. That approach has been used many times with respect to antipredator behavior. In rodents, and in mammals in general, conditioned fear responses include increased heart rate, defecation, and freezing behavior. In rodents (and mammals in general), there is evidence to suggest that one area of the brain that plays a key role in the conditioned fear response is the amygdala. Activity in this area of the brain increases as fear conditioning occurs, and experimental stimulation of the amygdala produces many of the same behaviors seen during conditioned fear responses. In addition, damage to the amygdala causes a reduction in the behaviors typically produced by conditioned fear responses (Applegate et al., 1983; Blanchard and Blanchard, 1969, 1972; Cohen, 1975; Quirk et al., 1995; Rogan et al., 1997).

If natural selection has shaped conditioned fear responses (mediated by the amygdala), then this suite of behaviors should be heritable. While little work has been done on this in natural populations, laboratory experiments, primarily using rodents, have found evidence for the heritability of conditioned fear responses (Figure 12.14) (Shumake et al., 2014). In addition, many artificial selection experiments on fear responses, including conditioned fear responses, have found strong responses to the selection pressure applied, suggesting an underlying heritability to these antipredator behaviors.

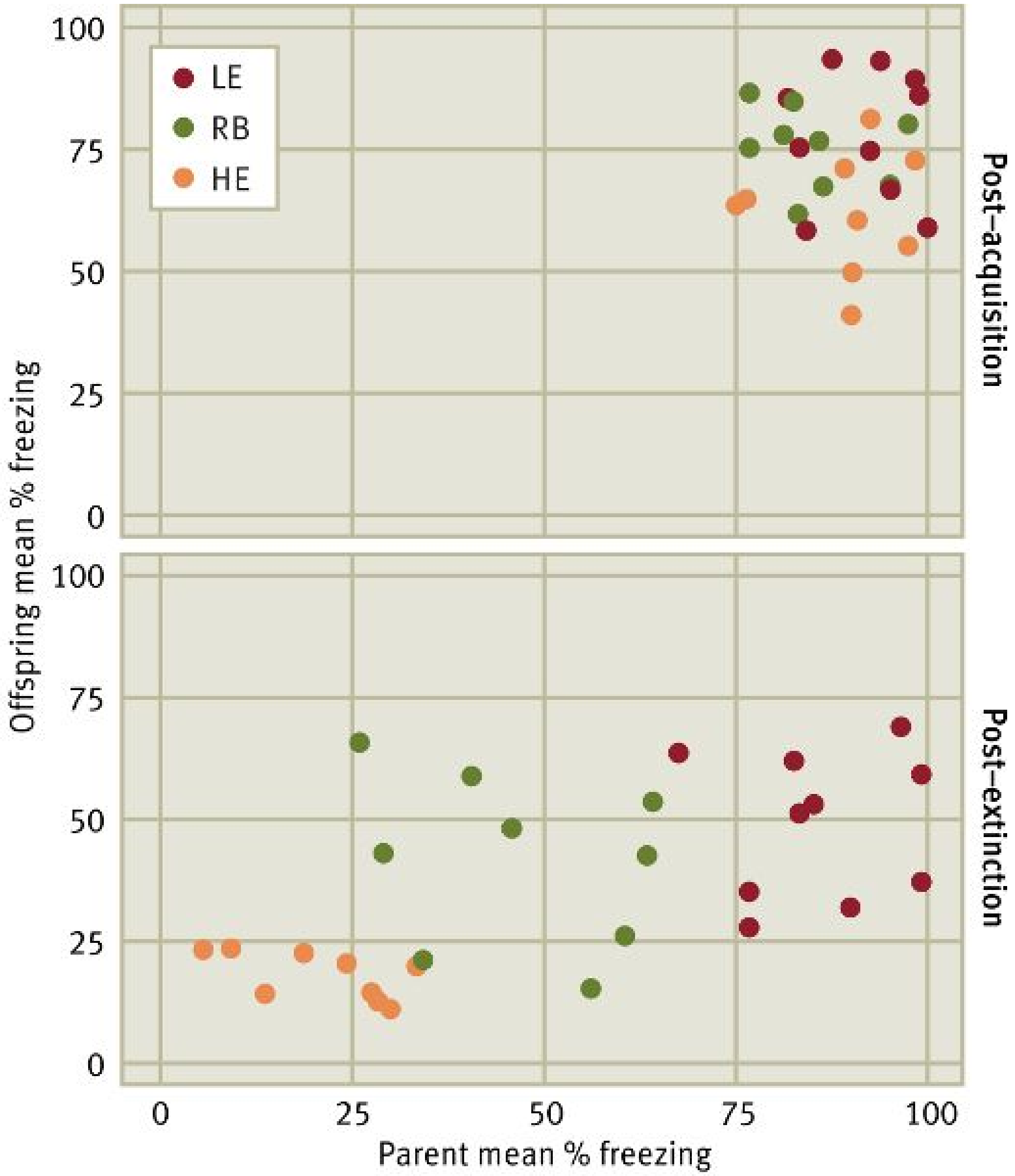


Figure 12.14. **Heritability of a conditioned response.** On the *x*-axis is the mean percent of individuals showing one conditioned fear response—in this case freezing—in parents, and on the *y*-axis is the corresponding figure for their offspring. Each point represents a single family. RB = Randomly bred line, LE = High “freezing score” line, HE = Low “freezing score” line.*(From Shumake et al., 2014)*

More work on the heritability of fear, particularly in natural populations, combined with work on variation and the fitness consequences of fear, will help us better understand this most basic of antipredator behaviors.

To test this idea, Warkentin marked 123 clutches of treefrog eggs. She found that less than half the eggs she kept track of survived to hatch, whereas the majority fell prey to wasp attacks. She then examined whether the eggs that survived responded by hatching and having the emerging tadpoles “flee” by dropping into the water. Warkentin found that eggs in clutches that were not disturbed by predators hatched at about six days. When comparing eggs from these undisturbed clutches to those clutches that had already suffered some predation by wasps, Warkentin found that hatching rates were different. Eggs hatched earlier when their clutch had been the victim of some wasp predation, with most eggs from attacked clutches hatching at four or five days (as opposed to six; Figure 12.16). Indeed, some embryos in clutches that were attacked ruptured their eggs, hatched, and dropped off branches immediately after such attacks. Similar results were found when the effect of snake predation on hatching rates was examined (Figure 12.17).

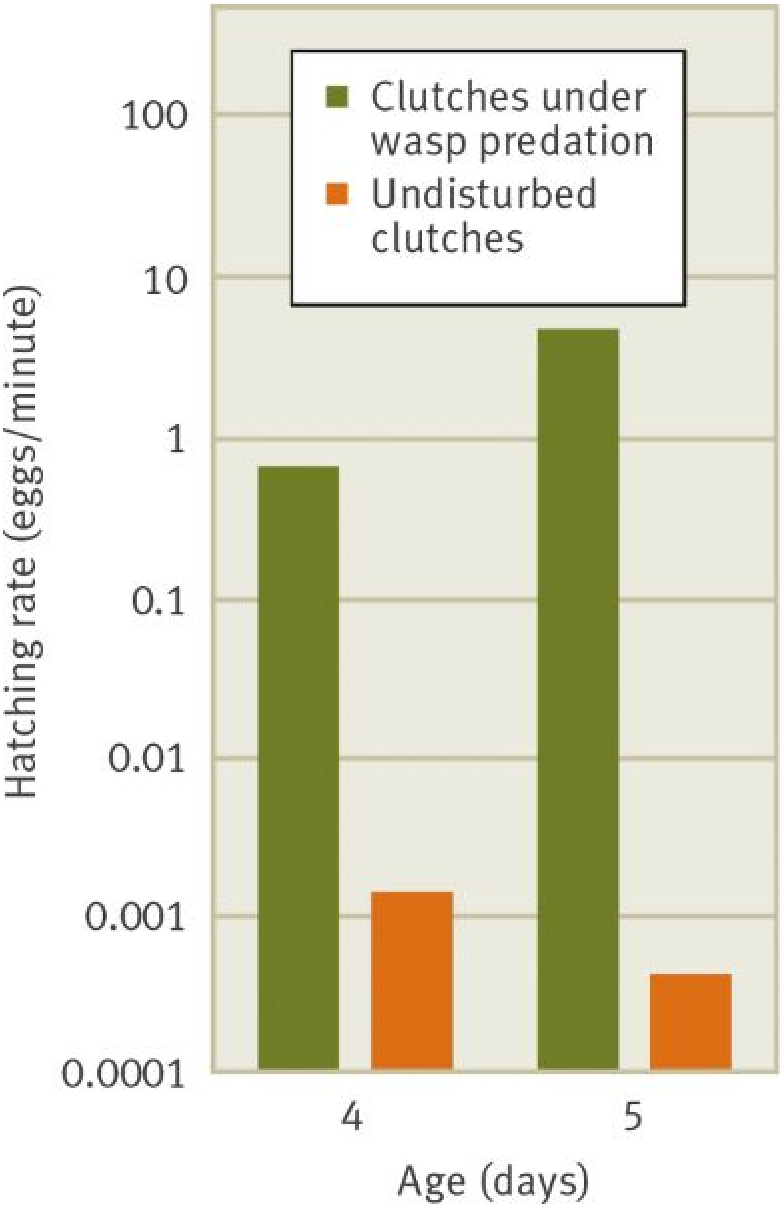


Figure 12.16. Wasp predation and development time. Red-eyed treefrogs respond to wasp predation by hatching early. Green bars represent the hatching time of clutches that suffered some wasp predation, and orange bars indicate undisturbed clutches. Embryos are capable of hatching sometime during day 4. *(Based on Warkentin, 2000)*

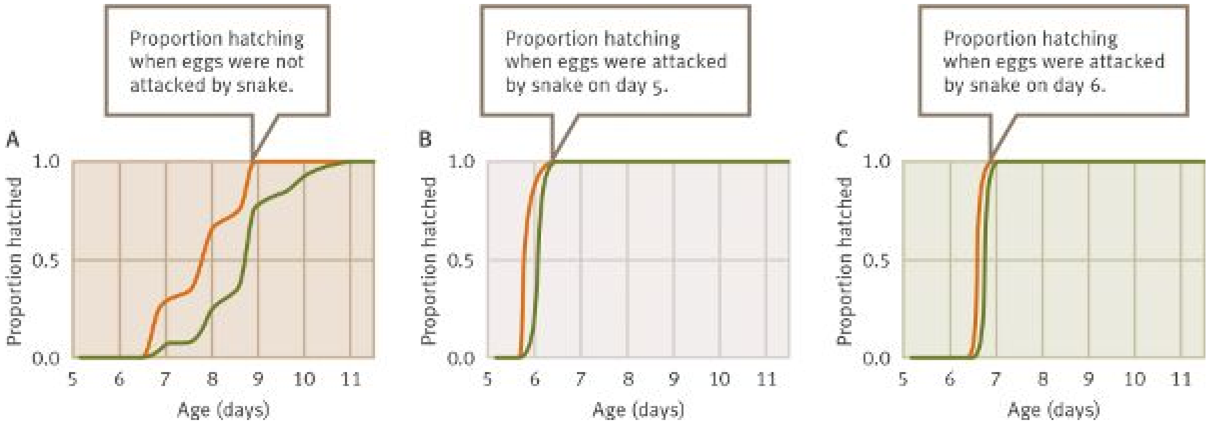


Figure 12.17. Snake predation and development time. Red-eyed treefrogs respond to snake predation by hatching earlier than normal. Notice the earlier hatching times when clutches were attacked by snakes in (B) and (C). Green and orange lines indicate replicate experiments. *(Based on Warkentin, 1995)*

Warkentin's work on predator avoidance raises an interesting question about proximate cues. What specific cues do the treefrog embryos use to determine when to shift from terrestrial to aquatic habitats? If the developing embryos survive an attack by snakes, survivors drop off branches into the water, but what specific cues are they homing in on? Warkentin hypothesized that the embryos may be using the vibrational cues associated with snake attacks as one proximate cue for when to switch from terrestrial habitats to aquatic ones.

To test her hypothesis, she released a snake into a cage and she recorded the vibrations associated with this predator. Because Warkentin hypothesized that the vibrations associated with snake attacks—and not just vibrations in general—were the key to a habitat shift away from predators, she also recorded a different vibrational cue: the vibrations associated with rainfall. She then played back vibrational recordings of two kinds of snake attacks and of a rainstorm to clutches of developing treefrog eggs (Figure 12.18). As predicted, the cues associated with snakes resulted in treefrogs that hatched earlier than treefrogs that had been played the recording with rainstorm cues (M. S. Caldwell et al., 2009, 2010; Warkentin, 2005; Warkentin et al., 2006, 2007).

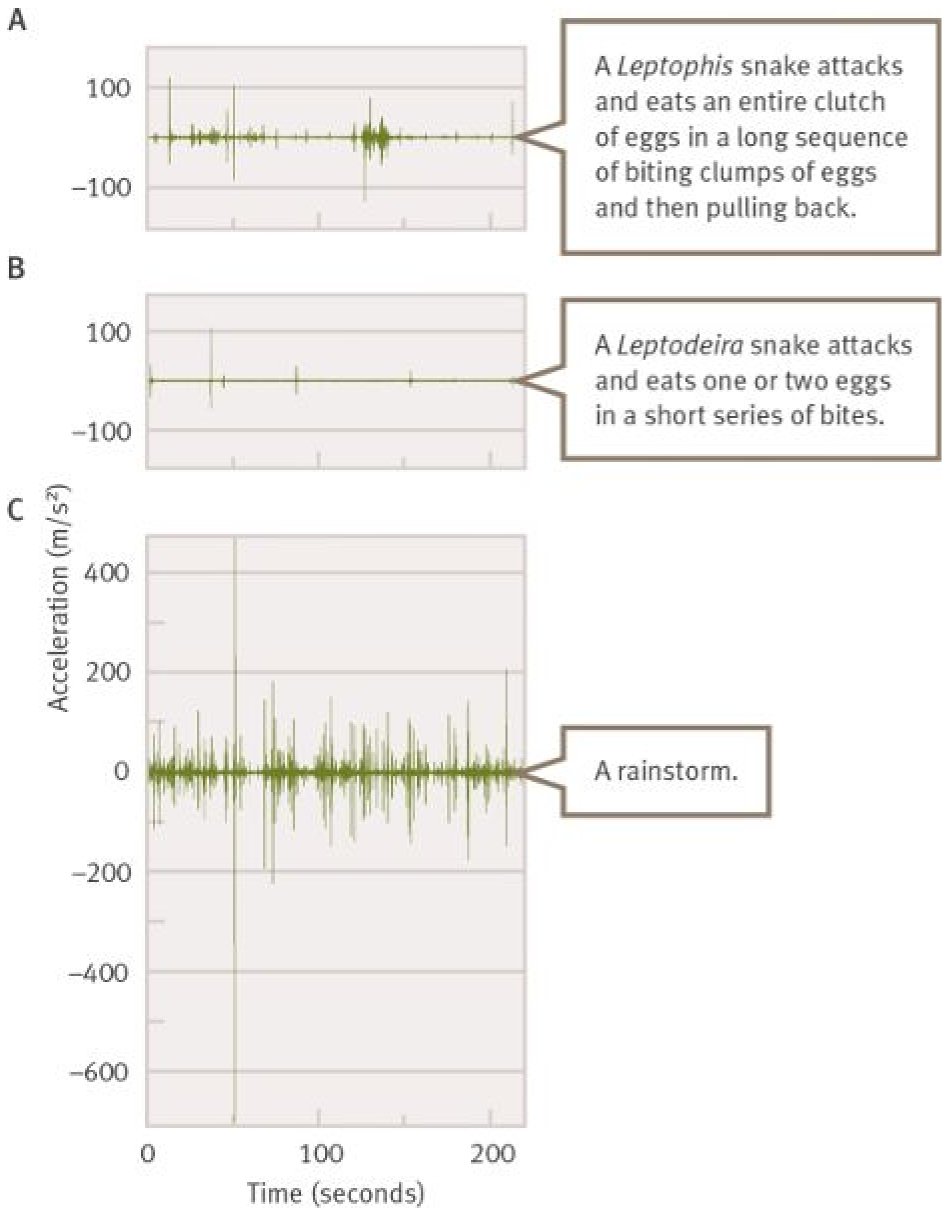


Figure 12.18. Sounds from red-eyed treefrog nests. Sounds recorded as waveform graphs at the nest of a red-eyed treefrog. *(From Warkentin, 2005, p. 62)*

APPROACHING PREDATORS

Animals sometimes approach predators when they encounter them. This may allow prey to gather important information about putative predators, and reduce their chances of mortality. This sort of behavior has been extensively documented in vertebrates, particularly in fish, birds, and mammals and in the literature goes by many different names, including approach behavior, boldness, investigative behavior, and predator inspection behavior (chapter 10: Curio et al., 1978; Dugatkin and Godin, 1992; Pitcher et al., 1986).

In vertebrates, approach behavior is characterized by a series of moves toward the predator interrupted by stationary pauses and sometimes alternating with moves away from the predator (Curio et al., 1983; Dugatkin, 1997a; Milinski, 1987; Pitcher et al., 1986). Approaches may culminate in prey retreating, prey rejoining a social group of conspecifics nearby, or an escalation in which prey actually attack the predator (see more on escalation below).

The Costs and Benefits of Thomson's Gazelles Approaching a Predator

Clare Fitzgibbon studied costs and benefits of approach behavior in natural populations of Thomson's gazelles (Fitzgibbon, 1994; Figure 12.19). In the Serengeti National Park (in Tanzania), gazelles live in groups that vary from fairly small (<10 individuals) to fairly large (>500), and gazelles have four main predators: lions, cheetahs, spotted hyenas, and wild dogs.

Figure 12.19. Gazelle antipredator behavior. (A) Gazelles are vigilant, searching for potential predators. (B) Many species, including the cheetah (pictured here chasing a gazelle) hunt gazelles. *(Photo credits: © Maggy Meyer / Shutterstock; Anup Shah / Minden Pictures)*

Fitzgibbon examined three, non–mutually exclusive benefits of approaching a predator. Approach behavior might

1. decrease the current risk of predation.
2. allow gazelles to gather information about a potential threat.
3. serve to warn other group members of the potential danger associated with predators.

In the course of her two-year field study, Fitzgibbon found some evidence for a decrease in the risk of predation. In particular, she found that cheetahs responded to gazelle inspection behavior, which is most common and most pronounced in large gazelle groups (Figure 12.20A), by moving farther between rest periods and between hunting periods (Figure 12.20B). This in turn could cause cheetahs to leave an area sooner than normal as a result of gazelle approach behavior, leading to decreased rates of mortality among potential prey.

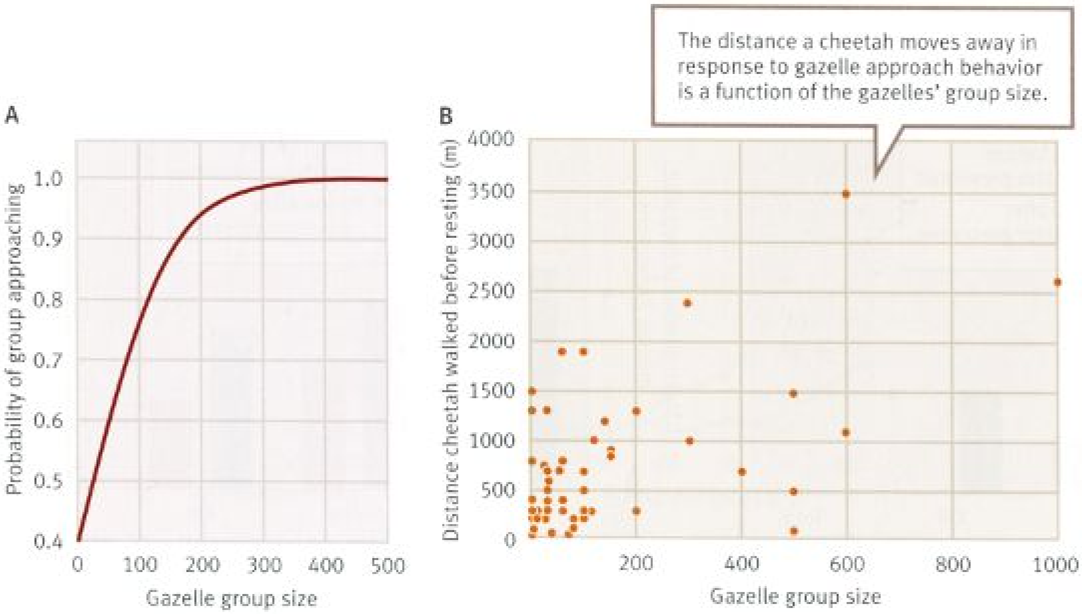


Figure 12.20. Approach behavior in gazelles. (A) The probability of approach behavior occurring in gazelles is a function of group size. (B) Cheetahs respond to gazelle approach behavior. *(Based on Fitzgibbon, 1994)*

The cost of gazelle approach behavior is paid primarily in terms of lost time/energy: gazelles spend approximately 4 percent of their waking hours involved in approach behavior. This time could otherwise be devoted to other activities—for example, foraging, mating, resting—and so it represents a real opportunity cost to the animals.

FEIGNING DEATH

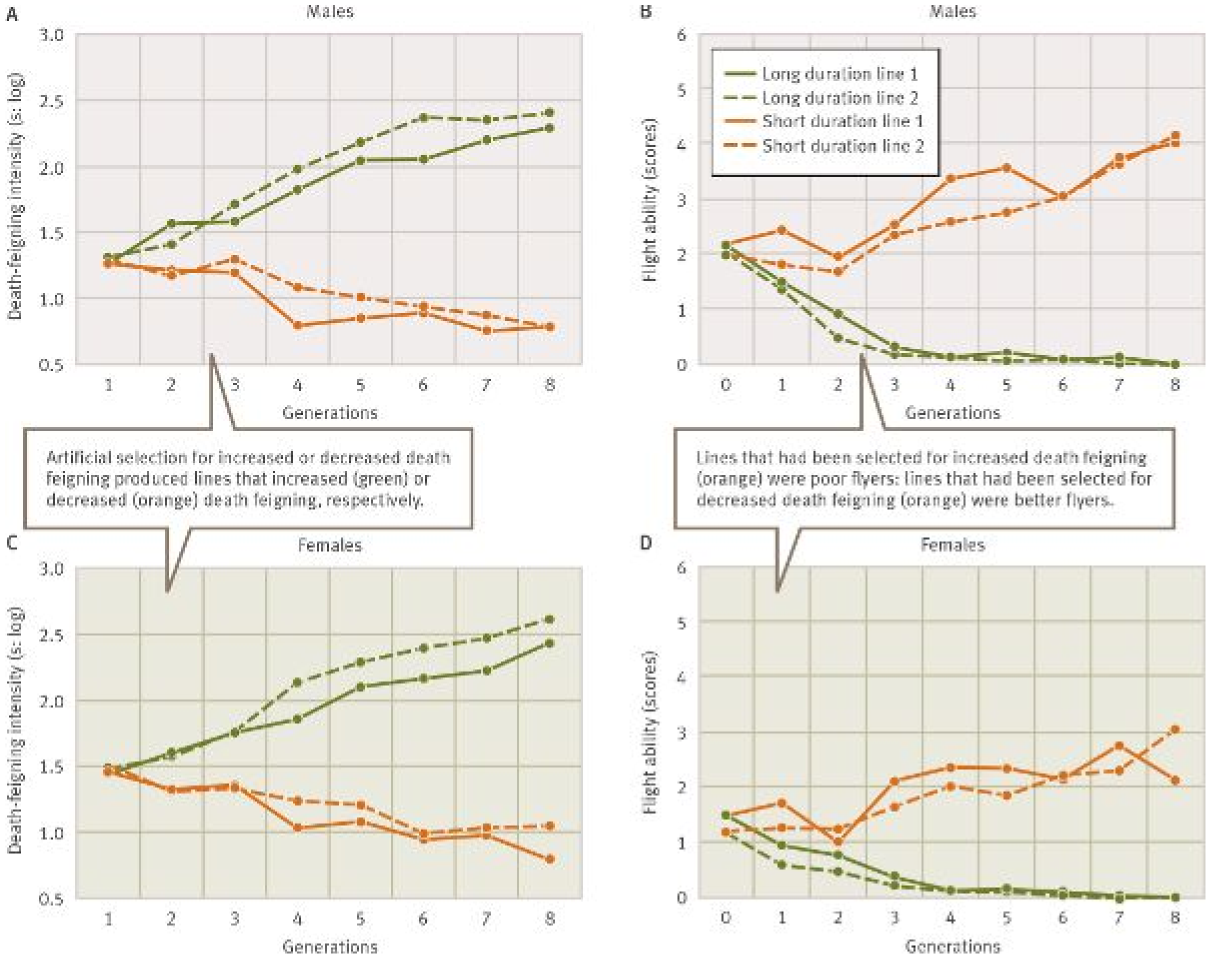
Faking, or feigning, death is an antipredator behavior seen in many species. Death feigning occurs in insects when, in response to a predator, an insect falls and then remains frozen, absolutely still. This is sometimes referred to as tonic immobility (Miyatake et al., 2004; Ruxton et al., 2004).

Tatsunori Ohno and Takahisa Miyatake have studied death feigning in the adzuki bean beetle (*Callosobruchus chinensis*; Ohno and Miyatake, 2007). When a beetle is on a branch and a predator approaches, beetles can either fly away or feign death, but they cannot do both at the same time. Ohno and Miyatake hypothesized that a negative genetic correlation existed between the intensity of death feigning and the ability to fly—those beetles that feigned death for a long period of time would be poor flyers, and those beetles that feigned death for shorter time periods would be especially good flyers.

The researchers established two behavioral assays—one for feigning death and one for flying ability. For the former, they exposed beetles to danger and measured how long the beetles remained frozen, feigning death. For the assay on flying ability, they dropped a beetle through a hole into a cube-shaped apparatus that had a grid on its bottom and tested whether the beetle dropped straight down (poor flyer), or whether it flew as it was falling and how far it flew (on a scale of 1–6). Next they ran an artificial selection experiment with two treatments. In the death-feigning (DF) treatment a random sample of 100 flies was selected, and the researchers measured the duration of death feigning for each fly. In the second treatment, the researchers selected beetles based on their flying abilities.

Two genetic lines were established within the DF treatment. In the “long-duration” line, the seven males and seven females who displayed the longest duration of death feigning were selected and allowed to breed with one another. In the “short-duration line,” the seven males and seven females with the shortest duration of death feigning were selected and allowed to breed with one another. This was repeated for eight generations—in each generation of the short-duration line, the males and females with the shortest times for feigning death were selected. The same process of selection and breeding of the seven males and seven females with the longest times for feigning death occurred over eight generations of the long-duration line.

Eight generations of artificial selection on death feigning produced dramatic differences between the selected lines (Figure 12.21). Individuals in the long-duration line showed death-feigning times that were about forty times as long as those in the short-duration line. In addition, Ohno and Miyatake found a negative genetic correlation between death feigning and flying abilities. Individuals in the long-duration line were very poor flyers, and, conversely, individuals in the short-duration line were adept flyers.



Artificial selection for increased or decreased death feigning produced lines that increased (green) or decreased (orange) death feigning, respectively.

Lines that had been selected for increased death feigning (orange) were poor flyers: lines that had been selected for decreased death feigning (orange) were better flyers.

Figure 12.21. Selection for death feigning. Data from two replications of the long-duration and short-duration selection experiments on death feigning in the adzuki bean beetle. Points on solid lines represent data from the first replicate; points on dashed lines represent data from the second replicate. There is a negative correlation with flying ability when selection is on death feigning. *(From Ohno and Miyatake, 2007, p. 558)*

Ohno and Miyatake ran a second artificial selection experiment. This time, they created two new genetic lines—one in which the best flyers (BF) in every generation bred with one another, and a second in which the worst flyers (WF) bred with one another. The same negative genetic correlation found in the DF treatment was uncovered here: after eight generations the beetles in the BF line were not only good flyers, but they displayed very short death-feigning times. Conversely, the beetles in the WF line were poor flyers, but they displayed death feigning for long periods of time.

Recent work by this group has also explored one of the proximate underpinnings of death feigning in beetles. They found that beetles in populations selected for long bouts of death feigning had higher brain concentrations of dopamine than beetles from populations selected for short bouts of death feigning (Nakayama et al., 2012; Figure 12.22).

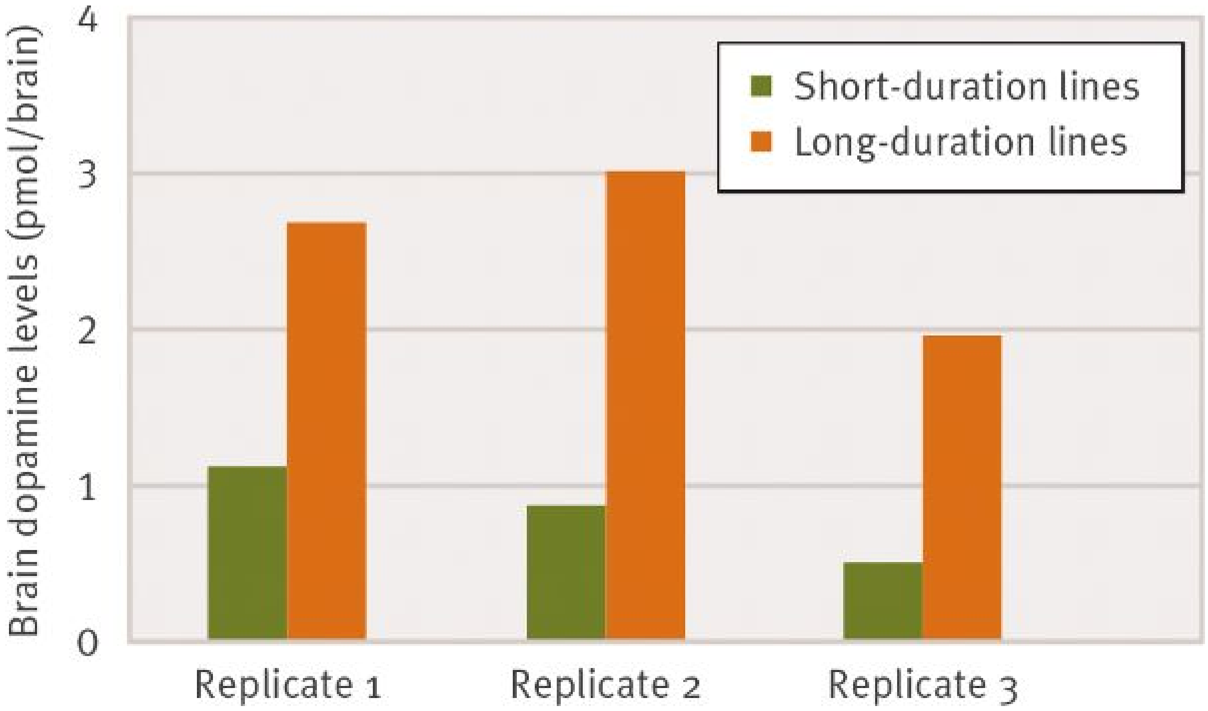


Figure 12.22. Dopamine and death feigning. In each of three replicates, adzuki beetles from lines selected for long periods of death feigning had higher concentrations of dopamine in their brains than did beetles from lines selected for short periods of death feigning. *(From Nakayama et al., 2012)*

SIGNALING TO PREDATORS

Prey sometimes transmit information to a predator to deter an attack, warning the predator of the dangers of contact, or that it has been sighted and may not succeed in capturing a prey. These signals are often visual but can also be auditory, as in the case of tiger moths that can produce warning sounds that cause bats to avoid them because the bats have learned to associate the sounds with a noxious taste (Barber and Conner, 2007). Here we will consider two case studies of signaling: (1) warning coloration in monarch butterflies and (2) tail flagging in ungulates.

Warning Coloration in Monarch Butterflies

During their caterpillar stage, monarch butterflies (*Danaus plexippus*) ingest milkweed plants, which contain cardiac glycosides. These chemicals are toxic to birds, but do not harm the monarchs, indeed, there is growing evidence they aid monarch butterfly resistance to infection: Lefevre et al., 2012; Gowler et al., 2015. These chemicals are sequestered and stored by the butterflies in their own tissue. If a bird predator eats a monarch, the toxins in the monarch make the predator violently ill (Figure 12.23). From that point forward, the color patterns of monarchs act as warning coloration for *that* predator that now avoids feeding on monarchs: birds learn to associate monarch color with illness.

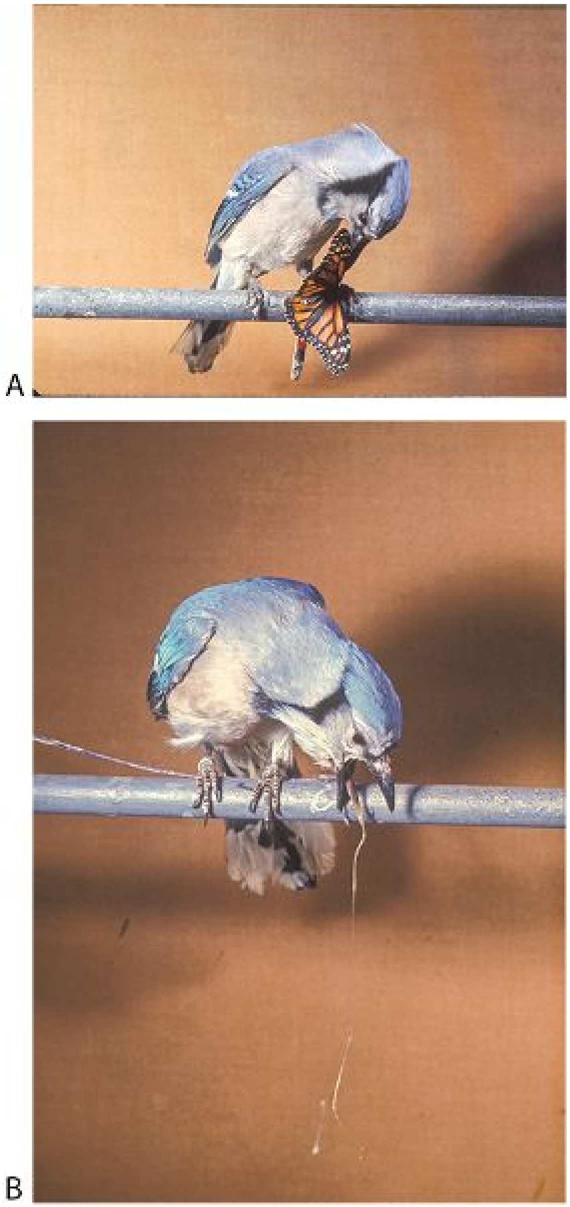


Figure 12.23. Monarch warning colors. (A) A bluejay holding the wing of a monarch butterfly that it is about to eat, and (B) a bluejay vomiting after eating a monarch butterfly. *(Photo credits: Lincoln Brower, Sweet Briar College)*

How could natural selection act on prey to produce the sort of warning coloration that we see in monarchs? If a predator must eat a monarch to learn how dangerous monarchs are, how could selection ever favor the monarch ingesting milkweeds and possessing a distinctive color pattern? How could natural selection favor a trait in which the individual in possession of the trait must die for the predator to learn about the danger? There are a number of ways that this could occur. R. A. Fisher suggested that if prey live in groups, such warning coloration could preferentially aid genetic relatives and so be favored by natural selection (R. A. Fisher, 1930). But the most likely explanation for the evolution of this sort of coloration is that the predator does not always kill the monarch before it senses the toxin, as touching the monarch may be enough to alert the predator to the presence of the toxin. The presence of the toxin and warning coloration may save the life even of a prey that is the victim of a predator's first encounter with a monarch.

Tail Flagging as a Signal

Signals can serve to warn a predator that it has been spotted. When the predator is an ambush hunter that relies on surprise, such a signal often causes it to move on and leave the area. Even when predators aren't strictly ambush hunters, prey may still benefit by signaling predators if signals reduce the probability of capture. Consider tail flagging in ungulates, where individuals "flag" their tails after a predator has been sighted (Figure 12.24). Such flagging occurs as part of a sequence of antipredator behaviors, and often it involves an individual lifting its tail and "flashing" a conspicuous white rump patch. Flagging often, but not always, occurs when a predator is at a relatively safe distance from its potential prey (Hirth and McCullough, 1977).

Figure 12.24. Tail flagging. In white-tailed deer, individuals often display a white patch while running from danger. At least a half dozen hypotheses have been put forth to explain the function of the patch. *(Photo credit: © Jim Cummings/ Shutterstock)*

Tail flagging could serve many functions. At various points in time, animal behaviorists have hypothesized that this behavior might

- warn conspecifics, both kin and nonkin, about the presence of a predator (Estes and Goddard, 1967);
- “close ranks” and tighten group cohesion, which might make predation less likely (Kitchen, 1972; McCullough, 1969; P. S. Smith, 1991) and increase the probability that group-related foraging and antipredator benefits are present in the future (R. J. F. Smith, 1986; Stankowitch, 2008; Trivers, 1971);
- signal to the predator that it has been sighted and should abandon any attack (the “pursuit-deterrence” hypothesis; Caro, 1995a; Caro et al., 1995; Woodland et al., 1980);
- entice the predator to attack from a greater distance, which may result in a failed attempt at capture (Smythe, 1977);
- cause other group members to engage in various antipredator activities, confusing the predator, and making the flagger less likely to be the victim of an attack (Charnov and Krebs, 1975); or
- serve as a sign for appeasing dominant group members, and only secondarily play a role in antipredator behavior (R. D. Guthrie, 1971).

Some evidence suggests that tail flagging can increase group cohesion (Bildstein, 1983; Hirth and McCullough, 1977; P. S. Smith, 1991), but here we will focus on the question whether tail flagging is a signal to the predator. Tim Caro's work on white-tailed deer, as well as the work of other researchers, provides some evidence of pursuit deterrence (Bildstein, 1983; Caro, 1994b; Caro et al., 2004; Woodland et al., 1980). Caro found that white-tailed deer that run fast flag their tails and are using this signal to communicate to the predator that an attack is unlikely to succeed because the fleeing deer will escape a pursuing predator. This sort of pursuit-deterrence signal is not only found in white-tailed deer nor is it restricted to tail flagging. For example, in a phylogenetic study involving 200 species and seventeen antipredator behaviors, Caro and his colleagues found that, in ungulates, snorting also serves as a signal to predators (Caro et al., 2004). This signal deters attack, perhaps because snorting indicates the health and vigor of the signaler.

FIGHTING BACK

Here we will examine two ways that prey, which are usually physically smaller and weaker than their predators, fight back when their life is in danger: chemical defense in beetles and mobbing behavior in birds.

Chemical Defense in Beetles

Thomas Eisner and his colleagues have studied how bombardier beetles use chemical weapons to defend themselves against predators, including swarming ants, orb-weaving spiders, and toads (Dean, 1980a,b; Eisner and Dean, 1976). In the bombardier beetle, *Stenaptinus insignis*, individuals blast potential predators with a highly noxious spray (Eisner and Aneshansley, 1982, 1999; Eisner et al., 2000, 2006).

A beetle can discharge its acidic spray twenty times before depleting its supply of chemicals, and beetles have two glands, each of which has two separate compartments. The larger compartment in a gland is referred to as the reservoir, and it contains hydroquanines and hydrogen peroxide. The smaller compartment, called the reaction chamber, holds a variety of catalases and peroxidases. When beetles are threatened by a predator, they mix the contents of the two compartments, causing a chemical reaction that produces a spray composed of acidic, noxious *p*-benzoquinones (Arndt et al., 2015; Di Giulio et al., 2015; James et al., 2013). The heat produced by this chemical reaction causes an audible pop, and the spray shoots out at a temperature of 100°C. The beetles themselves are not injured by their own noxious sprays, but predators are (Figure 12.25).

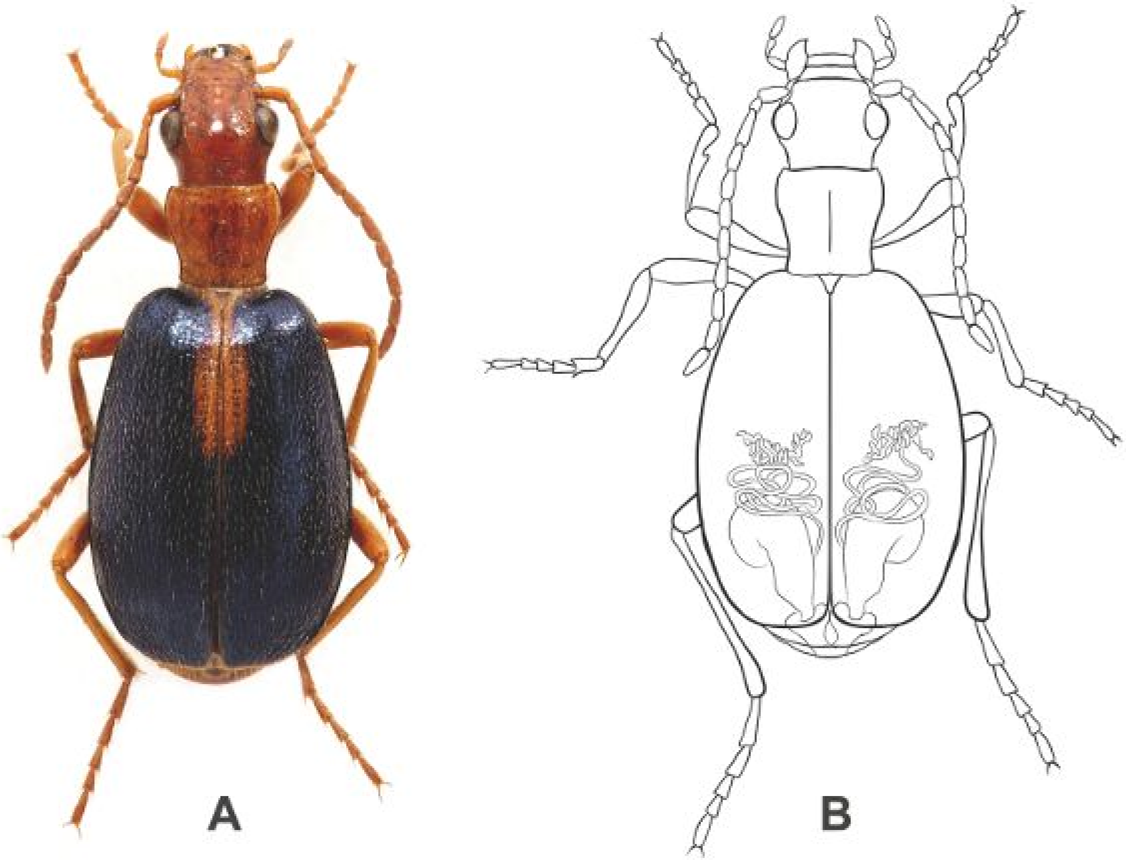


Figure 12.25. **Bombardier beetle chemical weapon system.** (A) The bombardier beetle, *Brachinus sclopeta*. (B) Schematic of the chemical defense system in *B. sclopeta*. Reprinted with permission from Elsevier. © 2015. *(From Di Giulio et al., 2015)*

S. insignis does more than just release an acidic spray when a predator attacks. Using high-speed photography, Eisner and Aneshansley have shown that the beetles selectively aim this spray at predators. When they are attacked from the front, they fire the spray forward; when attacked from the rear, they fire the spray backward (Eisner and Aneshansley, 1999; Figure 12.26).

Figure 12.26. Bombardier defenses. When the bombardier beetle, *Stenaptinus insignis*, is threatened, it releases chemicals that ward off predators. This bombardier beetle is being attacked from the front, and is directing its chemical spray forward. *(Photo credit: © Dr. Thomas Eisner, Visuals Unlimited, Inc.)*

How did such a complicated antipredator mechanism evolve? Researchers are still working on that question, but they have found a clue in the spray mechanism of *Metrius contractus*, which is the oldest of all extant species of bombardier beetles (Eisner et al., 2000). Like other bombardier species, it has a reservoir that contains hydroquanines and hydrogen peroxide and a reaction chamber that holds a variety of catalases and peroxidases, suggesting that possession of these traits is an ancestral characteristic. Unlike other species, however, which often discharge their defensive spray as a jet, *M. contractus*’s spray is discharged as a fine mist or a froth.

Again using high-speed photography, the researchers examined emission of this spray in more detail.

Eisner and his colleagues found that *M. contractus* emits its spray in a unique manner. When it is attacked from the rear, it produces a froth secretion, which builds up on the body of the beetle and wards off predators. When a beetle is attacked from the front, instead of spraying its attacker, it forces the chemical secretion it produces forward, along tracks on its forewings. Although it is not clear why, these mechanisms of discharging chemical weapons appear to lower the temperature of the disseminating chemicals from 100°C to approximately 55°C. This work on *M. contractus* hints that spraying an extremely hot chemical secretion may be a derived trait, but that frothing and using the forewing tracks to disseminate a somewhat reduced heat spray represents something similar to the ancestral version of chemical defense in bombardiers.

Social Learning and Mobbing in Blackbirds

Chemical weapons are only one way prey can counterattack their predators. Blackbirds (*Turdus merula*) sometimes **mob** their predators (Altmann, 1956; Sordahl, 1990). Once a flock of blackbirds spots a predator, they join together, fly toward the danger, and aggressively attempt to chase it away. Such group attacks often work well enough to force predators to leave the blackbirds' area.

Eberhard Curio and his colleagues examined whether young, predator-naive blackbirds learn what constitutes a predator by watching which species is mobbed and classifying such a species as predators (Curio et al., 1978). Is mobbing a form of cultural transmission that is useful in the context of antipredator activities?

In each trial of Curio's experiment, he and his team had a "model" and a "naive" bird, each in its own aviary. The experimental apparatus was designed so that each blackbird could see a noisy friarbird (*Philemon corniculatus*). The friarbird was a species that neither the model nor the naive blackbird had seen before, and it looked nothing like any known predator of blackbirds. The friarbird was presented in such a way that the naive blackbird saw the friarbird alone, but the model saw both a friarbird and, adjacent to it, a little owl, *Athena noctua*—a predator of blackbirds. From the viewpoint of the naive subject, the little owl was out of sight, so that when the model mobbed the little owl, the naive individual saw it mobbing a friarbird.

Curio’s team found that, once naive blackbirds had seen a model apparently mobbing a friarbird, the naive blackbirds themselves were much more likely to mob this odd new creature than if they had not been exposed to the model: information about what constitutes a danger was transmitted culturally. The researchers next asked whether the (now not so naive) blackbird subject would act as a model for a new naive blackbird. And if that worked, how many times could they get a former naive blackbird to successfully act as a model? The longer cultural transmission chains are, the more powerful cultural transmission may be in spreading antipredator behaviors through a population. Though their sample was small, they found that the blackbird cultural transmission chain can be six birds long. After the initial model (bird 1) perceived friarbirds as being dangerous, a new model (bird 2) then saw bird 1 respond to friarbirds. If bird 2 then responded as if friarbirds were dangerous, a new model (bird 3) then observed bird 2 respond to the friarbird as a predator. This procedure went on until six different birds acted as if the friarbird was a predator, and then the chain of information transfer was broken.

Predation and Foraging Trade-Offs

When animals spend time engaged in antipredator activity, they could potentially be doing something else—foraging, mating, resting, playing, and so forth (Lima and Dill, 1990; Figure 12.27). Or, rather than totally curtailing alternative behavior, antipredator behavior could create pressure to perform other behaviors in a different manner—for example, to forage in the vicinity of a refuge, to mate at times when predation is minimal, and so on. In either case, trade-offs between some other behavior and antipredator tactics are often common.

Figure 12.27. Foraging-predation trade-off. When animals are being vigilant for predators, it is often at the cost of other activities. A bird in the group can't forage for insects at the same instant that it scans the sky for hawks.

Predation pressure affects virtually every aspect of foraging—including when a forager begins feeding (Clarke, 1983; Lima, 1988a,b), when it resumes feeding after an interruption (De Laet, 1985; Hegner, 1985), where it feeds (Dill, 1983; Ekman and Askenmo, 1984; Lima, 1985; Schneider, 1984), what it eats (Dill and Fraser, 1984; Hay and Fuller, 1981; Lima and Valone, 1986), and how it handles its prey (Krebs, 1980; Valone and Lima, 1987). Consider Steven Lima and Thomas Valone's work on predation and foraging in the gray squirrel (*Sciurus carolinensis*; Lima and Valone, 1986; Figure 12.28). Early work by Lima had demonstrated that squirrels alter their foraging choices as a result of predation pressure from redtailed hawks (*Buteo jamaicensis*; Lima, 1985). Squirrels that could either eat their food items where they found them or carry the food to cover were more likely to carry items to an area of safe cover, particularly as the distance to safe cover decreased. The closer the refuge from predation, the more likely squirrels were to use such a shelter when foraging; when it was a quick run to reach safety, squirrels generally chose to do so. Squirrels were also much more likely to carry larger (rather than smaller) items to safe areas before continuing to forage.

Figure 12.28. Foraging/predation trade-off in squirrels. (A) When squirrels forage in open fields, they need to balance the risk of predation (in part a function of distance to cover) against the benefits associated with various food items. Here a squirrel is foraging at an experimental feeding station. (B) A squirrel heads for cover with a food item (part of a cookie) in its mouth. *(Photo credits: Steven Lima)*

Lima and Valone followed up the above study with one in which they presented squirrels with two types of food—a large chunk of cookie (associated with long handling times) or a small chunk of cookie (associated with short handling times; see chapter 11). Cookie chunks, rather than nuts, were used to avoid the confounding variable of food storage, as nuts are often buried, but cookies are always eaten. A combination of large and small items was placed either close (8 m) to an area of cover or farther from safety (16 m).

In order to make sense of Lima and Valone's results, we need two critical pieces of information. First, the profitability of small food items was greater than the profitability of large food items (see chapter 11). In the absence of predation, we would expect that squirrels would always take any small food item that they encountered. Second, the total handling time associated with larger food items was great enough that optimal foraging models predicted that larger items should be brought to cover, where it is safe, before being eaten, particularly when the distance to cover was not great. This was not the case for smaller items. Lima and Valone hypothesized that, if faced with predation, squirrels might sometimes pass up the smaller, more profitable food items and continue to search for larger morsels to bring back to cover. This, in fact, is what the squirrels did. Smaller items were rejected in favor of larger items that were brought back to cover.

Interview with Dr. Anne Magurran

Why study antipredator behavior in animals? Are there unique aspects about this sort of behavior?

Predation risk is an uncompromising form of natural selection. An animal that is captured by a predator will be unable to reproduce, so any activity or response that increases an individual's chances of survival is favored. The study of antipredator behavior can therefore tell us a lot about the process of evolution. But it is not simply a matter of prey evolving skills that allow them to evade predators more effectively. Predators will also experience selection to improve their capture success rate. This is sometimes called an "arms race" since better defenses are countered by improved hunting tactics, which in turn will select for improved antipredator behavior. I particularly like Darwin's description of this co-evolutionary game: "Wonderful and admirable as most instincts are, yet they cannot be considered as absolutely perfect: there is a constant struggle going on throughout nature between the instinct of the one to escape its enemy and of the other to secure its prey."

Interpopulational comparisons have proved particularly useful in terms of understanding the evolution of antipredator behavior. Why is that?

I believe there are two main reasons why interpopulational comparisons have been so productive. First, when we compare populations we are, to a large extent, comparing like with like. An investigation of the antipredator behavior of, say, blackbirds and robins could be confounded by all the other biological and ecological differences between the species. An intraspecies investigation, on the other hand, looks at groups of organisms that are broadly similar. It is a particularly powerful means of understanding the evolution of antipredator behavior when the degree of predation risk is the single most important thing that differentiates populations. Moreover, if there are multiple populations experiencing each level of predation risk, then we can, by virtue of this replication, be even more confident that the variation in behavior that we observe is related to the activities of predators as opposed to some other variable (such as the history of the population or the temperature of the environment).

Trinidadian guppies, *Poecilia reticulata*, are a classic example of an interpopulational comparison. A number of rivers draining Trinidad's Northern Range have barrier waterfalls that have prevented predators, though not guppies, from moving upstream. This means that the behavioral characteristics of guppy populations separated by very small distances, and exposed to similar ecological conditions, but differing in the types and numbers of predators that they coexist with, can be attributed to predation. It is also possible to perform simple manipulations in the wild, in which predators are added to or removed from populations, to show that a shift in predation risk does indeed result in heritable change—evolution—of behavior.

The second reason why interpopulational differences are so illuminating is that changes in predation risk—and hence evolution—can be tracked over relatively short time scales. In guppies, for instance, a change in escape response is detectable within about fifteen years of a shift in predation risk. I suspect that behavioral evolution occurs even more quickly than this in the guppy system—no one has looked carefully yet.

What is the most dramatic example of antipredator behavior that you know of?

There are many impressive antipredator behaviors and it is difficult to select a single example, but I think that the evasion tactics of schooling fish are particularly dramatic. Hundreds, or sometimes many thousands, of individuals engage in choreographed maneuvers, such as the flash expansion [in which tightly packed schools of fish "explode," and the fish swim off in all directions], that confuse and outwit their predators. Although it was originally thought that these seemingly cooperative tactics were for the "good of the species," we now know that they are underpinned by individual selection, and that the complex formations that emerge are based on simple decision rules. Unfortunately, this behavior offers little protection against modern fishing vessels since these are equipped with technology to locate and capture large shoals of fish.

Initially a great deal of work on predation focused on foraging/predation trade-offs. How would you summarize the findings from these studies?

One way of looking at this is in relation to what Richard Dawkins and John Krebs called the life-dinner principle. In other words, selection on an individual to remain alive is greater than the selection to find the next meal. So, all other things being equal, animals should invest more in predator avoidance than foraging. However, choices are rarely that simple. An individual that spent all its time in a refuge might avoid predators but would sooner or later die of starvation. This leads to a trade-off between the conflicting demands of foraging and predator avoidance. One resolution of this conflict is for an animal to select the habitat that allows it to minimize the risk of mortality (μ) while maximizing growth rate (g), typically by minimizing the ratio μ/g. Empirical studies—for example, experiments on creek chub, *Semotilus atromaculatus*, by Jim Gilliam and Doug Fraser—support these predictions. Of course, there is considerable variation, among individuals and species, in the trade-offs adopted. Sexually immature animals may place a higher priority on feeding so that they grow faster and reach the size class at which they are able to breed, whereas older ones may be more cautious to help ensure that they remain alive and continue to reproduce.

Your own work on predation pressure suggests that studying this phenomenon may have implications for understanding the process by which new species arise. Can you tell us a little about that?

Our work on guppies uncovered an interesting paradox. Population differences in antipredator behavior (as well as in life history and color pattern) arise over relatively short time periods (typically 10 to 100 generations). Reproductive isolation, in contrast, is slow to emerge and seems to take in excess of a million years to become established. When we looked at its evolution in detail, we found that some postmating isolation has arisen among populations that have been separated for long periods of time. It occurs in the form of gametic isolation (the reduced ability of foreign sperm to compete with native sperm) and as a reduction in hybrid viability. However, there is little evidence for pre-mating isolation, even among long-separated populations. In part this is because of female choice. Although females prefer certain male color patterns, particularly orange spots, they do not seem to discriminate against males from genetically divergent populations. Males show less discrimination of mating partner than females and use sneaky matings as well as consensual courtship to obtain copulations. Sneaky matings occur at a higher rate in populations that co-occur with predators, and are often directed at females preoccupied by predation avoidance.

Where do you see the study of predation and animal behavior heading over the next years?

To date, behavioral studies of predation, along with much of behavioral ecology, have focused on carefully designed, often laboratory-based, experiments. This work has been influential in understanding how animals interact with one another, whether they are predators and prey or individuals of the same species. However, it is now becoming clear that temporal variability in the natural world, such as changes in the presence and the abundance of species in ecological communities across diurnal, seasonal, and annual timescales, can profoundly influence behavior. For example, the predation risk experienced by guppies in their native streams in Trinidad can vary dramatically over short periods of time, but we know relatively little about how the fish respond to this variation in risk. So while it may be unwise to make predictions about future directions in a field like animal behavior, I believe that increasing attention will be paid to natural variability and how it shapes behavior. By learning how animals respond to natural change, we may also be better placed to ameliorate the rapid anthropogenic changes that many species now face.

Studies of this type will continue to use the observational and experimental approaches developed by Tinbergen and other pioneers in the field. However, this is an exciting era, as it is now possible to probe the genetic basis of behavior in real time, by tracking the expression patterns of genes using recently developed genomic tools. These techniques give researchers a much deeper understanding of how animals respond to the nuances of daily life, as well as revealing how the genome interacts with the environment in an increasingly changing world.

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SUMMARY

1. There are two basic types of antipredator behaviors: those that help prey avoid detection by predators, and those that are used once a prey encounters a predator. These two categories encompass most antipredator behaviors, but they are neither exhaustive nor mutually exclusive.
2. Studies using tools from genetics, neurobiology, endocrinology, and chemistry have helped animal behaviorists better understand proximate factors associated with antipredator behavior.
3. Predation pressure not only has an effect on how an animal behaves but also can have a dramatic effect on such life-history variables as development time—for example, when eggs will hatch.
4. If prey can avoid their predators in the first place, they not only can decrease the probability of being captured and eaten but also can reduce the costs associated with fleeing, fighting back against a predator, and so on. Three ways that animals avoid their predators are (a) blending into the environment, (b) being quiet, and (c) choosing a safe habitat.
5. Five types of behaviors that prey use once a predator has been encountered are (a) fleeing, (b) approaching a predator to obtain information, (c) feigning death, (d) signaling to the predator, and (e) fighting back.
6. Comparing a single species in populations with and without a particular predator is a powerful approach when studying how selection operates on antipredator behaviors.

DISCUSSION QUESTIONS

1. Pick your animal of choice, and sketch what a normal time budget (how much time it spends feeding, sleeping, mating, and so on) might look like for this animal. Now, besides the direct time spent looking for predators, examine how predation might directly or indirectly affect all the behaviors on your time budget.
2. Some prey, particularly birds, mob their predators and harass them until the predators leave. List some of the costs and benefits associated with such mobbing, and construct a hypothesis for what sorts of environments might favor mobbing.
3. Abrahams and Pratt (2000) used a thyroid hormone to manipulate growth rates of the fathead minnow (*Pimephales promelas*) in the study described in their paper, "Hormonal manipulations of growth rate and its influence on predator avoidance: Foraging trade-offs" in vol. 78 (pp. 121–127) of the *Canadian Journal of Zoology*. Thyroid treatment stunted growth rates, and the researchers found that such stunted individuals were less likely to risk exposure to predators to gain access to food. Why might that be? Is it possible to construct an argument that would predict the exact opposite of what was found? Also, what does this study tell you about the relationship between proximate and ultimate factors shaping antipredator behavior?
4. In addition to the three ways we discussed that animals avoid predators, can you think of any other predator avoidance behaviors? How do they work? Why do they work?
5. A number of studies have found that laboratory-raised animals can learn what constitutes danger by watching other animals respond to potential predators. How might such cultural transmission be employed by those interested in wildlife reintroduction programs?

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Greenwood, A. K., Ardekani, R., McCann, S. R., Dubin, M. E., Sullivan, A., Bensussen, S., Tavare, S., & Peichel, C. L. (2015). Genetic mapping of natural variation in schooling tendency in the threespine stickleback. *G3-Genes Genomes Genetics*, *5*, 761–769. A more detailed version of the work on genetics and schooling behavior we covered in this chapter.

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Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society, B–Biological Sciences*, *272*, 2627–2634. An overview of factors that affect antipredator behavior.

13

Communication

Communication is at the heart of much of social behavior. Signals are sent and received by individuals, both within and between populations, and even between species. As we will see throughout this chapter there are many different senses—visual, auditory, and so on—that are employed during bouts of communication.

Some environments are extremely “noisy,” making it difficult to send and receive signals. For example, the “soundscape” of an environment like the tropics is noisy and complex, making communication especially difficult (Planque and Slabbekoorn, 2008). In such auditory soundscapes, natural selection should favor communicating in ways that maximize the chances that auditory signals are not masked.

Evidence suggests that in neotropical rainforests, birds in one species monitor the auditory communication of birds in other species and adjust their own communication to minimize the chances that their own signals are masked (Luther, 2009). But the soundscape in neotropical rainforests also includes signals from insects, mammals, and even amphibians. Cicada species, for example, can be very noisy. Patrick Hart and colleagues hypothesized that neotropical birds might try to partition the soundscape with cicadas to increase the chances that their signals are not masked (Hart et al., 2015).

In particular, they tested the prediction that birds in the Costa Rican rainforest would partition the soundscape with *Zammara smaragdina*, a species of cicada that sings often and loudly in this environment, using a very broad band spectrum that could mask many bird songs. The researchers had acoustic recorders located one meter above the ground at seven separate locations and captured the song of *Z. smaragdina* and sixty-two different bird species. They then compared the number of bird species singing before versus after cicada choruses, and the total number of bird songs before versus after such choruses.

For the first three or so hours after dawn, birds from many species sing, but *Zammara smaragdina* do not start singing until some time between 8:40 and 10:40 a.m. The mean number of bird species singing, and the mean number of bird vocalizations, were both significantly lower in the 15 minute period after the cicadas started singing compared to the fifteen minutes before (Figure 13.1). In the cases when birds did sing concurrently with the cicadas, they used sounds that did not overlap with the frequencies of the sounds used by the cicadas. What’s more, on the few days when cicadas did not sing at all, the birds changed their singing patterns during the time period cicadas normally sing, suggesting that it was the cicada song per se that birds were responding to (Figure 13.2).

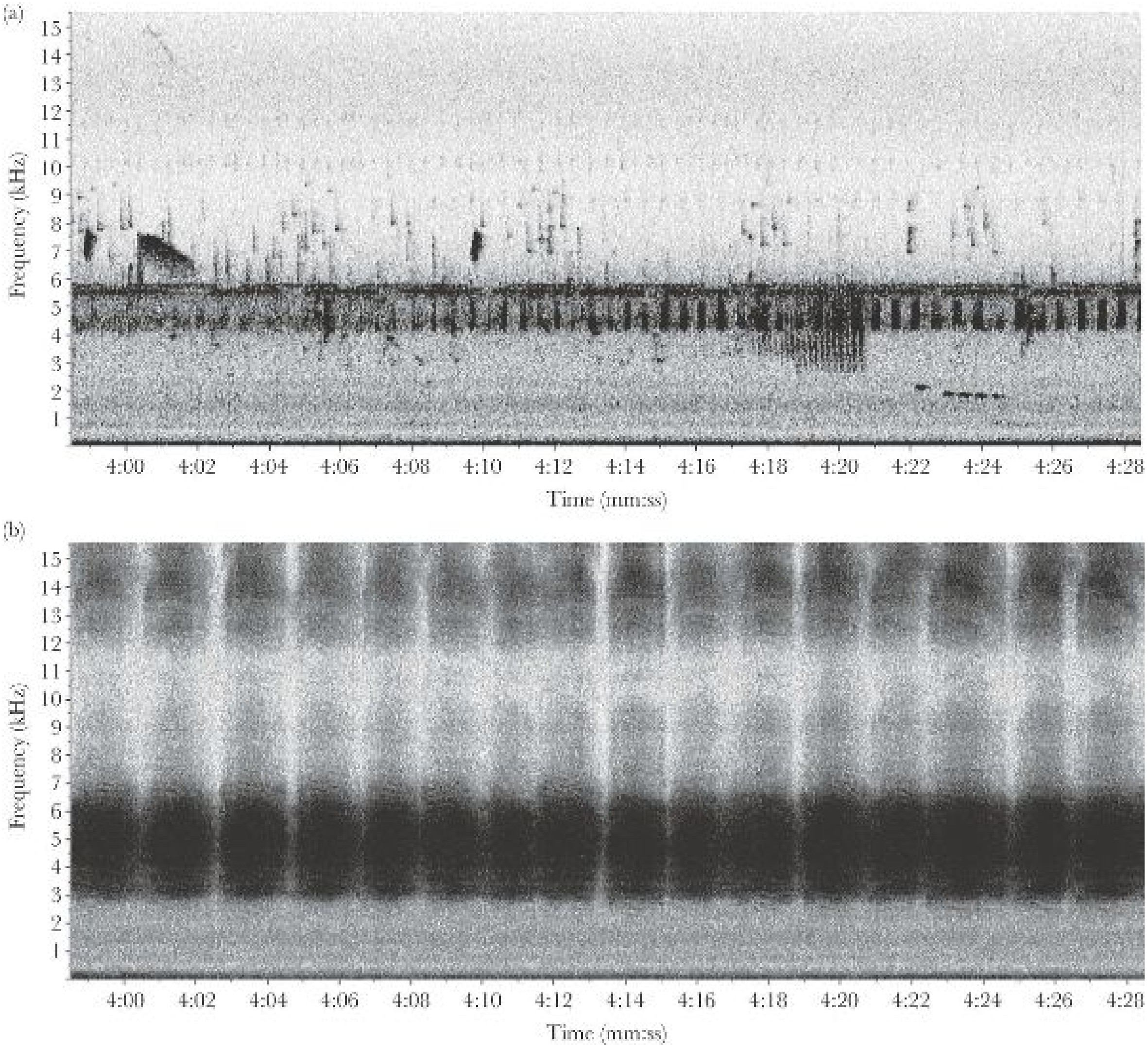


Figure 13.1. **Soundscapes.** (A) The soundscape of birdsong during a 30 second period (at 08:14 a.m.) before cicadas began singing. This soundscape includes vocalizations from at least seven different bird species (*Arremon aurantiirostris* call, *Picumnus olivaceus*, *Arremon torquatus*, *Catharus aurantiirostris*, *Arremon aurantiirostris* song, *Phaeothlypis fulvicauda*, *Formicarius analis*). (B) The soundscape 36 minutes later (08:50 a.m.), immediately after *Zammara* cicadas began singing. No bird vocalizations are present here, just the pulsing signal emitted by *Z. smaragdina*. By permission of Oxford University Press. *(From Hart et al., 2015)*

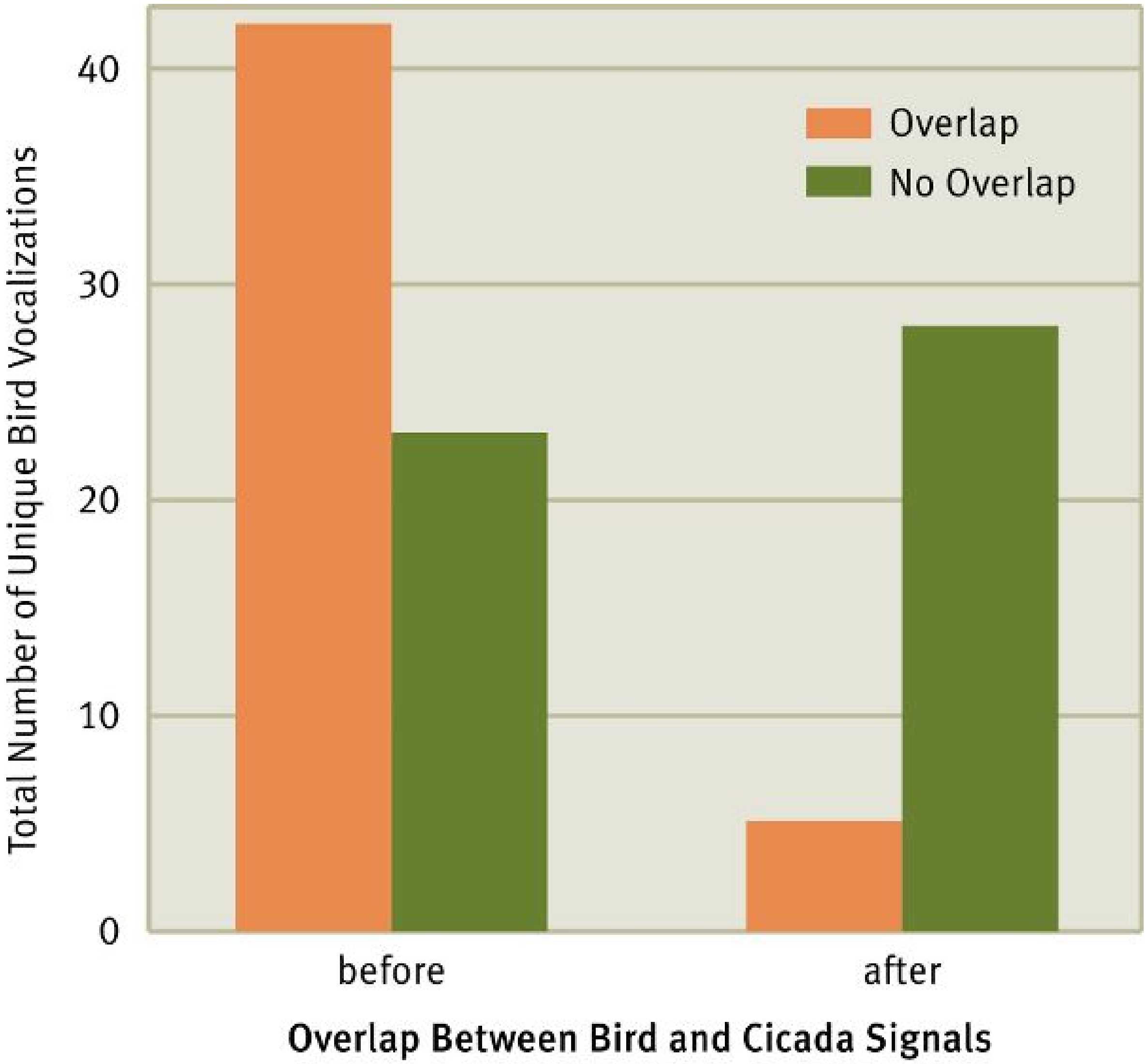


Figure 13.2. **Shifts in what is sung.** Dark bars show bird vocalizations that overlap with those of *Zammara* cicadas, and light bars show bird vocalizations that do not overlap in frequency with cicada calls. Before cicadas began singing (left bars), birds use many vocalizations that overlap with vocalizations used by cicadas. Once the cicadas began vocalizing (right bars), birds changed their songs so as to reduce overlap with cicada vocalizations. By permission of Oxford University Press. *(From Hart et al., 2015)*

* * *

Ethologists typically define *communication* as the transfer of information from a signaler to a receiver. This chapter will address both “how” and “why” questions about animal communication. We will begin by addressing one important question about communication—Is it honest? When do we expect individuals to communicate in a way that accurately conveys information, and when should communication be used to manipulate others? Subsequently, at the heart of the chapter, we will analyze communication systems in terms of the problems they solve. Communication is inherently social—it involves more than a single individual—and communication conveys information that is necessary to solve some problem or another. As such, we will organize the chapter around this functional, problem-solving approach to communication, examining communication as it relates to problems associated with foraging, mating, and predation.

Communication and Honesty

Regardless of the problem a communication network is in place to solve, we can ask whether natural selection should favor honest signals or deception (Dawkins and Krebs, 1978; Grafen 1990a; R. A. Johnstone, 1997; Mock et al., 2011). Richard Dawkins and John Krebs note:

> When an animal seeks to manipulate an inanimate object, it has only one recourse—physical power. A dung beetle can move a ball of dung only by forcibly pushing it. But when the object it seeks to manipulate is itself another live animal there is an alternative way. It can exploit the senses and muscles of the animal it is trying to control . . . which are themselves designed to preserve the genes of that other animal. A male cricket does not physically roll a female along the ground and into his burrow. He sits and sings, and the female comes to him under her own power. (Dawkins and Krebs, 1978, p. 282)

Dawkins and Krebs argue that communication is not so much the exchange of information between a signaler and a receiver but rather an attempt by the signaler to manipulate the recipient. They recognize that sometimes what is in the best interest of the signaler is also in the best interest of the recipient. But when what is good for the signaler is not good for the recipient, natural selection will favor signalers that send signals in whatever way best increases the fitness of the signaler, even if that means manipulating recipients. Natural selection will also favor recipients with the ability to unscramble what is honest and what isn’t, so it can act in ways that maximize its own fitness. Krebs and Dawkins refer to recipients as mind readers and describe an arms race between signaler and recipient in which the signaler is selected to better manipulate the receiver, which then is selected to better filter out only that information that benefits it, and so on (Krebs and Dawkins, 1984).

This is a different view from what Dawkins and Krebs refer to as the classic ethological approach of communication (Marler, 1968; W. J. Smith, 1968, 1977; N. Tinbergen, 1964). Implicit in the classic approach is that both parties usually benefit from the information exchange, and there is little selection pressure for either to be deceitful: the signaler and receiver have common interests, and selection favors the most economical way to share information.

Krebs and Dawkins recognize that the sort of cooperative signaling that is at the heart of the classic ethological approach may be occurring in some systems, particularly those involving kin or reciprocal exchanges (Bergstrom and Lachmann, 1997, 1998; Lachmann and Bergstrom, 1998; see chapters 9 and 10). They offer a way to distinguish between cases in which there is an arms race between manipulators and mind readers, and those in which cooperative signaling dominates.

Krebs and Dawkins propose that when communication is of the manipulator/mind-reader type, signals employed should be exaggerated, as one might expect from a salesman attempting to convince a prospective buyer that his product is the top of the line. When cooperative signaling is in play, natural selection should favor less exaggerated signals—what Krebs and Dawkins refer to as conspiratorial whispers. Because signaling often involves some costs—for example, energy costs or drawing attention from predators—natural selection should favor minimizing these costs through conspiratorial whispers, which reduce the conspicuousness of the communication itself (De Backer and Gurven, 2006; R. A. Johnstone, 1998; Noble, 1999).

While formal mathematical models of the conspiratorial whispers versus conspicuous display hypotheses have shown that this dichotomy oversimplifies communication systems, it is nonetheless a useful heuristic tool. There is, however, another means besides cooperative signaling by which we might expect communication to be honest. Honesty might evolve if the signals being sent are either impossible or, at the very least, difficult to fake. As an example, imagine that females produce more offspring when they mate with larger males. All males, even small ones, would be favored when they produced signals that make it appear to a female that they were large. But selection should favor females paying attention only to those cues that are honest indicators of large size. Females should cue in on honest signals. This appears to be the case in toads: Deep croaks can be produced only by large males because of the physiology of their vocal system. Because male toads can't fake deep croaks and females prefer larger males as mates, female toads can use croaks as an honest signal when choosing among males (Davies and Halliday, 1978; Figure 13.3).

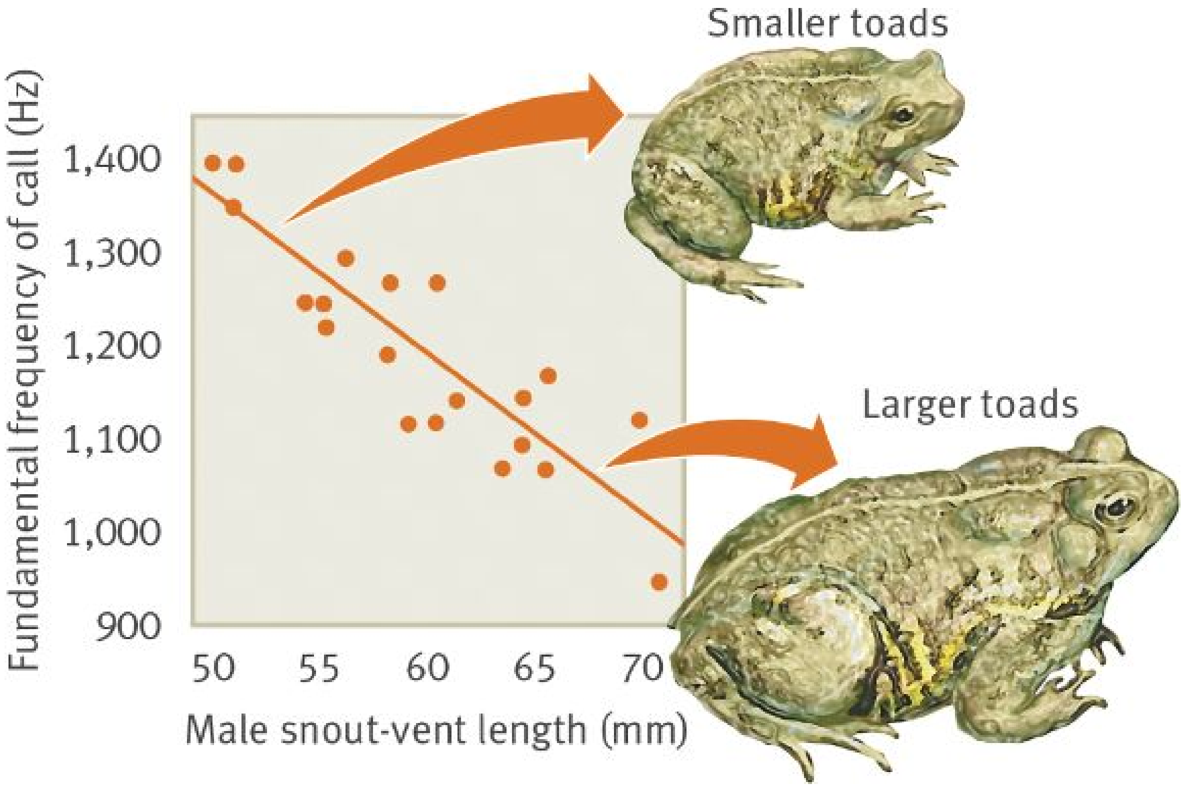


Figure 13.3. Toad size and croaks. The relationship between male size (as indicated by his snout-vent length) and the frequency of a male's call. Call frequency may be an honest indicator of size, and hence of fighting ability. *(Based on Davies and Halliday, 1978)*

Amotz Zahavi has suggested that honesty is also possible when traits are not impossible but just very costly to fake (Grafen, 1990a,b; Zahavi, 1975, 1977, 2003; Zahavi and Zahavi, 1997). Under Zahavi's handicap principle, if a trait is costly to produce, it may be used as an honest signal, because only those individuals that can pay the cost will typically adopt the signal in question. For example, imagine that females are using the length of a male's energy-costly song as a cue for the amount of resources he is able to garner. While a male that is not good at garnering resources could potentially use virtually all of his resources to sing, and thus could give the female a false impression of his resource-garnering skills, most often only the males that are genuinely good at gathering resources would be able to afford to sing, as singing is an energy-costly activity. Honest communication may be an outcome even when deception is possible in principle, as long as deception is costly (E. Adams and Mesterton-Gibbons, 1995; R. A. Johnstone, 1995, 1998; Mesterton-Gibbons and Adams, 1998; Zahavi and Zahavi, 1997).

Communication Solves Problems

In these next sections we will examine communication in terms of the problems associated with foraging, predation, and mating. In so doing, we will look at the costs and benefits of communication, the phylogenetic history of communication systems, the role of learning and social learning in shaping communication, as well as the underlying proximate basis for communication.

Before we look at communication in specific behavioral contexts like foraging and predation, it is worth noting that ethologists have also examined communication at a broader level, not confined to a single behavioral context. For example, Karen McComb and Stuart Semple studied the relationship between vocalization and group size in primates (McComb and Semple, 2005). When these researchers examined the published literature and compared vocalization *repertoire*—the number of different vocalizations used—and group size, they found a significant positive correlation (Figure 13.4). One possible explanation for this finding is that as group size increases, the benefits of a broad repertoire of sounds to communicate with other group members increases (Snowdon, 2009). However, because McComb and Semple's study was correlational, it is not clear yet whether increased group size favored increased vocalization repertoires or whether increased vocalization repertoire favored the evolution of increased group size (Freeberg et al., 2012) or both.

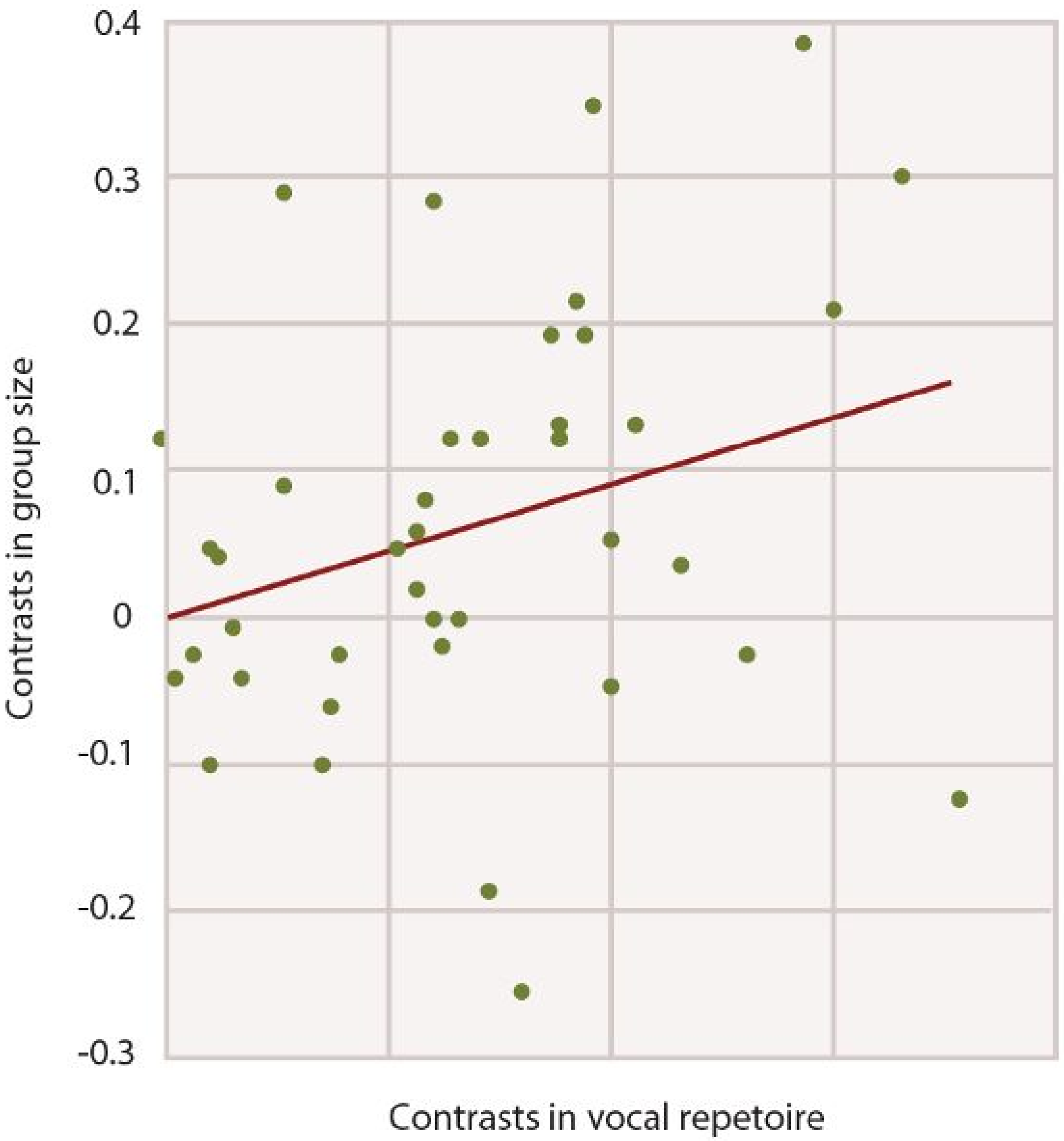


Figure 13.4. Vocal repertoire and group size. There is a positive correlation between vocal repertoire and group size in 42 species of primates. The *x*-axis and *y*-axis are measured in “contrasts,” which allow a statistical analysis that takes into account the phylogenetic relationship of the species studied (see chapter 2). Reprinted with permission of The Royal Society. © 2005. (*From McComb and Semple, 2005*)

PROBLEM: HOW TO COORDINATE GROUP FORAGING

When animals forage in groups, they face coordination problems. When new food sources are found, how can that information be transferred to other group members if such a transfer is beneficial to the signaler (Dornhaus et al., 2006; Fernandez-Juricic and Kowalski, 2011; Fernandez-Juricic et al., 2006; Galef and Giraldeau, 2001; J. R. Stevens and Gilby, 2004; Thierry et al., 1995; Torney et al., 2011)?

Food Calls in Birds

Colonial breeding cliff swallows (*Petrochelidon pyrrhonota*) live in nests that act as information centers (C. R. Brown, 1986; Ward and Zahavi, 1973). For some time, researchers thought that individuals living in nests passively received information—they simply observed their nestmates and followed them to potential resources. While this sort of system does allow for group foraging, it is not as efficient a solution to coordinating group behavior as *recruiting* foragers.

Charles Brown and his colleagues studied whether individuals are recruited to food sites (C. Brown et al., 1991). Using both playback experiments (playing tape-recorded bird calls) and provisioning experiments (putting food out to entice birds), Brown and his team found that cliff swallows gave off "squeak" calls, which alerted conspecifics that a new food patch—often a swarm of insects—had been found (Table 13.1). Squeak calls were emitted *only* in the context of recruiting others to a food site, suggesting that they served the specific function of facilitating group foraging, per se.

Table 13.1. Squeak calls attract others. The mean number of birds and squeak calls heard two minutes before and two minutes after insects were flushed by foraging cliff swallows. For each two-minute period, there were significantly more birds after insects were flushed than before, and significantly more squeak calls were heard after the insects were flushed than before. *(From C. Brown et al., 1991, p. 559)*

	Mean no. of birds		**Mean no. of calls/bird/2 minutes**		**No. of trials**
Period	**Before**	**After**	**Before**	**After**	**(*N*)**
May 8, 1990	37.8	240.3	0.062	0.267	11
May 9, 1990	9.5	20.5	0.000	0.137	4
May 24, 1990 A.M.	9.7	22.7	0.000	0.100	6
May 24, 1990 P.M.	30.8	88.7	0.053	0.171	9
May 27, 1990	7.9	45.4	0.031	0.133	7

	Mean no. of birds		**Mean no. of calls/bird/2 minutes**		**No. of trials**
Period	**Before**	**After**	**Before**	**After**	**(*N*)**
May 29, 1990	8.8	54.8	0.000	0.098	5
May 30, 1990	8.5	38.5	0.033	0.109	2
June 15, 1990	25.9	102.1	0.032	0.134	7

Recruiters also obtain benefits from calling because the increased group size that results from recruiting makes it more likely that some group members will find and track the insect swarm and thus provide further foraging opportunities (C. Brown, 1988; C. Brown et al., 1991). This tracking behavior may be important, as swallows must often return to the colony to provision young, and might have difficulty relocating an insect swarm without the help of others.

Swallows are not the only birds that emit food calls. When ravens, who are scavengers that can often survive for days if they uncover a large food patch, find a new food source, they often emit a very loud yell that attracts other ravens to the caller’s newly discovered bounty (Boeckle et al., 2012; Figure 13.5).

Figure 13.5. Raven yells. Under certain conditions, ravens emit a loud “yell” upon uncovering a new food source. Such yells attract other birds. *(Photo credit: © Marcin Perkowski / Shutterstock)*

Bernd Heinrich and John Marzluff have studied both proximate and ultimate questions associated with communication and foraging in common ravens (*Corvus corax*; Heinrich, 1988a,b; Heinrich and Marzluff, 1991). On the proximate end, it appears that yelling is, in part, a response to hunger level, as hungry birds call more often than satiated birds (Figure 13.6). In terms of the costs and benefits of calling, it appears that yelling by juvenile ravens attracts other juvenile ravens to a food resource, allowing them to overpower resident adult ravens. Most of the juvenile ravens are unrelated “vagrants,” and one way an immature vagrant that comes upon a food source that is being defended by an adult territorial male can gain access to this source is to yell (P. G. Parker et al., 1994). Yelling attracts others that, together with the signaler, can overpower those originally found at the food source (Heinrich and Marzluff, 1991).

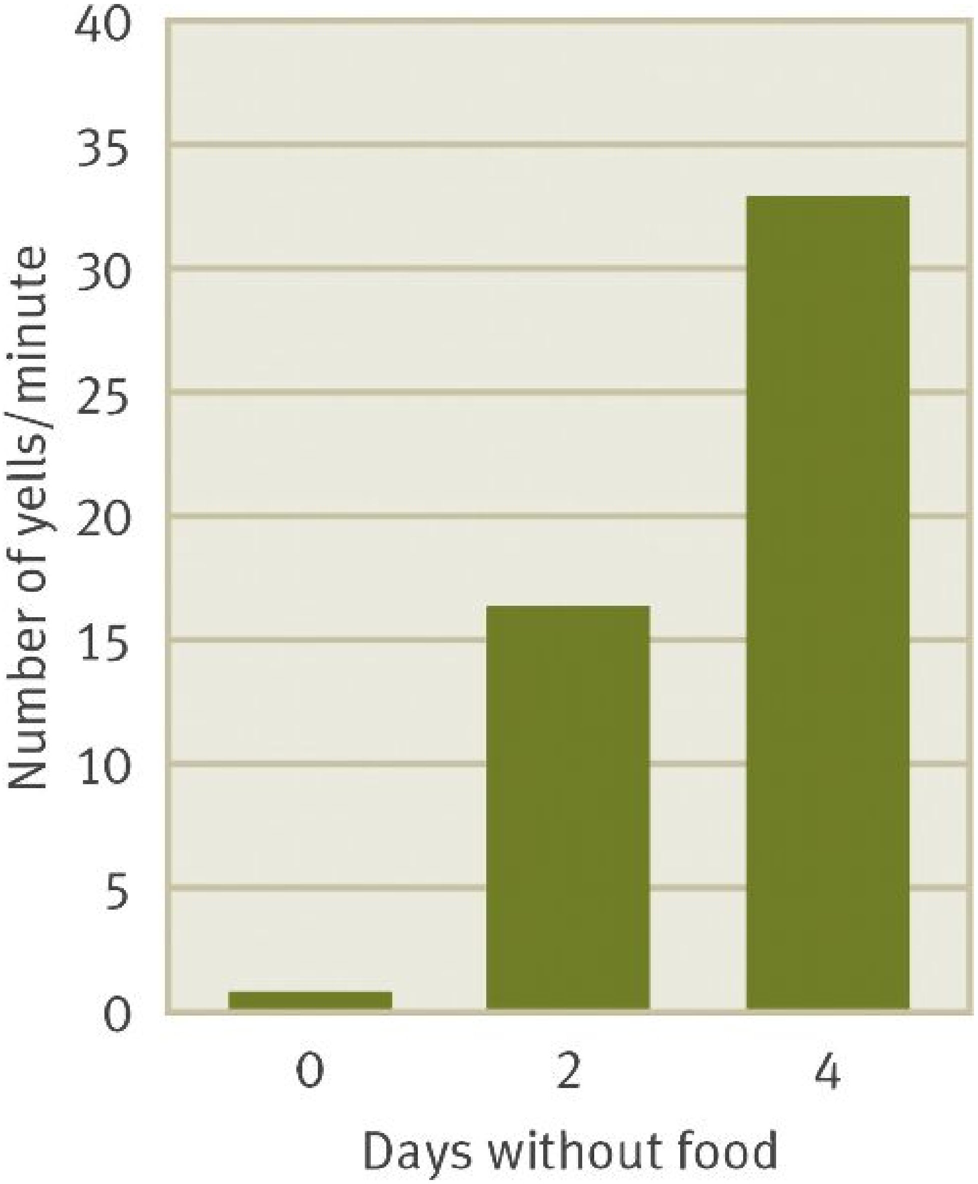


Figure 13.6. Yellers are hungry. In ravens, "yelling" is often associated with foraging—in particular, calling others to a food bonanza. Immature ravens yell more when hungry. *(Based on Heinrich and Marzluff, 1991)*

Ravens also communicate about food when they roost together at night, and this form of communication appears to involve some type of learning (Marzluff et al., 1996). While many populations of ravens roost at the same spot for years, Marzluff and his team studied juvenile ravens in the forested mountains of Maine, where individuals form roosts near a newly discovered food source—for example, a large animal carcass. They found that such roosts are very mobile and ravens move to where new prey has been discovered. Marzluff's team hypothesized that these mobile roosts served as information centers that provided roostmates with the chance to share information about prey that they had discovered when away from the roost.

They ran a series of experiments to test their ideas on communication at evening roosts. Such roosts contain both knowledgeable individuals that know about nearby prey, and naive individuals that do not. Yet, when birds leave the roost in the morning, they all tend to go in the same direction, hinting that they communicate with one another, and that one or a few knowledgeable individuals lead the way. In one experiment, Marzluff's team captured ravens and denied them information about the prey environment. When these individuals were released and joined a roost, they tended to follow, rather than lead, other birds out of the roost in the morning.

Marzluff's team ran a second experiment in which they again captured ravens, but this time they brought the captured birds to a location where there was a new prey item that the researchers themselves had placed into the environment. This information was unavailable to birds that were not captured, as they were not brought to the location of the new food source. When captured birds were released and joined roosts, they tended to lead other roostmates out of the roost and to the newly discovered prey item: birds that had learned the location of prey acted as leaders (Figure 13.7). Indeed, Marzluff found that the same individual would act as a leader when it learned the location of new prey, and as a follower when it was denied information that others in the nest knew. While it is not clear exactly how information about who is a knowledgeable forager and who is not is spread at the roost, researchers noted that before the ravens departed from the roost in the morning, they emitted “honking” sounds. Whether knowledgeable birds were more likely to emit such sounds remains to be tested.

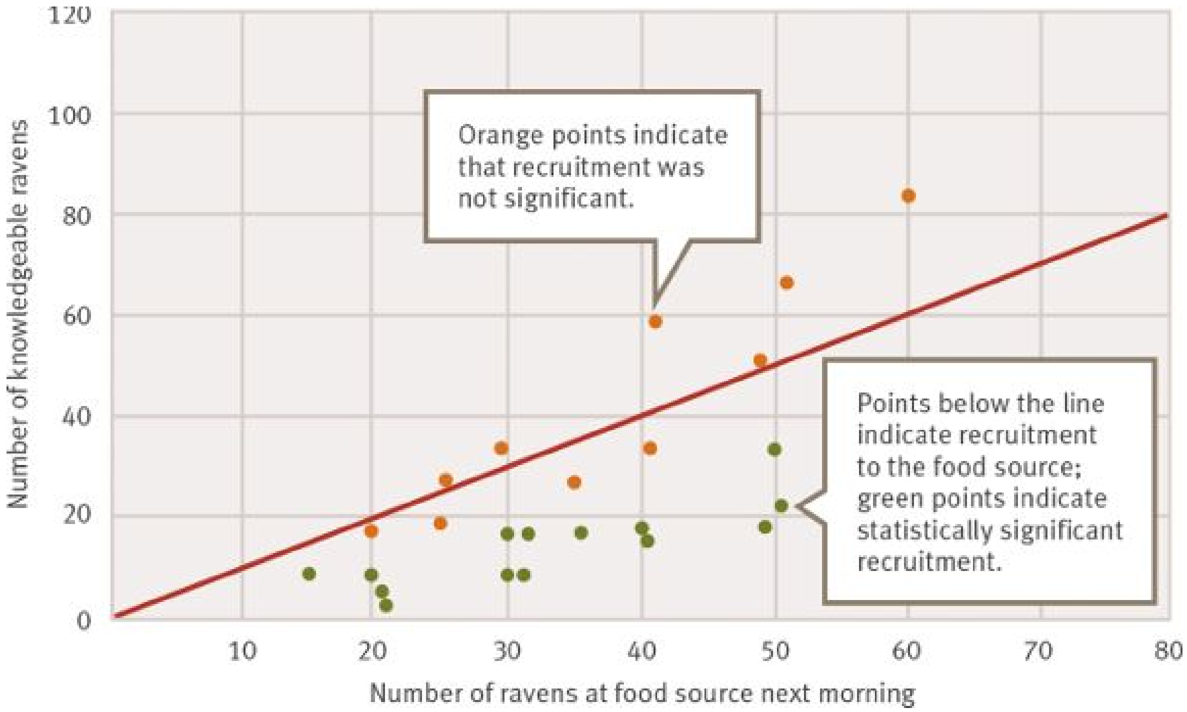


Figure 13.7. Raven recruitment. The line denotes when the number of ravens that knew of the prey source equals the number of ravens at the prey source the next day. Points below the line indicate recruitment because they are instances in which more birds arrived at food after roosting than birds that previously knew of the food's location. *(Based on Marzluff et al., 1996, p. 99)*

Honeybees and the Waggle Dance

In honeybees, collecting food for the hive often involves thousands of workers covering large areas (Visscher and Seeley, 1982; Figure 13.8). Such a system poses logistical problems for honeybees: How do they keep track of the changing distribution of resources (nectar, pollen) through time? How are they able to monitor the needs of others in the colony? How do foragers communicate information about any food they uncover to other members of their hive? The answer to that last question, in part, lies in the now famous waggle dance of the honeybee.

Figure 13.8. Honeybee foraging. Honeybee foraging involves a complex communication system, including waggle dances. The waggle dance, along with other informational cues, gives bees in a hive information about the relative position of newly found food sources. *(Photo credit: Juniors Bildarchiv GmbH / Alamy Stock Photo)*

The waggle dance of the honeybee was first studied experimentally by Karl von Frisch (von Frisch, 1967). Thomas Seeley describes the waggle dance as

> a unique form of behavior in which a bee, deep inside her colony's nest, performs a miniaturized reenactment of her recent journey to a patch of flowers. Bees following these dances learn the distance, direction and odors of these flowers and can translate this information into a flight to specified flowers. Thus the waggle dance is a truly symbolic message, one which is separated in space and time from both the actions on which it is based and the behaviors it will guide. (Seeley, 1985, pp. 84–85)

The waggle dance has an almost mystical quality to it (Munz, 2005). Fortunately, it is possible to maintain that air of the amazing while studying this behavior in detail, as ethologists have now been doing for more than half a century (Grueter and Farina, 2009; Seeley, 1985, 2012). To see this, imagine that a worker bee has just returned from a cluster of flowers that is 1,500 meters from her nest, and that these flowers are located 40 degrees west of an imaginary straight line running between the worker's nest and the sun (Figure 13.9). How can a worker communicate this information about a new food source to others in the hive?

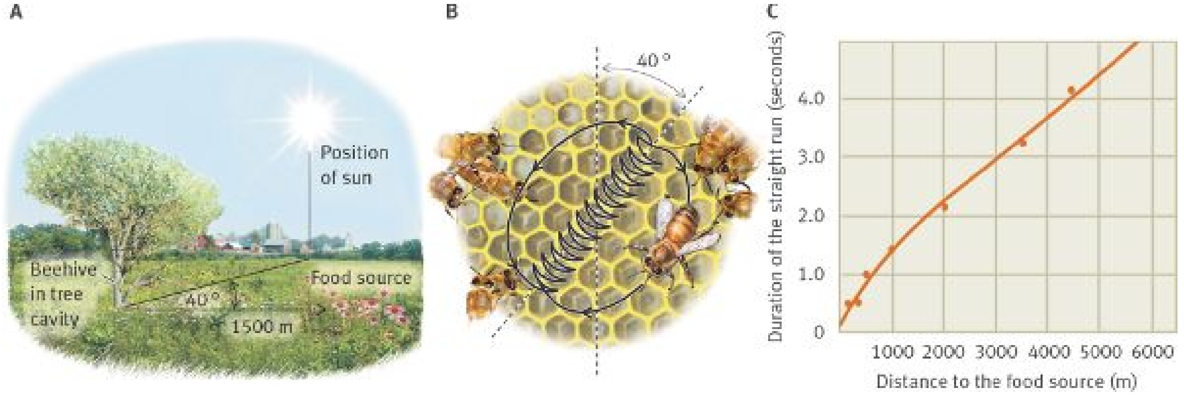


Figure 13.9. Honeybee waggle dances. (A) Imagine a patch of flowers that is 1,500 meters from a hive, at an angle 40 degrees west of the sun. (B) When a forager returns, the honeybee dances in a figure-eight pattern. In this case, the angle between a bee's straight run (up and down a comb in the hive) and a vertical line is 40 degrees. (C) The length of the straight run portion of the dance translates into the distance from the hive to the food source. *(Based on Seeley, 1985)*

Upon returning to the nest, the worker bee quickly starts "dancing" up and down a vertical honeycomb within the hive; her sisters and half-sisters stay near her, making as much physical contact as possible with both her and each other in the process. While dancing vigorously by waggling her abdomen, the worker conveys crucial information to her relatives in the hive. The dance provides topographical information (north, east, south, west, northwest, and so on) for finding the food source from which she has just returned. When compared with a straight up-and-down run along a comb, the angle at which the forager dances provides information about the position of the food source of interest in relation to the hive and to the sun. Furthermore, the longer the bee dances—in a part of the waggle dance known as the "straight line"—the farther away the bounty. Every extra 75 milliseconds of dancing translates into the resource being about an additional 100 meters from the hive. The more precise the information conveyed in the waggle dance, the greater the ability of other bees to find the food source, the more food brought back to the hive, and consequently the greater the inclusive fitness of the forager, because a hive is largely composed of individuals that are closely related to one another.

Ross Crozier and his colleagues studied the genetics of the honeybee dances by examining the point at which bees shift from other types of dances to the waggle dance (Johnson et al., 2002; Oldroyd and Thompson, 2007; Oxley and Oldroyd, 2010). When resources are close to the hive, honeybee foragers tend to use what is called a round dance. When the resources are at greater distances, bees switch to a sickle dance, and when food is very far from a hive, foragers use the waggle dance (Figure 13.10).

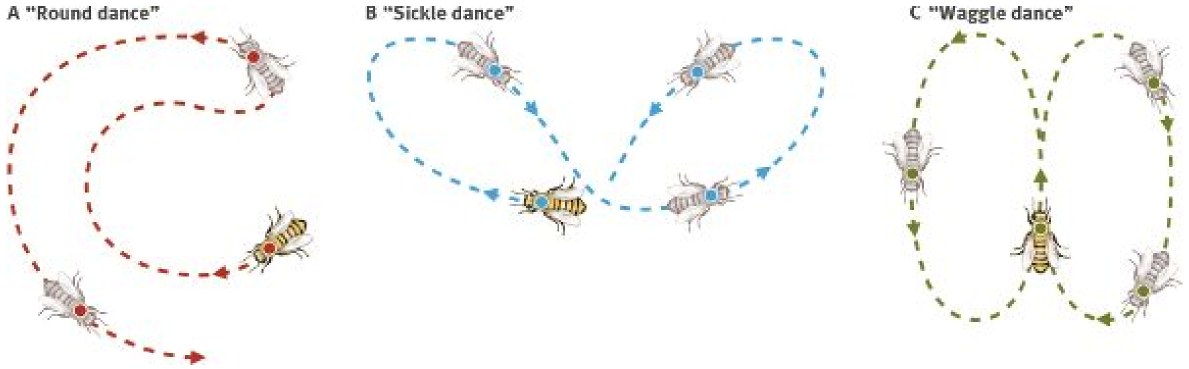


Figure 13.10. Different honeybee dances. Three honeybee dances. Each honeybee at its initial starting point is shown in full color, and the same bee is shown in fainter colors as it moves along the path of its dance. *(Based on Johnson et al., 2002, p. 171)*

Crozier and his team ran a series of experiments in which they mated individuals from populations of bees that differed in terms of when they shifted from using the round dance to the sickle dance, and finally when they shifted from the sickle dance to the waggle dance. For example, in one population that the researchers studied, bees transitioned from the round to the sickle dance when food was more than 20 meters from the hive, and they shifted from the sickle dance to the waggle dance when food was 60 meters or more from the hive. The results of the genetic crosses undertaken by Crozier and his colleagues suggest that the transition across dance types is controlled at a single locus (Johnson et al., 2002).

Ethologists have also studied developmental changes associated with the honeybee waggle dance. Jurgen Tautz and his colleagues examined how hive temperature during development affected the waggle dance behavior of bees (Tautz et al., 2003). Tautz's team raised bees in one of three temperatures: 32°C, 34.5°C, or 36°C. When bees in these treatments matured, they were individually marked and placed into foster hives and they were trained by Tautz and his colleagues to feed at an artificial food source placed 200 meters from the hives. The researchers observed differences in the waggle dance behavior in bees raised at different temperatures.

Bees from the 32°C treatment were less likely to use the waggle dance when they returned to the hive than were bees from either of the other treatments—60 percent of foragers from the 32°C treatment waggle danced versus 90 percent of foragers from the 34.5°C and 36°C treatments (this difference, however, was not statistically significant because of the large amount of variance found within treatments). In addition, bees from the 32°C treatment made significantly fewer circuits—trips around the figure eight in the waggle dance—than bees from the 36°C treatment (Figure 13.11).

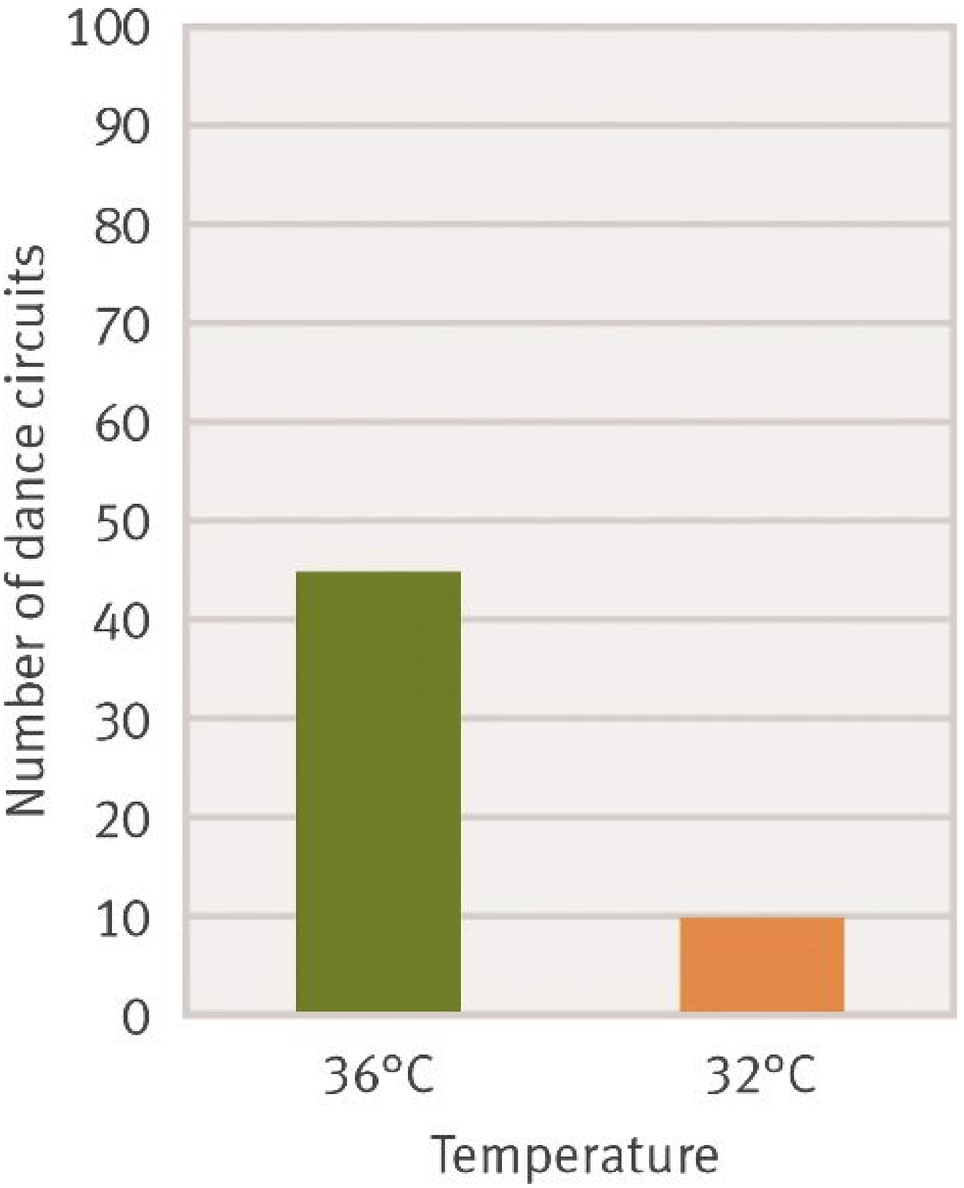
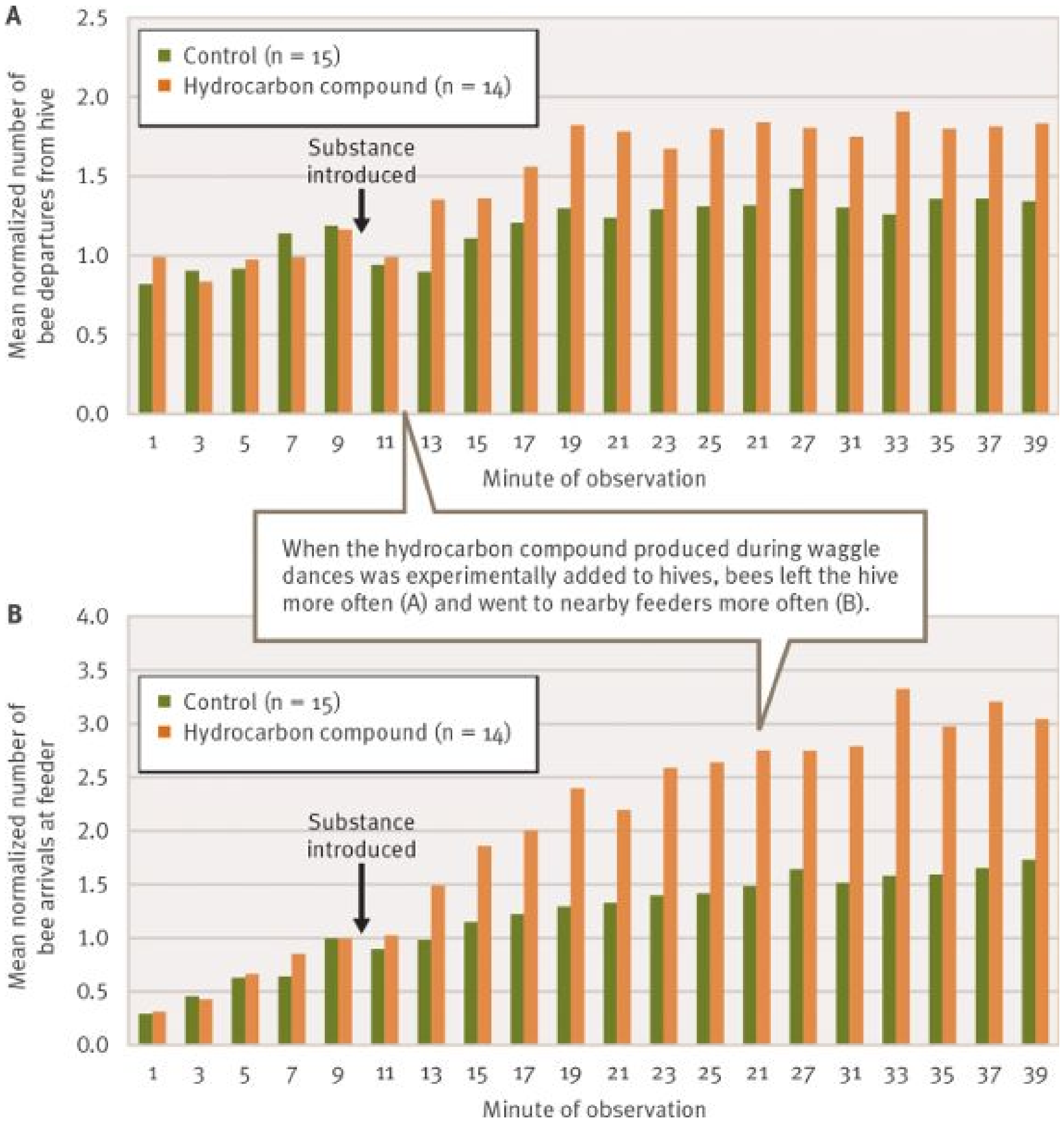


Figure 13.11. Number of dance circuits. The number of figure-eight circuits in a waggle dance when honeybees were raised at a temperature of 36°C or 32°C. *(Based on Tautz et al., 2003, p. 7345)*

Tautz and his colleagues also found that bees raised in the 36°C treatment fared much better in individual learning tasks than did bees raised in the other treatments. These results suggest that differences in temperature during early development can have important effects for both individual bees and the hive as a whole. When bees were raised in colder temperatures, they were both poor learners and less efficient at communicating important foraging-related information to other members of their hive. Because the food that foragers bring into a hive is eventually transferred into energy that keeps the hive temperature high, a dangerous feedback loop is put into play: Lower temperatures lead to bees that are both poor foragers and poor communicators, which in turn leads to less energy for the hive and hence to lower hive temperatures, which then leads to even worse foragers, and so on.

Animal behaviorists have also investigated what chemical cues cause bees to leave a hive to forage in response to the waggle dance (Thom et al., 2007). Thom and Dornhaus (2007) found four different hydrocarbons that were emitted by bees during waggle dances. When synthetic versions of these hydrocarbons were placed in a hive, bees increased their tendency to exit the hive, suggesting a link to foraging. Follow-up work by Thom and his team found that when this compound was added to hives, individually marked bees increased their departures from a hive by almost 50 percent compared with controls, and they more than doubled their visits to a nearby feeder (Gilley et al., 2012; Giley, 2014; Figure 13.12; Box 13.1).



When the hydrocarbon compound produced during waggle dances was experimentally added to hives, bees left the hive more often (A) and went to nearby feeders more often (B).

Figure 13.12. Hydrocarbon dance compounds. (A) When a hydrocarbon compound produced during the waggle dance was added to a hive, more honeybees exited the hive than in a control treatment. (B) More honeybees were also found at a nearby feeder. *(From Gilley et al., 2012)*

Box 13.1. SCIENCE AT WORK

What is the research question? How does the honeybee waggle dance communicate information to would-be foragers?

Why is this an important question? The honeybee waggle dance is one of the few instances of nonhuman communication where place and time are communicated symbolically.

What approach was taken to address the research question? Many different approaches, including recording behavior within hives, experimental manipulation of foraging sites, manipulation of the hive environments, genetic breeding studies, and molecular genetic analyses have been employed to study this question.

What was discovered? Two of the key components of the waggle dance convey the location of food sources to naive foragers are the angle that a returning forager uses during the straight run part of the waggle dance (an indication of compass direction) and the duration of the straight run (indicating distance from the hive). Both convey information about the location of food sources to naive foragers.

What do the results mean? Animals are capable of complex, sophisticated forms of communication, some of which use symbolic representation.

Chemical and Vibrational Communication in Foraging Ants

Like honeybees, ants often forage in groups and can cover large areas during their foraging bouts. And like honeybees, ants face the problem of how to communicate foraging-related information to those in their nest. They solve this communication problem primarily by using chemical markers and sound production through vibrations (stridulation; Billen and Morgan, 1997; Holldobler and Wilson, 1990; Vander Meer et al., 1997; E. O. Wilson, 1971). Here we begin by looking at chemical communication in the leaf-cutting ants of the genus *Atta* and then examine vibrational communication in this group (Holldobler and Roces, 2001).

Ants in the genus *Atta* consume more vegetation in the neotropics than any other group in that ecosystem. Leaf-cutter ants subsist entirely on the fungus they grow on leaves and on the sap produced by the plants whose leaves they harvest (Littledyke and Cherrett, 1976). These ants live in nests containing a queen and often hundreds of thousands of workers and have an elaborate, caste-based system for obtaining leaves. Leaves must first be cut, then carried to the nest, ground up, chewed and treated with enzymes, placed into the fungus garden, and subsequently cultivated. Bert Holldobler and E. O. Wilson liken the system to an assembly line where different castes handle different tasks (Holldobler and Wilson, 1990; D. S. Wilson, 1980; E. O. Wilson, 1980a,b; E. O. Wilson and Holldobler, 2005a,b).

From a proximate perspective, two chemicals are especially important in long-distance foraging communication in *Atta* species: methyl 4-methylpyrrole-2-carboxylate and 3-ethyl-2,5methylpyrazine (Morgan, 1984). These substances are produced in the poison gland of leaf-cutter ants and are used to recruit other workers to foraging sites that are relatively long distances from their nest. Recruitment pheromones, which fade slowly, are placed along the trails leading to trees where leaves are being harvested. These pheromones are also deposited along branches and twigs, bringing recruited foragers very close to the leaves they need to harvest. Recruitment pheromones are incredibly powerful:

> The discoverers of methyl 4-methylpyrrole-2-carboxylate . . . estimated that one milligram of this substance (roughly the quantity in a single colony), if laid out with maximal efficiency, would be enough to lead a column of ants three times around the earth. (Holldobler and Roces, 2001, p. 94)

When leaf-cutters are in the vicinity of the leaves, they rely on a second type of communication called stridulation to determine the precise leaves on which to work; certain areas with certain leaves are cut until there is virtually nothing left (Figure 13.13). Holldobler and Roces hypothesized that *Atta* workers were cutting the tenderest leaves (Holldobler and Roces, 2001). They further hypothesized that because *Atta* workers raise and lower their gasters (part of their abdomen) in a manner similar to the way they create stridulatory vibrations, the ants were using vibrational cues to recruit other workers to the best leaves in the vicinity, increasing the amount of high-quality food brought back to the nest (Markl, 1968).

Figure 13.13. Leaf-cutters foraging. Leaf-cutter ants can ravage foliage in their path. The ants don’t attack all the leaves, however, but instead they often strip some leaves to the stalk (for example, those that are most tender or have fewer secondary compounds present), while leaving other leaves untouched. *(Photo credit: © Dong Lin / Fisher Lab/ California Academy of Sciences)*

Holldobler and Roces tested whether workers in *Atta cephalotes* stridulate while they are cutting leaves. What they found was that workers were stridulating while they were cutting the leaves, and the vibrations were being sent along the length of a leaf in a long series of vibrational “chirps” (Figure 13.14). Next, the researchers offered workers leaves that were either tough or tender. In addition, in a follow-up experiment, tough and tender leaves were both dipped in sugar water and offered to ants. While only 40 percent of the ants stridulated when cutting tough leaves (with no sugar water), 70 percent did so when the leaves were tender (with no sugar water), and almost 100 percent stridulated when either type of leaf was dipped in sugar water (Roces et al., 1993).

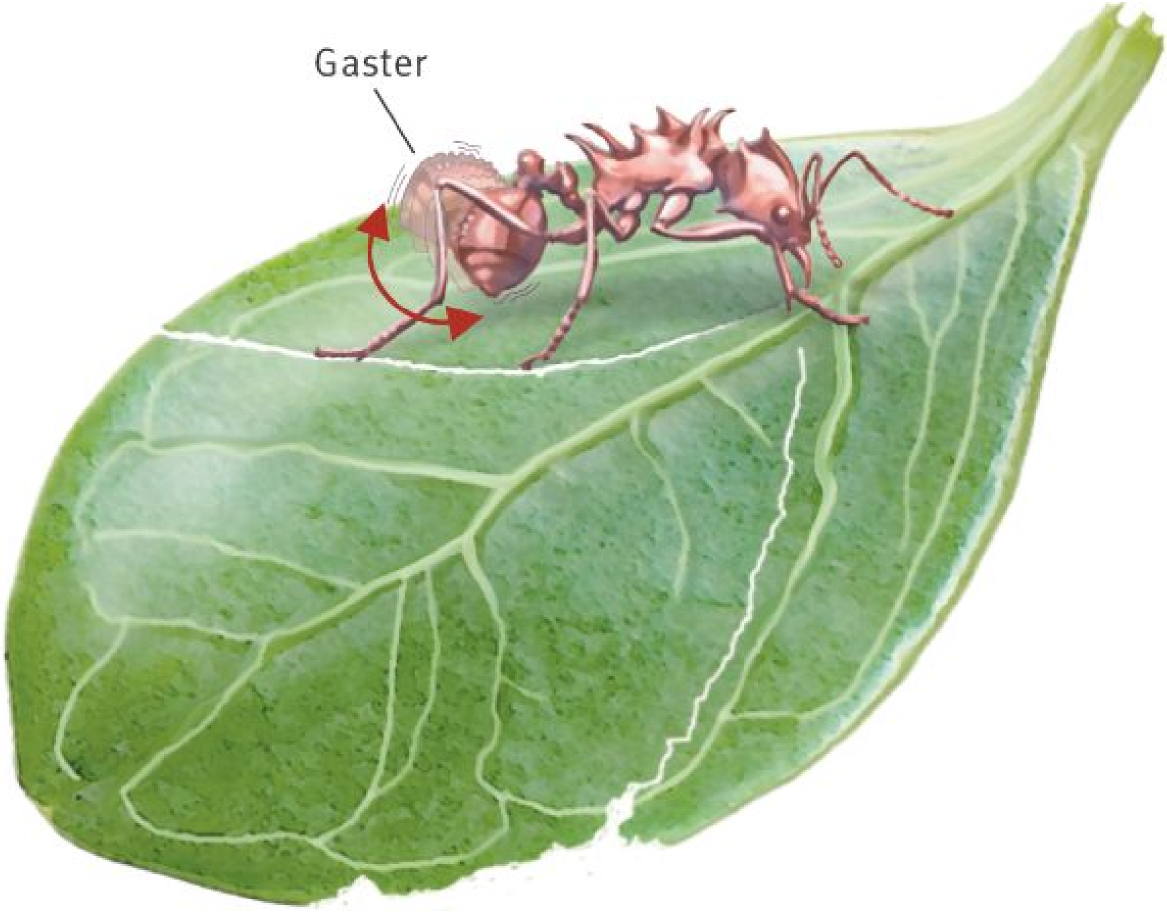


Figure 13.14. Stridulating communication. A schematic of a leaf-cutter ant cutting a leaf and stridulating its gaster up and down. *(Based on Holldobler and Roces, 2001)*

To test for the potential recruiting nature of stridulatory communication, Holldobler and Roces hooked one leaf to a vibrator and used a similar leaf that was not vibrated as a control (Holldobler and Roces, 2001). When given the choice to cut either of the leaves, ant workers preferred the vibrating leaf, suggesting that these cues were not only produced by workers, but also used to recruit workers (Roces and Holldobler, 1996). Stridulation was also found to serve a second role in communication. In *A. cephalotes*, a caste of very small ants, called minim workers, exists. These minim workers cannot cut leaves, but they are often found hitchhiking rides on leaves on the backs of leaf-cutters. Minims protect these other leaf-cutting workers from attack by parasitic flies, so it is in the interest of leaf-cutting ants to have minims find them (Eibesfeldt and Eible-Eibesfeldt, 1967; Feener and Moss, 1990). Hitchhiking minims apparently use the vibrational cues created by stridulating leaf-cutting nestmates to locate the leaf-cutters (Roces and Holldobler, 1995; Figure 13.15).

Figure 13.15. Minim workers hitchhiking on a leaf. The stridulating signals emitted by leaf-cutters are used in numerous contexts. One such venue is between leaf-cutters and "minimum" workers (minims), who use these signals to eventually hitch rides on cut leaves that are carried on leaf-cutters' backs. *(Photo credit: Bert Holldobler)*

PROBLEM: HOW TO FIND AND SECURE A MATE

Animals use many different types of communication when assessing potential mates (see Box 13.2). In this section, we will examine the role of (1) vocal communication (birdsong) and (2) tactile communication (ripples by insects that live in water), as they relate to intrasexual and intersexual selection.

Box 13.2. CONSERVATION CONNECTION

Anthropogenic Change and Animal Communication

The type of communication system that natural selection favors in a population depends, in part, on the ecology and environment in which that species lives. For example, many forest-dwelling birds that breed in leks (see chapter 7) will display courtship behavior only when the light breaks through the forest canopy through small gaps at certain times of the day. Altering that environment can disrupt courtship activity.

In the Guianian cock-of-the-rock (*Rupicola rupicola*), orange-colored males will often display to females when yellow-orange wavelength light from small gaps in the canopy reaches the ground (Endler, 1997; Endler and Thery, 1996). The courtship dance and song that then takes place is dramatic, as described by Pepper Trail, who studied these birds in Suriname: “The normally silent males burst into ringing choruses of raucous, crowing calls and drop from their resting perches. . . . Each male stands erect and violently beats his wings, flashing the dramatic, usually concealed, black and white primary feathers” (Trail, 1995). Males may then repeat this greeting display (Figure 13.16), and females choose from among the displaying males.

Figure 13.16. Communication in cock-of-the-rocks. (A) A male cock-of-the-rock. (B) A group of males displaying and singing to attract females. *(Photo credits: WILDLIFE GmbH / Alamy Stock Photo)*

Humans clear-cutting the area of the lekking arena, or even areas in its vicinity, will change the way light enters the lekking arena and might radically disrupt the courtship communication between male and female cock-of-the-rocks (Endler, 1997). Of course, it is difficult to predict exactly how, but such clear-cutting might produce constant light during daytime hours, which could (1) stop males from displaying at all because of increased exposure to predators, (2) induce males to display so often that they become energetically drained, or (3) lead to females no longer being able to assess male quality accurately. Any or all of these effects could affect population size.

Birdsong

Birdsong has been studied by naturalists, ethologists, behavioral ecologists, neurobiologists, comparative psychologists, evolutionary biologists, and even physicists (Beecher, 2008; Berwick et al., 2011; Brumin and Naguib, 2009; Catchpole and Slater, 1995; D. F. Clayton, 2004; Mooney, 2009; Podos and Warren, 2007; Podos et al., 2004; Slater, 2003; Mindlin, 2103; Bolhuis and Moorman, 2015). Birdsong has many functions associated with colony formation, flocking, foraging, and other behaviors (Kroodsma and Byers, 1991), but here we will focus on its role in sexual selection. In particular, we will examine how and why birdsong is used to attract and secure mates. We will begin with two studies that address ultimate questions regarding the fitness consequences of birdsong and the phylogeny of birdsong, and then we will examine the proximate underpinnings of birdsong (for an in-depth case study of social learning and birdsong, see the discussion in chapter 7 of Freeberg's work on cultural transmission in the cowbird).

In most species of songbirds, males don't just learn *a* song; they learn *many* different songs: the song sparrow (*Melospiza melodia*) sings approximately ten different songs, the western marsh wren (*Cistothorus palustris*) sings more than a hundred songs, and the brown thrasher (*Toxostoma rufum*) sings an incredible thousand different songs (Beecher and Brenowitz, 2005). Because repertoire size may be a proxy cue for a male's age and/or genetic quality, ethologists have hypothesized that females may use the size of a male's song repertoire when choosing between mates (Hosoi et al., 2005; MacDougal-Shackleton, 1997).

Aki Hosoi examined the role of repertoire size in the mating success of male brown-headed cowbirds (*Molothrus ater*). Male cowbirds sing between two and eight different perched songs (songs sung from a perch, generally near the ground, rather than in flight) during the mating season. Earlier studies indicated a correlation between the size of the perched song repertoire and mating success, but no work had specifically examined whether female mate choice per se was affected by song repertoire in cowbirds (O'Loghlen, 1995; O'Loghlen and Rothstein, 1993, 1995, 2002). To examine whether male repertoire size had an effect on female mate choice, Hosoi and her colleagues brought female cowbirds from two populations in California into an experimental aviary (Hosoi et al., 2005). They implanted the captured females with subcutaneous estradiol to increase the probability that they would respond to male song during experimental manipulations.

Hosoi and her team exposed each female in the experiment to five different song treatments—a *single* song sung three times in succession by a male Santa Barbara cowbird (treatment 1; smaller repertoire) or by a male Ventura cowbird (treatment 2; smaller repertoire), three *different* songs sung in quick succession by a male Santa Barbara cowbird (treatment 3; larger repertoire) or by a male Ventura cowbird (treatment 4; larger repertoire), and a control in which females were exposed to the song of males from a different species (song sparrow). The length of time that a female displayed ritualized "copulation-solicitation displays" (CSDs) to different songs was recorded and used as a measure of female choice.

Female cowbirds displayed longer CSDs when they heard cowbird versus song sparrow songs, regardless of how many songs were sung. Comparing across the four treatments, females show a marked increase in CSD times when exposed to males with larger song repertoires (Figure 13.17). When females were exposed to males from their own population, they preferred larger song repertoires in the majority of trials. Females exposed to male cowbirds from a different population also preferred males with larger song repertoires (Soma and Zsolt-Garamszegi, 2011; but see B. E. Byers and Kroodsma, 2009) (Box 13.3).

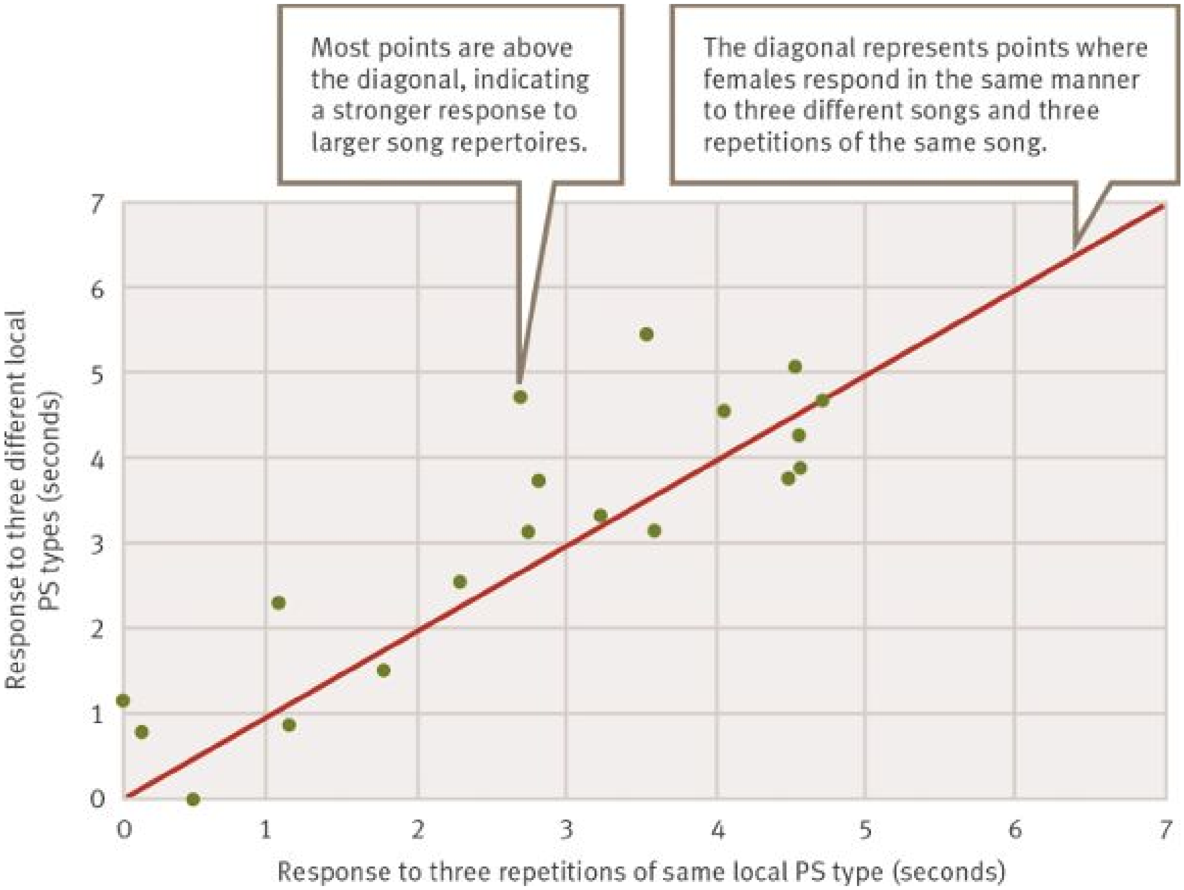


Figure 13.17. Same versus different songs. Female cowbirds had longer copulation-solicitation displays (CSDs) when they were exposed to three different songs than to the same song played three times. Each point represents the CSDs of one female. *(From Hosoi et al., 2005, p. 89)*

Box 13.3. SCIENCE AT WORK

What is the research question? Does the number of different songs a male sings affect his mating success?

Why is this an important question? Some work suggests that the size of a male's song repertoire affects his mating success, but whether females prefer large song repertoires in males was not known.

What approach was taken to address the research question? Female brown-headed cowbirds (*Molothrus ater*) were exposed to males that sang different numbers of songs. Males were from either the same population as the female, a different cowbird population, or a different species.

What was discovered? Females engaged in more copulation-solicitation displays when exposed to cowbird males with larger song repertoires.

What do the results mean? Female choice of mates in cowbirds is affected not only by characteristics of a male's song, but by the number of different songs he sings.

Phylogenetic studies of birdsong also point to a relationship between sexual selection and the evolution of birdsong (Brenowitz, 1997; J. J. Price and Lanyon, 2002a,b, 2004a,b). Many phylogenetic studies of sexual selection look at a single trait—for example, feather length—and map that trait onto a phylogenetic tree. This approach is more difficult to use when song is the trait of interest, as many components of song—repertoire size, amplitude, frequency, and so on —can vary across groups. To obtain an accurate assessment, phylogenetic analysis of birdsong and sexual selection need to incorporate many measures of song—frequency, rate of pauses, maximum note length, and so forth (J. J. Price and Lanyon, 2004a). And, if researchers are interested in sexual selection and communication, it is especially useful for them to analyze components of song that are costly to produce, and hence hard to fake.

Jordan Price and Scott Lanyon mapped six components of birdsong onto a molecular phylogeny of seventeen species of blackbirds from two groups of New World blackbirds—caciques and oropendolas (J. J. Price and Lanyon, 2004a). The caciques and oropendolas are well suited for analysis involving sexual selection and song, as variation in mating systems exist in these groups, with some species being monogamous, and others being polygynous. In addition, some species of caciques and oropendolas are sexually monomorphic for size (males and females are the same size), while others are sexually dimorphic (males are much larger than females) (Price, 2009). This variance is important, as much work suggests that sexual selection operates more strongly in polygynous mating systems and in systems that are sexually dimorphic in size (Figure 13.18).

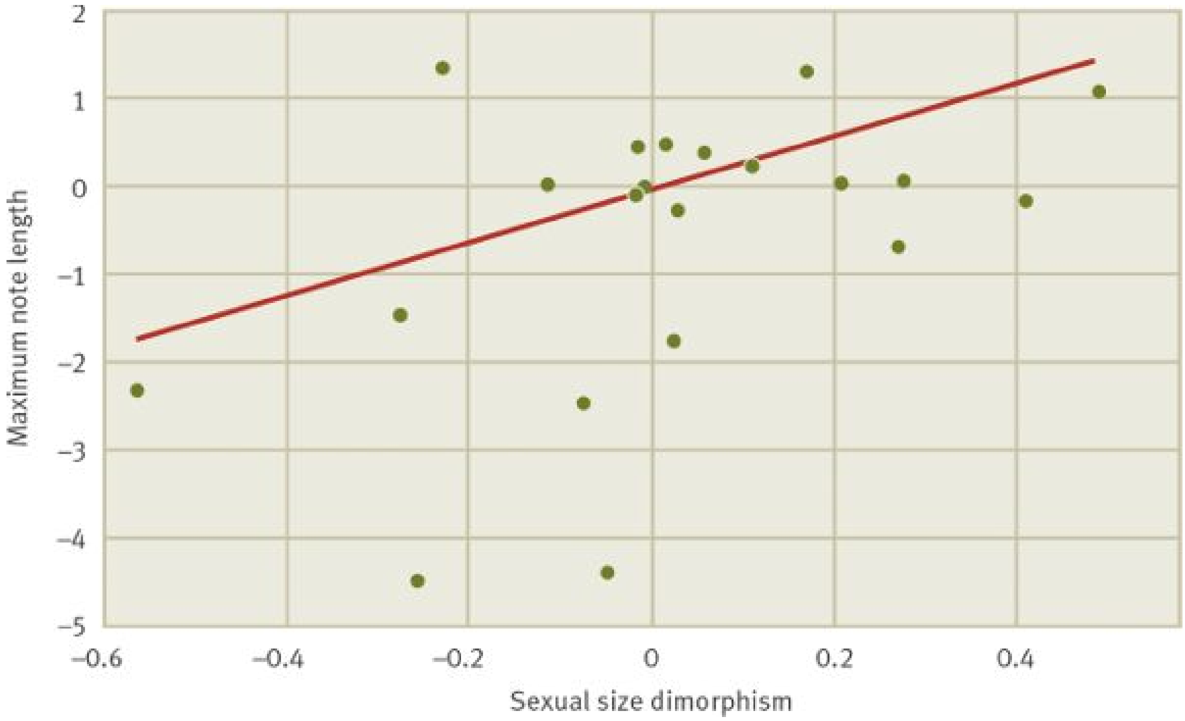
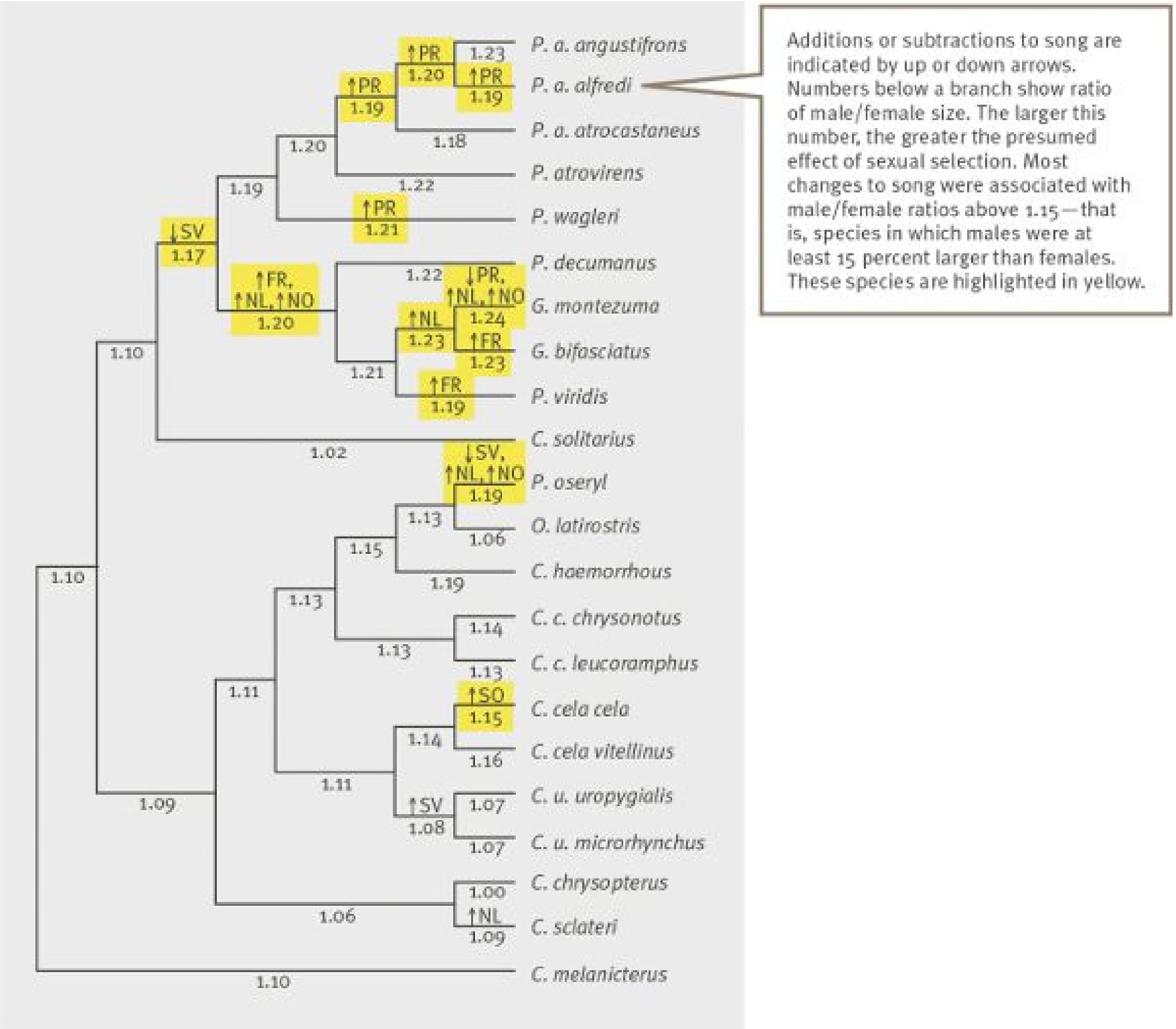


Figure 13.18. Sex differences and songs. Across seventeen species of blackbirds, the maximum note length of songs increased as the size difference between males and females increased. The *x*- and *y*-axes have been transformed into independent contrasts and can take negative values. *(From J. J. Price and Lanyon, 2004a, p. 490)*

Price and Lanyon's phylogenetic analysis found evidence that evolutionary changes in song were most often associated with sexually dimorphic species, where sexual selection is strong. For example, in one oropendola species, *Psarocolius oseryi*, in which males were much larger than females, phylogenetic analysis found changes in three components of song. More generally, in the phylogenetic tree that Price and Larson constructed, in eight of the ten branches that showed clear changes in song components, males were at least 15 percent larger than females (Figure 13.19). When sexual selection *is* powerful, and there is strong competition for access to females, natural selection acts strongly on the many components that make up male song.



Additions or subtractions to song are indicated by up or down arrows. Numbers below a branch show ratio of male/female size. The larger this number, the greater the presumed effect of sexual selection. Most changes to song were associated with male/female ratios above 1.15—that is, species in which males were at least 15 percent larger than females. These species are highlighted in yellow.

Figure 13.19. Phylogeny, sexual selection, and song. A phylogeny of oropendola and cacique birds with changes in song characters mapped on. Above the branches are song characters as they are added or dropped from the song repertoire. SO = song output, SV = song versatility, FR = frequency range, PR = pause rate, NL = maximum note length, and NO = note overlap. Numbers below branches show male/female size ratios. *(From Price and Lanyon, 2004a)*

In addition to the evolutionary literature on birdsong, much work has also addressed birdsong from a proximate perspective. Part of this work centers on a paradox. As we have seen, birdsong is incredibly diverse in terms of structure, pattern, tempo, frequency, and repertoire size. At the same time, the vocal organ used in birds, the syrinx, varies little between different species in this group. How is it possible that morphological (structural) invariance in the syrinx can translate into great diversity in birdsong?

Table 13.2. The different ways to sing. The costs and benefits of different song lateralization patterns. *(Based on Suthers, 1999)*

Song Lateralization Pattern	Species	Advantages	Disadvantages
Independent bilateral sound formation	Brown thrasher and gray catbird	Two independent voices increase spectral and phonetic complexity.	Expensive in use of air supply. Best suited for a low syllable repetition rate.
Unilateral dominance	Waterslager canary	Conserves air, favoring shorter minibreaths and longer phrases. Separation of phonatory and inspiratory motor patterns to opposite sides of syrinx. Both may facilitate higher syllable repetition rates.	Use of one voice limits frequency range and certain kinds of spectral and temporal complexity.
Alternating lateralization	Brown-headed cowbird	Enhances spectral contrast between notes. Efficient use of air supply. Extended frequency range for overall song.	Two-voice complexity limited to note overlap.
Sequential lateralization	Northern cardinal	Extended frequency range. Conserves air supply.	Lacks spectral complexity of two voices.

The avian syrinx has two compartments—left and right—and the two sides of a bird’s brain can control these compartments independently (Suthers, 1997; Suthers et al., 2004; Suthers and Zollinger, 2004; Riede and Goller, 2014; Table 13.2). This one piece of information sets the stage for moving from *invariance* in the structure of the syrinx to *variance* in the song output. That is, although the syrinx as a whole varies little in structure, its *parts* can be changed to create new permutations that may give rise to new sounds (Suthers, 1999).

Over a hundred years ago, theorists suggested that two different sides of the syrinx contribute differentially to the frequency component of birdsong. But strong evidence of this phenomenon did not arise until 1968 (Greenewalt, 1968; Stein, 1968). Independence of the two sides of the syrinx allows songbirds to switch off one side at any time. This, in turn, facilitates variation in song production in that it permits some species to

- operate both sides of the syrinx independently throughout their song without one side being dominant, as in brown thrashers (*Toxostoma rufum*) and gray catbirds (*Dumetella carolinensis*; Suthers et al., 1994, 1996; Suthers and Hartley, 1990).
- have one side of the syrinx dominate song generation, as in canaries (*Serinus canaria*; Nottebohm and Nottebohm, 1976).
- alternate which side of the syrinx dominates during a song, as in brown-headed cowbirds (*Molothrus ater*; Allan and Suthers, 1994).
- have one side of the syrinx dominate for certain frequencies, and the other side dominate for the remainder of the frequencies used in a song (sequential lateralization), as in the northern cardinal (*Cardinalis cardinalis*; Suthers, 1997; Suthers and Goller, 1996).

Variance in the structure of respiratory muscles and in labia tissues, as well as variance in how these are used, can affect the structure and timing of birdsong (Reide and Goller, 2014): though the syrinx itself is relatively invariant, variation around other anatomical structures can produce variation in the output of birdsong.

These sorts of proximate analyses help us to better understand the construction of communication systems that are designed to address problems that arise during sexual selection in songbirds.

Ripple Communication and Mate Choice in Aquatic Insects

In 1972, Stim Wilcox discovered a new form of communication called ripple communication in water striders, insects that live in freshwater lakes, ponds, streams, and small rivers. In water striders, ripples are typically produced by an up-and-down movement of the legs, with both right and left legs in synchrony and in contact with the water surface (Wilcox, 1995). The water striders produce ripples: waves with different amplitudes and frequencies for different kinds of behaviors, including signals for calling mates, courtship, copulation, postcopulation, mate guarding, spacing, territoriality, and food defense. These signals can range from 0.2 seconds during the courtship behavior of the water strider, *Rhagadotarsus anomalus* (Wilcox, 1972), up to 30 seconds in other water strider species (Polhemus, 1990).

In *R. anomalus*, males produce ripple signals that can travel more than 60 cm, and females find such ripple signals attractive. Wilcox ran playback experiments that demonstrated that females from as far away as 60 cm were attracted to mating ripple signals—ripples that are different from those produced by aggressive males (Wilcox, 1972; Figure 13.20). Females would often grasp males and even begin to oviposit (lay eggs) in response to playbacks of calling signals. In addition, Wilcox hypothesized that ripple calls designed to attract mates also serve as a means for species identification, as *R. anomalus* are often found in the same streams and ponds as other water striders (Polhemus and Karunaratne, 1993).

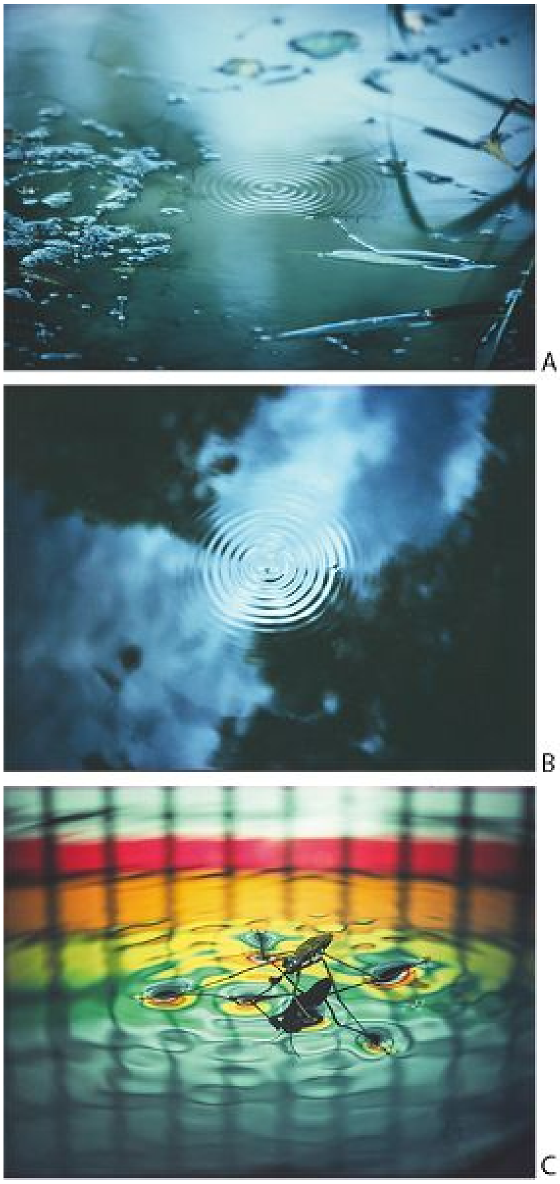


Figure 13.20. Ripple communication by water striders. (A) The concentric circles of these ripples in a pond are part of the communication used by the water strider, *R. kraepelini*. (B) A close-up of the male water strider (*R. kraepelini*) and the ripples he is making. (C) An experimental setup to study ripple communication, in which an *A. remigis* female is making a signal induced via a magnet glued to her leg. In nature, female water striders don't emit such signals. *(Photo credits: Stim Wilcox)*

PROBLEM: PREDATORS

Vervet monkeys living in the Amboseli National Park in southern Kenya face danger from many predators: leopards hide in the bush, crowned eagles fly above, and snakes slither about below. When encountering these predators, vervets communicate information in a remarkable fashion. Vervets don't just give an alarm call when a predator is sighted; they emit specific alarm calls for specific types of danger and different calls elicit different responses by groupmates (Figure 13.21) (Cheney and Seyfarth, 1990; Manser, 2013). When an eagle is spotted, vervets emit a "cough" call. When other vervets hear the cough call, they look into the air or hide in the bushes, where they tend to be safe from avian threat. If a leopard is spotted, a "barking" alarm call is given, and vervets respond by heading up trees, where their agility makes them relatively safe from leopard attacks. When a python or cobra is sighted, vervets emit a "chutter" call. Since snakes often hunt vervets by hiding in the tall grass, a chutter call gets other vervets to stand and scan the grass around them for snakes.

Figure 13.21. Vervet alarm calls. Vervets give different alarm calls depending on what type of predator has been sighted. (A) Vervets stand up after hearing a chutter alarm call. When a leopard (B) is detected, vervets give a barking alarm call and (C) climb trees for safety. *(Credits: Photo "Chlorocebus aethiops 1 MHNT" by Roger Culos licensed under Creative Commons Attribution-Share Alike 3.0 Unported license; Photo by Martina Blersch licensed under CC BY-SA 4.0 International; Photo by Harvey Barrison licensed under CC BY-SA 2.0)*

This sort of complex alarm calling has also been found in other primates such as chimpanzees and tamarins, as well as in birds

(Crockford and Boesch, 2003; Crockford et al., 2012; Kirchhof and Hammerschmidt, 2006; Suzuki, 2016). In blue monkeys (*Cercopithecus mitis*), males not only give specific alarm calls for specific predators but they can gauge the distance of predators from the alarm calls given by others in their group (Papworth et al., 2008; Zuberbuhler, 2009). For more about the complex, often cognitively challenging aspects to communication and signals in the context of predation, see Box 13.4.

Box 13.4. COGNITIVE CONNECTION

Can Elephants Distinguish Between Humans Based On Voice?

Elephants in the Ambosseli National Park face many dangers, including threats from humans. But, the threat that humans present to elephants differs across the ethnic group, sex, and age of the humans involved. Maasai pastoralists, who spend much time grazing their cattle, are more dangerous to elephants than are individuals from the Kamba, because the former sometimes come into conflict with elephants over access to watering holes and grazing patches, while the latter do not (Moss et al., 2011). On occasions when Maasai pastoralists spear elephants over conflicts associated with grazing sites, it is Maasai adult males, not adult females or children, that attack the elephants.

Prior work had demonstrated that elephants could distinguish between Maasai and Kamba people based on olfactory cues (Bates et al., 2007). Karen McComb and her team wanted to know whether elephants could use human voice to discern the level of threat posed by a human (McComb et al., 2014; Plotnik and de Waal, 2014). They presented playbacks of human voices to forty-eight elephant family groups and noted the response of the elephants. Depending on which type of human voice they heard, the elephants displayed differences in defensive behaviors, including bunching together, listening, smelling, and retreat behavior. The elephants' defensive behaviors were stronger in response to voices that were associated with human groups that were more dangerous: defensive behaviors were stronger in response to Maasai adult males vs. Kamba adult males, Maasai males vs. Maasai females, and Maasai adult males vs. Maasai boys (Figure 13.22).

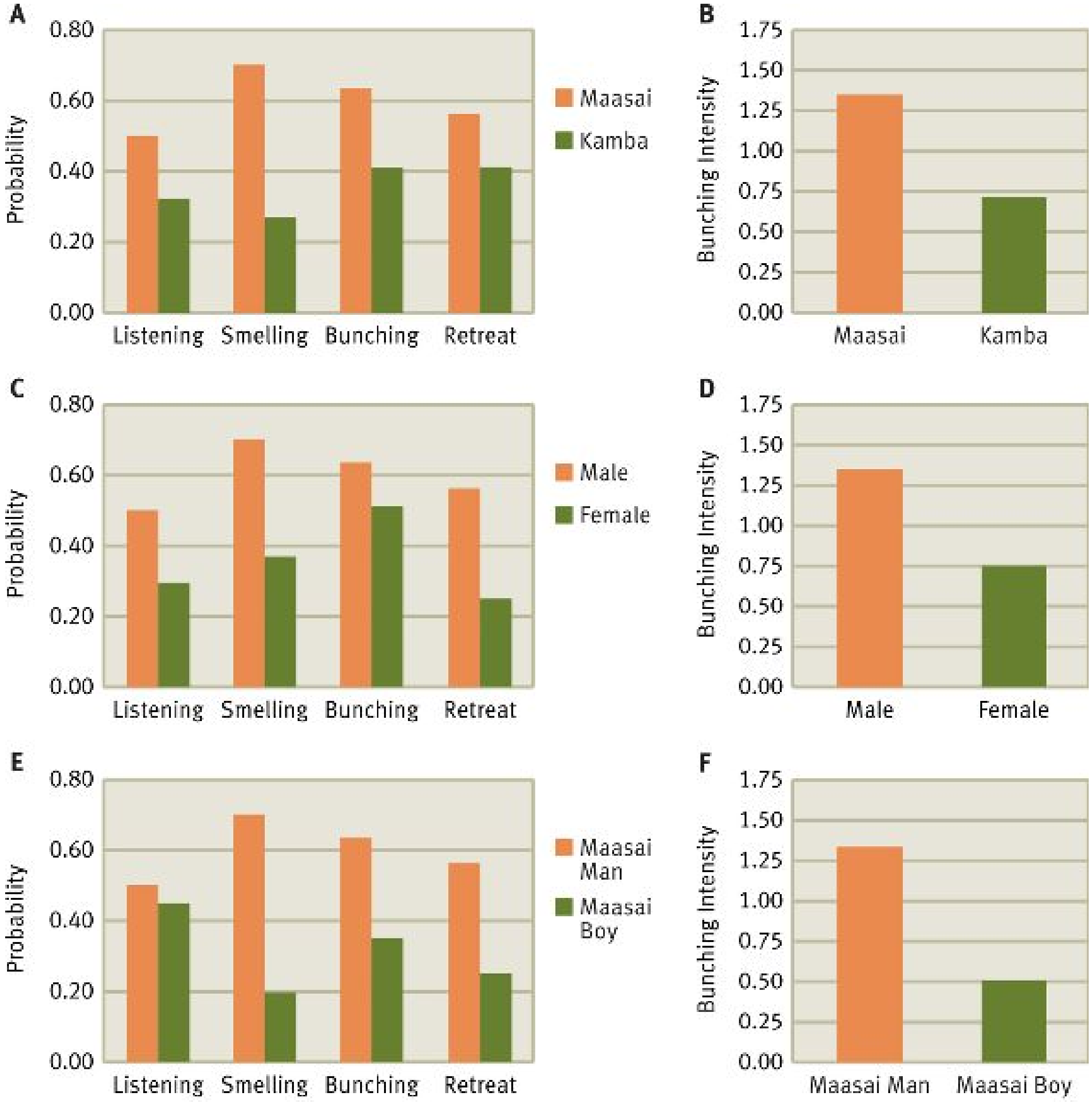


Figure 13.22. **Elephants assess threat level from human voice.** Four defensive behaviors were measured in elephants—listening, smelling, bunching, and retreat. A stronger defensive response was seen when comparing (A and B) Maasai males vs. Kamba males, (C and D) Maasai males vs. Maasai females, and (E and F) Maasai males vs. Maasai boys. *(From McComb et al., 2014)*

This sort of cognitively complex attribution behavior by elephants may be especially important to their survival, as humans encroach more and more into elephant habitats (see Box 13.5).

Box 13.5. SCIENCE AT WORK

What is the research question? Can elephants gauge how dangerous humans are using vocal cues?

Why is this an important question? If animals can use signal characteristics to gauge how likely a signaler was to be dangerous, such a trait would be favored by natural selection.

What approach was taken to address the research question? The behavior of elephants was noted in response to playbacks of human voices that were associated with different levels of threat to the animals.

What was discovered? Elephants displayed more defensive behaviors when exposed to human voices that were associated with greater risks.

What do the results mean? Elephants use human vocal cues to detect differences associated with risk between humans from different populations (the Maasai, who sometimes kill elephants, and the Kamba, the who rarely do), different sexes (human males are more dangerous than females), and age (older humans are more dangerous than children).

Development, Learning, and Alarm Call Communication in Meerkats

When parental care is present and lengthy, natural selection will often favor developmental pathways in which young individuals learn about communicative signals from adults (Platzen and Magrath, 2005). This should be especially true when signals are complex, as in the alarm calls of vervets. Indeed, the evidence suggests that young vervets do learn about alarm calls from older individuals (Seyfarth and Cheney, 1986). Meerkats also have prolonged parental care and learn complex alarms calls for terrestrial and avian predators.

Meerkat pups spend the first three weeks of their lives underground, and then they emerge and join groups of juveniles (six to twelve months old) and adults. Once above ground, pups are subject to predation pressure from avian and terrestrial predators. Linda Hollen and Marta Manser examined the development of the response to alarm calls in maturing meerkat pups (Hollen and Manser, 2006). They studied eleven groups of free-ranging meerkats in the Kalahari Desert, using both data from the field and experimental manipulation through playback experiments in which meerkats were exposed to recorded alarm calls.

Behavior observations indicate that, compared with adults, pups *initially* were more likely than adults to ignore alarm calls emitted in the presence of dangerous predators. Other evidence also suggests that pups don't react as appropriately to alarm calls as adults do. After hearing an alarm call, pups often moved to shelter when they observed adults only briefly looking up and scanning for aerial predators. And even when pups displayed antipredator behaviors similar to those of adults, they reacted more slowly than did adults (Figure 13.23). As time passed, however, pups began to display more adultlike, adaptive, responses to alarm calls, and evidence strongly suggests that these changes are in part due to pups learning about alarm calls and predators from adults (Hollen et al., 2008).

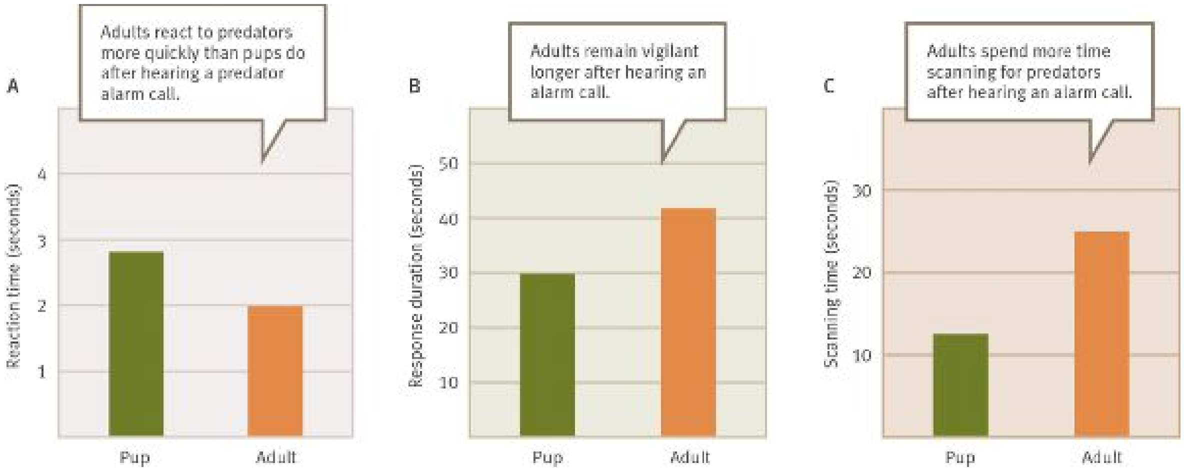


Figure 13.23. Age differences in reaction to alarm calls. In meerkats, a pup's response to alarm calls was not as strong as the response seen in adults: (A) time until reaction after hearing playback of alarm call, (B) duration of response to playback of alarm call, and (C) length of time spent scanning the environment for predators after hearing alarm call. *(Based on Hollen and Manser, 2006, p. 1350)*

When Not to Pay Attention to Signals

When signals such as alarm calls become less reliable, natural selection should favor paying less and less attention to them. This raises the question of whether animals that receive inaccurate information from a signaler respond by eventually ignoring the signaler (Beauchamp and Ruxton, 2007; Blumstein et al., 2004; Hollen and Radford, 2009). James Hare and Brent Atkins examined this in Richardson's ground squirrels (*Spermophilus richardsonii*; Figure 13.24). Hare and Atkins designed an experiment with juvenile ground squirrels in one of two treatments. In one treatment, juveniles heard a recorded alarm call and then saw a predator (a stuffed badger). They then heard the same alarm call, which was paired with the presentation of the predator nine more times (for a total of ten presentations). In a second treatment, ground squirrels again heard an alarm call, but now they did not see a predator. In this treatment, the same alarm call was repeated ten times but was not followed by presentation of a predator (Hare and Atkins, 2001).

Figure 13.24. Alarm calls in Richardson's squirrels. Over time, when predator alarm calls are unreliable, juvenile squirrels begin to ignore such false alarm cues. *(Photo credit: John Cancalosi/naturepl.com)*

Hare and Atkins examined how long the squirrels remained vigilant and the extent to which juvenile squirrels in the two treatment conditions turned in the direction from which an alarm call emanated (postural change). No differences across the two groups were found in their response to the first alarm call, which was expected, as the squirrels had no knowledge beforehand as to which alarm calls would be reliable and which would not. Even after hearing five alarm calls, no differences in vigilance duration were found across the two treatment groups, although there was a difference in postural change: Squirrels that had heard unreliable calls were less likely to look in the direction of the call than were squirrels that had heard reliable calls. After hearing the alarm call ten times, differences in vigilance duration between the two groups of squirrels emerged. Squirrels in the group in which the alarm was paired with a reliable caller (that accurately alerted them to the presence of a predator) responded to alarm calls by remaining vigilant and looking in the direction of the call. Squirrels in the other treatment—in which the information they had been receiving was inaccurate—ignored the alarm calls, and they were unlikely to look in the direction from which the calls emanated (Figure 13.25). Given enough information, Richardson's ground squirrels can distinguish between reliable and unreliable calls (Pollard and Blumstein, 2012).

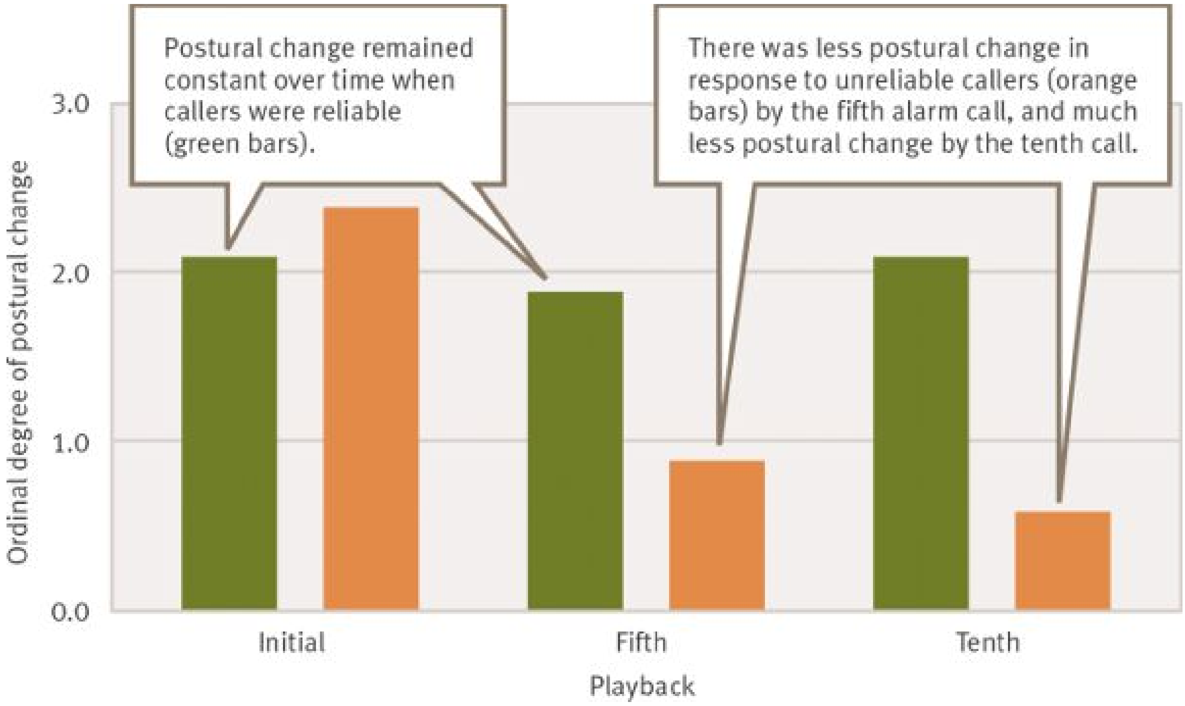


Figure 13.25. Responses to reliable and unreliable alarm calls. Postural change—elevation of the head in the direction of the perceived threat—differed depending on whether the alarm caller was a reliable source. Reliable alarm calls are shown in green; unreliable alarm calls are shown in orange. *(From Hare and Atkins, 2001, p. 110)*

Interview with Dr. Rufus Johnstone

What do ethologists mean when they speak of communication? How did you come to study this phenomenon?

Different people have defined communication in different ways. I would say, though, that it entails the use of specialized structures or behaviors (signals) by one individual to modify the behavior of others. The key feature of this definition is the emphasis on specialized signals, by which I mean traits that have been favored by natural selection specifically because of their influence on the behavior of receivers. There are plenty of cues that can provide receivers with useful information but have not been selected for that reason. Consider, for instance, a field mouse that rustles the grass as it moves and draws the attention of a predator such as an owl. The rustling noise provides the predator with a cue to the prey's location, but selection has not favored noisy mice for this reason—quite the reverse! So I would not see this as a true instance of communication, nor the rustling as a true signal. By contrast, when a peacock displays its train or a nightingale sings, their behavior has been favored by selection because of the responses it elicits from others.

Animal signals are so striking and so diverse, one can't help being fascinated by them. Just think of a bowerbird's elaborately decorated bower, or the complex song of a humpback whale, or take a look at the gape of a parrot finch chick—what could possibly have driven the evolution of such an extreme display? But more than any individual example, what most appealed to me about the study of communication was the idea that there might be unifying principles of signal evolution underlying this great diversity of different displays.

What is meant by *honest communication*? When do animal behaviorists expect to find this type of communication, and when don't they?

Again, different people use the word *honesty* in different senses. In everyday speech, it usually carries "intentional" connotations. That is, an honest individual is one who bears no intent to deceive but rather means to convey reliable, truthful information. In this sense, however, the concept of honesty is inapplicable to many animals (though not perhaps to all), who lack any awareness of the responses their signals may evoke (or the meanings they may convey). Nevertheless, biologists often speak of honest and dishonest signals—one might, for instance, describe the aposematic coloration (bright warning colors) of a palatable hoverfly that mimics a wasp as dishonest. This is not to imply that the hoverfly is engaged in intentional deceit. Rather, a dishonest signal in this sense is one that elicits a response that is beneficial to the signaler, but detrimental to the receiver. In this case, the hoverfly obviously benefits when its bright colors deter a predator, but the predator loses out because it has forgone a potentially palatable meal. Conversely, an honest signal is one that elicits responses that are beneficial for the receiver as well as for the signaler. The aposematic coloration of the wasp model, for instance, unlike that of the hoverfly, is honest—the wasp gains if its black and yellow stripes deter attack, but so too do the predators that avoid it.

When do we expect to find honest communication? To begin with, if there is no evolutionary conflict of interest between signaler and receiver, then there should be no selection for deceitful signals, because what benefits the receiver also benefits the signaler. This is typically the case when we consider communication between close relatives. A nice example is the waggle dance of the honeybee. When a worker returns to the hive with food, the waggle dance she performs conveys information to her fellow workers about the direction and distance of the food source. There is no evolutionary incentive for deceit here, because the worker benefits by recruiting others to the food; all share the same evolutionary interest in the productivity of the colony.

What about communication between individuals with conflicting interests? Even here, we might expect that honest communication is the norm. The reason is that in the long run, selection will favor receivers that ignore a consistently dishonest signal, and that attend only to signals that provide reliable information at least some of the time. Moreover, signals that are costly to produce or maintain are likely to provide such information, because it only pays signalers to employ them if they are of high quality or in great need—this is Zahavi's handicap principle. Of course, there are plenty of examples of dishonesty, but deceitful signalers must typically exploit some underlying system of reliable communication—and dishonesty cannot be too frequent or too costly to receivers if the system is to persist.

How does an ethologist build a mathematical model of something as complex as communication?

Constructing a model always involves a lot of simplification. This is not necessarily a bad thing—in fact, a model that is too detailed and complex is often rather unhelpful because it is likely to be applicable only to one specific system, and it may be very difficult to understand the results it yields. The best models are those that strike a good balance between generality and specificity. The difficulty lies in identifying which factors to include, and which you can omit. In modeling communication, a distinction is often made between efficacy and strategy. The details of signal design have an important influence on the ease with which receivers can detect and identify a signal (its efficacy), but strategic issues of honesty and reliability depend principally on the costs of signal production, the benefits of eliciting certain responses, and the fitness consequences of those responses for the receiver. So many strategic models ignore the details of signal form and focus solely on costs and benefits. This approach has generated many insights, although in the long run, I suspect it will be necessary to integrate both efficacy and strategy in a more comprehensive analysis.

Do you think communication is more important in some behavioral venues (for example, foraging, aggression, cooperation) than others? If so, why?

I think that communication plays an important role in almost every behavioral interaction. In any social context, individuals are likely to benefit from information about those with whom they interact—their nature, identity, motivation, and physiological state may all be relevant. So we would expect animals to attend to behavioral and morphological cues that provide such information. But whenever receivers do attend to a cue, selection will favor those individuals who tend to elicit the most beneficial responses—leading to the elaboration of cues into true signals. In fact, many behaviors that are not obviously displays may be modified in this way. When a parent bird, for instance, brings food to the nest, it is engaging in parental care. But this behavior may also indicate to its mate that the offspring are hungry, or that the focal parent is a good provider, encouraging the mate to work harder or deterring it from seeking an alternative partner. Indeed, it may be that frequent feeding is partly driven by the need to impress the mate, rather than simply to supply the young. So cooperation over offspring care might entail communication, even if there are no obvious display behaviors involved. In general, I think it is very difficult to fully understand the evolution of social foraging, aggression, cooperation, or any other type of interaction without thinking about the information that an individual’s actions convey to others in this way—and in that sense, communication is always important.

Do you think of human communication via language as fundamentally different from all other forms of communication?

Human language is certainly exceptional. I don't think all of its striking features are individually unique to our species. Other animals, for instance, employ apparently arbitrary signals to convey information about the external world—the usual example is the alarm calling of vervet monkeys, who make distinct vocalizations to alert others to the presence of leopards, eagles, and snakes. Similarly, other species can produce varied signals by combining distinct display elements in different ways—songbirds provide a good example. But there is no animal signaling system even remotely comparable to human language in complexity, flexibility, and scope of reference. What's more, from a strategic perspective talk is cheap; honesty among humans is not maintained by the costs of faking an exaggerated display, but by social sanctions. This is very different from the costly signals with which ethologists are often concerned.

Dr. Rufus Johnstone is a professor at the University of Cambridge (England). Dr. Johnstone's game theory models of animal behavior have shed light on many questions surrounding the evolution of communication.

SUMMARY

1. Communication is defined as the transfer of information from a signaler to a receiver.
2. One framework to study communication begins by assuming that the exchange of information between signaler and receiver is an attempt by the signaler to *manipulate* the recipient and the recipients to mind read whether the transmitted information is accurate.
3. Zahavi's handicap principle hypothesizes that honest signaling can evolve when traits are very costly to fake.
4. Communication systems are designed to solve problems that animals encounter in their natural environments.
5. When animals forage in social groups, they face coordination problems. Communication systems that solve these problems have been favored by natural selection.
6. Animals communicate to attract mates. Male birds use birdsong to attract females during the mating season, male water striders use ripple communication to signal their location to female water striders, and so on.
7. Animals use communication to warn others in their family or group about predators.

8. Work on the costs and benefits of communication, the phylogenetic history of communication systems, the role of learning and social learning in shaping communication, and the underlying proximate basis for communication is providing ethologists with a much improved picture of signaler-receiver dynamics.

DISCUSSION QUESTIONS

1. Bacteria often release chemicals that affect other bacteria in their vicinity. Would you consider this communication? If so, why? If not, would you consider the chemical trails that ants use to direct one another to a food source communication? How does that differ from the bacteria case, if at all?
2. One problem examining whether a communication system more resembles exaggerations or conspiratorial whispers is that it is difficult to know how to define those terms for any given animal social system. How might you tackle this problem? Consider using a comparative study involving many species.
3. Imagine you are studying a group of amphibian species that vary in their habitats, some living in dense, murky water, and others living in very clear ponds. What kind of communication problems exist in each environment? What sorts of differences in communication systems would you expect to see across such species?
4. Suppose you are studying a heretofore unexamined species of primates. During your observations, you note that individuals often throw heavy rocks against trees, causing a large “booming” sound. You speculate that individuals are communicating to one another using this technique. How might you go about testing this hypothesis?
5. How has research on birdsong provided insight into both proximate and ultimate questions regarding communication?

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14

Habitat Selection, Territoriality, and Migration

The abiotic and biotic components of an animal’s habitat and/or territory set the stage on which natural selection operates. How quickly selection can act when a habitat changes has been a long-standing question in the fields of both evolutionary biology and animal behavior. One powerful way to study this question is to work with species that have been, or can be, domesticated (chapter 2), as changes in habitat in these instances are clear and salient.

Steelhead trout (*Oncorhynchus mykiss*) are one of a few fish species to have been fully domesticated. Domestication in this species centers on changes associated with living in the more crowded environment of a hatchery (vs. a natural stream) (Figure 14.1). Work on domestication to hatchery conditions in steelhead trout has found large scale, heritable changes in these fish in less than a decade. Mark Christie and his colleagues designed a breeding experiment to test whether changes in response to life in a hatchery environment might be occurring even more quickly than that, and if so, how such changes were manifesting themselves (Christie et al., 2016). They bred pairs of wild-caught steelhead trout (W × W pairs) and pairs of steelhead trout that were first-generation hatchery fish (H × H pairs). Offspring from all pairs were raised in the hatchery environment (maternal effects were ruled out in a separate set of experiments). An mRNA molecular genetic analysis then examined differences in the offspring of W × W versus H × H matings.

Figure 14.1. **Steelhead trout.** (A) in a stream, (B) in a hatchery. *(Photo credits: Paul Vescei; Robert Clay / Alamy Stock Photo)*

What Christie et al. found were heritable differences in gene expression in a surprisingly large number of genes—723 of them—in the offspring of H × H vs. W × W pairs. Many of these differences in expression pattern were in genes whose function was associated with wound healing, immunity, and metabolism; for these genes, offspring from H × H matings generally showed higher levels of gene expression—producing more functional products—than offspring from W × W matings.

Given that the crowded conditions of the hatchery environment likely facilitate aggression and the spread of disease, the differences in gene expression in wound healing, immunity, and metabolism make adaptive sense and suggest that natural selection can act strongly in response to major changes in habitat (stream versus hatchery) in as little as two generations.

* * *

Almost every aspect of an animal’s behavior is affected by where it lives. This is true for animals that remain in a single place, as well as for those that move from place to place. From an ethological perspective, habitat choice is interesting not only because the habitat of an animal affects its behavior—what sorts of antipredator strategies will be successful, what types of foraging behaviors will yield the most food, what mating opportunities will be available—but also because the behavior of an animal affects its choice of habitat. For mobile animals, individuals can decide where to live, and in that sense they have some control over the ecological and evolutionary forces operating on them (Odling-Smee et al., 2003; Laland et al., 2016).

To better understand the relationship between animal behavior and habitat choice, let’s walk through a hypothetical scenario. Imagine a male bird that lives near a large marsh (Figure 14.2). Where should he spend his time during the day? To answer that, the bird must balance many factors. If it is the mating season, one factor would be this: Where are the females? Females may prefer the safety of the reeds, so perhaps a male should go there. The reed area, however, may be home to parasites, so there are both costs and benefits to staying in the reeds. Even if the reeds do not have parasites, courting a mate is energetically expensive, and it may be that prey are not found in the reeds, but over the marsh water, so there might be reason to spend time over the marsh first. However, predators may also prefer the area over the marsh, so, as with the reed area, there are costs as well as benefits to spending time over the marsh. Other factors may also play a role in determining where our bird goes. Temperature will vary both across the day and across the marsh, and this may affect where the bird spends time. The point is that the choices faced by animals are complex and multidimensional.

Figure 14.2. Habitat choice. Imagine a red-winged blackbird deciding where to form a territory. Many factors—mates, temperature, predators (such as the hawk in the upper left of the drawing)—play a role in the decision making. Habitat choice also affects availability of prey, such as the presence of dragonflies (not drawn to scale) shown flying above the marsh.

Suppose our bird ends up flying between the reeds and the marsh water but does not spend that much time in any one area. We might speak of those areas as being his **home range**. Suppose he flies between the reeds and the marsh area, but that he regularly returns to a particular area in the central part of the reeds and actively tries to keep intruders outside of this area. Now we can speak of this individual as having a **territory**—an area occupied and defended by the bird. It might be that while our bird frequents the central marsh area as his home range, he only keeps intruders out of half of that area. In that case, his home range would be twice as big as his territory.

Animal behaviorists have made much progress in understanding habitat choice and territoriality. In some cases, abiotic factors dominate habitat choice; in other cases, biotic factors do. The abiotic factors that affect habitat choice include heat, availability of water, wind, refuge from danger, availability of specific nutrients, and so on. The biotic factors affecting habitat selection include the location of mates, food, predators, and parasites. We will examine some of these in more depth in the remainder of the chapter.

Even animals with home ranges and territories, however, can make dramatic shifts in the habitats in which they live, periodically moving long distances, from one region to another, through **migration**. The most dramatic examples of this are the large-scale migrations seen in insects, reptiles, fish, mammals, and birds. Let's imagine that we continue studying our bird, which wanders about his home range and defends his territory. Six months after watching our subject, we note that he leaves the marsh we have been studying and spends the next half year 2,000 miles south of where we first saw him. At the end of these six months, our bird returns back to the central reed area of the marsh and starts back where he began. In this case, we have home ranges and territories mixed in with large-scale migration. We might, in fact, get any number of permutations here. It may be that 2,000 miles south, our bird has another home range or territory or neither.

Animal behavior researchers do more than observe and record migration: they test hypotheses. For example, we can now track animals over very long distances. We also have a much better handle on the physiology and resultant behavioral changes associated with switching from a "nonmigratory" to a "migratory" mode, as well as the costs and benefits of migration. This opens the door to study experimentally what a generation ago might have been logistically impossible.

Having introduced habitat selection, territoriality, and migration, this chapter will delve into the following topics:

- Models of habitat choice and territoriality
- Territoriality and learning
- Family dynamics and territoriality
- Migration and navigation
- Parasites and migration
- Mapping migration onto a phylogeny

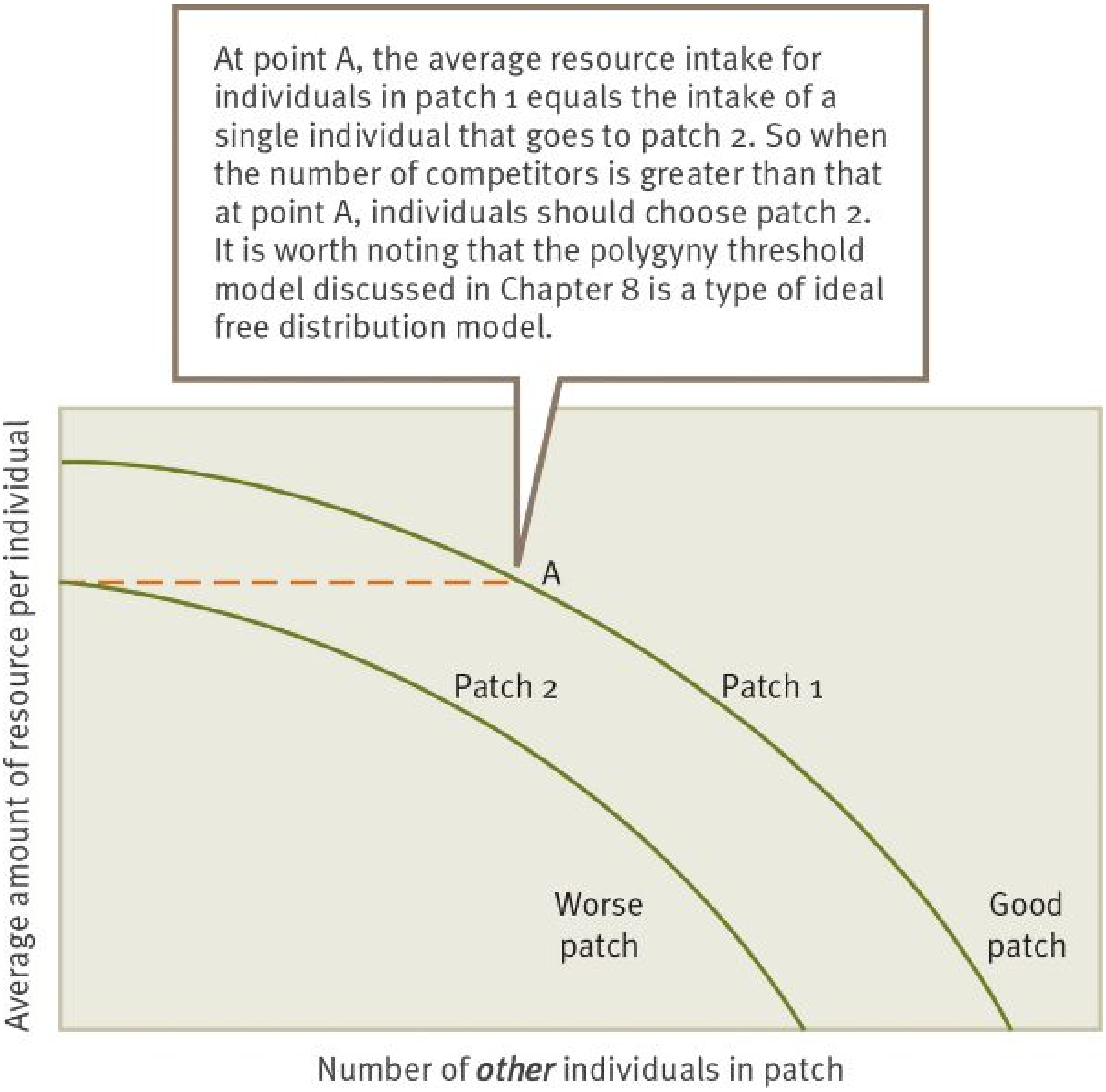
Habitat Choice

While territoriality implies the defense of a set area, **habitat choice** centers on how animals distribute themselves in space and time with respect to resources in their environment (Bateson, 1990; J. S. Brown and Rosenzweig, 1985; Kacelnik et al., 1992; Kennedy and Gray, 1993; D. W. Morris, 1994; Rosenzweig, 1981, 1985, 1990, 1991). Although ecologists have examined how animals distribute themselves into different habitats, ethologists specifically focus on the costs and benefits of habitat choice and the role of behavioral decision making.

THE IDEAL FREE DISTRIBUTION MODEL AND HABITAT CHOICE

Work in natural history has long suggested that animals distribute themselves in relation to the distribution of resources. If two habitats differ in terms of the amount of food available, and one habitat has more food than the other, more animals tend to be found where there is more food. In a sense, this finding is intuitive, but animal behaviorists want to understand why this is such a common finding and what behavioral rules animals use to distribute themselves between habitats (Herrnstein, 1961, 1970). The **ideal free distribution (IFD)** model was developed to address these sorts of issues (J. L. Brown, 1969; Fretwell, 1972; Fretwell and Lucas, 1970; Orians, 1969; G. A. Parker and Stuart, 1976).

The IFD model is used to predict the equilibrium frequency of individuals in different patches (Figure 14.3). To see how this model works, consider the case where individuals choose between two habitats—H1 and H2—with resources R1 and R2, respectively. Suppose that H1 provides five food units/minute (R1), and H2 provides three food units/minute (R2). Imagine that we are studying a population that has N individuals, that all individuals can move freely from habitat 1 to habitat 2, and that moving between food patches has no costs associated with it. How many individuals should end up in habitat H1 and how many in habitat H2?



At point A, the average resource intake for individuals in patch 1 equals the intake of a single individual that goes to patch 2. So when the number of competitors is greater than that at point A, individuals should choose patch 2. It is worth noting that the polygyny threshold model discussed in Chapter 8 is a type of ideal free distribution model.

Figure 14.3. The ideal free distribution. Imagine two different habitat types, or patches: a high quality patch (1) and a patch of lower quality (2). The first individuals that make a decision where to go should choose patch 1. Once the average resource intake at patch 1 drops to the point labeled A, individuals start to fill patch 2. *(Based on Fretwell, 1972)*

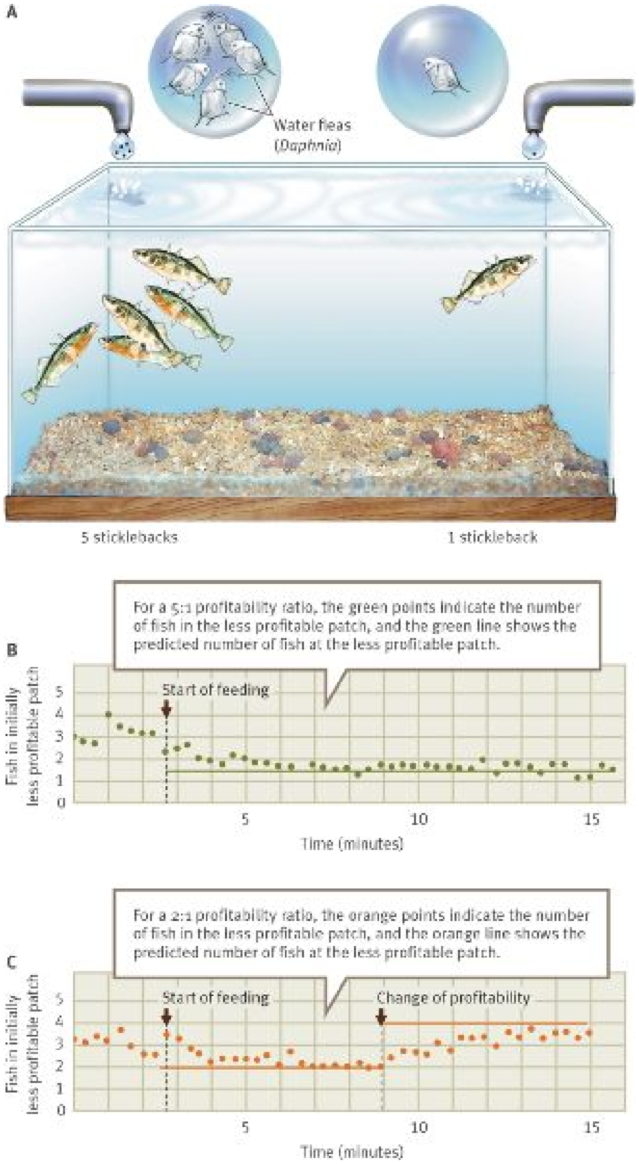
The IFD model predicts that the equilibrium distribution of individuals into patches should be that distribution at which, if any individual moved from the patch it was in, it would suffer a reduced payoff: at the IFD equilibrium, any individual that moved from H1 to H2, or vice versa, would obtain fewer resources as a result of its move. Mathematically, it can be shown that this translates into individuals settling in habitats in proportion to the resources available in that patch. The equilibrium proportion of individuals in H1 and H2 should be reached when R_1/N_1 =

R_2/N_2—when the per capita intake rate of individuals in both patches is equal. $R_1/N_1 = R_2/N_2$ is also known as the resource matching rule, as the distribution of individuals at equilibrium matches the distribution of resources across patches (Herrnstein, 1970; Fagen, 1987; Houston, 2008).

The IFD Model and Foraging Success

The IFD model has been applied to cases in which the resource driving habitat choice ranges from availability of mates to safe refuge from predators (Höglund et al., 1998; G. A. Parker and Stuart, 1976). Here we will focus on two studies where the critical resource is food, and in particular we will address (1) whether animals distribute themselves as the matching resource rule predicts, and (2) at such a distribution, whether all individuals receive approximately the same amount of food, as predicted by the IFD model.

One of the earliest tests of IFD models of foraging was conducted by Manfred Milinski (Milinski, 1979). In an elegantly simple experiment, Milinski had six stickleback fish in a tank that had two feeders that provided food—water fleas (*Daphnia magna*)—at opposite ends of the tank. The foraging behavior of fish was then observed in two treatments. In one treatment, water fleas were released from the two feeders in a 5:1 ratio (five times as much food at one feeder than the other); in the second treatment, the ratio of water fleas released from the feeders was 2:1. Milinski found that, after some initial sampling, the fish in both treatments distributed themselves under feeders in a ratio similar to the resource matching rule (Figure 14.4). For example, in the treatment in which five times more food was available at one feeder, five of the six fish were found at that feeder. While Milinski's study was the first experimental work demonstrating the resource matching rule, it was not designed to examine the feeding success of each individual and hence could not determine whether individual foraging success was approximately equal across the two feeding patches (Box 14.1).



For a 5:1 profitability ratio, the green points indicate the number of fish in the less profitable patch, and the green line shows the predicted number of fish at the less profitable patch.

For a 2:1 profitability ratio, the orange points indicate the number of fish in the less profitable patch, and the orange line shows the predicted number of fish at the less profitable patch.

Figure 14.4. Sticklebacks and the ideal free distribution. (A) When sticklebacks are presented with two foraging patches that produce food at a 5:1 ratio (5 water fleas being dropped into the tank from the left feeder versus 1 water flea being dropped into the tank from the right feeder), they distribute themselves in accordance with predictions from the ideal free distribution model. (B) Using this setup researchers also tested the ideal free distribution model for a 5:1 profitability ratio and then for a 2:1 ratio. The arrow on the left indicates the start of feeding; the arrow on the right in panel (C) indicates the point at which the profitabilities of the more and less profitable patches were reversed. *(Based on Milinski, 1979)*

Box 14.1. SCIENCE AT WORK

What is the research question? Do sticklebacks distribute themselves among food patches in accordance with the predictions of the ideal free distribution model (IFD)?

Why is this an important question? The IDF is a simple but powerful model that can be applied to many questions regarding habitat choice, as well as other behavioral decisions.

What approach was taken to address the research question? Groups of six fish were placed in an aquarium that had two feeding patches whose profitability could be manipulated experimentally.

What was discovered? The sticklebacks distributed themselves across patches in accordance with the relative profitability of the patches, as predicted by the IFD.

What do the results mean? Sticklebacks can assess the profitability of patches in their environment and use a simple resource-matching rule to distribute themselves between food patches.

Using individually recognizable mallards (*Anas platyrhynchos*) living in a pond at Cambridge University, David Harper ran an experiment similar to that of Milinski (Harper, 1982). Harper had two observers who were stationed 20 meters apart throw pre-cut, pre-weighed pieces of food (bread) into the pond. The observers acted both as data takers *and* as the food stations themselves. Harper varied the profitability of a patch by varying either the number of pieces of food added to that patch or the weight of each piece (Figure 14.5).

Figure 14.5. Ducks feeding at a pond. (A) One of the first controlled experiments on the ideal free distribution model involved ducks feeding at a pond. (B) To test the ideal free distribution model, food was thrown into a pond from two locations, and the distribution of ducks to each feeding station was recorded.

When equal amounts of food were thrown into patches by both observers, ducks quickly distributed themselves in a 1:1 ratio (Figure 14.6). In addition, as predicted by the IFD model, when one patch had twice as much bread as the other, the ducks distributed themselves in a 2:1 ratio.

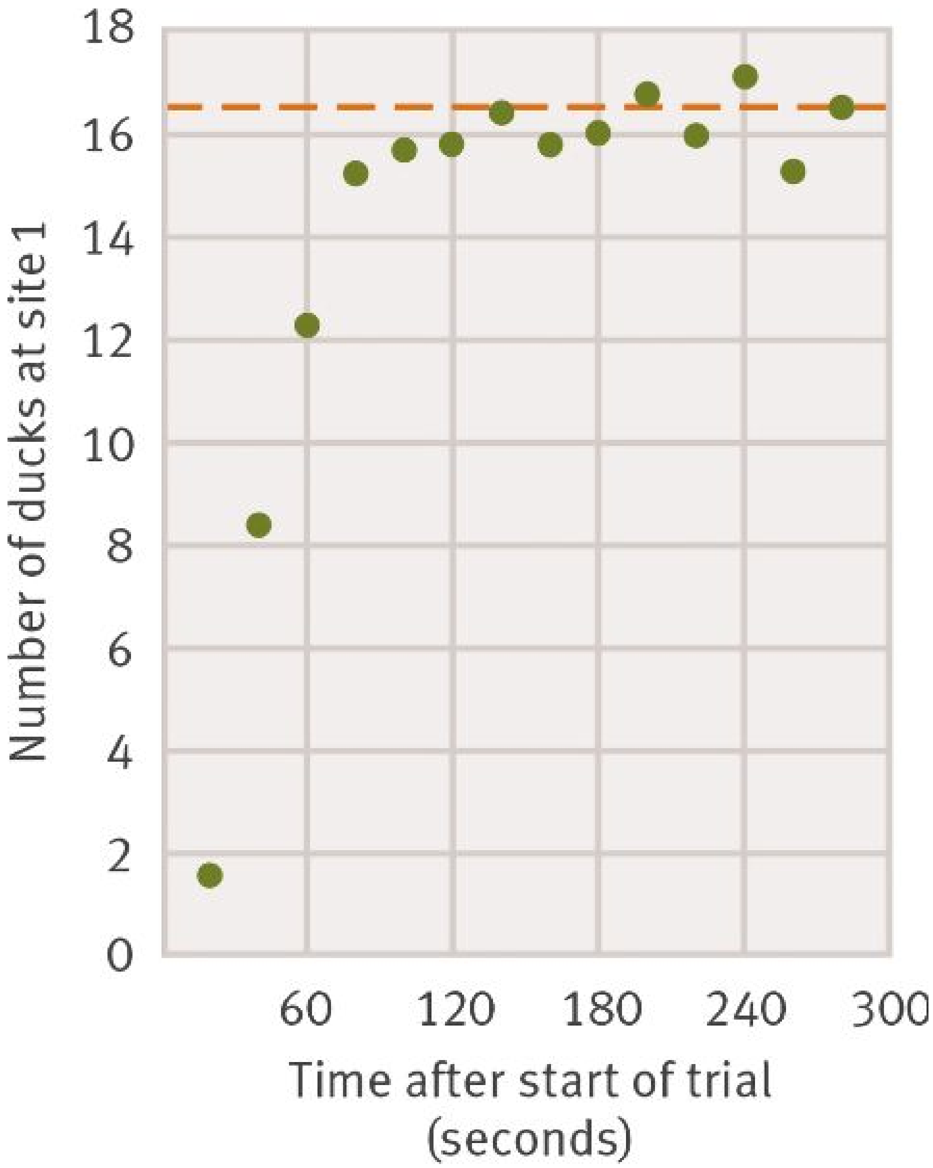


Figure 14.6. Testing the ideal free distribution in ducks. The two foraging patches created when two observers threw bread into a pond from different locations had equal profitability. The dashed line represents the predicted number of ducks at site 1. *(Based on Harper, 1982)*

During trials of his experiment, Harper noticed that some ducks seemed to be very aggressive and tended to receive a disproportionate amount of food within the patches. What this meant was that, although individuals distributed themselves across food patches in a manner similar to the resource matching rule, all individuals were *not* receiving the same amount of food across patches. The ducks' behavior might be better represented by a modified IFD model, know as the ideal despotic distribution model, that takes into account such aggression (G.

A. Parker and Sutherland, 1986; Sutherland, 1983; Sutherland and Parker, 1985).

AVOIDANCE OF DISEASE-FILLED HABITATS

Potential exposure to disease-causing agents can also affect habitat choice. Given the obvious effects of disease on fitness, natural selection should act strongly on any behavioral traits that help minimize an animal's exposure to disease. The two most likely ways this might occur are through (1) the avoidance of habitats that contain pathogens and (2) the avoidance of individuals that are already ill. We will touch on the former here.

One means by which individuals may reduce the risk of infection from parasitic diseases is by producing offspring in habitats that have low parasite levels (Kiesecker and Skelly, 2000). Amphibians are particularly good for testing whether such disease avoidance behaviors are in play, as they host many parasitic pathogens (Blaustein and Bancroft, 2007; Kiesecker et al., 2001, 2004) and are able to distinguish between oviposition sites based on a wide variety of characteristics (Duellman and Trueb, 1994).

Kiesecker and Skelly examined whether gray treefrogs (*Hyla versicolor*) base their decisions about where to oviposit (lay eggs) on levels of parasite infection by trematode parasites that are known to affect both larval performance and mortality (Kiesecker and Blaustein, 1997, 1999; Kiesecker and Skelly, 2000). The ponds used by *H. versicolor* are also home to the snail *Pseudosuccinea columella*, an intermediate host for a trematode parasite. The presence of this snail may serve as a cue to the frogs that an oviposition area is risky in terms of trematode infections (Figure 14.7).

Figure 14.7. Oviposition and parasite infection level. (A) The gray treefrog (*Hyla versicolor*) bases choice of oviposition site in part on parasite infection level. (B) A trematode parasite uses the snail *Pseudosuccinea columella* as an intermediate host. Frogs attempt to oviposit (lay eggs) in sites with low snail densities, and hence low trematode levels. *(Photo credits: David Brabiner / Alamy Stock Photo; © Walther Ishikawa)*

Kiesecker and Skelly addressed two related questions in their study of habitat selection and disease avoidance in frogs: (1) Do ovipositing gray treefrogs distinguish between sites with and without *P. columella* snails, and (2) if they do respond to presence or absence do they also take into account the density of snails present (Kiesecker and Skelly, 2000)? To address these questions, they set up twenty-five artificial ponds and ran five treatments: no snails (control), five infected snails, five uninfected snails, ten infected snails, and ten uninfected snails (Figure 14.8). They then assessed oviposition behavior of naturally occurring gray treefrogs. Although controls (ponds with no snails) made up only 20 percent of the ponds, 66.1 percent of all eggs deposited by *H. versicolor* were laid in such ponds, providing evidence that gray treefrogs were favoring ponds with no snails. In addition, the frogs responded to the density treatments in a manner suggesting that they can distinguish between infected and uninfected snails. Ponds containing uninfected snails received 33.5 percent of the eggs laid, and ponds containing infected snails received only 0.4 percent of the eggs laid (Box 14.2).

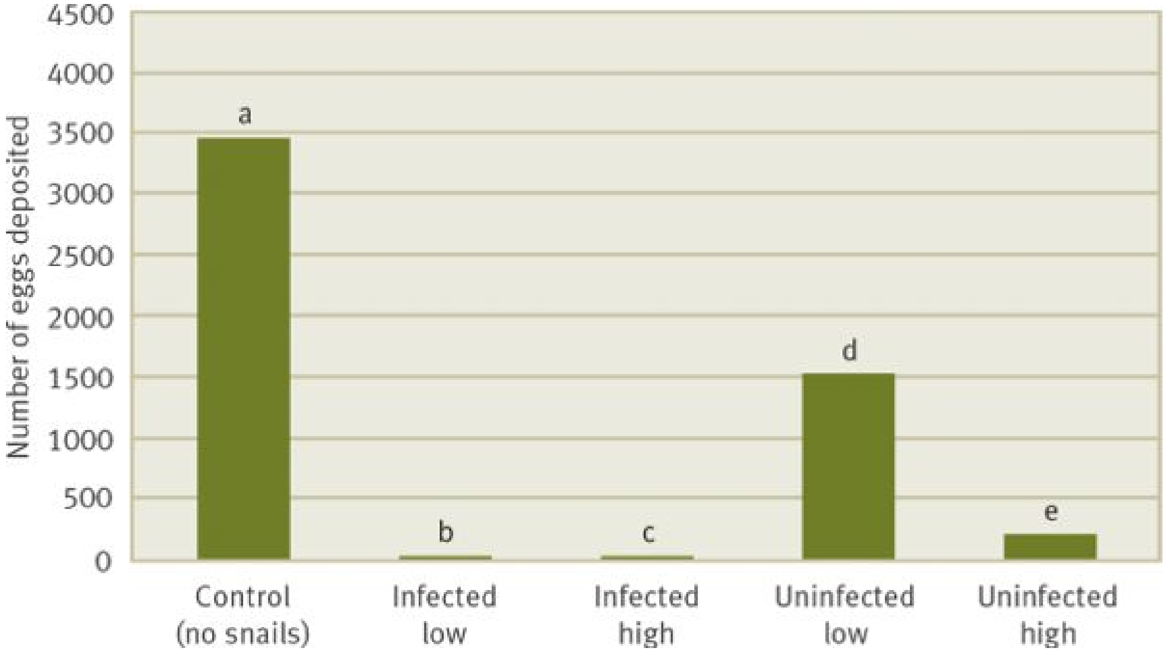


Figure 14.8. Parasites and oviposition sites. *Hyla versicolor* laid more eggs at control sites (with no snails) (A) than at sites with experimentally low (B) or high (c) levels of parasites. Frogs also preferred sites with low densities of snails (d) over sites with high densities of snails (e), even if the snails were uninfected. *(Based on Kiesecker and Skelly, 2000, p. 2941)*

Box 14.2. SCIENCE AT WORK

What is the research question? Do gray treefrogs (*Hyla versicolor*) use information regarding risk of parasitization when selecting oviposition sites?

Why is this an important question? Parasite load in a habitat can have important consequences for individuals and their progeny.

What approach was taken to address the research question? Researchers exposed gray treefrogs to experimental ponds that differed in risk of infection.

What was discovered? Frogs showed a preference for laying eggs in ponds that had the lowest probability of their offspring being parasitized.

What do the results mean? Animals can detect cues associated with risk of parasitization and use such cues when assessing where to deposit their eggs.

STRESS HORMONES, SPATIAL MEMORY, AND HABITAT CHOICE IN RATS

When animals make choices about which habitat to occupy, and where within that habitat to spend time, they may remember certain attributes about such habitats available. Ethologists have studied spatial memory and habitat choice in numerous ways, including by examining the hormones that affect it (de Quervain, 2006; de Quervain et al., 1998, 2000; Joels et al., 2006; Oitzl et al., 2010; Sapolsky, 2003; Schwabe et al., 2010). For example, in many animals, high levels of glucocorticoid hormones—often called stress hormones—interfere with spatial memory skills (McEwen and Sapolsky, 1995; Sapolsky, 1999; Sapolsky et al., 2000).

Dominique de Quervain and his colleagues used a water maze to examine how one glucocorticoid hormone—corticosterone—affects spatial memory and habitat choice in rats (de Quervain et al., 1998). In this experimental setup, rats are put into a large tank of dark and murky water. Some distance from where the rat enters the water, there is a single small platform that is slightly submerged but close enough to the surface to serve as a resting place for the rat: The platform is a place of refuge within the otherwise inhospitable habitat of the water tank. When first put into the tank, rats swim around randomly, but eventually they come across the hidden platform and use it as a refuge. As they are put through more and more trials in the water maze, rats become better and better at finding the platform.

On the basis of prior work on rodents, de Quervain and his colleagues hypothesized that a stress-induced increase in corticosterone would impair a rat's spatial memory regarding the position of the platform in their habitat. To test this hypothesis, they gave rats eight trials in the water maze, and then they divided the rats into four groups (Figure 14.9). In group 1, rats received a shock thirty minutes before their ninth trial in the water maze. In group 2, the shock came two minutes before the ninth trial, and in group 3 it was administered four hours before the ninth trial. A fourth group—the control group—received no shock before their ninth trial. De Quervain and his team found that rats in groups 2 and 3 spent about as much time near the platform as did rats in the control group: shocks that were administered two minutes or four hours before a trial did not impede spatial memory for the location of the platform. Rats in group 1—those that experienced the shock thirty minutes before the trial—did show impaired memory for the location of the platform (Figure 14.10). De Quervain and colleagues then measured corticosterone levels in rats in all four groups. As predicted, they found that, compared with the control group, only rats in group 1—the group with decreased ability to find the area of the platform in their tank—had higher levels of corticosterone, suggesting an important memory-inhibiting role for this hormone.

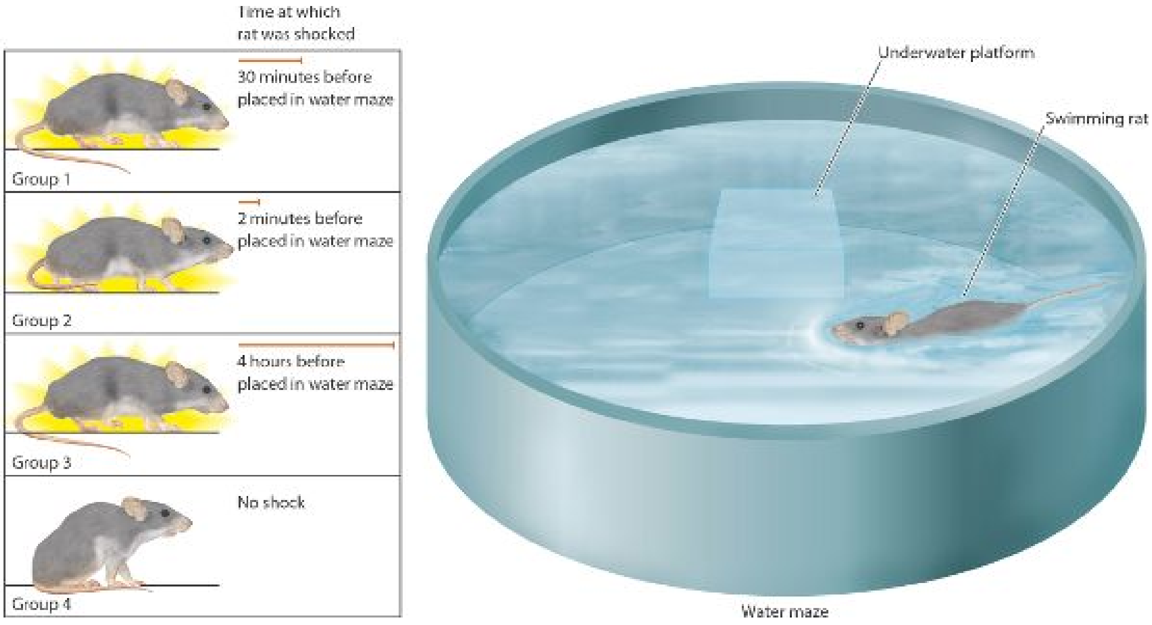


Figure 14.9. Water maze apparatus and learning trials. Stress and learning in rats was studied using a water maze in murky water that had a platform that the rats could not see but could learn to find. In group 1, rats received a shock thirty minutes before their ninth trial. The shock was administered two minutes before the ninth trial in group 2 rats, and four hours before the ninth trial in group 3 rats. Rats in group 4, the control group, received no shock before their ninth trial.

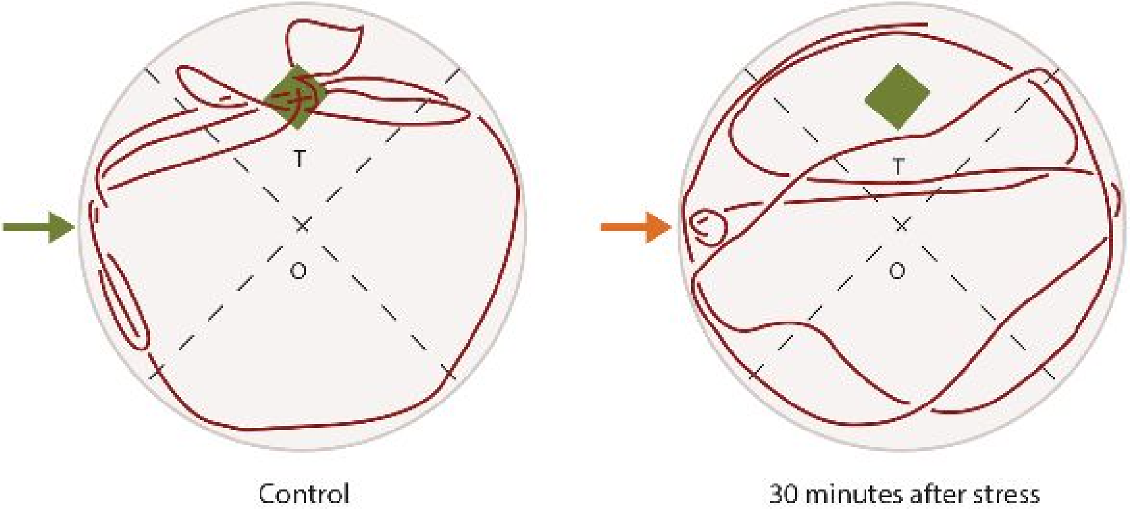


Figure 14.10. Shock and spatial memory in rats. The swimming path of a control rat on its ninth trial was near the target (T), indicating that its memory for the location of the platform was not impaired, whereas the swimming path of a rat that was shocked thirty minutes before the ninth trial was random, indicating that its memory for the location of the platform was impaired by the shock. Nature Publishing Group. © 1998. *(From de Quervain et al., 1998)*

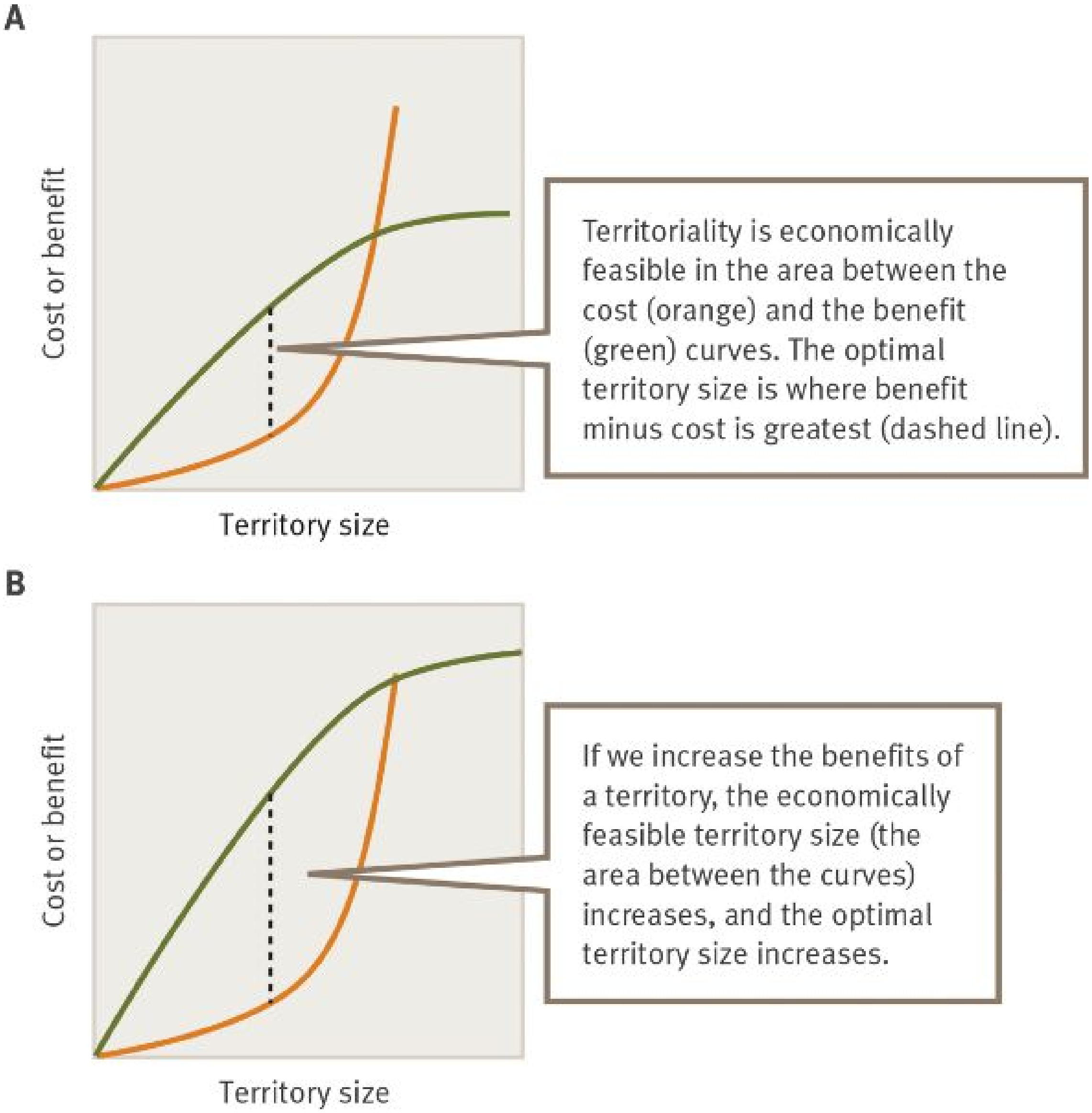
De Quervain and colleagues examined the role of corticosterone on spatial memory and habitat choice in two follow-up experiments. In one of these, they injected rats with the drug metyrapone, which inhibits the production of corticosterone by blocking certain chemical reactions in the adrenal glands, where corticosterone is produced. When rats were injected with metyrapone, individuals that were shocked before their trial in the water tank did not show impaired memory compared with control animals. When corticosterone production was blocked, rats retained the ability to find the platform, again suggesting that corticosterone was associated with spatial memory tasks in rats.

In another follow-up experiment, instead of shocking rats thirty minutes before their last trial in the water maze, de Quervain and his colleagues injected rats with corticosterone thirty minutes before a trial. If corticosterone changes in response to stress were behind the impairment of spatial memory, then rats that had their corticosterone levels experimentally increased should also show impaired spatial memory in the water maze, and indeed, rats injected with corticosterone (but not shocked) thirty minutes before being placed in the water maze tank also showed impaired memory when they tried to find the platform.

Taken together, the work by de Quervain and his team is a good example of how the behavioral endocrinology of spatial memory can be studied in a controlled environment. The combination of behavioral experiments with measurements of corticosterone and experimental manipulations of corticosterone, as well as manipulation of chemicals that block the production of corticosterone, allows us a much deeper understanding of the role that endocrinology plays in spatial memory and habitat choice.

Territoriality

Territoriality is defined as the occupation and defense of a particular area. Territories can provide their owners with exclusive access to food, mates, and safe haven from predators, and are typically vigorously defended from intruders. Such defense can be costly, in terms of both time and energy. Models of territoriality consider both the costs and benefits of owning a territory: when the benefits are greater than the costs, territory defense will be favored by natural selection (Figure 14.11).



Territoriality is economically feasible in the area between the cost (orange) and the benefit (green) curves. The optimal territory size is where benefit minus cost is greatest (dashed line).

If we increase the benefits of a territory, the economically feasible territory size (the area between the curves) increases, and the optimal territory size increases.

Figure 14.11. An economic model of territoriality. (A) The zone between the curves indicates where territoriality is economically feasible, and the dashed line shows the optimal territory size. (B) When the benefits of territoriality increase, so do the range of economically feasible territory sizes and the optimal territory size.

Most of our discussion of territoriality will focus on territories that contain either a single individual or a family, but territories are sometimes defended by groups of individuals. This sort of group territoriality can result in dramatic between-group interactions, in which groups attempt to enlarge their own territory by taking over another group's territory. For example, chimps sometimes engage in between-group raiding. Between-group interactions often appear to be war-like, and in fact resemble the raiding behavior that is common among many tribal populations of humans (Boehm, 1992). During raids, all-male chimpanzee patrol groups travel into areas that border their territorial boundaries (Bygott, 1979; Goodall, 1986; Nishida, 1979). In contrast to excursions for food, in which foraging chimps often emit vocalizations, chimps in patrols move in a wary fashion and remain silent (Goodall, 1986). These raids often involve the killing of a small number of members of the raided group and the capture of females. Occasionally, raiding parties from two groups will meet one another. In such instances, rather than engaging in extremely violent interactions, both groups engage in hostile vocalizations and then withdraw (Goodall, 1986). Although all-out warfare does not emerge when two raiding parties meet, raiding can, in the long run, amount to the slow extinction of one group: in the Mahale Mountains of Tanzania, raiding led to a larger group eradicating a smaller group of chimps (Nishida et al., 1985; see also Goodall, 1986, for evidence of this at Gombe).

TERRITORIALITY AND LEARNING

Most models of territoriality assume that animals are capable of assessing various characteristics about a potential territory—how much food is in the area, how safe the area may be from predators—but many of these models do not explicitly consider how learning affects the establishment and maintenance of a territory. But a few learning-based models have been constructed, and below we examine two models that examine how learning affects decisions regarding both the acquisition and subsequent maintenance of territories.

Territoriality and Learning During Settlement

Judy Stamps has studied the role of learning in territory formation among juvenile *Anolis aeneus* lizards (Stamps, 2001). These lizards form territories early in life, and Stamps has examined where and how juveniles decided to stake out a territory (Figure 14.12). Because much of the work on territoriality has centered on the distribution of food resources, her initial inclination was to test for the importance of food availability in structuring territoriality in *A. aeneus*. Yet despite numerous experiments manipulating food availability, Stamps did not uncover a clear-cut effect of food availability on territory formation. Rather, in subsequent experiments, she found that safety from predators and suitable temperature appeared to be the most important attributes of a desirable territory. But *how* do juvenile lizards determine which territories are suitable with respect to temperature and predation pressure? More specifically, do lizards *learn* what areas are best from their interactions with other lizards (Stamps and Krishnan, 1999, 2001)?

Figure 14.12. Territorial lizards. (A) Juvenile *Anolis aeneus* are territorial, and their territory formation has been studied in the context of habitat choice and learning. (B) *Anolis aeneus* stake out territories in areas such as those depicted here. *(Photo credits: Judy Stamps)*

Stamps had noticed that juvenile *A. aeneus* watched what other lizards were doing, and she hypothesized that they might be determining territory quality as a result of their interactions with conspecifics. If another individual has already determined a territory is safe and has temperatures that will not cause overheating, then it may be a good territory. This sort of decision-making process, in which individuals use the choices of others to determine the quality of a potential territory, has been called “conspecific cueing” (Donahue, 2006).

Stamps tested a conspecific cueing model of territoriality by examining whether a territory that had been occupied by an owner sometime in the past but was currently vacant would be viewed as attractive to other lizards (Stamps, 1987a). In this experiment, a juvenile was allowed to observe two very similar territories, one that was currently occupied and one that was vacant. When given the choice between these two areas, with the territory owner now removed, juveniles showed a preference for the previously inhabited area (Figure 14.13). Furthermore, juveniles that had not observed the territories during the initial part of the experiment but were given a choice between these territories displayed no preference for the previously occupied territory, suggesting a visual component to conspecific cueing in *A. aeneus* (Stamps, 1987b).

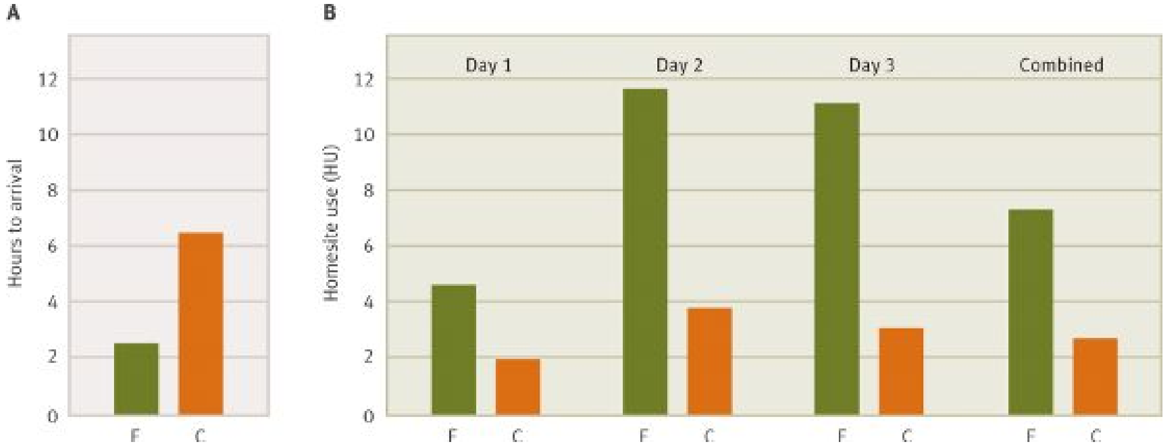


Figure 14.13. Conspecific cueing and territorial lizards. (A) Focal juveniles not only spent more time on experimental (E) versus control (C) homesites but also arrived at experimental homesites more quickly. (B) Juvenile lizards were drawn to experimentally manipulated homesites (E) over control (C) homesites. Control territories remained empty prior to the focal’s choice, while experimental territories had formerly contained a territorial juvenile. *(Based on Stamps, 1987a)*

CONFLICT WITHIN FAMILY TERRITORIES

While genetic relatives often cooperate, we have seen that is not always the case. Under certain conditions, family members on a territory may differ on decisions about when a territory member should leave a territory and breed on its own. For example, it may be in an individual's best interest to leave its natal territory and breed, while it may be in the best interest of other family members on the territory for that individual to remain at home, not to breed, but instead to help family members. Conversely, it may be in an individual's interest not to breed, but in the interests of other family members for that individual to breed on its own territory. There is a burgeoning literature on **optimal skew theory**, which studies the distribution of breeding within a group and whether there will be cooperation or conflict over reproductive activities (see chapter 9). For an example of conflicting interests in terms of breeding and territory use, we turn to Steve Emlen's work on parent-offspring conflict over breeding opportunities in white-fronted bee-eaters (*Merops bullockoides*; S. T. Emlen and Wrege, 1992).

Young male white-fronted bee-eaters often remain on their natal territory and aid their genetic relatives, usually their parents, in raising their siblings. When breeding opportunities for young males are rare, no conflict exists between young males and their parents—it is in the best interest of all parties for the young male to remain at home and help his parents. The situation gets more complex when breeding opportunities away from the natal nest become available to such a young male. Now it may be in the best interest of a young male to breed on his own territory, but in the best interest of this male's parents for him to remain at home and help raise his siblings. This leads to conflict between offspring and parent.

Box 14.3. COGNITIVE CONNECTION

Nest Complexity and Cerebellar Foliation

Many animals modify the habitat or territory they inhabit by constructing a nest. Nests vary in their complexity, from simple to construct to more elaborate and difficult to construct, requiring greater motor abilities and manipulative skills by the builder. Motor abilities and manipulative skills are positively correlated with certain cerebellar characteristics, in particular with the amount of folding—more technically, foliation—in the cerebellum. Such a correlation has been found between cerebellar folding and tool use in birds (Iwaniuk et al., 2009).

Sue Healy and her colleagues hypothesized that the amount of folding in the cerebellum, measured by what is known as the cerebellar foliation index (CFI), would be positively correlated with nest complexity (Hall et al., 2013). They gathered CFI measures and information on nest building behavior in 64 species of birds. Healy and her team focused on platform nesting, which requires collection of nest material but little manipulation (nests are just piles of collected materials), and cup nesting, which involves both collecting material and manipulating that material into cup-like nests. Platform nesters and cup nesters were also compared to birds that built no nests at all. As hypothesized, they found that for a given cerebellar volume, CFI scores were highest in cup nesters, followed by platform nesters and then birds that that built no nests at all (Figure 14.14).

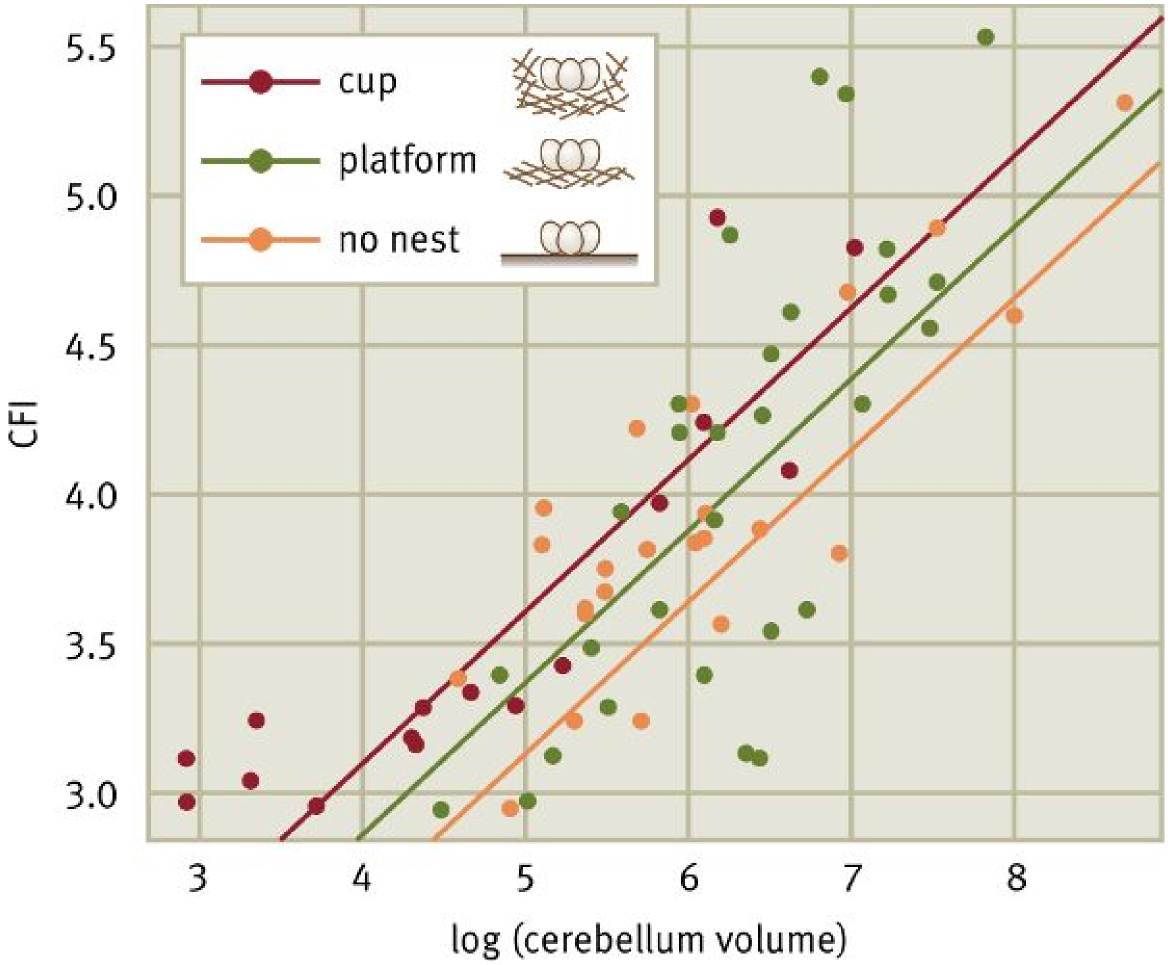


Figure 14.14. **Nest complexity and cerebellar foliation index (CFI).** For a given cerebellum volume, CFI was greatest in cup nesting species, followed by platform nesters and, lastly, birds that did not build nests. *(From Hall et al., 2013)*

Work in other taxa such as primates and sharks has also found that skills associated with object manipulation increase with CFI, suggesting that cerebellar folding as a mechanism for increasing manipulative skills, and potentially more complex behaviors in general, may be conserved in many vertebrates.

To understand this conflict, consider the following: Pairs of white-fronted bee-eaters without helpers raise an average of 0.51 offspring per clutch. Every helper a pair has adds approximately 0.47 offspring. Keeping in mind that young males that breed for the first time will rarely have a helper of their own, let's start our cost-benefit analysis from the perspective of a young male's parents. If their son attempts to breed, he will, on average, produce 0.51 offspring. But if instead he helps them, he will add, on average, 0.47 offspring to their next clutch. Since the young male's parents are twice as related to their own offspring (r = 0.5) as they are to grand-offspring (r = 0.25), parents have an incentive to keep their son around to help: the benefit they receive if their son stays—0.47 × 0.5—is greater than the benefit they obtain if their son leaves—0.51 × 0.25.

The genetic accounting is different from the young male's perspective. Because he is equally related (r = 0.5) to his own offspring and to his siblings (individuals he would assist if he were to help his parents), there is no incentive for such a male to resist his parents' attempt to suppress his breeding. And, indeed, Emlen and Wrege found that in bee-eaters, parental suppression of offspring breeding is met with little resistance on the part of their son. But when a breeding pair tries to suppress the reproductive efforts of its more distant kin, or even nonkin, where the costs, benefits, and genetic relatedness are different, their actions are met with much stiffer resistance than when they attempt to suppress the reproduction of their own offspring.

Migration

> Twice each year, billions of birds, entire species, swarm across the globe, traveling thousands of miles as they follow the sun to populate regions that are habitable for only part of the year. The spatial scope of these migrations exceeds all other biological phenomena. So fantastic are they that ancient civilizations devised a host of myths to explain the periodic appearance and disappearance of such vast numbers of animals. Those apocryphal stories were concocted in part because what we know to be true seemed then so completely beyond the pale. It seemed more likely that swallows buried themselves in the mud at the bottom of ponds than that they flew all the way from Europe to Africa and back twice each year. But the truth turned out to be more amazing than the myth. (Able, 1999, p. vii)

From wildebeests swarming across the African plains to monarch butterflies heading by the tens of millions to Mexico each year, migration is seen across many different animals and is certainly one of the most spectacular of all animal behaviors. In some species, annual migration is obligatory, occurring like clockwork; in other species, it occurs only when conditions become poor in what is called irruptive migration; in still other cases, only a portion of a population will migrate, while the rest stays put (Able, 1999). No matter where a species falls on this migration continuum, ethologists can ask questions such as how do they know where to go, when to go, how to go, how to prepare (Able, 1999; Alerstam, 1990; Baker, 1978; Gauthreaux, 1980; Heape, 1931; Ramenofsky and Wingfield, 2007; Salewsk and Bruderer, 2007; R. Wiltschko and Wiltschko, 2003; Figure 14.15)?

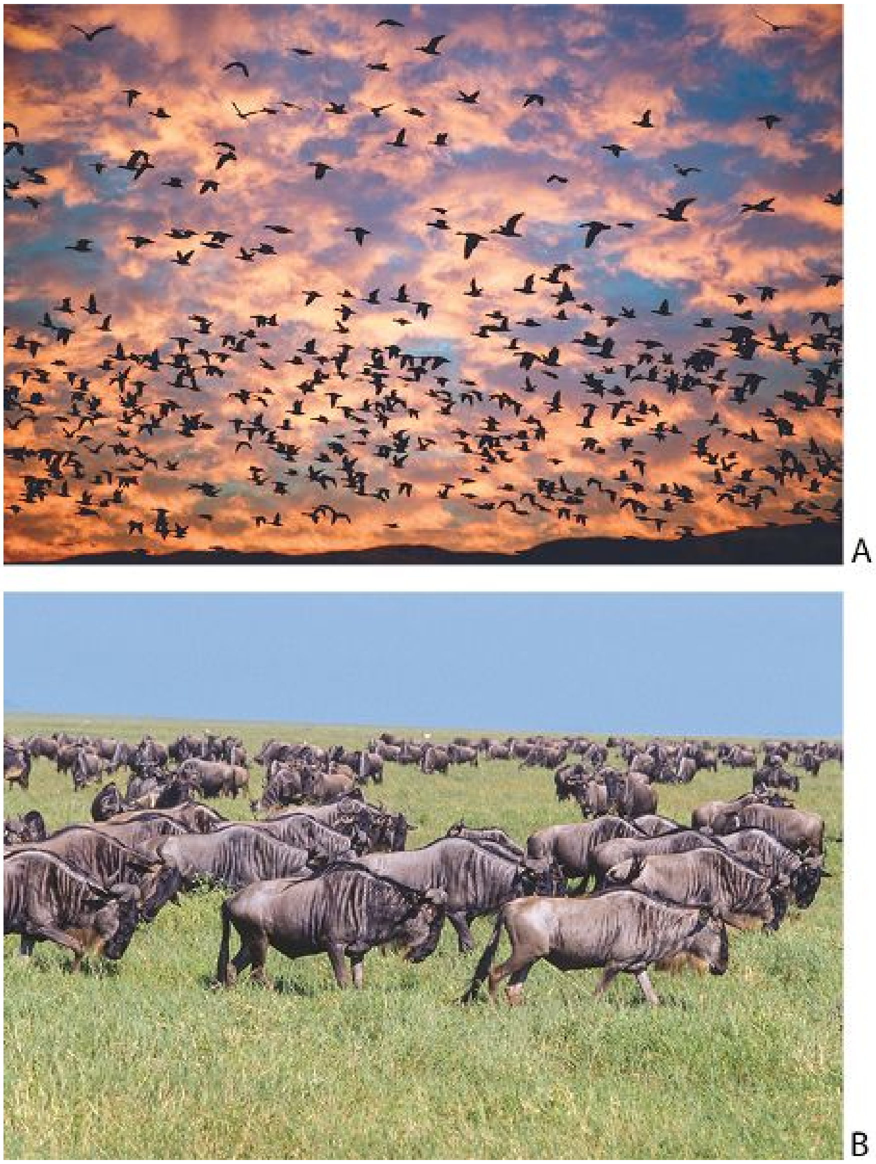


Figure 14.15. Animal migration. In some species of birds and mammals, massive yearly migrations take place. Here we see migration in (A) geese and (B) gnu. *(Photo credits: © Adam Jones/Visuals Unlimited; © Joe McDonald/Visuals Unlimited)*

MULTIPLE MIGRATORY ROUTES

Avian migration is so spectacular, covering such huge stretches of distance, that we tend to think of *a* migration path taken by individuals. In fact, there are often numerous different paths taken by migrators in the same species. With the advent of small geo-locator devices that provide positional data of migrating individuals, and related platform transmitter terminals that are used to infer mortality during migration, animal behaviorists have begun to test the fitness consequences of taking one migratory route over another.

Each autumn, common cuckoos (*Cuculus canorus*) living in the United Kingdom migrate south to their wintering grounds in Central Africa. Tracking cuckoos from nine locations in the UK, Hewson et al. (2016) reconstructed the migratory routes used in these nocturnally migrating birds. On the autumn migration south (but not on the spring migration back north), cuckoos used two different migratory routes: a southwest route via Spain or a southeast route via Italy or the Balkans. Both paths ended in the same general location (in central Africa), and individual birds were consistent across years in which path they flew during the autumn migration.

Morality rates differed across the two migratory paths. Although the southwest migratory route was 12% *shorter*, mortality, particularly up to the crossing of the Sahara desert, was *higher* along this path. Most of the mortality on the more dangerous southwestern route occurred in Europe. Although it is difficult to ascertain specific causes of mortality, severe drought and a related increase in wildfires near Spain (a stopover point on the migration) may in part be responsible (Figure 14.16).

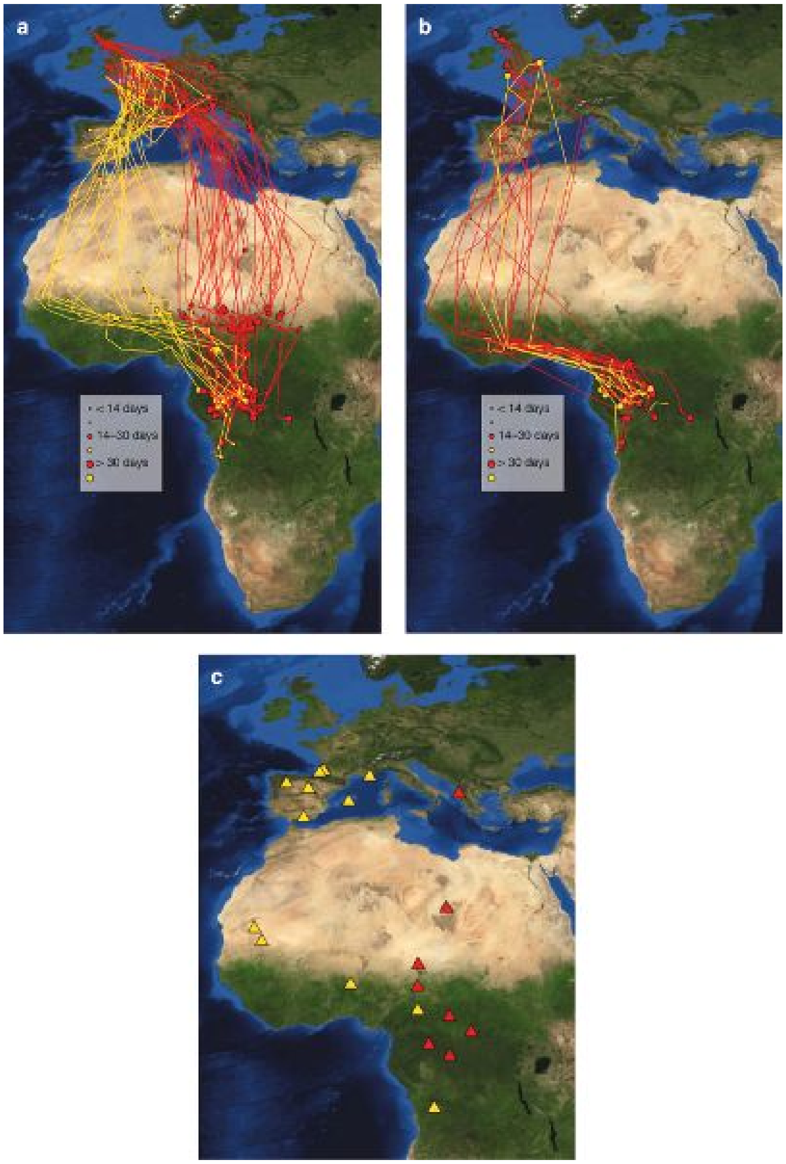


Figure 14.16. **Migratory paths south in cuckoos.** (A) Two different autumn migration routes south (circles represent stopover points) (B) Spring migration routes north (circles represent stopover points), and (C) spots where mortality occurred during the autumn migration (red = southeast route, yellow = southwest route). Reprinted by permission from Macmillan Publishers Ltd. © 2016. *(From Hewson et al., 2016)*

Cuckoo populations in general are declining in the United Kingdom, and mortality related to the choice of migration route is, in part, responsible for population-level variation in this decline. While populations from all of the nine UK sites had some individuals who took the southwest route and other who flew southeast, there is a negative correlation between population size in a UK population and the proportion of birds that migrated using the southwest route (Box 14.4).

MIGRATION AND NAVIGATION

Migration involves navigating through complex environments, and migrators need to use cues to assess where they are in relation to where they are heading. These cues can come in many forms—the position of the sun, the position of the stars, landmarks on the ground, the odor of a stream, and so on—but one way or another, migrating animals must determine if they are heading where they want to go, and if not, how they can get back on track (Bruderer and Salewski, 2008; Dingle, 2008; J. L. Gould and Gould, 2012; Zink, 2011; see Box 14.5).

Box 14.4. SCIENCE AT WORK

What is the research question? Are there fitness consequences associated with alternative migration routes?

Why is this an important question? The fitness consequences of long-term migration behavior have been notoriously difficult to study.

What approach was taken to address the research question? The migratory routes of common cuckoos (*Cuculus canorus*) were tracked during their autumn migration to Central Africa. Mortality rates were estimated along two alternative routes.

What was discovered? Cuckoos used two different migratory routes: a southwest route via Spain or a southeast route via Italy or the Balkans. The southwest migratory route was 12% shorter, but mortality was *higher* along this path.

What do the results mean? Choice of migratory route has fitness consequences in cuckoos. This choice has consequences not only at the level of the individual, but at the population level as well: populations with more individuals that migrate along the more dangerous route decline more quickly than other populations.

Box 14.5. CONSERVATION CONNECTION

Migration Patterns, “Stopovers,” and Conservation Biology

Information on animal migration patterns, including the location of “stopovers,” where migrating individuals feed and rest, informs both ethologists and conservation biologists interested in understanding migratory behavior and minimizing human obstacles to such migration (Morales et al., 2010; Sawyer and Kauffman, 2011; Shamoun-Baranes et al., 2012). Obtaining such information is difficult, in part because tracking migrating individuals over long distances can be hard, but also because it is a challenge to use data on a small sample of migrating animals to make accurate estimates of migratory patterns for the *populations* from which the sample animals come.

In 2007, Jon Horne and his colleagues developed a mathematical model that takes global position data (GPS data) and, using sophisticated mathematical algorithms, estimates where important “stopovers”—likely associated with foraging, resting, and mating—occur. The model then uses such data from individuals to estimate large-scale population migration patterns (Horne et al., 2007). Hall Sawyer and his colleagues used the model to estimate the migration patterns, including stopovers, of mule deer (*Odocoileus hemionus*) across a pristine area of Wyoming. One of the reasons they chose this population is that the migration area of these deer was being considered as a location for 2,000 gas wells and over 1,600 kilometers of gas pipes. Sawyer and his team captured forty-seven mule deer, placed a GPS radio collar on each one, and then released the animals. They then tracked the migratory behaviors of these deer and used their model to map out a population-level migration route, which they superimposed onto a map with the proposed sites for the gas wells and pipelines (Figure 14.18). When they presented their data on migration paths and stopover sites to the oil industry, this led these companies to modify the use patterns of gas wells and pipelines (wells and pipelines were used less in important areas during migratory season). The oil companies also made improvements to key habitats along migration routes, especially at highly frequented stopover sites (Sawyer et al., 2009).

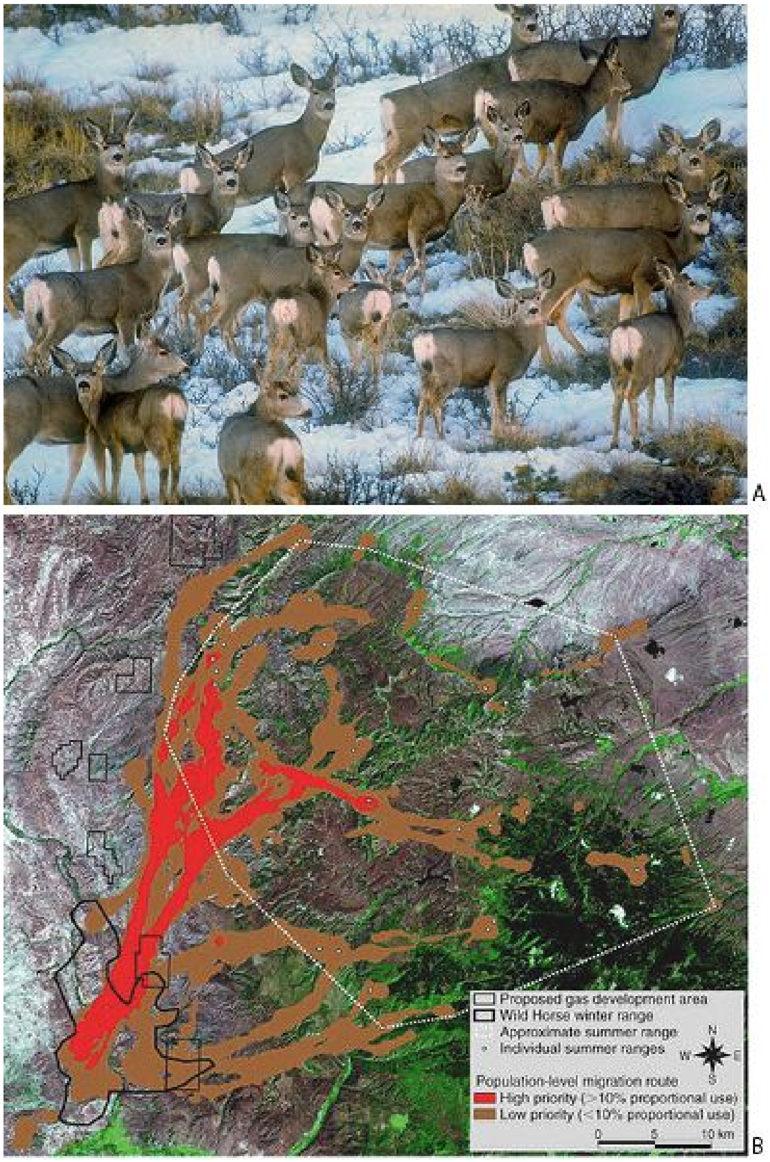


Figure 14.18. Migration patterns and oil company gas wells and pipelines. (A) Mule deer. (B) The migratory behavior of mule deer and the proposed placement of gas wells and pipelines are shown on a GPS map. (*Photo credit: Art Wolfe/Photo Researchers; from Sawyer et al., 2009,* reprinted by the permission of the Ecological Society of America)

Migration and the Sun Compass

Both because the sun is such a large, prominent object and because it provides information about direction, ethologists have long speculated that migrating animals use the sun to help them navigate (Guilford and

Taylor, 2014). While other factors, for example, the use of magnetic cues, play a role during monarch migration (Guerra et al., 2014), here we shall examine how monarch butterflies use the sun to guide them on their journeys.

Tens of millions of monarch butterflies (*Danaus plexippus*) migrate each year from North America to the mountain ranges of central Mexico. During this annual migration, the air is so thick with monarch butterflies that branches of trees have been known to collapse from the weight of too many butterflies (Figure 14.17). Monarch butterflies travel up to 6,000 miles on their migratory trip, and they almost always navigate successfully without getting lost, even on their first migration (recent work has looked at monarch brain structure as it relates to migration; Reppert et al., 2016; Philipps-Portillo et al., 2016; Shlizerman et al., 2016).

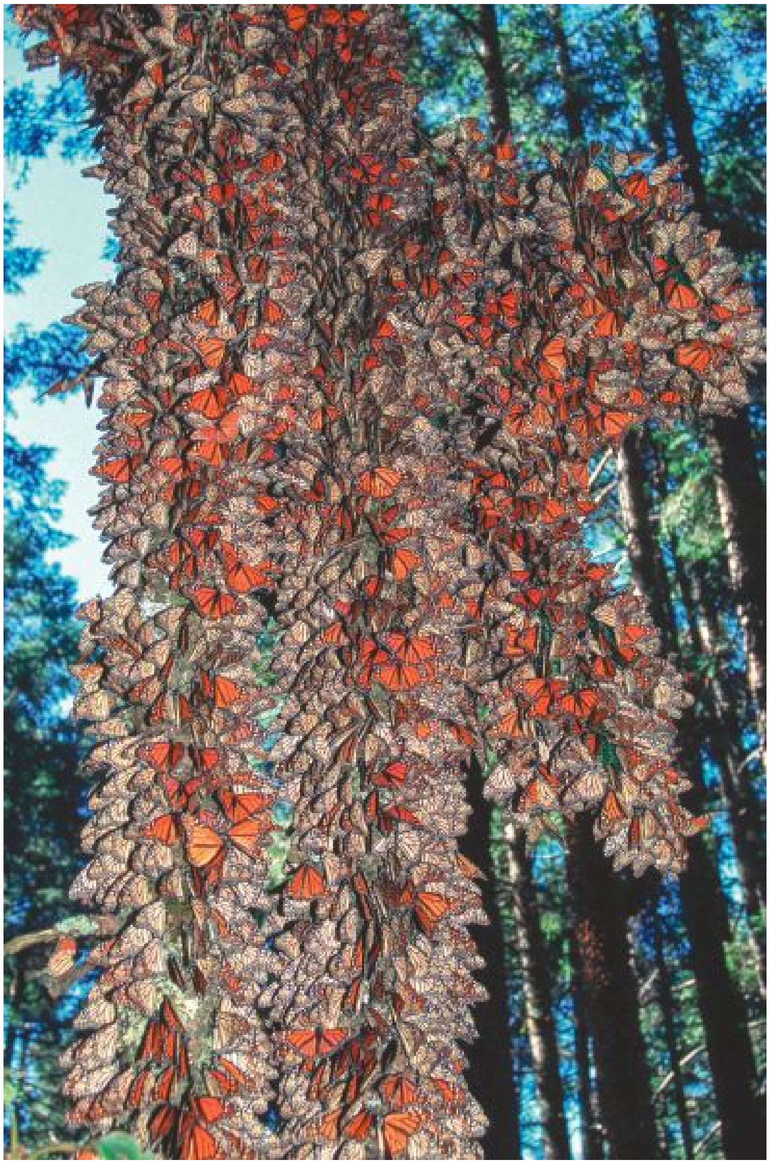


Figure 14.17. Monarch migration. Migration of monarch butterflies can involve tens of millions of individuals. *(Photo credit: © Thomas Marent/Visuals Unlimited, Inc.)*

As they travel south, monarch butterflies use the position of the sun to help them navigate (Mouritsen and Frost, 2002; Perez et al., 1997). To examine the role of solar navigation in monarch migration, Sandra Perez and her colleagues ran a "clock-shift" experiment (Perez et al., 1997). The idea was to experimentally manipulate the amount of daylight and darkness animals are exposed to such that they experience a light-dark cycle that is different from the normal cycle at that time of year. For example, more hours of daylight are typically experienced in the summer than in the winter, but clock-shift experiments allow an experimenter to take an animal during the winter and expose it, in the laboratory, to the light-dark cycle it typically experiences in the summer. This manipulation of its biological clock tricks the animal into acting as if it were summer.

At the start of the experiment, Perez and her team raised one group of monarch butterflies in a laboratory and slowly shifted the butterflies' body clocks back six hours—when the real time, for example, was noon, the clock-shifted monarchs acted as if it were six hours later. The researchers also kept a second control group of butterflies in the laboratory, but these butterflies' body clocks were not shifted. During the period of autumn migration south, Perez and her team released individual monarch butterflies that they had raised in the laboratory. They then watched these individual butterflies and noted their position by using handheld compasses. The control butterflies headed south, just as wild populations of monarch butterflies typically do in the autumn migration (Figure 14.19). The clock-shifted butterflies, however, flew almost due west, which is just where Perez and her team expected them to fly if they were using a sun compass to help them navigate during their migration. That is, the six-hour clock shift caused the butterflies to misinterpret the information that the sun was conveying about direction and to fly west rather than south.

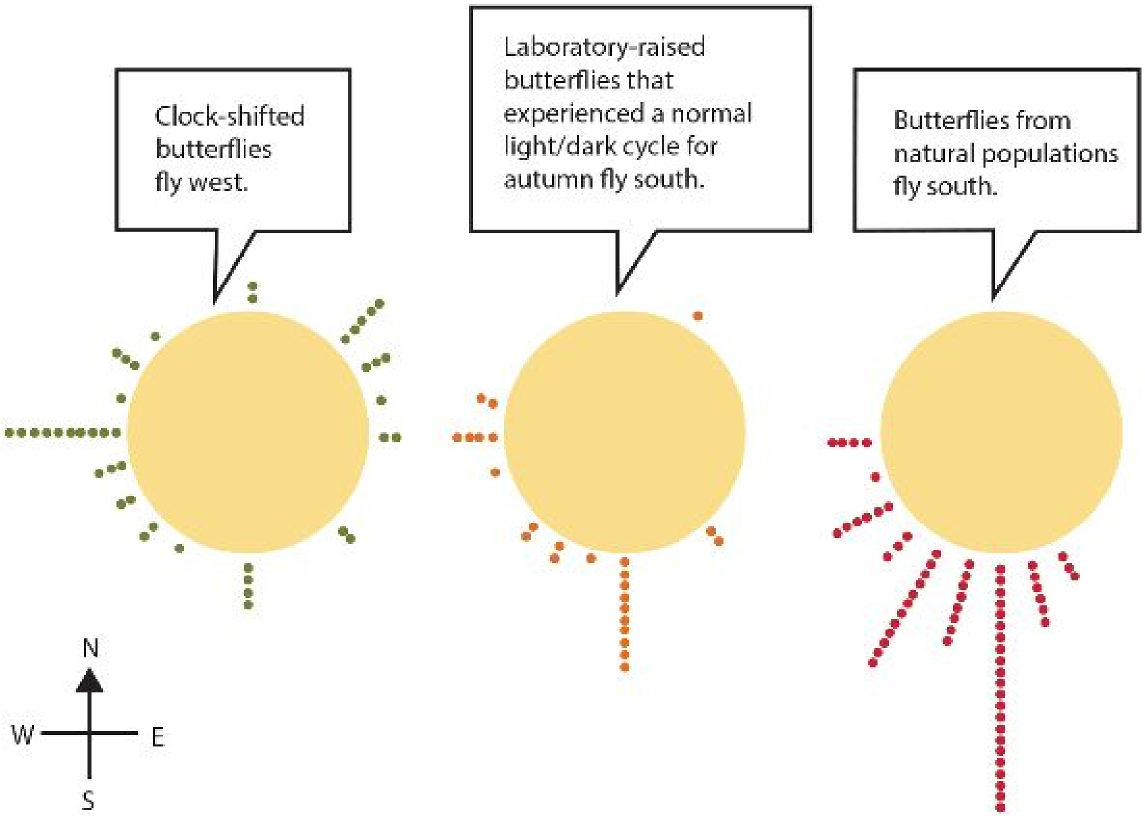


Figure 14.19. Clock-shifted monarch butterflies and navigation. The diagrams show the mean body position of monarch butterflies during the first five minutes of autumn migration. Nature Publishing Group. © 1997. *(From Perez et al., 1997, p. 29)*

Henrik Mouritsen and Barrie Frost also examined monarch butterflies' use of a sun compass to navigate. They built a miniature flight simulator (Figure 14.20) that allowed them to follow the orientation of a tethered monarch butterfly for much longer than the five-minute time frame in the Perez experiment (Mouritsen and Frost, 2002). Using this flight simulation device and the clock-shift protocol discussed above, Mouritsen and Frost's data point to an important role for the sun compass in monarch butterfly migration.

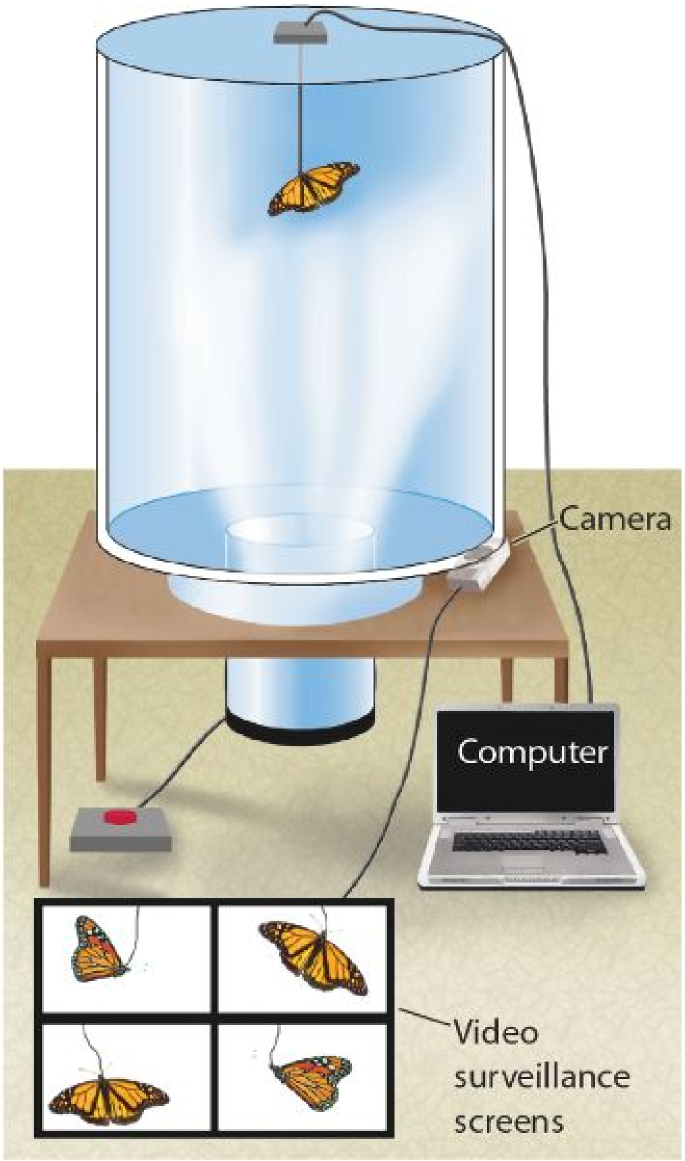


Figure 14.20. Insect flight simulator. A flight simulator for monarchs was constructed in the laboratory, and a butterfly was tethered to this device. The pipe at the bottom of the simulator directed a constant flow of air up toward the butterfly so that it could fly; a video camera was connected to the bottom of the simulator (so that the researchers could see when the butterfly was flying, gliding, or stopping; the four images show the images from different time periods); an encoder (recording the butterfly's direction) was attached to the butterfly from the top of the flight simulator and was connected to a computer that kept a timed record of all the butterfly's movements. With this setup, researchers could track the direction the butterfly was orienting toward and whether it was actively flying or gliding. *(From Mouritsen and Frost, 2002, p. 10163)*

Indigo Buntings and Navigating By the Stars

The majority of passerine birds migrate almost exclusively at night (Able, 1999). What cues might such birds use when cues from the sun are absent? Using indigo buntings (*Passerina cyanea*), a nocturnal migratory species that travels 2,000 miles each winter from the northeastern United States to the Bahamas, Mexico, and Panama, Stephen Emlen ran one of the earliest studies of how migrating individuals might use the stars to help them navigate (S. T. Emlen, 1967, 1970, 1975; Figure 14.21).

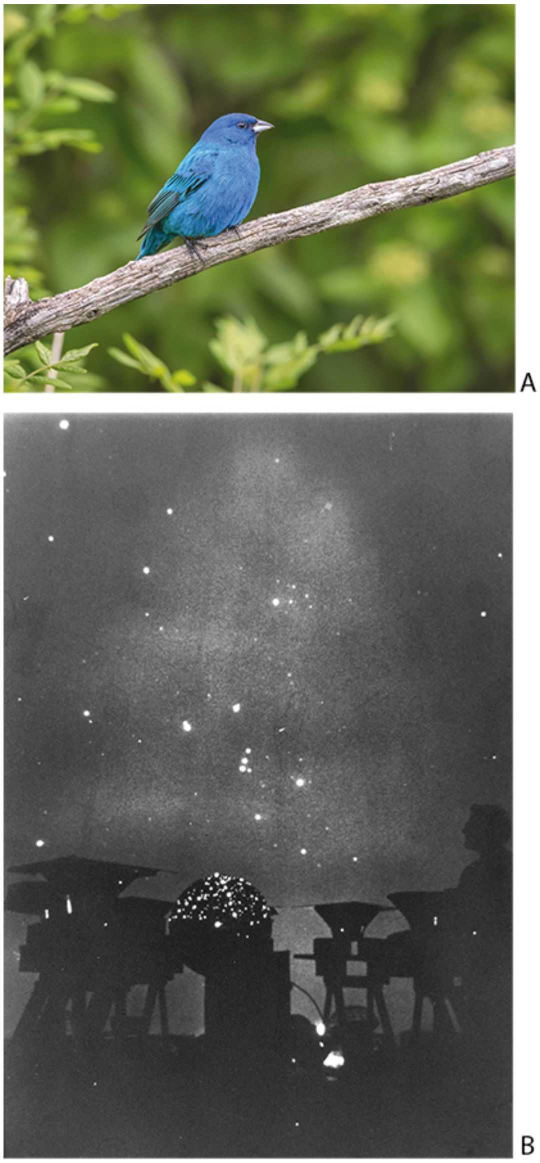


Figure 14.21. Bunting migration. (A) Indigo buntings can use the stars as a navigation tool. (B) A planetarium like the one in which indigo buntings in funnel-shaped cages were shown the stars. *(Photo credits: © FotoRequest / Shutterstock; © Stephen Emlen)*

Emlen built funnel-shaped test cages for buntings, and at the bottom he placed an ink pad. The cages were constructed such that each time a bunting tried to fly out, the location of its footprint was marked by ink, so its orientation pattern was easily recorded (Figure 14.22). When these cages were placed under a starlit sky, the buntings oriented their attempts in the direction they would normally migrate—toward the south in September and October, and toward the north in April and May. In addition, these patterns all but disappeared on cloudy nights when stars were not visible, suggesting a role for star-based navigation.

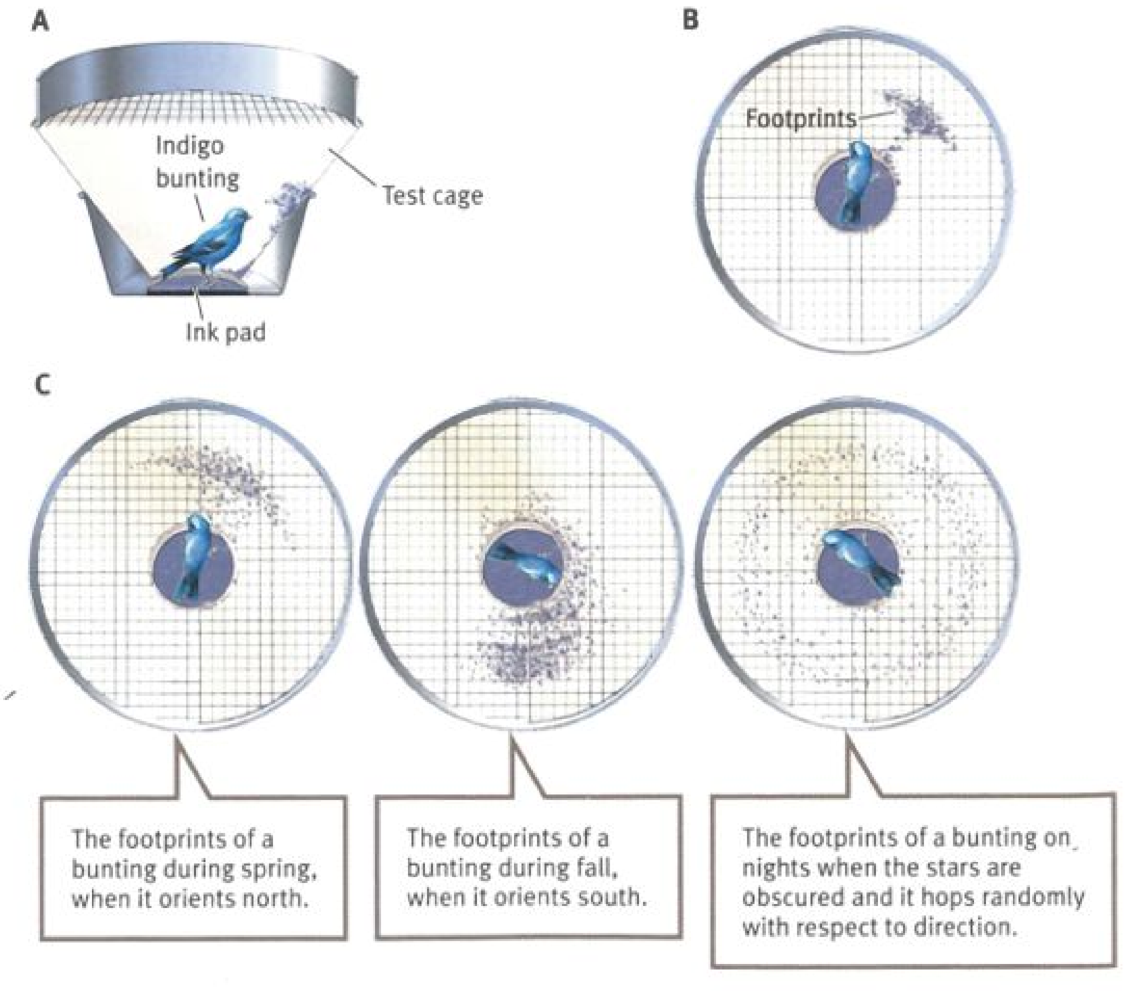


Figure 14.22. Migration and orientation. (A) A cross-sectional view and (B) a top view of the circular test cage used by Emlen in his orientation/migration work in indigo buntings. The funnel portion of the cage was made of white blotting paper, with an ink pad at the bottom. The entire apparatus was placed in an outdoor cage. The migration tendencies of the buntings were recorded as the bird tried to hop out of the funnel. (C) Each time the bunting hopped in one direction, it left black footprints on the blotting paper. *(Based on S. T. Emlen, 1975; reprinted by permission of Stephen T. Emlen)*

Emlen repeated his experiments inside a planetarium, where he could control what the birds saw in a simulated nighttime sky. Results were similar to those obtained in the field, but Emlen was now able to artificially shift the position of the North Star. In response to this manipulation, buntings shifted to the new south or new north (depending on the season).

The Earth's Magnetic Field and Animal Migration

The hypothesis that the earth's magnetic field might affect animal navigation and migration has been in the behavioral literature for more than a century, but the first experimental work on this idea was not undertaken until the late 1960s and early 1970s, when it was found that magnets placed on the backs of pigeons disoriented birds navigating across a fifteen- to thirty-mile route (Keeton, 1971; W. Wiltschko, 1968; R. Wiltschko and Wiltschko, 1995, 2003).

Evidence that the magnetic field of the earth is important in migration has now been found in a wide diversity of animals, including birds, amphibians, reptiles, and insects (Freake et al., 2006; Maeda et al., 2008; Wajnberg et al., 2010; R. Wiltschko and Wiltschko, 2006; Kishkinev and Chernetsov, 2014; Brothers and Lohmann, 2015; Putman, 2015; Shaw et al,. 2015). To see how magnetic fields can affect navigation and migration, let's examine the behavior of the bobolink (or rice bird; *Dolichonyx oryzivorus*), which has one of the longest round-trip annual migrations of any animal—12,400 miles. These birds spend the summer months in the northern United States and Canada and then migrate to South America (primarily Brazil, Paraguay, and Argentina) before they return to the Northern Hemisphere (Figure 14.23). Do they use the earth's magnetic field to help guide them on this incredible journey?

Figure 14.23. Magnetic fields and bobolinks. Research has examined whether bobolinks use the earth's magnetic field to help guide them on their annual migration, which involves a 12,400-mile round-trip. *(Photo credit: "Bobolink" by USFWSmidwest on flickr, licensed under CC BY 2.0)*

To answer that question, Robert Beason and Joan Nichols examined the direction to which the birds oriented at the time of their fall migration to South America (Beason and Nichols, 1984). They first brought birds into a planetarium and projected the star patterns that matched the autumn sky in the Northern Hemisphere. When the birds were given correct visual cues with respect to migration, they oriented south (toward South America). Beason and Nichols could also use equipment in the planetarium to manipulate the magnetic polarity that the birds experienced. When the visual cues and the magnetic polarity provided the same information—the northern sky was associated with magnetic north—the birds again oriented in the correct southern direction.

The most critical treatment in the Beason and Nichols experiment was the one in which the visual cues were correct, but the magnetic polarity was reversed: that is, the appropriate star pattern for autumn in the north was displayed, but the magnetic field was reversed so that the visual cues suggested south was in one direction and the magnetic cues indicated south was in the opposite direction. In this treatment, the birds headed toward the magnetic south, indicating that magnetic cues were critical in the annual round-trip migration.

How are the bobolinks able to sense changes in magnetic polarity? To find out, when their experiment was complete, Beason and Nichols autopsied the bobolinks, focusing on the head area of the birds. They found high levels of an iron-rich, magnetically sensitive substance, most likely magnetite, in the bobolinks. In particular, this magnetically sensitive substance was consistently found around the olfactory nerves and the bristles that project into the nasal cavity, as well as in the tissue between the nasal cavity and the eyes (Freake et al., 2006; Lohmann and Johnsen, 2000).

MIGRATION, TEMPERATURE, AND BASAL METABOLIC RATE

Long migrations require much energy on the part of migrants, and many animals increase foraging, leading to greater body fat levels, just prior to migration. In birds, metabolic rates differ between migrating and nonmigrating species. Walter Jetz and his team looked at published data on 135 species of migratory and nonmigratory birds. They found that after correcting for differences in body size, birds' basal metabolic rate (BMR)—defined as the minimum maintenance energy requirement of an endotherm—was significantly higher in migrating species (Jetz et al., 2008; Figure 14.24). Higher metabolic rates *might* help animals maintain the increased metabolic costs associated with large-scale migrations, but Jetz and his colleagues hypothesized that there were other possible explanations for this relationship between increased BMR and migration.

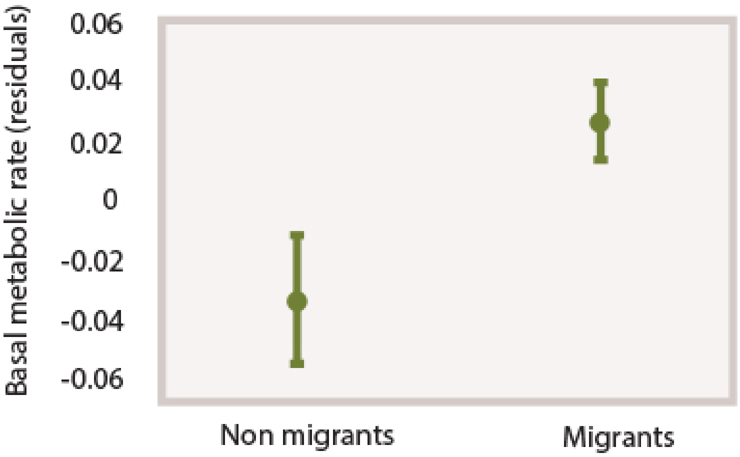


Figure 14.24. Basal metabolic rate and migration. Individuals in migrant species have higher basal metabolic rates than those in nonmigratory species. The *y*-axis takes into account differences in body size between migratory and nonmigratory species using "residuals" from statistical analysis. *(From Jetz et al., 2008)*

Species that live in colder environments tend to have high BMRs. And species that migrate tend to be found in colder environments than species that are sedentary. So the relation between BMR and migration could just be a by-product of the fact that migratory species tend to live in colder places (Kvist and Lindstrom, 2001; Lindstrom and Klaassen, 2003; Londono et al., 2015; McNab, 2016). To examine this possibility, Jetz and his colleagues used statistical analyses that could evaluate whether migratory behavior or habitat temperature better explained patterns of BMR. Their analysis found that BMR was more tightly correlated with environmental temperature than the tendency to migrate (Jetz et al., 2008). Natural selection favors both migration and higher BMR in bird species in cold environments, thus leading to a spurious correlation between these two variables.

MIGRATION AND DEFENSE AGAINST PARASITES

The energy expended during long migration can reduce immune responsiveness, making animals more susceptible to disease (Buehler et al., 2010; Hoffman-Goetz and Pedersen, 1994; Leffler, 1993). In addition, long-distance migrants also face new parasites and diseases upon arrival at their migratory end point. While nonmigratory birds must combat parasites in one environment, migratory birds face that challenge in two very different environments, combating a larger and more diverse array of potential parasites. Anders Møller and Johannes

Erritzøe hypothesized that migratory birds should therefore invest more heavily in immune function compared with related resident relatives (Møller and Erritzøe, 1998).

They tested their hypothesis by comparing the size of two immune defense organs—the spleen and a lymphoid organ called the bursa of Fabricus—in pairs of bird species. One member of each pair was from a migratory species, and the other pair member was from a closely related species that was nonmigratory. The researchers assumed that a larger size in either of these defense organs would provide better immunological resistance to parasites (John, 1994; Toivanen and Toivanen, 1987): in nine of ten pairwise comparisons, the bursa of Fabricus was larger in birds from the migratory species, while in nine of thirteen pairwise comparisons, the spleen was larger in birds from the migratory species.

Møller and Erritzøe note that differences in sexual selection pressure, mating systems, and the pattern of nest use and reuse are also known to affect investment in immune defenses (Møller and Erritzøe, 1996). As such, they reanalyzed their data, using only pairs of species that were known not to differ on any variable (besides migratory tendencies) that might affect the size of immune defense organs. While this comparison lowered their sample size to six pairwise comparisons for both the bursa of Fabricus and the spleen, their initial findings remained unchanged, suggesting selection on the immune system of migratory species.

A PHYLOGENETIC APPROACH TO MIGRATORY BEHAVIOR

Migratory behavior has been studied in a phylogenetic context (Outlaw and Voelker, 2006; Outlaw et al., 2003; Winger et al., 2012; Zink, 2002). Outlaw and Voelker examined migratory behavior in the family Motacillidae, which includes the pied wagtail (*Motacilla alba*), the golden pipit (*Tmetothylacus tenellus*), and the yellow-throated longclaw (*Macronyx croceus*; Figure 14.25). They set out to test what is known as the evolutionary precursor model of migration, which posits that migration will be associated with species that live in open or edge habitats (so-called nonbuffered areas) rather than species that live in forests (buffered areas; Chesser and Levey, 1998; Levey and Stiles, 1992). The underlying logic here is that open and edge habitats exhibit much greater seasonal variation in food resources than do forest habitats, and that this variation might select for migration in the birds that occupy such open and edge habitats.

Figure 14.25. Migratory behavior in Motacillidae birds. Migratory behavior has been studied in a phylogenetic context in the avian family Motacillidae, which includes such species as (A) the pied wagtail (*Motacilla alba*), (B) the golden pipit (*Tmetothylacus tenellus*), and (C) the yellow-throated longclaw (*Macronyx croceus*). *(Photo credits: © Paul Crabtree; © Markus Lilje; © Paul van Giersbergen)*

To test this model in a phylogenetic context, Outlaw and Voelker categorized the migratory behavior of forty-nine species in the Motacillidae family as either migratory or sedentary, and their habitat as either open/edge or forest. Using a published molecular genetic phylogeny of Motacillidae, they found that the evidence did not support the evolutionary precursor model—there was no association between migration and habitat in terms of open/edge versus forest. Species that were associated with open/edge habitats were no more likely to migrate than were species that lived in the forest.

Outlaw and Voelker's phylogenetic analysis also suggests that the ancestral state of migration in Motacillidae was "sedentary" and that the ancestral habitat was likely open/edge (Figure 14.26). Migratory behavior then evolved independently in many species in Motacillidae, but these species were just as likely to live in the forest as in open/edge habitats. Outlaw and Voelker's analysis did, however, find one ecological variable that was associated with migration. Species that lived at higher altitudes were much more likely to migrate than species that lived at lower altitudes. Overall, their analysis found numerous independent evolutionary transitions from sedentary to migratory and that these transitions were most likely in species that lived at high latitudes.

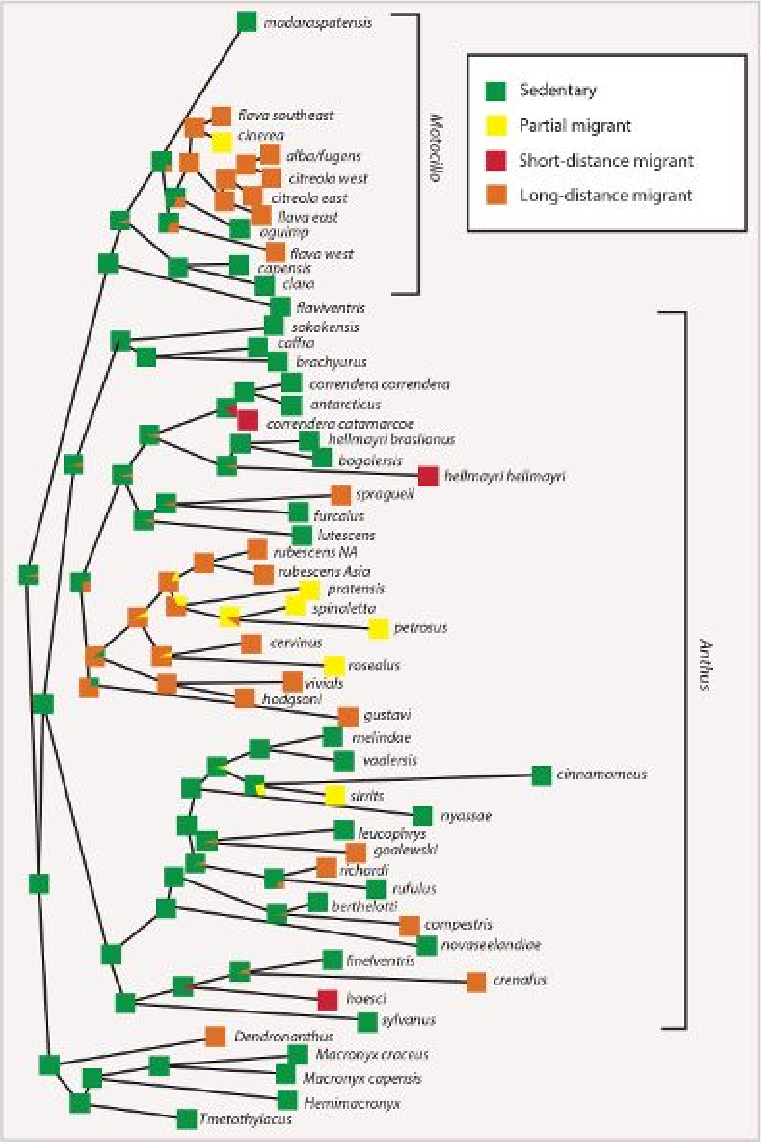


Figure 14.26. Phylogeny of migration. A reconstructed phylogeny of migratory behavior in Motacillidae birds. Shading at the terminal tips (where there are no branches coming off that taxon) indicates the state of the extant taxon. On other nodes, the portion of color in the square indicate the probabilities of ancestral states. The hypothesized primitive state is sedentary. Reprinted by permission of the American Ornithologists' Union. (*From Outlaw and Voelker, 2006*)

Interview with Dr. Judy Stamps

Of all the systems you could have chosen to study territoriality, how did you end up working with small lizards?

I originally began studying social behavior in lizards because of a comment made by my professor in an undergraduate animal behavior class. He suggested that lizards might be a good choice for studying stereotyped behavior patterns (displays) because many lizards use stereotyped behavior—head-bobbing patterns—to communicate with each other. So I began by studying the displays of male *Anolis* lizards in captivity. After several years of studying lizards in the laboratory, I became curious about their behavior under natural conditions and made a preliminary field trip to their native habitat, in the West Indies, to observe their behavior there. This first trip not only convinced me that these lizards were doing some pretty interesting things in nature but also that the place they were doing them (the West Indian island of Grenada) had obvious attractions of its own. So my first fieldwork focused on the social behavior of adult lizards in the West Indies.

While observing adults in the field, I noticed that tiny hatchlings exhibited many of the same behavior patterns as adults, including head-bob displays, chasing, fighting, and the defense of territories. In addition, since territory size typically scales with body size, hatchlings that weighed only 2 grams had commensurately small territories, on the order of only 0.5 square meter in size. As a result, it was possible to study an entire “neighborhood” of territories in a small area in the field and to manipulate structural features of habitats under natural conditions to determine the features that free-living juveniles preferred in their territories. After several months of playing around with juvenile lizards, it was obvious that they were much more amenable to both laboratory and field studies of territorial behavior than adults, and from that point on, I focused on the juveniles.

You’ve modeled territoriality in terms of learning. What spurred you to take on this approach?

Many hours spent observing juveniles in the field convinced me that I needed to consider the role of learning in territorial behavior. For instance, it was quite apparent that a juvenile who entered a neighborhood for the first time had no idea where any of the territory boundaries were, and that it only became aware of their locations as a result of being chased from one territory to the next by the residents. Similarly, two juveniles of similar size meeting for the first time engaged in an extended, strenuous fight, involving lengthy exchanges of a wide array of head-bob patterns, and culminating in physical combat, in which the two parties grabbed one another by the jaws, and then banged one another against the perch. It seemed that this “knock down, drag out” fight made a strong impression on both combatants, because when they encountered each other again the next morning, both seemed reluctant to venture near that opponent, and instead they began to exchange head-bob displays from adjacent perches, across an intervening “no-man’s-land” that eventually became the border between their two territories. Other observations indicated that if an individual was summarily attacked the first time it ventured into a novel area, it almost never returned to that area. In contrast, if an individual received a comparable attack in an area it had used for an extended period of time, its first response was to flee, but typically it returned to the area within an hour or so, and persisted in using its familiar area in the face of repeated attacks by its opponent. These and other observations suggested that salient experiences, both positive (a snooze on a familiar, comfortable perch with a full stomach) and negative (being attacked by an opponent), had important effects on the subsequent social and spatial behavior of these animals.

Inspection of the psychology literature revealed that scientists studying the effects of positive and aversive stimuli on space use had already described very general behavioral phenomena that could account for the behavior of these lizards. For instance, rodents who receive aversive stimuli (for example, electric shock) as soon as they first venture into an unfamiliar area are unlikely to return to that area, whereas comparable individuals who receive the same stimulus in an area in which they have previously been rewarded are much more likely to return to that area. Translated into territorial terms, these studies suggest that territorial animals may be behaving like little psychologists, delivering punishment to one another in an attempt to dissuade members of their own species from using a particular area.

Does being bigger usually mean you are guaranteed a good territory? If not, what else plays a role in territory acquisition?

In some situations, large body size can be helpful in acquiring a good territory, because if two individuals are competing for an area that is novel to both of them, and if one is larger than the other, the larger one is capable of delivering more punishment to its opponent during aggressive interactions than vice versa. However, size is not everything, because individuals who are already in possession of an area typically retain possession of that area, even when competing with larger opponents, a phenomenon called the “prior residency advantage.” The prior residency advantage may be attributable to the fact that a resident knows more about an area than does a newcomer, as a result of which the resident is likely to fight more vigorously for that area, and persistently return to that area even after losing one or more fights to a larger newcomer.

Regardless of the reason, the prior residency advantage means that animals can acquire space by being the first to settle in an area, rather than by being bigger than their opponents. This means that in many species, the ability to find newly vacant territories, and the ability to settle in them before anyone else finds them, plays an important role in territory acquisition. Thus, the prior residency advantage may explain why some birds establish territories weeks or months in advance of the time that the territory will be needed for reproduction: The early bird gets the territory.

Are there any general patterns in territoriality that emerge when you look across taxa?

There are a number of general patterns that occur in territorial species from a wide range of taxa. I have already mentioned the prior residency advantage, which occurs in virtually all territorial animals. Another generalization is that individuals in territorial species exhibit site tenacity, meaning that a given individual tends to remain in the same area for an extended period of time. Site tenacity is observed in all territorial species, but the reverse is not the case (for example, not all species with site tenacity defend areas in which they live). The basic elements of territorial behavior (stay in an area and use aggressive behavior to discourage other individuals from remaining in or returning to that area) are exhibited by a very large array of species, ranging from sea anemones to primates, but taxa with a long evolutionary history of territoriality typically add certain refinements to this basic pattern. For instance, territory owners in birds, mammals, frogs, lizards, and insects may produce songs, olfactory signals, conspicuous visual displays, or other conspicuous signals using other sensory modalities. These broadcast signals indicate to other inhabitants of the area that the territory is occupied, as well as providing additional information about the sex, condition, and (sometimes) identity of the territory owner. Territory owners in species with a long evolutionary history of territoriality are also likely to be able to recognize different categories of conspecifics, and tailor their aggressive behavior accordingly.

Dr. Judy Stamps is a professor emeritus at the University of California, Davis. Her long-term work on lizards and territoriality has led to new ideas on both territoriality and the role of learning in territory formation.

SUMMARY

1. Both biotic and abiotic factors affect habitat choice in animals. Abiotic factors include heat, availability of water, wind, refuges from danger, and the availability of specific nutrients, and biotic factors include the location of potential mates, food, predators, and parasites.
2. Territories provide exclusive access to food, mates, and protection from predators, and are defended from intruders. Defense can be costly, in terms of both time and energy.
3. The ideal free distribution model examines habitat choice as a function of resource distribution. This model predicts that the equilibrium distribution of individuals into patches (or habitats) should be that distribution at which, if any individual moved to a patch (or habitat) it was not in, it would suffer a reduced payoff.
4. Animals use the presence of cues about parasitization when judging the suitability of a habitat.
5. The proximate cues underlying memory and habitat choice and migration are being investigated by ethologists.
6. Animals can learn about territory quality through a process known as conspecific cueing, wherein they judge the suitability of a territory by whether it previously was occupied by an owner sometime in the past.
7. Ethologists studying migration focus not only on salient costs (for example, the energy needed for travel) and benefits (breeding in a warmer climate) of migration but also on more subtle factors such as the immunological costs of being a migrant and the various cues that migrants use to locate their breeding and nonbreeding grounds.
8. Phylogenetic studies of migration have tested the evolutionary precursor model of migration, which posits that migration will be associated with species that live in open or edge habitats rather than species that live in forests.

DISCUSSION QUESTIONS

1. Make a general list of the costs and benefits of territoriality. Using that list, determine what sort of environments would generally favor the formation of long-term territories.
2. The ideal free distribution model predicts that animals will distribute themselves among patches in proportion to resources. What sort of cognitive abilities, if any, does this assume on the part of animals? Would bacteria potentially distribute themselves in accordance with the predictions of IFD models? If so, how?
3. Suppose that young individuals watch older conspecifics choose their territories and subsequently use such information in their habitat-choice decisions about valuable resources. Outline one scenario by which such observational learning could increase competition for prime habitat sites, and one in which it would decrease competition for such sites.
4. Consider Møller and Erritzøe’s work on immune defense organs and migration behavior. Can you make any predictions regarding how a migrating species might fare against local parasites (in both its habitats) as compared to resident species? What is the logic underlying your hypothesis?

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15

Aggression

In this chapter we will examine how the outcome of aggressive contests can determine where individuals rank within a dominance hierarchy, and how that subsequently affects access to tangible resources such as food and mates. But the outcome of aggressive contests can, in principle, have even more broad-ranging effects.

Using the banded kokopu fish (*Galaxias fasciatus*) from New Zealand, Abbas Akbaripasand and his colleagues examined whether aggressive interactions affect not just access to tangible resources, but also habitat selection. These fish live in streams, within which there are many smaller pools. A single group of kokopus reside in a pool and, as a result of many one-on-one aggressive contests, a dominance hierarchy emerges within the group, with fish at the top of the hierarchy having preferential access to food in the pool. Akbaripasand hypothesized that this would result in slower growth rates for subordinate fish, and that, as a result, subordinates would sometimes opt to leave the pool they reside in and search for another pool (Akbaripasand et al., 2014).

The researchers found that the amount of food that a fish received, and its rank in a hierarchy, were indeed predictors of movement and, in particular, shifts to new pools. Subordinate individuals were more likely to move to new pools than dominant individuals, and such habitat shifts were likely in the best interests of subordinates. Although the average amount of food in pools that subordinates left and those they moved to was approximately equal, the growth rate was significantly higher in subordinate fish *after* such a move, likely because fish tend to move to pools with fewer competitors (Figure 15.1, Box 15.1).

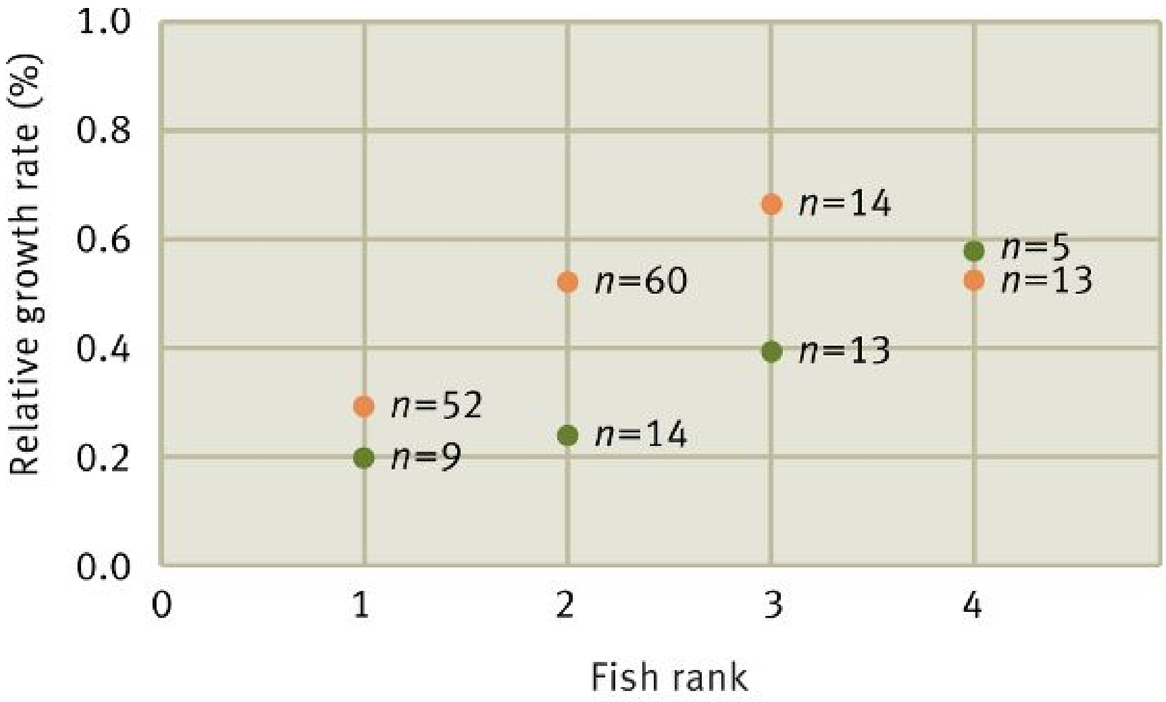


Figure 15.1. **The benefits to subordinates leaving.** On average, the relative growth rate of banded kokopus (*Galaxias fasciatus*) was greater after moving (orange circle) than it was before (green circle). *(From Akbaripasand et al., 2014)*

Box 15.1. SCIENCE AT WORK

What is the research question? How does aggression influence habitat choice?

Why is this an important question? One understudied effect of aggression may be to cause some animals to leave their current habitat in search of another.

What approach was taken to address the research question? Growth rate and rank in hierarchy were assessed in group-living banded kokopu fish (*Galaxias fasciatus*).

What was discovered? Subordinate fish had lower growth rates than more dominant fish, and were more likely to leave their group and move to another pool in their stream.

What do the results mean? Rank in a dominance hierarchy impacts behavioral decisions such as habitat choice.

* * *

Animals fight over obtaining food, securing space (territories, home ranges), providing safety for their family members, and many other things. The array of weapons that have evolved for use in fights is astonishing. From extinct Trilobite arthropods exquisitely preserved in the fossil record to modern arthropods, fish, mammals, and reptiles, ethologists and paleontologists have found an incredible array of physical body parts that are used as weapons (Figure 15.2). Most often these weapons are found on males, and they tend to be associated with the systems in which males can defend some resource that is spatially restricted. Weapons are often, but not always, honest indicators of male size and fighting ability (D. J. Emlen, 2008; chapter 7).

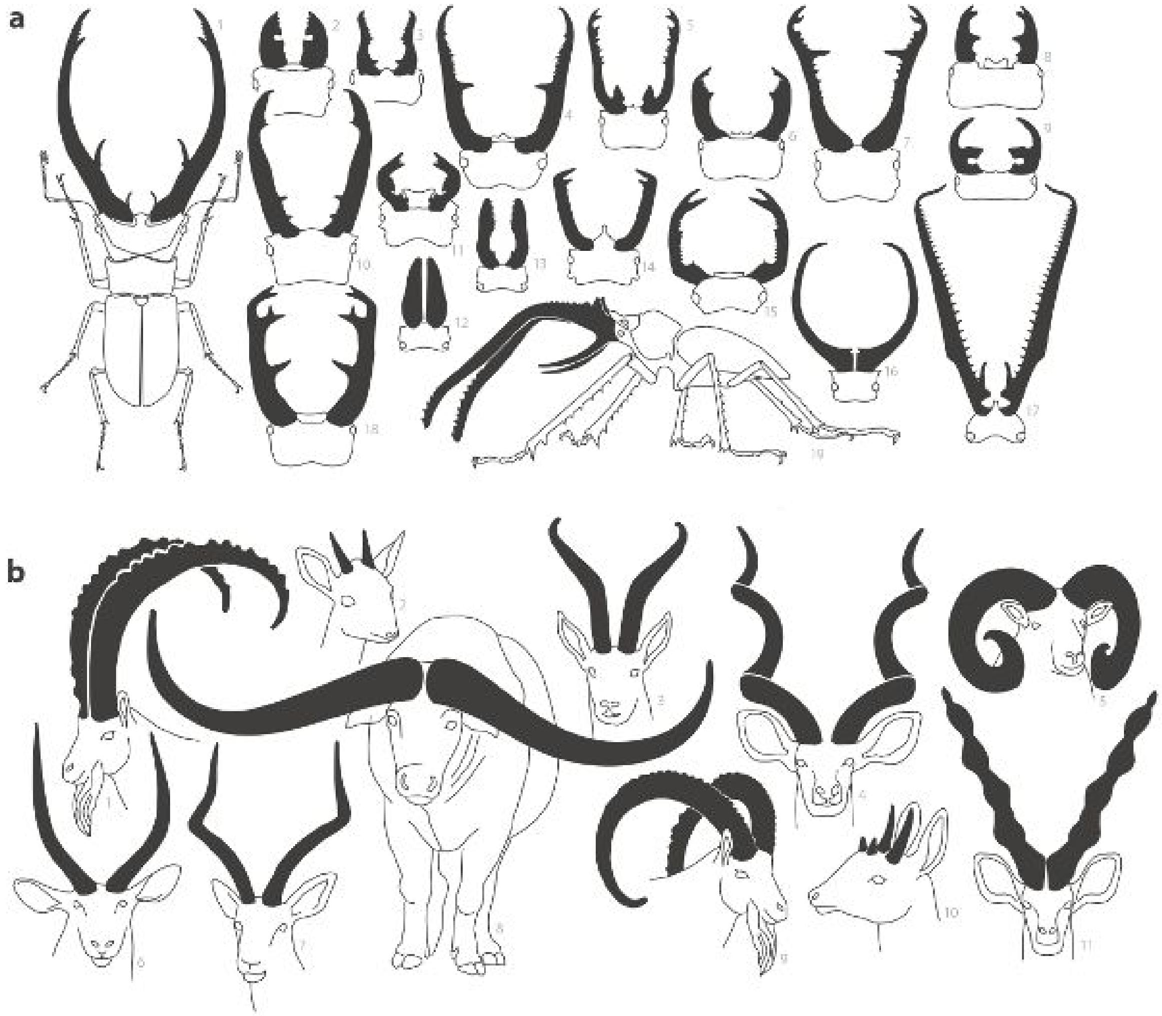


Figure 15.2. **Animal weapons.** An incredible array of weapons have been found in many groups, including (A) modern stag beetles: 1. *Cyclommatus elaphus*, 2. *Odontolabis latipennis*, 3. *Prosopocoilus serricornis*, 4. *Hexarthrius mandibularis*, 5. *P. bison*, 6. *Dorcus titanus*, 7. *Prosoposoilus giraffa*, 8. *D. alcides*, 9. *Aegus punctipennis*, 10. *Cyclommatus giraffa*, 11. *Mesotopus tarandus*, 12. *Colophon primosi*, 13. *Poecilus sericeus*, 14. *Weinreichius perroti*, 15. *Rhaetulus speciosus*, 16. *Sphaenognathus feisthameli*, 17. *Chiasognathus grantii*, 18. *O. femoralis*, 19. *Chiasognathus grantii* (side view); and (B) modern Bovids: from left to right. 1. Spanish ibex (*Capra pyrenaica*), 2. dik-dik (*Madoqua kirkii*), 3. Grant's gazelle (*Gazella granti*), 4. kudu (*Tragelaphus strepsiceros*), 5. bighorn sheep (*Ovis canadensis*), 6. waterbuck (*Kobus ellipsiprymnus*), 7. impala (*Aepyceros melampus*), 8. long-horned African buffalo (*Pelorovis antiquus**), 9. Asiatic ibex (*Capra ibex*), 10. chowsingha (*Tetracerus quadricornis*), 11. markhor (*Capra falconeri*). *Asterisks denote extinct species. © by and republished with permission of Annual Reviews, Inc. *(From Emlen, 2008)*

Aggression, also called agonistic behavior, occurs when animals either send threating signals (e.g., an animal flashes its canine teeth) and/or engage in some sort of physical combat. Most aggressive behavior studied by ethologists is conspecific aggression, though aggression between members of different species has also been investigated. Ethologists generally do not consider predator-prey interactions as aggression, though there is some debate on this matter. In this chapter, we examine conspecific aggression, focusing on major theoretical and empirical questions.

Aggression has been studied in relatively solitary species in which individuals fight when they occasionally interact at a territory boundary, as well as in species that live in social groups year-round. When aggression occurs in group-living species, and individuals interact with each other many times, we can measure **dominance hierarchies**—rank orderings of the individuals based on the results of pairwise aggressive interactions—in such groups. Where an individual places in a dominance hierarchy can be studied from both proximate and ultimate perspectives. Individuals at the top of hierarchies often have access to more food, more mating opportunities, and safer territories than individuals at the lower end of hierarchies (see chapter opening). At the proximate level, ethologists might study how levels of various hormones may differ between individuals that hold different ranks in a hierarchy.

Ethologists and naturalists have long been fascinated with animal aggression, and the literature in this area goes back to at least the time of Darwin (Archer, 1988; Drummond, 2006; Huntingford and Turner, 1987; Mock and Parker, 1997). Thomas Henry Huxley, one of the leading intellectual figures of the nineteenth century and Darwin's most vociferous defender, argued that interactions in the animal world resulted in a bloodbath. Huxley thought that aggression, often extreme aggression, was the norm for animals, and he made his claim in no uncertain terms:

> From the point of view of the moralist, the animal world is on about the same level as the gladiator's show. The creatures are fairly well treated, and set to fight; whereby the strongest, the swiftest and the cunningest live to fight another day. The spectator has no need to turn his thumb down, as no quarter is given . . . the weakest and the stupidest went to the wall, while the toughest and the shrewdest, those who were best fitted to cope with their circumstances, but not the best in any other way, survived. Life was a continuous free fight, and beyond the limited and temporary relations of the family, the Hobbesian war of each against all was the normal state of existence. (T. H. Huxley, 1888, p. 163)

In contrast, Peter Kropotkin in his book *Mutual Aid* describes a world that seemed almost antithetical to that of Huxley's:

> In all these scenes of animal life which crossed before my eyes, I saw mutual aid and mutual support carried on to an extent which made me suspect in it a feature of the greatest importance for the maintenance of life, the preservation of each species and its further evolution. (Kropotkin, 1902, p. 18)

To some extent and under certain circumstances, toned-down versions of both views capture aspects of animal behavior at different times and under different conditions. But rather than asking whether animals are being aggressive or cooperative, modern ethologists are interested in the costs and benefits that favor animals in a population fighting or not fighting with one another, or cooperating or not cooperating with each other. It is also important to note that cooperation and aggression are not the flip sides of a coin—individuals in groups often cooperate with each other in order to compete, often aggressively, with individuals in other groups (Dugatkin, 1997a; Gadagkar, 1997). In wasps, for example, while cooperation is common within hives, when individuals from other hives try to enter a nest, wasp guards often respond with vigorous and sometimes deadly defensive behaviors (Gamboa et al., 1986; Figure 15.3). And this is not unique to the social insects. In green woodhoopoe birds (*Phoeniculus purpureus*), individuals increase the amount of grooming they dispense to *others within their group* when they enter areas where conflicts with another group of woodhoopoes is likely. The amount of self-grooming, which is an indicator of stress, did not increase in these situations (Radford, 2003, 2008, 2011). Grooming others may solidify bonds within groups, leading to an increased probability of victory should between-group hostility increase.

Figure 15.3. **Intruder aggression.** When a wasp (left) approaches a nest, guards at the nest assess whether it’s a hive mate or an intruder. Intruders are aggressively repelled.

This chapter will focus on (1) proximate mechanisms of aggression; (2) models of aggression, including the hawk-dove game, the war of attrition model, and the sequential assessment model; and (3) the implications of experience, particularly social experience, on aggressive interactions and hierarchy formation, including the effects of winning and losing in one aggressive interaction on subsequent interactions, and the effects of observing or being observed on future aggressive interactions.

Fight or Flight?

In the “fight or flight” response (chapter 3), a surge in adrenaline and norepinephrine produces a quick increase in blood sugar, which, along with oxygen, is delivered to strategic areas such as the brain, skeletal muscles, and heart. Systems such as the digestive and reproductive systems are often temporarily shut down at this point. This response most often occurs when prey must decide to fight off a predator or flee. The same sort of response—albeit not as dramatic—occurs when animals encounter aggressive individuals from their own populations.

An individual can choose to fight or flee from a potentially antagonistic opponent.

We can think about the decision whether or not to fight against conspecifics at a number of different levels. From an ultimate perspective, this decision revolves around the costs and benefits of aggression. When the benefits of victory, on average, outweigh the costs of fighting, natural selection will favor aggressive behaviors, and ethologists predict that animals will fight; otherwise, they should not (see Box 15.2). From a proximate perspective, we ask questions about immediate causation and aggression. And, as in the case of responding to predators, when animals opt to fight or flee from others in their own population, ethologists often focus on the endocrinological underpinnings of such behavior and have found similar hormonal responses across different species. Dominant individuals typically display increased androgen levels—for example, increased testosterone—and are more likely to fight than flee. Likewise, winners of fights tend to have their circulating levels of androgens increase. Subordinates, who are more likely than dominants to flee than fight, usually lose aggressive interactions in which they are involved. Subordinates tend to have higher circulating levels of glucocorticoid stress hormones such as cortisol or corticosterone than dominants when going into fights, and even higher levels when a fight is over. But it is not always the case that subordinates and losers are the only individuals that display high levels of circulating stress hormones. For example, dominant individuals defending territories often must expend a large amount of energy fending off competitors, leading to high glucocorticoid levels. Similarly, high-ranking individuals in a hierarchy are often challenged by many subordinates in their group, and this too can lead to increases in glucocorticoid levels.

Box 15.2. CONSERVATION CONNECTION

Breeding Programs Can Lead to More Aggressive Animals

Reintroduction plans for endangered species sometimes include captive breeding programs in which animals are bred for many generations in a controlled environment. These breeding programs are common in fish, because it is relatively easy to maintain breeding populations of fish bound for reintroduction for many generations. The goal of many of these breeding programs is to both minimize inbreeding and to increase population size to a large enough number that endangered animals can be introduced back in their natural environments. But breeding programs themselves introduce new selection pressures on animals by radically changing the environment from one that animals would experience in the wild. The effects of these new selection pressures on traits like aggressive behavior are being investigated by both ethologists and conservation biologists.

Jennifer Kelley and her colleagues designed an experiment to examine whether breeding programs change the level of aggression in animals compared with that found in natural populations—and if so, how (Kelley et al., 2006). The researchers compared the aggressive behaviors seen in a natural population of the endangered butterfly splitfin fish (*Ameca splendens*) from El Rincon, Mexico, with the aggressive behaviors observed in a captive-bred population that is housed in the London Zoo (Figure 15.4).

Figure 15.4. **Captive breeding and increased aggression.** Butterfly splitfin fish have bred in captivity, and this breeding program has inadvertently produced more aggressive individuals. *(Photo credit: © Gunther Schleussner)*

Kelley and colleagues first observed the aggressive behavior of males to determine whether the general repertoire of aggressive behaviors was similar in the natural population and the captive-bred population they were studying. In general, these behaviors were similar, though some of the captive populations displayed territoriality that was not seen in natural populations. Kelley's team next compared the aggressive behavior of males from both populations in a more controlled environment. They exposed males from both the natural and captive-bred population to a structured tank environment containing gravel, aquatic plants, and small shelters or to an unstructured (bare) tank environment. In addition, the number of males in each tank was manipulated to create high-density and low-density treatments in both the structured and unstructured populations.

Captive-bred males showed much higher levels of aggression than males from the natural population. This increased aggression in captive-bred males was greatest when fish were in high-density populations in the structured environment: this is somewhat surprising, given that structured environments typically reduce, rather than increase, aggression (Naslund and Johnsson, 2016). Although the experimental protocol used could not disentangle genetic changes underlying increased aggression from the effect of experiences (being raised in either a natural or captive-bred population), it is likely that both play a role in the differences found (Ruzzante, 1994).

This work has implications for reintroduction programs in the butterfly splitfin fish and for reintroduction programs in general. In the case of the butterfly splitfin fish, because natural environments will be closer to the structured environment in Kelley and her colleagues' experiment, a reintroduction of captive-bred males into a natural environment could lead to high levels of aggression in the reintroduced population. The fact that butterfly splitfin males are aggressive toward one another does not necessarily mean that they would also be more aggressive toward fish in other species. But if they are, this increased aggression could restructure interspecific interactions.

In general, reintroduction programs based on captive population breeding need to take into account the way that captive breeding programs may inadvertently select for more aggressive animals, and they must consider the implications of introducing such individuals back into natural populations.

If fighting is costly, then once it is clear that an animal is losing a fight, it will often be beneficial for it to signal subordination and reduce future costs (Enquist and Leimar, 1990; Geist, 1974b; Hurd, 1997; Vitousek et al., 2014). That signal may inhibit its aggressive behaviors, refraining from charging, biting, or rapidly approaching the dominant animal. One means to communicate subordinate status is via color change. Color change may be a particularly good communication vehicle in aggressive contests, because color change can quickly indicate an individual's relative rank in a hierarchy and whether it will engage in aggressive behaviors (S. Rohwer, 1982; T. J. Roper, 1986).

Because fish have tight hormonal and neuronal control over the expansion of pigment cells, they are particularly adept at quick color change over short time periods and have been the subject of numerous experiments on color change and aggression (Baerends et al., 1986; D. M. Guthrie and Muntz, 1993; Rhodes and Schlupp, 2012; Skold et al., 2013). For example, researchers have studied color change in Atlantic salmon (*Salmo salar*), a species in which aggression is most often associated with territorial defense. During fights, males go through a sequence of behaviors, including circling, charging, and biting. Losers, who often have increased levels of cortisol, swim close to the surface to avoid future aggressive interactions with individuals that have defeated them. In terms of signaling relative status in a dominance hierarchy, dominant males develop dark vertical eye bands and subordinate individuals develop darker body color (Keenleyside and Yamamoto, 1962; Figure 15.5). In other species, such as the swordtail (*Xiphoporus helleri*), males display a red lateral stripe when dominant, but a black stripe when subordinate (Rhodes and Schulpp, 2012).

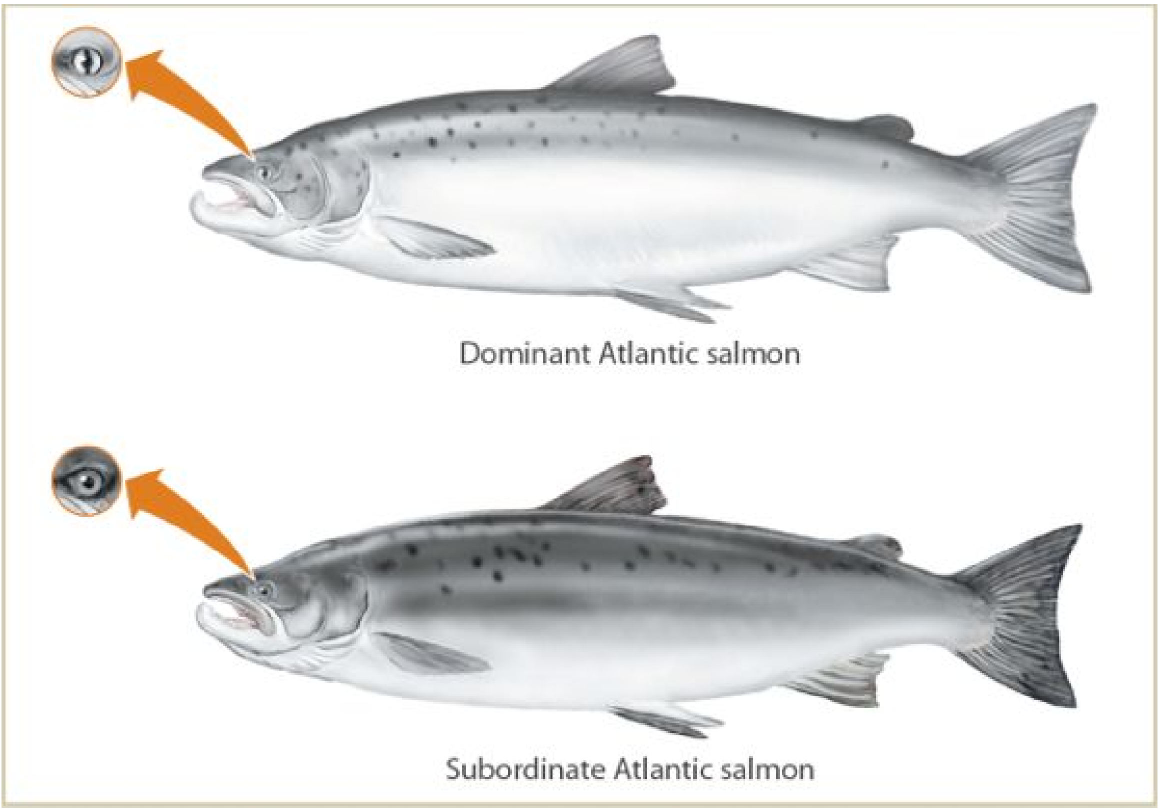


Figure 15.5. **Color as a signal.** In Atlantic salmon, subordinate individuals often assume a much darker body color. Dominants' body color remains light, but they develop dark vertical eye bands.

Two caveats are in order before we move to the next section. First, many hormones, not just androgens and glucocorticoids, affect decisions about whether or not to fight. Second, while androgens and glucocorticoids tend to play the same role in aggression and submission across many species, not all chemical messengers associated with aggression and submission have similar effects across species. As a case in point, let's briefly examine the role of the neurotransmitter serotonin in aggressive behavior.

How levels of serotonin (and its chemical precursors) affect aggression differs across taxa. In mammals, low serotonin levels are often linked with high levels of aggression but lower social status (Coccaro, 1992; Raleigh et al., 1991; Sheard, 1983). The situation can be complex, however, as the effect of serotonin (and its chemical precursors) may depend on whether animals were raised in social or asocial environments and on what specific type of aggressive behavior is being studied (Balaban et al., 1996; Raleigh and McGuire, 1991; Chichinadze et al., 2014). In fish, subordinate individuals have increased serotonin levels, leading to reduced fighting behavior (Clotfelter et al., 2007; Winberg et al., 1992, 1997; Winberg and Thornqvist, 2016). Yet a different picture emerges when we look at the relationship between serotonin, aggression, and social status in crustaceans (D. H. Edwards and Spitzer, 2006; Huber et al., 1997, 2011; Kravitz, 1988). In crustaceans, increased serotonergic function leads to enhanced aggression and high social status. When lobsters are paired up in fights, they generally escalate their aggressive behaviors through a series of ritualized combats (Huber and Kravitz, 1995). Once an individual loses a fight, however, it avoids aggressive interactions for days. But losers can be made more aggressive if they are given injections of serotonin (Huber et al., 1997; Figure 15.6). Furthermore, if fluoxetine (Prozac), an inhibitor of serotonin, is injected into the lobster at the same time as serotonin, this effect disappears, suggesting an important role for serotonin in lobster aggression.

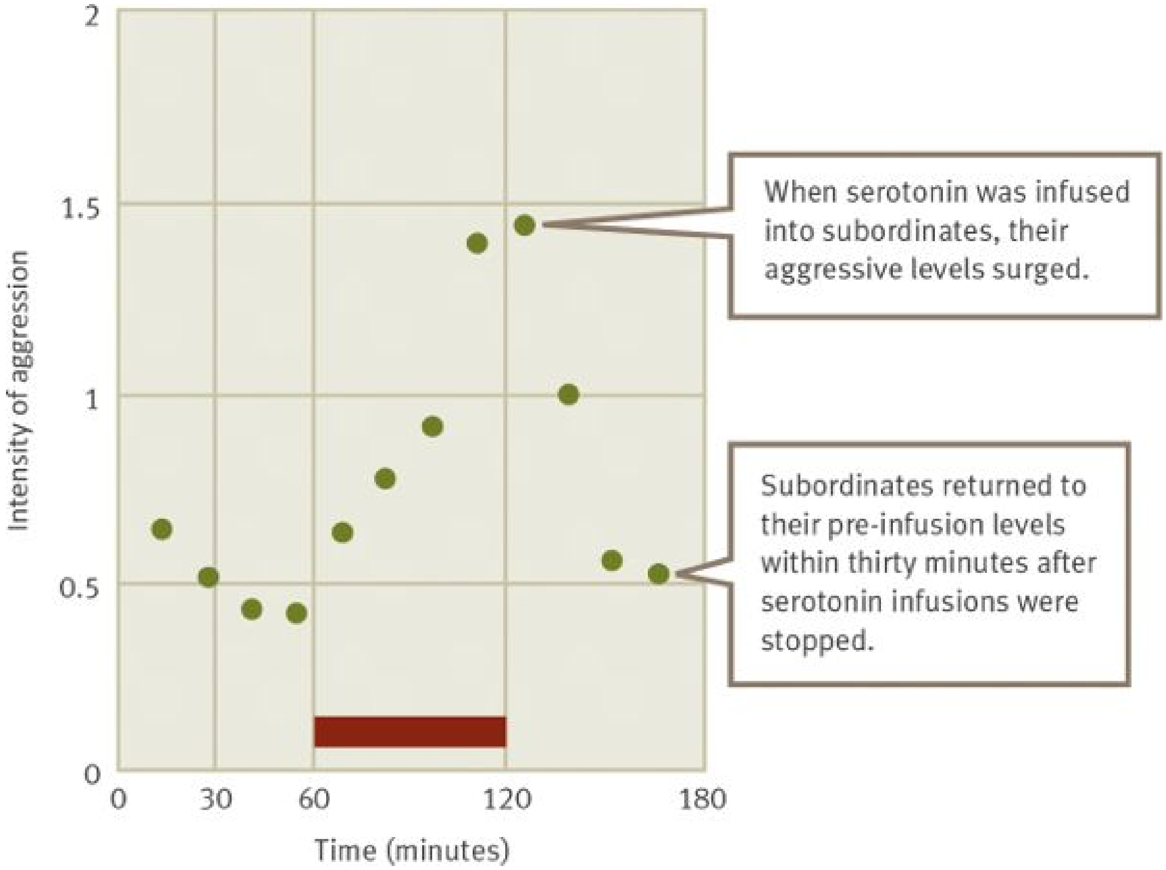


Figure 15.6. **Serotonin and aggression.** A small lobster was made subordinate by being matched against an individual that was 30 percent larger than it was, and then serotonin was continuously infused into subordinates (red bar). The intensity of the aggression over time is shown here. *(Based on Huber et al., 1997)*

While serotonin appears to play an important role in aggression across this wide spectrum—crustaceans, fish, and mammals—the neuroendocrinological effect of serotonin differs dramatically across these groups.

Game Theory Models of Aggression

As we learned in chapter 10, game theory models of social evolution are used when the fitness of an individual depends on both its own behavior and on the behavior of others. Evolutionary game theorists have built a suite of models that examine the evolution of fighting behavior (Riechert, 1998). We will focus on the three best-developed game theory models of aggression—the hawk-dove game, the war of attrition model, and the sequential assessment model. All three of these game theory models share certain characteristics. All assume a cost to fighting, though the cost can take many different forms, ranging from opportunity costs—the cost associated with not doing something else—to the cost of physical injury, up to and including mortality costs (Enquist and Leimar, 1990).

All game theory models also include a variable that represents the value of the resource being contested. In some cases, the value of a resource will be fairly easy to estimate. When two individuals, for example, are contesting an item of food, the value of the resource will be straightforward to calculate. In other cases, such as an individual's access to reproductively active members of the opposite sex, resource value can be much more difficult to calculate. The net value of a resource affects not only an animal's decision to fight but also how long and/or how hard it is willing to fight (Figure 15.7).

Figure 15.7. **Deciding to fight.** (A) One of the many resources animals will fight over is food, as shown here by these vultures that are fighting over a carcass. (B) Males also fight over females. Here, male elephant seals are fighting over access to reproductively active females. *(Photo credits: © Petra Christen / Shutterstock; Chuck Place / Alamy Stock Photo)*

Two individuals contesting a resource may not assign the same value to that resource. Imagine that two animals—one of which is starving, and the other of which is hungry, but not starving—are contesting a prey item that has just been discovered. A prey item may be *valued* differently by putative fighters. To a starving animal, it might make the difference between life and death, while to a less hungry animal the value might be much lower. In that case, the starving animal might fight harder for the food than its opponent does (Figure 15.8). As another example, consider the value of territory to a potential intruder and to a territory holder. Above and beyond the fact that the territory holder might be on a territory because it is a good fighter to begin with, it may well be that a territory holder will value its territory more than a challenger, because it has already invested time and energy in learning where the resources in such a territory are located (Kokko et al., 2006). These sorts of asymmetries in value have been documented many times in the ethological literature (Barnard and Brown, 1984; Elias et al., 2010; Ewald, 1985; Mohamad et al., 2010; Tibbetts, 2008; Verrell, 1986).

Figure 15.8. **Value estimation.** When two animals contest a resource, the hungrier animal may fight harder or longer to obtain it. If one of these cats is hungrier than the other, it may be willing to risk more to obtain the remains of the fish.

THE HAWK-DOVE GAME

The earliest game theory model of the evolution of aggression is Maynard Smith and Price's **hawk-dove game** (Maynard Smith, 1982; Maynard Smith and Price, 1973).

Imagine that individuals can adopt one of two behavioral strategies when contesting a resource: (1) hawk, in which a player escalates and continues to escalate until either it is injured or its opponent cedes the resource; or (2) dove, in which a player displays as if it will escalate, but retreats and cedes the resource if its opponent escalates (this strategy was originally labeled “mouse”).

If we let V = the value of the contested resource and C = the cost of fighting, we can fill in the potential payoff matrix for the hawk-dove game (Table 15.1). This matrix shows that if a hawk interacts with a dove, the hawk receives the entire value of the resource (V), while the dove receives nothing. We assume that if two doves encounter each other, on average, they receive half the value of the resource (for example, they split a food item in half). When two hawks interact and fight, we assume that only the loser pays the cost of fighting (for example, the cost of being injured). As such, each hawk has a 50 percent chance of obtaining the resource (V/2) and a 50 percent chance of being injured and not receiving the resource (C/2), with an expected payoff equal to (V − C)/2.

Table 15.1. The payoff matrix for the hawk-dove game. Both player 1 and player 2 choose between the hawk strategy (always be aggressive) and the dove strategy (bluff, but retreat if opponent escalates). V = value of resource, C = cost of fighting. Payoffs to player 1 are shown above the diagonal line, and payoffs to player 2 are shown below the diagonal line.

		Player 2	
		hawk	**dove**
Player 1	hawk	(V – C)/2	V
		(V – C)/2	O
	dove	O	V/2
		V	V/2

The evolutionarily stable strategy (ESS; see chapter 10) to this game depends on whether the value of the resource or the cost of fighting is greater. If V is greater than C, then hawk is an ESS, as the hawk-hawk payoff, $(V - C)/2$, is positive and thus greater than the payoff dove obtains when it meets hawk (0). Dove, however, is not an ESS, as the dove-dove payoff ($V/2$) is less than the payoff hawk obtains when it meets dove (V). When V is greater than C, hawk is the only ESS. This makes sense, since $V > C$ implies that the cost of fighting, paid only by hawks, is low compared with the prize that awaits the winner of any contest (V), and as a result, hawks do well. The situation is a bit more complicated when the cost of fighting is greater than the value of the resource. Now, neither hawk nor dove is an ESS: instead a mixture of hawks and doves may now be an evolutionarily stable strategy (see math in Box 15.3).

Box 15.3. MATH

The Hawk-Dove Game

Consider a hawk-dove game, where $C > V$.

If $C > V$, then hawk is not an ESS, as hawk's payoff against other hawks, $(V – C)/2$, is now negative, while dove's payoff against hawk is 0. Using the same calculations as we did for the case of $V > C$, we can see that dove is not an ESS either.

To see if some combination of hawks and doves is an ESS, let p = the frequency of hawks, and $1 – p$ be the frequency of doves. Hawk's payoff is then:

$$p(V - C)/2 + (1 - p)V, \qquad (1)$$

where the first term is hawk's payoff against other hawks and the second is hawk's payoff against dove.

Dove's payoff can be calculated as:

$$p(0) + (1 - p)V/2, \qquad (2)$$

where the first term is dove’s payoff against hawk and the second term is dove’s payoff against other doves.

When (1) = (2), the fitness of hawks is equal to the fitness of doves, and we then have our equilibrial frequency of hawks and doves. A little algebra shows that (1) = (2) when $p = V/C$.

There are more complicated varieties of the hawk-dove game than the one examined above (Mesterton-Gibbons and Adams, 1998; Riechert, 1998; Mesterton-Gibbons et al., 2014; Mesterton-Gibbons and Sherratt, 2014). One interesting version of this game adds in a new strategy called bourgeois. When using the bourgeois strategy, an individual plays hawk if it is a territory holder, but plays dove if it does not own a territory.

Bourgeois Butterflies

In the speckled wood butterfly (*Pararge aegeria*), territories are not fixed in space; rather than having a territory with a set place in three dimensions, a male has a territory that is an open patch delineated by well-lit areas that emerge when the sun breaks through the clouds. When a male comes upon an empty well-lit patch, he occupies it and by doing so secures a mating advantage compared with males not in sunlit territories.

When a male speckled wood butterfly comes upon a territory that has another male in it, a contest involving exaggerated spiral flights upward that sometimes include physical combat ensues and is settled as follows: resident wins, intruder retreats (Sherratt and Mesterton-Gibbons, 2015). In fact, there is very little aggression at all when males come upon occupied territories, perhaps because a prolonged fight over a short-lived resource, such as a sun patch, is not worth the costs. Rather, once a male is aware that a territory is occupied, he simply leaves (Figure 15.9). What makes the “resident wins” rule so dramatic is that an individual need only be the resident of a sun patch for a few seconds to secure victory over an intruder. In a study by Nick Davies, a male butterfly (M1) was experimentally made a territory owner (Davies, 1978). M1 then always defeated M2, an intruder male. But when M1 was removed from his territory and M2 then occupied it, even if M2 was resident for only a short time, M1 would now defer to M2 when he was reintroduced into his original sun patch. The only escalated contests occurred when two males both acted as if they were the owner of a sun patch (see Mesterton-Gibbons and Sherratt, 2016, for a theoretical approach to this case). This happens naturally when two butterflies come to a sun patch at about the same time but do not notice the other individual for some period (this can also be simulated experimentally). In such cases, fights can and do occur between the speckled wood butterfly males (see Kemp and Wiklund, 2004, for an alternative view).

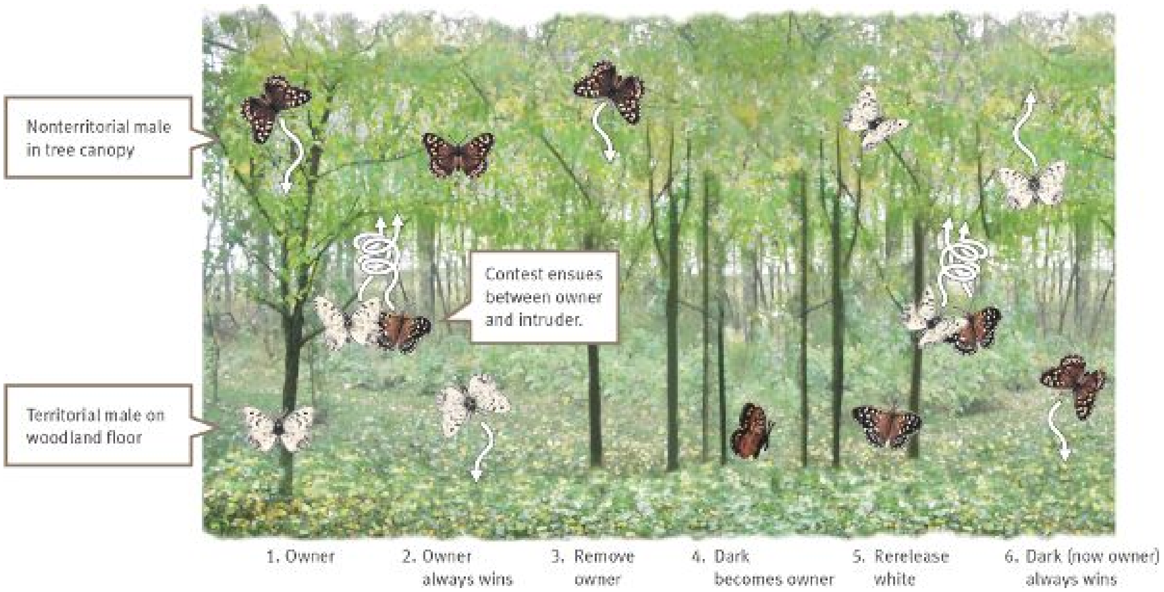


Figure 15.9. **Conventional rules.** Territory ownership and contest rules were investigated in the speckled wood butterfly (*Pararge aegeria*). *(Based on Dawkins and Krebs, 1978, p. 299)*

THE WAR OF ATTRITION MODEL

Some agonistic encounters are settled by displaying aggressively, but not actually fighting. To better understand what sorts of behavior natural selection might favor in such scenarios, theoreticians developed the **war of attrition model** (D. T. Bishop et al., 1978; Chatterjee et al., 2012; Hammerstein and Parker, 1982; Maynard Smith, 1974; Maynard Smith and Parker, 1976; G. A. Parker, 1974a; T. Uehara et al., 2007, Riechert, 2013; Helgesson and Wennberg, 2015).

The war of attrition model of fighting behavior makes a number of assumptions: (1) individuals can choose to display aggressively for any duration of time; (2) display behavior is costly—the longer the display, the more energy expended; and (3) there are no clear cues such as size, territory possession, and so forth that contestants can use to settle a contest (Riechert, 1998).

In the war of attribution game, let V = the value of the resource being contested, and define *x* as the length of a contest. The evolutionarily stable strategy to the game is not a single contest length, but a distribution of contest lengths. More technically, the probability that a contest lasts *x* units of time is equal to $(2/V)e^{-2x/v}$ (G. A. Parker and Thompson, 1980): rather than predicting a set time for aggressive display, the war of attrition model predicts that animals will choose randomly from a specific exponential distribution of contest lengths defined by the probability function $(2/V)e^{-2x/v}$. The model predicts that all contest lengths from this ESS function—any choice of display time from this function—lead to equal fitness gains to individuals.

This predicted distribution of contest lengths matches certain display durations in nature (Broom and Ruxton, 2003; Crowley et al., 1988; S. A. Field et al., 1998; G. A. Parker and Thompson, 1980; Stoewe et al., 2006). Recall the dungflies discussed in chapter 8. Females arrive at fresh dung patches to lay eggs, and males aggregate at such patches for access to females. There is intense male-male competition at such patches. The question, in terms of the war of attrition model, is how long should a male stay at a given patch? If he stays too long, he will encounter fewer and fewer females with time. If he leaves too quickly, he will pay the cost of moving and may miss the opportunity to mate with females at the patch he left.

Using detailed measurements of the costs and benefits of dungfly mating, Parker and Thompson found that males’ stay times—the time they remained at a patch—were exponentially distributed, as predicted from a war of attrition model (G. A. Parker and Thompson, 1980). When Parker calculated the mean time to find and move to a new patch from the dungfly fieldwork, he found that it was approximately four minutes (Curtsinger, 1986; G. A. Parker and Maynard Smith, 1987). When the travel time between patches is about four minutes, in accordance with the predictions of the war of attrition model, the stay times observed in the dungflies translate into approximately equal fitness for all males (Figure 15.10).

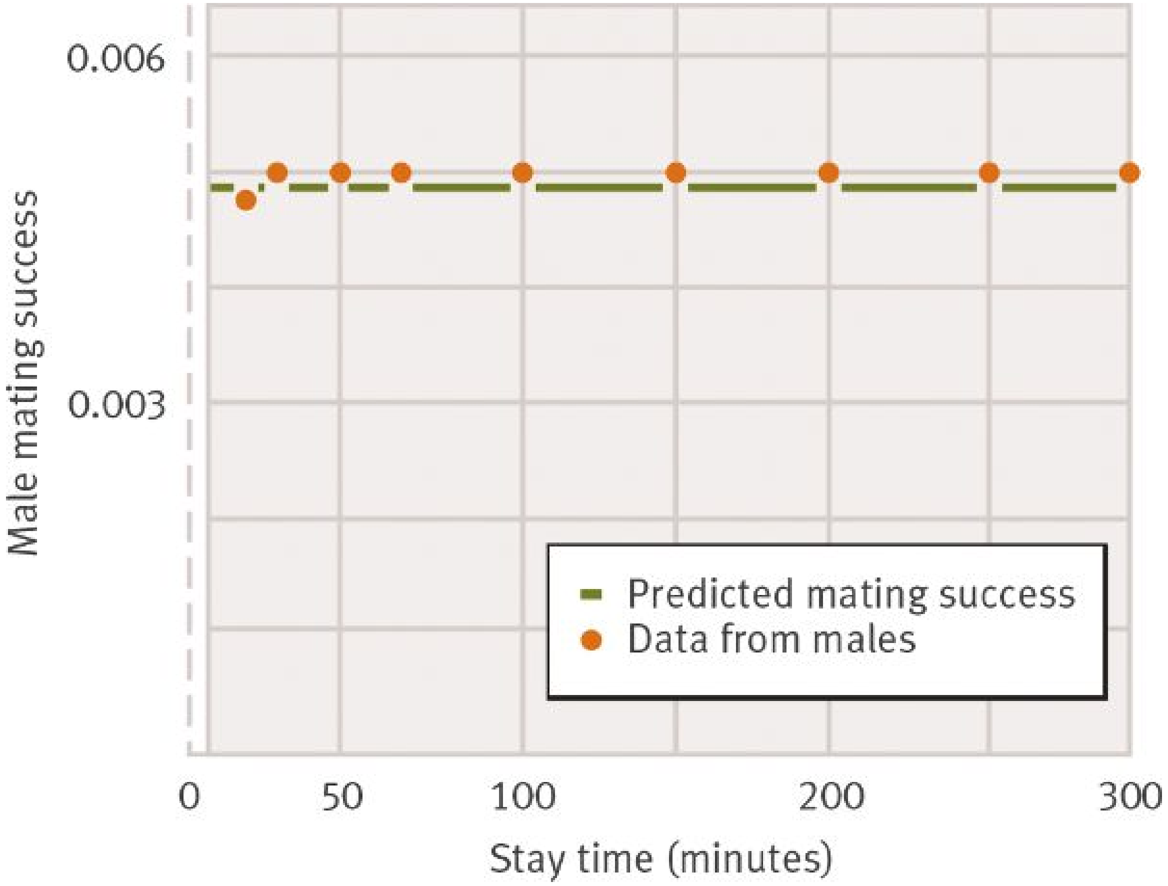


Figure 15.10. **War of attrition over females.** Male dungflies appear to engage in wars of attrition when determining how long to stay on a dung patch where females may alight. Assuming it takes four minutes to move from patch to patch, male mating success appears equal for a wide range of "stay times." *(From Maynard Smith, 1982, p. 31)*

THE SEQUENTIAL ASSESSMENT MODEL

A third game theory model of aggression, developed by Magnus Enquist and Olof Leimar, is called the **sequential assessment model** (Enquist and Leimar, 1983, 1987, 1990; Enquist et al., 1990; Leimar and Enquist, 1984). The sequential assessment game is designed to analyze fights in which individuals continually assess one another in a series of "bouts" (Arnott and Elwood, 2009; Hurd and Enquist, 2005).

In the sequential assessment model, individuals assess their opponent's fighting abilities. Assessing an opponent's fighting ability, Enquist and his colleagues argue, is analogous to a process of statistical sampling (Enquist et al., 1990). A single sample—for example, a single assessment of fighting ability—introduces significant random error. The more sampling (assessment), the lower the error rate, and hence the more confident an individual can be in whatever is being estimated—in our case, the opponent's fighting ability. After some period of sampling, one individual will eventually determine that its odds of winning a fight are so low that it should end any further aggressive interaction with its opponent.

The sequential assessment game examines contests in which the level of aggression varies from relatively mild to very dangerous. At the evolutionarily stable solution to the sequential assessment game, individuals should begin with the least dangerous type of aggressive behavior and sample (probe) each other with respect to that behavior for some period of time. Soon, however, all the information about an opponent with respect to that behavior will be exhausted. At that point, the next most dangerous behavior is predicted to be the most common behavior among protagonists. Again, at some point, information about an opponent and that behavior B will reach saturation; depending on the behavioral repertoire of the animals in question, more and more dangerous behaviors will be added to the sequence. Because gauging the probability of winning a fight is most difficult when fighting ability is similar to your opponent's fighting ability, the sequential assessment model predicts that the more evenly matched opponents should engage in the more dangerous behaviors.

Studies testing various predictions of the sequential assessment game have produced mixed results. Some studies find partial support of the model's basic predictions (Brick, 1999; DiMarco and Hanlon, 1997; Hack, 1997; Jennions and Backwell, 1996; Jensen and Yngvesson, 1998; Koops and Grant, 1993; McMann, 1993; Molina-Borja et al., 1998; I. C. Smith et al., 1994). Other studies support the majority of the basic predictions of the sequential assessment game (Leimar et al., 1991). One such study examined contest behavior in the fish *Nannacara anomala*.

Sequential Assessment in Nannacara Anomala

The predictions of the sequential assessment game have been tested in *N. anomala* (Figure 15.11). In this species, males form hierarchies, and aggressive interactions in males of this species range from changing color (least dangerous) and approaching through tail beating, biting and mouth wrestling, up to circling, which is the most dangerous of the aggressive activities, in which fish repeatedly attempt to bite each other while they swim in a circular pattern (Figure 15.12).

Figure 15.11. **Testing models of aggression in fish.** *Nannacara anomala* have a suite of aggressive behaviors they use during contests. *(Photo credit: Magnus Enquist)*

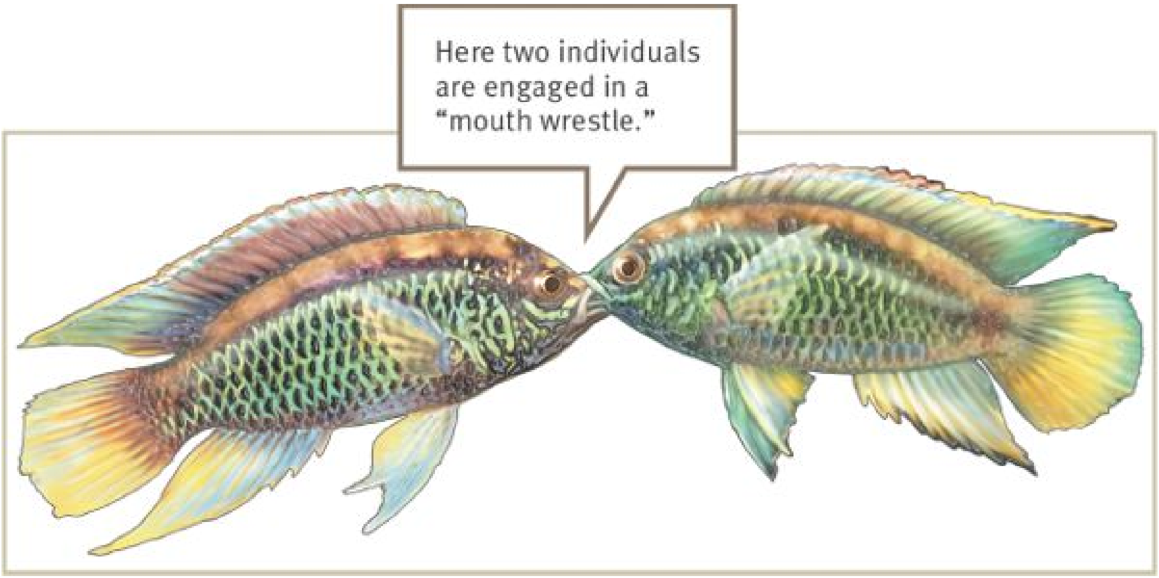


Figure 15.12. **Sequential assessment.** Much work on the sequential assessment model has been done studying escalated fighting behavior in *Nannacara anomala*.

Enquist and his collaborators staged pairwise interactions among male fish to test predictions of the sequential assessment game (Enquist et al., 1990). All trials were videotaped to allow a detailed analysis of subtle behavioral changes through time. Overall, interactions between aggressive males matched the predictions of the sequential assessment model well.

One of the most basic predictions of the sequential assessment model is that the more evenly matched the opponents are, the longer the fights and the more phases a fight should go through. In *N. anomala*, as in many fish, individuals are able to assess weight asymmetries (Enquist et al., 1987), and weight differences appear to have a very large effect on contest outcome—heavier fish are more likely to emerge victorious from a contest. In accordance with the predictions of the sequential assessment model, fights take longer when fish are more closely matched for weight than they do when large asymmetries exist.

The sequential assessment model also predicts that when numerous behaviors are used in aggressive contests, they should be used in approximately the same order across all fights. While some fights are predicted to last longer and contain more elements than others, the *order* in which new aggressive behaviors appear in a fight should be similar in all contests, and shorter contests should simply have fewer types of behavior. Again, the behavior of *N. anomala* matches the model's prediction. Males typically begin aggressive interactions with some sort of visual assessment, progress to tail beating, then to biting and mouth wrestling, and occasionally to circling. How many acts in this sequence are played out depends on differences in an opponent's weight, but the order in which these acts are displayed tends to be the same, regardless of weight differences (Box 15.4).

Box 15.4. SCIENCE AT WORK

What is the research question? Does the sequential assessment game predict bouts of aggression in *Nannacara anomala*?

Why is this an important question? Early models of aggressive behavior did not consider contests involving bouts where aggression escalates over time through the choice of progressively more dangerous aggressive behaviors.

What approach was taken to address the research question? A sequence of aggressive interactions was recorded in pairs of fighting *N. anomala* and the temporal pattern of aggression was compared to that predicted by the sequential assessment game.

What was discovered? The following predictions of the sequential assessment game were supported: 1) initial bouts should involve relatively less dangerous types and over time contestants should begin to employ more dangerous tactics, and 2) fights between equally matched fish took longer and involved more escalated forms of aggression.

What do the results mean? Game theory models of aggression can predict not just whether a fight will take place, but also the temporal sequence of aggressive interactions.

Winner, Loser, Bystander, and Audience Effects

Prior experience with an opponent can provide important information about potentially aggressive interactions in the future. If animal 1 has recently defeated animal 2, then animal 1 may decide to be more aggressive during its next interaction, and animal 2 may decide to be less aggressive. Indeed, experience with other individuals can be secondhand, but still important. Suppose that animal 3 has recently seen animal 2 lose a fight to animal 1. If animals 3 and 2 interact at some point in the future, animal 3 may be more aggressive after seeing animal 2 lose the contest with animal 1; observation, as well as direct interaction, provides information that may affect aggressive interactions. Ethologists have also found that *being* observed can affect the behavior displayed during, and the outcome of, aggressive interactions. Here we will examine the effect of direct and secondhand experience by focusing on what are referred to as winner effects, loser effects, bystander effects, and audience effects.

WINNER AND LOSER EFFECTS

In sports, individual athletes, as well as teams, go on winning streaks and losing streaks—winning itself sometimes leads to more winning, and losing to more losing. A similar phenomenon exists in nonhumans, wherein winning an aggressive interaction increases the probability of future wins (**winner effects**) and losing an aggressive interaction increases the probability of losing future fights (so-called **loser effects;** Landau, 1951a,b, Mesterton-Gibbons et al., 2016).

Winner and loser effects are defined as an increased probability of winning at time T, based on victories at times T − 1, T − 2, and so on, and an increased probability of losing at time T, based on losing at times T − 1, T − 2, and so on, respectively. Although loser effects are more common than winner effects, both have been documented in many species (Chase et al., 1994; Lindquist and Chase, 2009).

At the proximate level, loser effects are often associated with increased circulating levels of glucocorticoid stress hormones. Increased glucocorticoids are sometimes also seen in winners, but winners usually, though not always, return to baseline hormone levels much faster than losers. Losers tend to have low levels of testosterone, and winners tend to have high levels, but the precise effects of testosterone on winning are less understood (Hsu et al., 2005). To get a better understanding of the behavioral dynamics of winner and loser effects, as well as some of the proximate underpinnings of these effects, let us examine two case studies.

Winner and Loser Effects in Copperhead Snakes

The outcome of male-male aggression impacts male mating success in copperhead snakes. Gordon Schuett has studied the behavioral dynamics and endocrinological underpinnings of aggression in copperheads, focusing on winner and loser effects (*Agkistrodon contortrix*; Schuett, 1997; Schuett and Gillingham, 1989). The experimental protocol Schuett used had a trial arena that housed a female in the center and one male at each end. Two males who had not been involved in any aggressive interactions for six to twelve months prior to this study were pitted against each other, and in all pairs one male was approximately 10 percent larger. In all thirty-two trials, the larger male won the fight and gained access to a reproductively active female.

Ten winners and ten losers from these contests above were chosen, and each was matched against a same-sized male copperhead that had no prior experience. Schuett found that prior winners were not more likely to win again, nor were they more likely to win than their opponents that had no experience to obtain access to a female—no winner effects were uncovered. A loser effect, however, was found. Losers were more likely to lose again and to cede access to reproductively active females to other males. Schuett then examined how individuals that had now lost twice (in the initial “size contests” and then in loser effect treatments) fared against opponents that had no experience and that were about 10 percent smaller. Would the loser effect outweigh the positive size advantage that the losers possessed, or vice versa? Results pointed to the strength of the loser effect in copperheads—two-time losers lost all contests with smaller opponents (Figure 15.13).

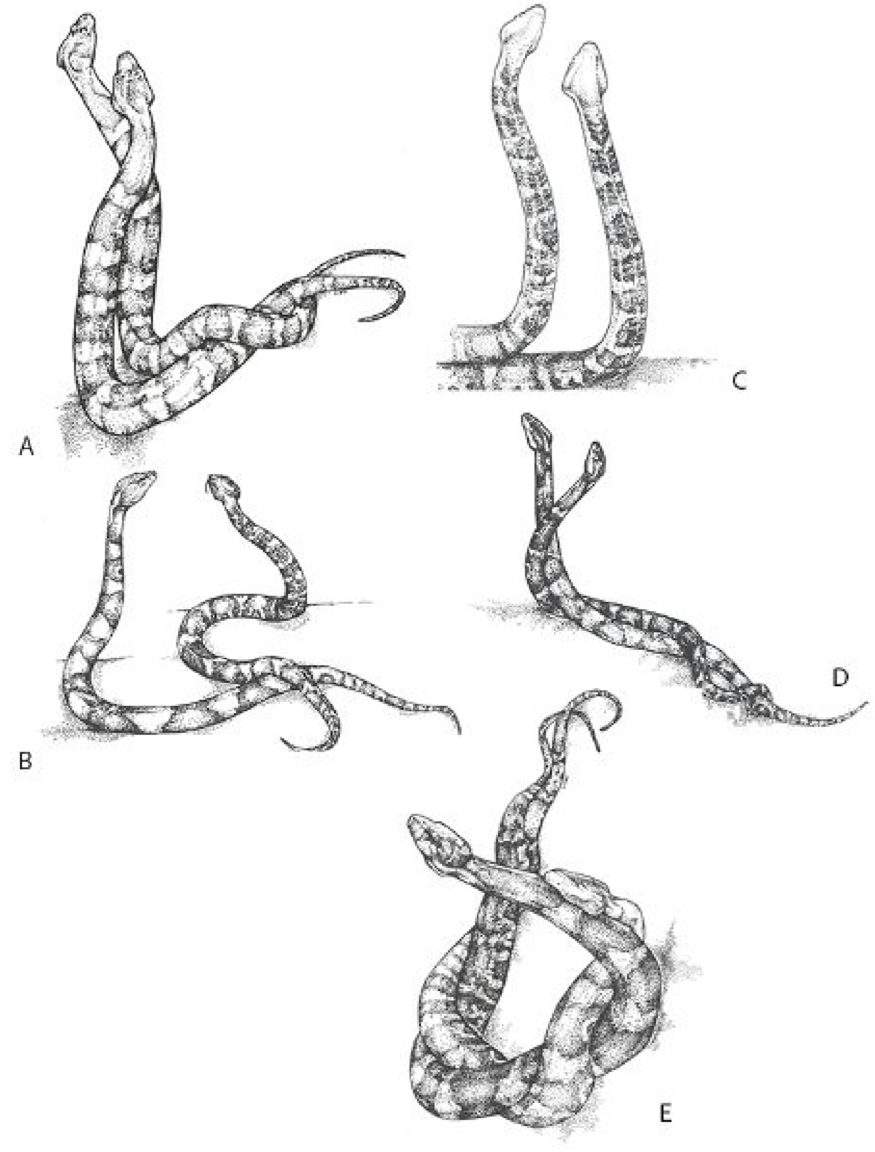


Figure 15.13. **Winner and loser snakes.** In copperhead snakes, losses can have a significant effect on future contest outcome. Snake fights in *Agkistrodon contortrix* include aggressive behaviors such as (A) ascend, (B) ventrad-to-ventrad sway, (C) ventrad-to-dorsad sway, (D) hook, and (E) stiffen. Reprinted by permission. *(Based on Schuett and Gillingham, 1989, p. 248)*

Schuett and his team also examined the hormonal correlates of the loser effect (Schuett et al., 1996; Schuett and Grober, 2000). They allowed pairs of males to fight when a female was present, and the snakes were kept together until one male was dominant to the other. At that point, the individuals were separated and a blood sample was collected for hormonal analysis. In addition to this treatment, two controls were run: In the first, a lone male in his home cage was used, and in the second, a single male and a female were placed in the arena. Plasma corticosterone levels were measured in winners, losers, and both classes of control males, and researchers found that plasma corticosterone was significantly greater in losers than in winners or controls (Figure 15.14).

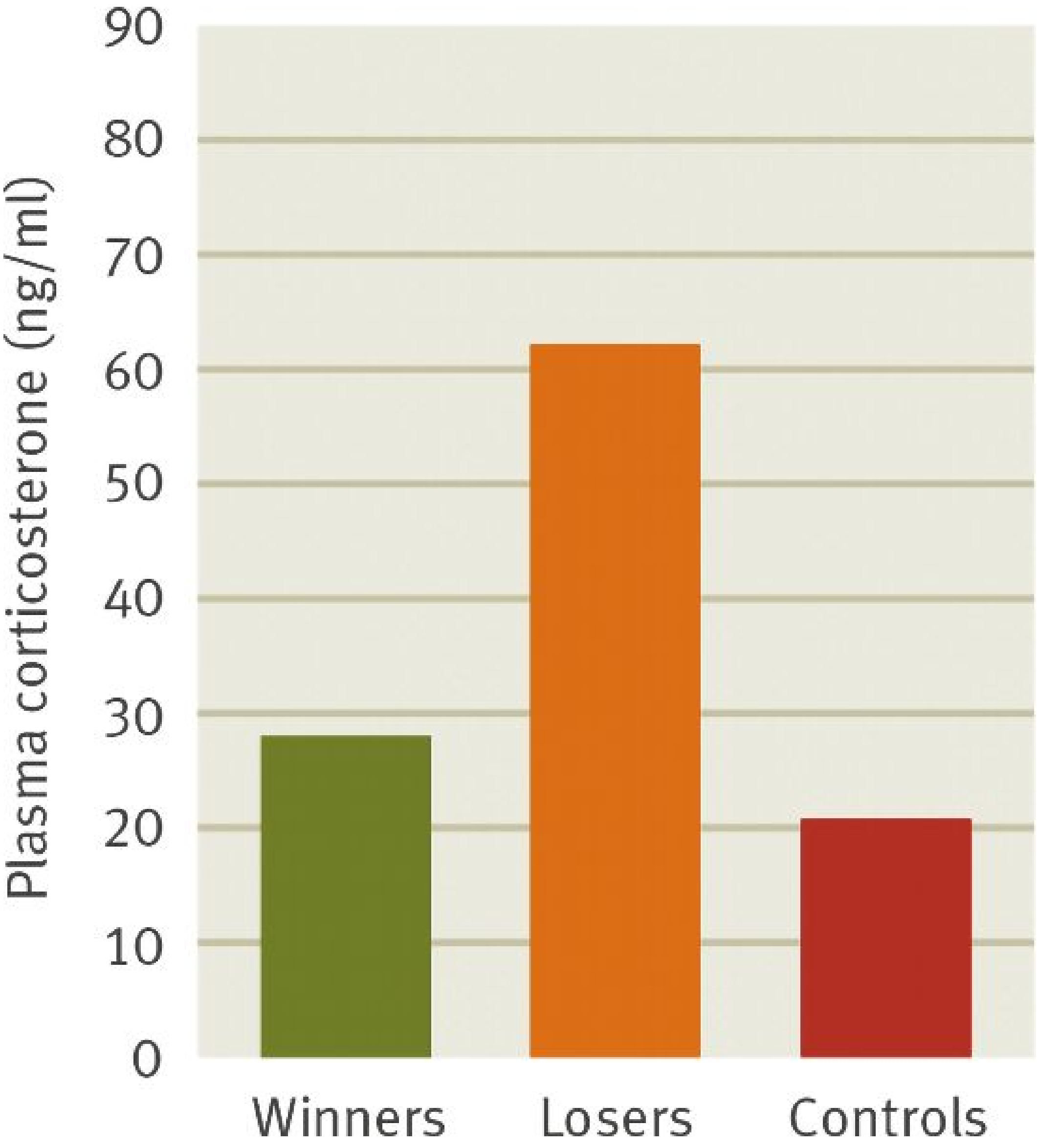


Figure 15.14. **Hormones, winning, and losing.** In copperhead snakes, losers show increased levels of plasma corticosterone compared with controls. No such change was found in winners. *(Based on Schuett et al., 1996)*

Increased levels of corticosterone produced dramatic effects in terms of both fighting and courtship behavior in male copperheads. Not only do males that lose fights, and consequently have raised corticosterone levels, act subordinate and rarely, if ever, challenge other males, but they almost never court any females that are in the vicinity of where they fought.

Winner and Loser Effects in Rivulus Marmoratus

Yuying Hsu and her colleagues have examined winner and loser effects in the fish *Rivulus marmoratus* (Hsu and Wolf, 1999, 2001; Hsu et al., 2009; Huang et al., 2011; Lan and Hsu, 2011). They looked not only at the effect of wins and losses on the next aggressive interaction in which an individual was involved but also at the effect of wins and losses that had occurred two moves back in time (penultimate wins and losses).

Hsu and her team subjected fish to a number of combinations of wins (W), losses (L), or neutral (N, no win, no loss) events. By comparing fish in the WW versus LW and the LL versus WL treatments, Hsu and Wolf were able to document the first experimental evidence that the penultimate (next-to-last) aggressive interaction a fish experiences also affects its current probability of winning or losing (Hsu and Wolf, 1999). For example, fish experiencing WW were significantly more likely to win a fight than fish experiencing LW. If the penultimate interaction had no effect on current aggressive interactions, one would expect no such difference across the WW versus LW treatments. Comparing numerous other treatments, Hsu and Wolf found that, while penultimate interactions were important, wins and losses two moves back in time had less of an effect on current outcome than wins and losses one move back in time.

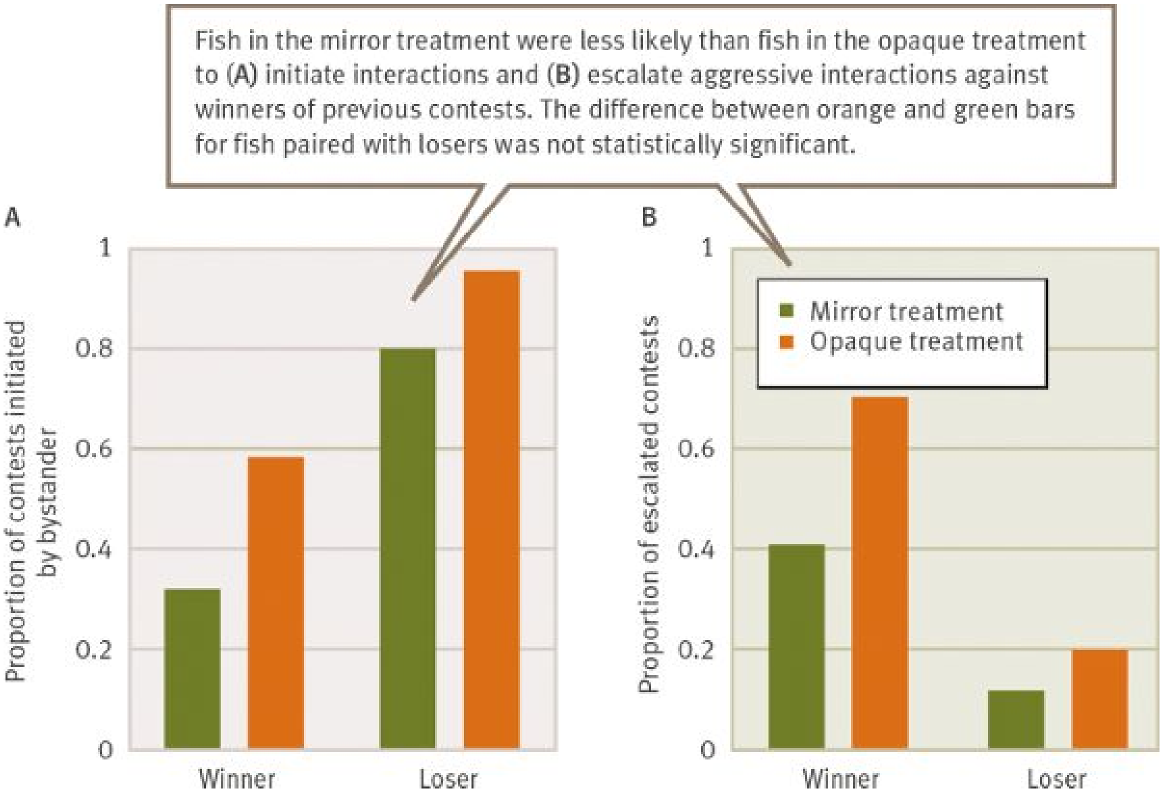
BYSTANDER EFFECTS

Bystander effects—sometimes called “eavesdropper effects”—occur when the observer of an aggressive interaction changes its assessment of the fighting abilities of those it has observed. Through observation, bystanders learn beforehand something about the opponents they may face in the future (Coultier et al., 1996; Johnsson and Akerman, 1998; Oliveira et al., 1998). A number of mathematical models have found that bystander effects can have important consequences on the dynamics of hierarchy formation (Chase, 1974, 1982, 1985; Dugatkin, 2001b; Earley, 2010). Experimental work has found bystander effects in birds, mammals, and fish (McGregor, 2005).

Bystander effects have been examined in the green swordtail fish (*Xiphophorus helleri*), a species in which males establish linear dominance hierarchies (Beaugrand and Zayan, 1985; Franck et al., 1998). In these experiments, eavesdroppers first observed aggressive interactions and were then paired with one of those they had observed. For example, Ryan Earley and I had eavesdroppers on one side of an experimental tank and a pair of swordtails that were involved in aggressive interactions on the other side. In one treatment, the eavesdropper could observe the pair of fish through a one-way mirror (mirror treatment), in which he could see the fish that were fighting but they could not see him and so would not be affected by the eavesdropper's presence. In the other treatment, the (potential) eavesdropper could not see the pair because of an opaque partition in the tank (opaque treatment; Earley and Dugatkin, 2002, 2005).

After this observation period, the eavesdropper was pitted against either the winner of the observed fight or the loser of the observed fight. The opaque partition treatment served as a control for winner and loser effects. Since the (potential) eavesdropper in the opaque partition treatment could not observe the interaction between pairs of individuals in the opaque partition treatment, the dynamics of the subsequent interaction between the eavesdropper and the winner, or between the eavesdropper and the loser, were the result of winner and loser effects, respectively. In contrast, both bystander effects and winner and loser effects could affect contests between the eavesdropper and winners and losers in the one-way mirror treatment. When comparing the dynamics of contests involving eavesdroppers in the opaque treatment (where only winner and loser effects are possible) and the one-way mirror treatment (where winner, loser, and bystander effects are possible), the contribution of bystander effects, if any, can measured.

Eavesdroppers who observed a contest in the one-way mirror treatment were much more likely to try to avoid the winner of that contest than were fish in the opaque treatment—eavesdropping per se affected future interactions with winners (Figure 15.15). In addition, eavesdroppers avoided observed winners regardless of how badly they had defeated their prior opponent.



Fish in the mirror treatment were less likely than fish in the opaque treatment to (A) initiate interactions and (B) escalate aggressive interactions against winners of previous contests. The difference between orange and green bars for fish paired with losers was not statistically significant.

Figure 15.15. **Eavesdroppers, winners, and losers.** In one condition, swordtail fish could observe aggressive interactions between a pair of other fish (one-way mirror treatment; green bars), but in the other condition, such interactions were blocked from view by an opaque partition (opaque treatment; orange bars). *(Based on Earley and Dugatkin, 2005, p. 90)*

In general, eavesdroppers responded in a similar way to all losers, regardless of whether they had witnessed the losers' defeat. But there is one piece of evidence that suggests that eavesdroppers behave differently with losers as a result of having observed them lose. In the one-way mirror treatment, eavesdroppers were less likely to initiate aggressive behavior and win against (1) losers that had persisted in their fights or (2) losers that had escalated their aggressive actions. This was not the case for the opaque treatment, suggesting the presence of subtle bystander effects when the eavesdroppers are interacting with losers (Box 15.5).

Box 15.5. SCIENCE AT WORK

What is the research question? Do swordtails who observe aggressive interactions between others change their own behavior when interacting with those they have observed?

Why is this an important question? Such bystander effects would indicate sophisticated and subtle behavioral strategies in observers.

What approach was taken to address the research question? A swordtail either could observe a pair of fish fighting or was placed behind an opaque partition and not permitted to observe fights. This fish was then paired with either the loser or the winner of the pairwise fight.

What was discovered? When allowed to observe fights, swordtails used the information they obtained when interacting with those they observed.

What do the results mean? Observers modified their behaviors differently when paired with those they had seen win versus lose a fight, suggesting that complex behavioral strategies are employed by these fish.

Ethologists have also studied the underlying proximate mechanisms associated with bystander effects. In the cichlid fish *Oreochromis mossambicus*, when eavesdropping males watch a fight between a pair of other males, their androgen levels rise (Figure 15.16). When Rui Oliveira and his team measured the levels of testosterone in the urine of eavesdroppers before they saw a fight and after they observed a fight, they found a significant increase in testosterone levels (Oliveira et al., 1998, 2001, 2002, 2005). This increase in testosterone may better prepare the eavesdropper for future aggressive interactions by indirectly affecting attention, learning, and memory in ways that might prove beneficial to observers. For example, the increase in testosterone may be beneficial for the eavesdropper if the winner of the observed fight subsequently attacks others, including the eavesdropper, in the immediate vicinity.

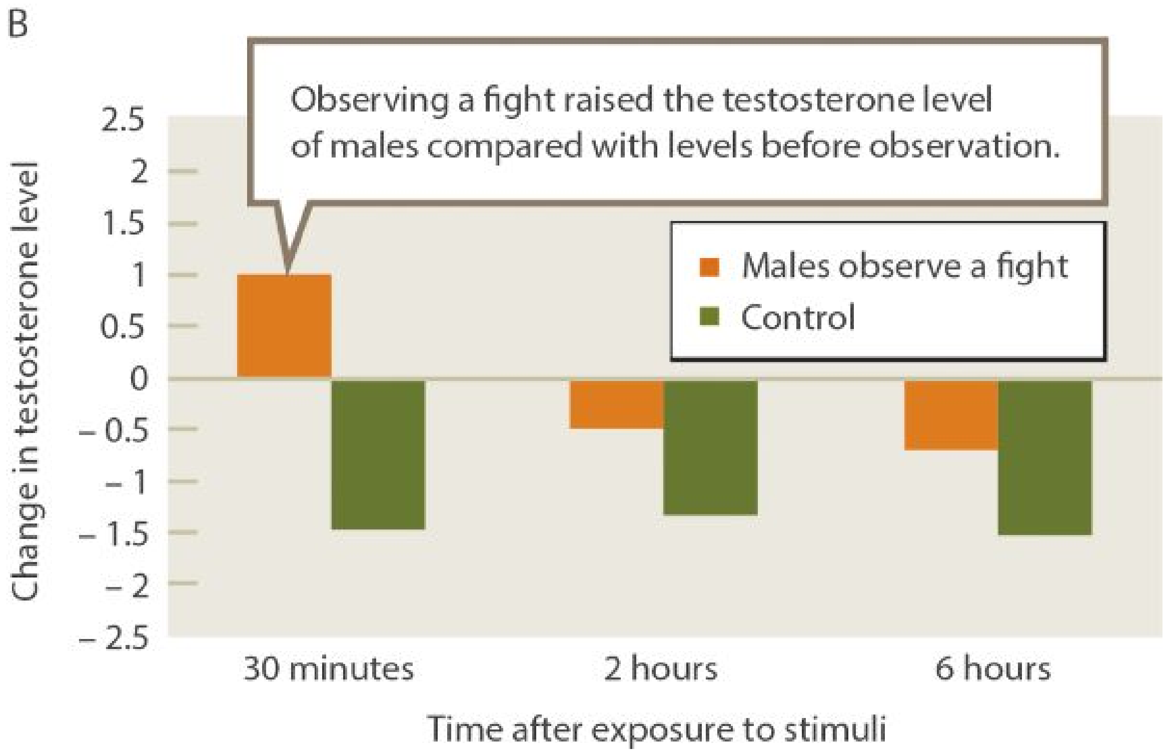


Figure 15.16. **Eavesdropping and testosterone.** The level of testosterone increases after eavesdropping on a fight in *Oreochromis mossambicus*. Orange bars show the difference in testosterone in experimental males before versus after observing a fight between two other males. A spike in testosterone occurs and lasts at least thirty minutes. The decrease in testosterone in control males is likely due to the normal daily decrease in testosterone from late morning (when experiment was undertaken) to evening (six hours later). *(From Oliveira et al., 2001)*

AUDIENCE EFFECTS

Not only do bystanders change their estimation of the fighting ability of those they observe, but individuals involved in aggressive interactions change their behavior if they are watched. The latter is referred to as the **audience effect**, and it has been studied in a number of species (Doutrelant et al., 2001; Dziewerzynski et al., 2012; Evans and Marler, 1994; McGregor and Peake, 2000; Overduin-De Vries et al., 2012; Plath et al., 2009; Zaccaronia et al., 2013; Cruz and Oliveira, 2015; Lappan and Morino, 2014; Hedwig et al., 2015; Seagraves et al., 2016). Here we will examine audience effects found in the context of aggression and “recruitment screams” in chimpanzees.

Wild chimpanzees emit screams during pairwise aggressive interactions. The screams of those winning a fight are very different from those losing a fight, and researchers have studied “aggressor screams” vs. “victim screams” (Slocombe and Zuberbuhler, 2005). Victim screams may, in part, function to entice support from observers—for example, a scream by a victim may entice an observer to intercede and break up the fight. Kate Slocombe and Klaus Zuberbuhler examined this possibility in a population of wild chimpanzees in the Budongo Forest of Uganda (Slocombe and Zuberbuhler, 2007; Fedurek et al., 2015).

Slocombe and Zuberbuhler began their work by categorizing pairwise aggressive interactions between chimps as either mildly or severely aggressive. From their observations, they were able to gather data on eighty-four screaming bouts, and they found evidence suggesting a cognitively complex form of audience effects (Snowdon, 2009). When they compared the screams of victims in mildly aggressive interactions, no differences were found when an audience was present or absent. When interactions involved severe aggression, however, victim screams were sometimes much longer and more intense when there was an audience present (compared with when there was no audience). But this audience effect was seen only when at least one of the audience members held a rank in the hierarchy that was equal to or above the rank of the aggressor (Figure 15.17). This screaming strategy was successful, as victims that emitted longer and more intense screams were often able to entice support from high-ranking observers that often intervened and broke up fights.

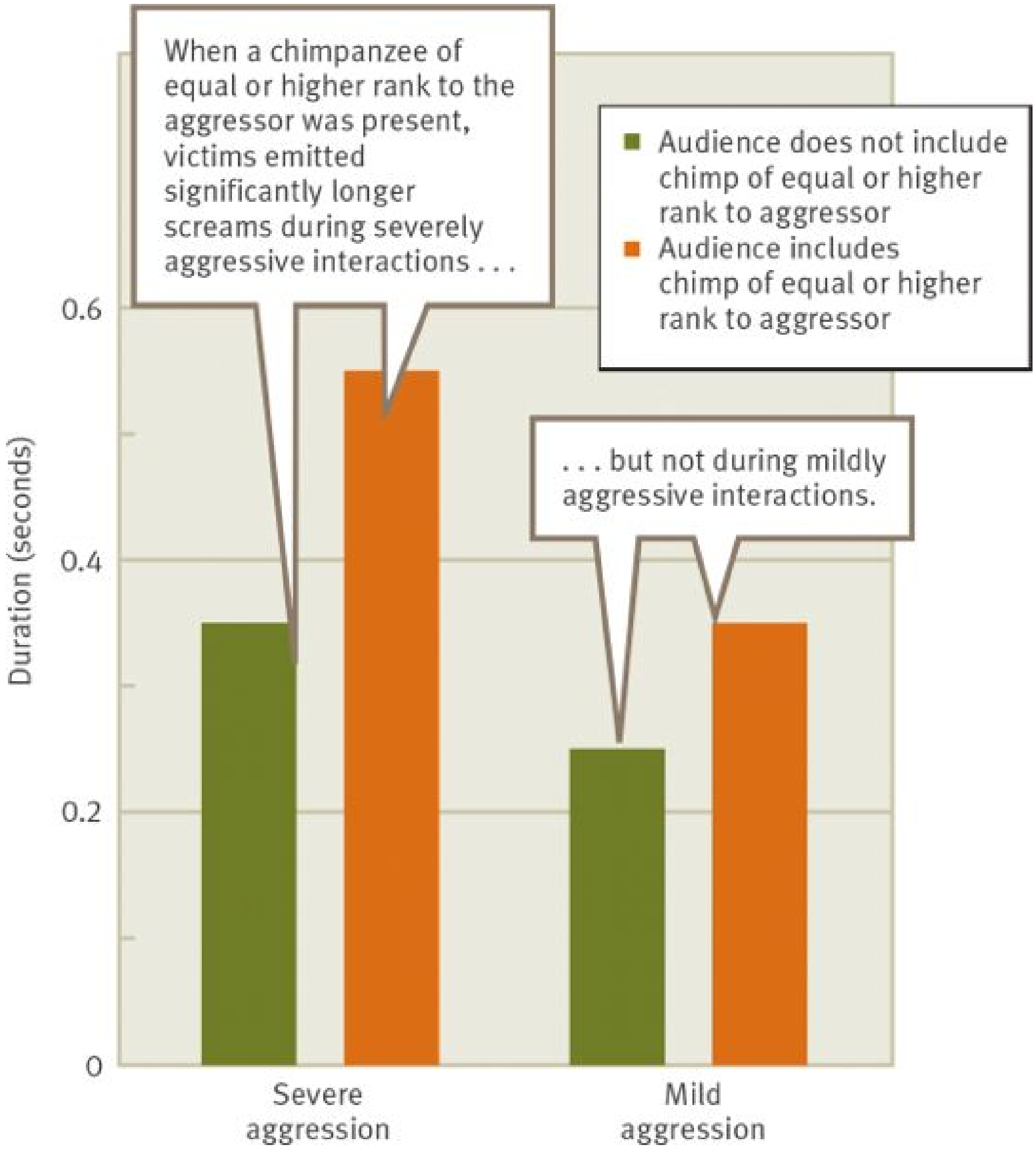


Figure 15.17. **Audience effects in chimpanzees.** Chimpanzees that were victims in severe aggressive interactions emitted distinctive screams. Significantly longer screams were emitted when fights were watched by an audience that included a chimp of equal or higher rank to the aggressor (orange bars) than when the audience did not contain such an individual (green bars). No significant difference was found when victims were involved in mildly aggressive interactions. *(Based on Slocombe and Zuberbuhler, 2007)*

Aggression and Social Network Theory

Taken together, the work on winner, loser, bystander, and audience effects suggests that group-living animals are embedded in complex **social networks**, within which information flows between individuals. Recently animal behaviorists have begun using social network analysis (SNA) that incorporates visualization techniques, descriptive measures, modeling, and simulations to examine the dynamics of social networks (Dugatkin and Hasenjager, 2015; Hasenjager and Dugatkin, 2015).

As an example of how social network theory can inform aggression, consider the policing behavior seen in troops of pig-tailed macaques (*Macaca nemestrina*). Policing involves a small number of males in a group, on occasion, breaking up fights that occur between others. Jessica Flack and her colleagues ran a "behavioral knockout" experiment in which they removed policing individuals from a group to examine the effects of such removals. Using many of the mathematical tools underlying social network analysis, Flack et al. (2006) found that when policing males were removed, aggressive behaviors became more common and affiliative behaviors less so (Flack et al., 2005). But social network analysis also uncovered other complex, more subtle effects: those remaining after policers were removed had fewer play partners and fewer grooming partners. What's more, the "reach"—a technical term that measures how quickly information can flow within a group—of the remaining monkeys decreased with respect to both play and grooming behavior, reducing the spread of pro-social behaviors. Rather than a single group in which macaques interacted with most other individuals, removal of the policers led to the formation of smaller subgroups, whose members interacted primarily with one another.

Box 15.6. COGNITIVE CONNECTION

Aggression, Observation, and Gene Expression

In the cognition box in chapter 7, we examined how gene expression in *c-fos* and *egr-1* genes in the brains of female *Astatotilapia burtoni* fish were affected by watching males compete with each other. Here we look at two related issues: whether gene expression in these same genes change in *male Astatotilapia burtoni* who 1) are engaged in an aggressive interaction that is being watched by another male and/or 2) are watching an aggressive interaction between other males.

Julie Desjardins and her colleagues set up an experiment in which a pair of males engaged in aggressive interactions, while a third male watched this contest (Desjardins et al., 2015). They experimentally manipulated the size of the two contestants relative to each other, and relative to the observer. In a control condition, pairs of males fought, but no other fish observed the contest. After contests were complete, *c-fos* and *egr-1* gene expression levels in many different areas of the brain were measured in contestants and observers.

Males fought more intensely when watched by another male than when they were not being watched (Figure 15.18). The results with respect to *c-fos* and *egr-1* gene expression were complex, but in general, what Desjardins and her team found was that *c-fos* and *egr-1* gene expression patterns changed in similar ways in both observers and contestants who were being watched, but not in contestants who were not being watched. Watching or being watched during aggressive interactions has a similar effect on *c-fos* and *egr-1* gene expression in the brains of male fish, suggesting that aggression likely triggers similar gene expression pathways regardless of what role a fish plays in aggressive contests (fighter or observer). The researchers also found evidence that this pathway is likely linked to anxiety and stress, because when observers were larger than the fighters, changes in *c-fos* and *egr-1* gene expression in fighting males were especially pronounced in the brain areas that were homologous to areas in the mammalian brain known to be associated with stress responses.

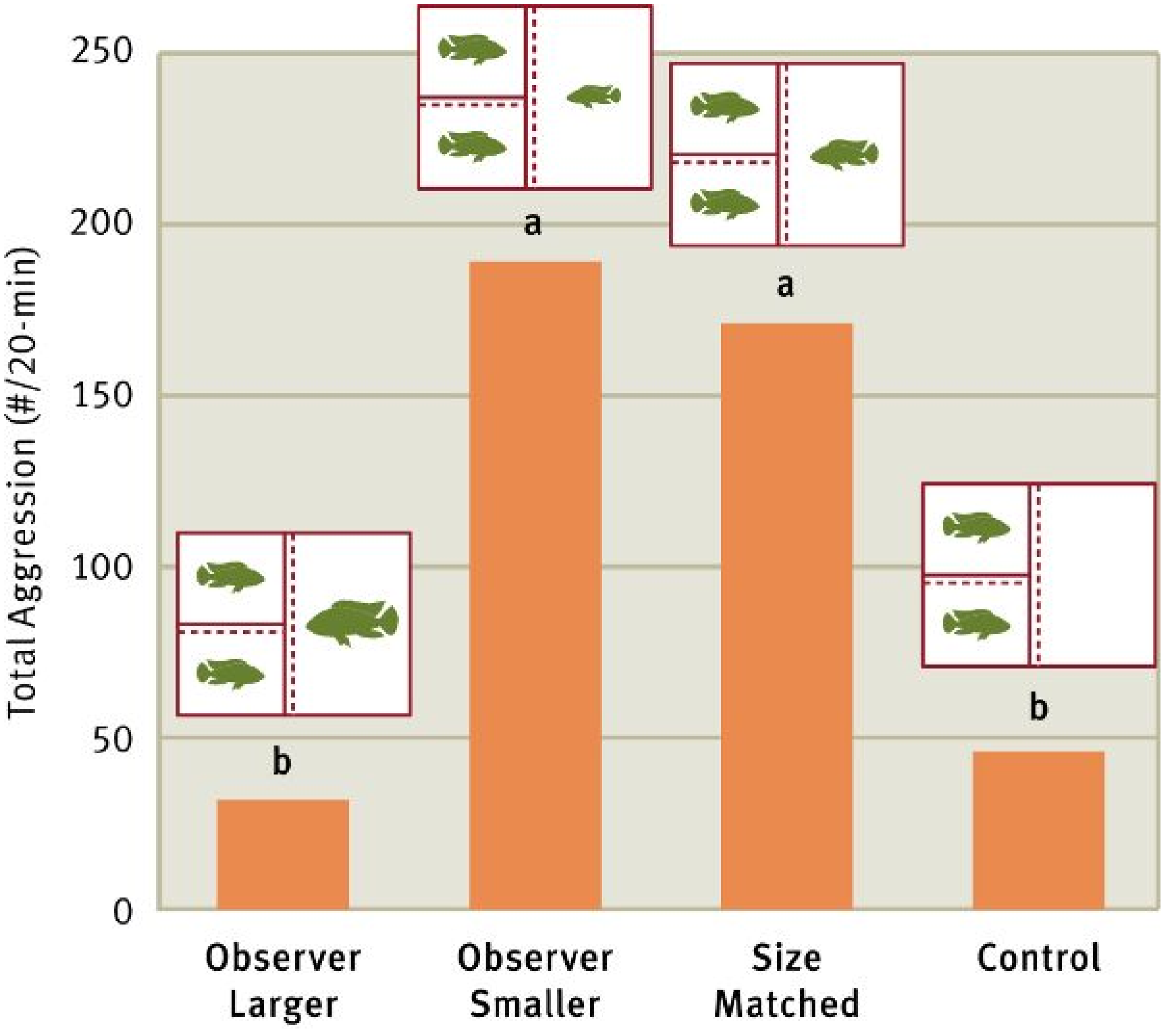


Figure 15.18. **Males fight more when being watched.** Male *Astatotilapia burtoni* fought more intensely when watched by another male than when they were not being watched. Reprinted with permission from Elsevier. © 2015. *(From Desjardins et al., 2015)*

Interview with Dr. Karen Hollis

As a psychologist, what drew you to the study of animal aggression?

I first became interested in aggression as a graduate student working with *Betta splendens*, a territorial freshwater fish native to Southeast Asia. Although my project addressed a question of underlying learning processes, not aggression per se, it afforded me a serendipitous observation of aggressive behavior, one that provided the raw material for years of subsequent research. My project required me to transport each *Betta* male in its home tank to another room where it would have the opportunity to display to a rival. After a few days of this procedure, I noticed that when I approached the shelf on which the males were located and reached for a particular male's tank, it became quite agitated. After a few more days, each male that I selected began to display—at me. And at eye level that display looked quite ferocious! I recognized that some features of my appearance obviously had become a learned cue for the subsequent interaction with a territorial rival. At that time, associative learning in *B. splendens* was pretty well established (even if the experimenter-as-signal was a little unconventional). However, what was even more interesting to me was the realization that this kind of learning could be a wonderfully adaptive mechanism, providing a territory owner with a definitive competitive edge: Confronting a potential usurper with a full-blown aggressive display could be a very effective aggressive strategy for a territory owner. A few years later, as a postdoctoral student at Oxford, I had the opportunity to conduct those experiments with blue gouramis, *Trichogaster trichopterus*, and, as the data showed pretty convincingly, the best defense is, indeed, a good offense.

What do animals usually fight over? Do they display different types of aggression depending on what the fight is about?

No matter what the situation—from nest-mate aggression and sibling rivalry to parent-offspring conflict and territorial behavior—aggression is all about resources. Moreover, as behavioral ecologists have demonstrated quite convincingly across a variety of taxa, particular forms of aggressive behavior emerge under particular selection pressures. For example, aggressive behavior in the context of resource-defense polygyny is a mating strategy in which individuals of one sex, typically males, defend a resource that is in short supply, critical for females, and defendable, both in terms of the reliability of its location and its quality. That resource—and, thus, what males fight over—could be anything that meets these criteria. Many species of freshwater fish, including my own study species, blue gouramis, defend a location where aspects of the habitat, such as the temperature and pH of the water, are favorable for the development of eggs and fry. Territorial lizards defend spots safe from predators. Some birds defend shady spots, necessary for the development of eggs. And, of course, many animals, from territorial male bumblebees and green frogs to sunbirds and burrowing owls, defend food sites.

Aggression also appears in another mating strategy, called harem defense, in which a few males defend a group of females directly, rather than a needed resource. Harem defense polygyny is characteristic of grizzly bears, red deer, and elephant seals. Because the benefits of winning are tied more directly to reproductive success whenever males are defending access to reproductively active females than when they are defending only the resources to which females are drawn, and because only a few males, namely those powerful enough to mount this kind of defense, are able to reproduce, the aggressive behavior differs enormously. Males are much more aggressive, and injuries are potentially more lethal, wherever harems are concerned. So, yes, aggressive behavior differs dramatically, depending on what the fight is about, as predicted by evolutionary theory.

How flexible are the aggressive strategies employed by animals? What role does learning play in aggressive behavior?

Many of the learning phenomena studied by animal learning psychologists map nicely onto naturally occurring aggressive behavior and, thus, demonstrate the flexibility of—and modulating influence on—aggression. For example, the “dear enemy effect”—where two adjoining territory holders form a temporary alliance to fight intruders that are threats to both of them—obviously depends upon habituation. Habituation is the progressive decrease in responsiveness resulting from repeated presentation of a stimulus. Although some instances of attenuated responsiveness are merely the result of sensory adaptation or muscular fatigue, true habituation is a phenomenon of neural memory: The response to repeated sensory stimulation is chocked off somewhere in the brain—or nerve net—of the animal. Aggression between territorial neighbors, which is initially both intense and frequent, gradually wanes to a point of sporadic and relatively mild aggressive interactions. Yet, while neighbors spare one another from their territorial aggression, producing dear enemies, newcomers face its full measure. Laboratory experiments on habituated aggression have reproduced successfully the basic components of the dear enemy effect. That is, the habituated response is stimulus-specific: Neighbors, and only neighbors, no longer elicit aggressive behavior. Moreover, habituation itself is neither permanent nor ephemeral, lasting just long enough to handle the time intervals observed in natural settings.

Other examples abound. Many species of territorial fish are capable of recognizing their competitors, even when they do not belong to the same species; fish of other species whose ecological requirements overlap with the territory holder are driven away while noncompetitive species are permitted to remain within the territory.

In short, individuals not only learn which species to attack, but also make fine discriminations between different species of the same genera.

Finally, in the same way that animals can use signals to determine when or where an aggressor might appear and, thus, focus their aggression in cost-effective ways, inhibitory learning—the ability to learn that a cue predicts the absence of a particular event for some period of time—provides a mechanism to avoid useless energy expenditure at times when, or places where, rivals are less likely to occur. For example, territory owners often exhibit “spontaneous” aggressive displays, favoring particular locations—locations, as the research shows, where they have encountered rivals in the past—and ignoring places where rivals have not appeared and, thus, are unlikely to pose a threat.

What do you predict will be the next major breakthrough in the study of animal aggression?

To me, science is like a very large construction project, with different teams of professionals arriving on site at particular points to contribute their special expertise, then making way for the next group, and so on. Only, in the case of science, the project never really ends. Not only does the edifice get renovated over and over again, but also those teams of experts return with new and improved technology. In the study of aggression, behavioral ecologists have laid an extensive and solid foundation of intra- and interspecific behavioral similarities and differences, all of which reflect particular selection pressures. It’s now time for geneticists to step on site with their array of exciting new tools.

In particular, I predict that genomic analyses will allow us to explore the vast expanse of questions that lie between genes and the expression of aggressive behavior. Concerning intraspecific differences, what does an ESS look like from a genetic perspective? What are the genetic and developmental differences that separate individuals that become harem defenders from those that are forced to adopt surreptitious strategies to obtain copulations? Single nucleotide polymorphisms (SNPs), locations on the genome where individuals differ by just one chemical compound, already have been implicated in the aggressive threat behavior of monkeys, making this approach a very promising one for addressing individual differences in aggression. At the interspecific level, to what extent do the genomes differ between closely related species that express different types of male-male competition? Conversely, to what extent might the aggressive behavior of convergent species possess similar genetic mechanisms? In short, I predict not only that geneticists and molecular biologists will add a completely new wing to the edifice that is our science of animal behavior, but also that the connectors between these and other groups of behavioral scientists will get easier and easier to traverse.

Table 15.2. Matrix for exercise in question 2.

	Hawk	Dove
Hawk	(V/2) – C	V
	(V/2) – C	0
Dove	0	V/2
	V	V/2

Dr. Karen Hollis is a professor emerita at Mount Holyoke College. Her work on animal learning and Pavlovian conditioning represents a classic example of how researchers can integrate biological and psychological approaches to animal behavior.

SUMMARY

1. Individuals from many species tend to fight over resources (space, mates, food, and so on).
2. Ethologists and evolutionary game theorists have built a series of models that examines the evolution of fighting behavior. Three game theory models of aggression are the hawk-dove game, the war of attrition model, and the sequential assessment model. In all three of these game theory models, a cost to fighting is assumed.
3. There are many varieties of the hawk-dove game. One version adds a new strategy: bourgeois. The bourgeois strategy instructs an individual to play hawk if it is a territory holder and dove if it does not own a territory.
4. The war of attrition model examines aggression when the choice available to individuals is more continuous—for example, “fight for *x* seconds, then stop.” Rather than establishing a set time for fighting, the war of attrition model predicts an ESS distribution of contest lengths.
5. In the sequential assessment model, individuals constantly assess and update their assessment of their opponents’ fighting skills. A single sample (assessment) introduces significant error; the more sampling (assessment) an individual does,

the lower the error rate and hence the more confident that individual can be in whatever is being estimated.

6. Winner and loser effects are usually defined, respectively, as an increased probability of winning at time T, based on victories at times T − 1, T − 2, and so on, and an increased probability of losing at time T, based on losing at times T − 1, T − 2, and so on.
7. Bystander effects occur when the observer of an aggressive interaction between two other individuals changes its assessment of the fighting abilities of those it has observed. Not only do bystanders change their estimation of the fighting ability of those they observe, but individuals involved in aggressive interactions change their behavior if they are watched. This latter phenomenon is referred to as the audience effect.

DISCUSSION QUESTIONS

1. In 1990, Enquist and Leimar published a paper, “The evolution of fatal fighting,” in *Animal Behaviour* (vol. 39, pp. 1–9). Based on reading their paper, as well as your own thoughts on the costs and benefits of extreme aggression, when do you think fighting to the death might be likely to be favored by natural selection?
2. The classic hawk-dove game we examined in this chapter assumes that losers pay a cost (C) that is not paid by winners. In Table 15.2 above, we are assuming that both hawks in a fight pay a cost. For the case of both $V > C$ and $V < C$, calculate the ESS for this new game.
3. A number of studies have suggested that loser effects are both more common and more dramatic than winner effects. Construct a hypothesis as to why this might be. How could you test your hypothesis?
4. If stress-related hormones such as cortisol often inhibit learning and/or memory, how might that compound the difficulties subordinate fish face in trying to raise their rank in hierarchies?

SUGGESTED READING

Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour*, *77*, 991–1004. A review of assessment and the role it plays in animal aggression.

Edwards, D. H., & Spitzer, N. (2006). Social dominance and serotonin receptor genes in crayfish. *Current Topics in Developmental Biology*, *74*, 177–199. A detailed analysis of serotonin and aggression in crayfish.

Emlen, D. J. (2008). The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 387–413. An excellent review of the wide variety of animal weapons and their function.

Hsu, Y. Y., Lee, I. H., & Lu, C. K. (2009). Prior contest information: Mechanisms underlying winner and loser effects. *Behavioral Ecology and Sociobiology*, *63*, 1247–1257. A review of the proximate underpinnings of winner and loser effects.

Maynard Smith, J., & Price, G. (1973). The logic of animal conflict. *Nature*, *246*, 15–18. The classic paper introducing ethologists to mathematical models (game theory) of aggression.

Riechert, S. E. 2013. Maynard Smith & Parker’s (1976) rule book for animal contests, mostly. *Animal Behaviour*, *86*, 3–9. A review of a number of ethological models of aggression.

16

Play

In chapter 6, we discussed stone play and cultural transmission in the Japanese macaques (*Macaca fuscata*) living in Iwatayama National Park (Kyoto). But stone play has been documented in *many* Japanese macaque populations, and the list of ways that monkeys use stones during play is continually growing (Figure 16.1). During bouts of play, which most often occur before feeding, macaques have been seen gathering stones, stacking stones, licking stones, throwing stones, rolling stones in their mouths, flipping stones, scattering stones, rubbing stones, washing stones, spinning stones, wrapping stones in leaves, and more (Nahallage et al. 2016) (Table 16.1). When in engaged in such play, macaques appear focused on the activity, and in chapter 6, we discussed findings that suggested stone play may facilitate the development of perceptual and cognitive skills in young monkeys and slow the deterioration of cognitive processes often seen in older individuals.

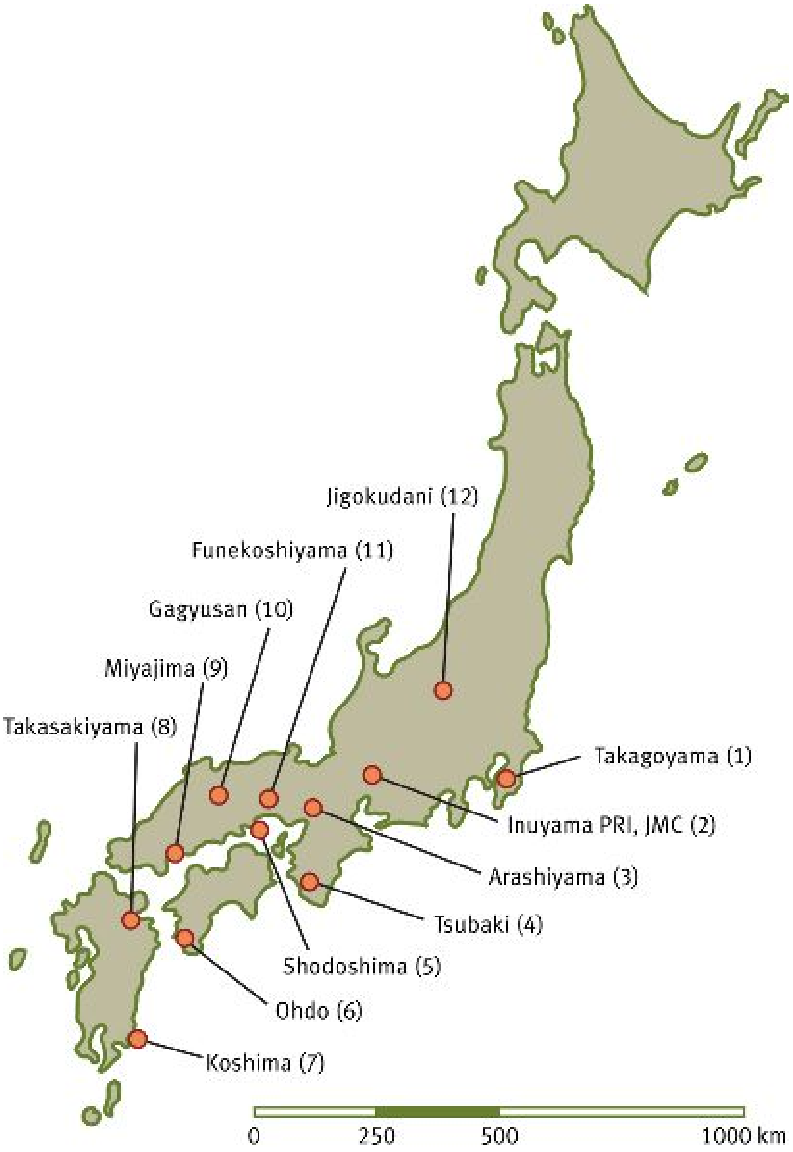


Figure 16.1. **Stone play is common in Japanese macaques.** A map showing populations of Japanese macaques where stone play has been recorded. *(From Nahallage et al., 2016)*

Table 16.1. Different types of stone play. *(From Nahallage et al., 2016)*

Investigative activities	**Sound producing activities**
Pick	Rub on Surface
Hold	Roll in Hand
Bite	Rub Together
Lick	Scatter
Sniff	Clack
Cuddle	Rub with Hand

Put in Mouth
Move in Mouth
Collecting/gathering activities
Gathering
Pick Up
Pick Up and Drop
Grasp Hand
Locomotor activities
Move and Push
Grasp Walk
Carry
Carry in Mouth
Toss Walk

Pound on Surface
Slap
Rub with Mouth
Rub in Mouth
Tap in Mouth
Flint
Flip
Flint in Mouth
Complex manipulative activities
Wrap in Leaf
Combine with Other Objects
Throw
Stone Grooming
Shake in Hand
Rub on Fur
Wash
Put in Water
Spin
Swipe
Throw and Sway
Throw and Jump
Throw and Run

The frequency of stone play in Japanese macaques is influenced by both biotic and abiotic factors. In general, stone play seems to be most common when macaques are under low stress conditions. In some populations, for example, monkeys play more when it is warm and sunny than when it is cloudy, rainy, and/or cold. Play is also in more common when the levels of intergroup aggression are low. This has led researchers to suggest that the frequency of play behavior can be used by conservation biologists and ethologists as an indicator of the psychological well-being of animals (Vicino and Marcacci, 2015; Nahallage et al., 2016; see Box 16.1).

Box 16.1. CONSERVATION CONNECTION

Play Behavior as a Measure of Environmental Stress

The Conservation Connection in chapter 2 (Box 2.3) discussed ways that conservation biologists use fluctuating asymmetry as a cue of environmental stress. Are there other such cues—perhaps more behavioral cues—that can be used to gauge the way populations studied by conservation biologists are under environmental stress of one sort or another? Recently, ethologists have suggested that play behavior may be such a cue.

Anita Stone observed the foraging behavior, time spent traveling, play behavior, and other social behaviors of juvenile squirrel monkeys (*Saimiri sciureus*) in Eastern Brazilian Amazonia. What she found was that during the dry season, when fruit availability was low, young individuals spent more time foraging and much less time playing (Figure 16.3). This decrease in play was likely due both to the increased time spent foraging and to the high energy expenditure necessary for play—energy that was not available during the dry season (Stone, 2008).

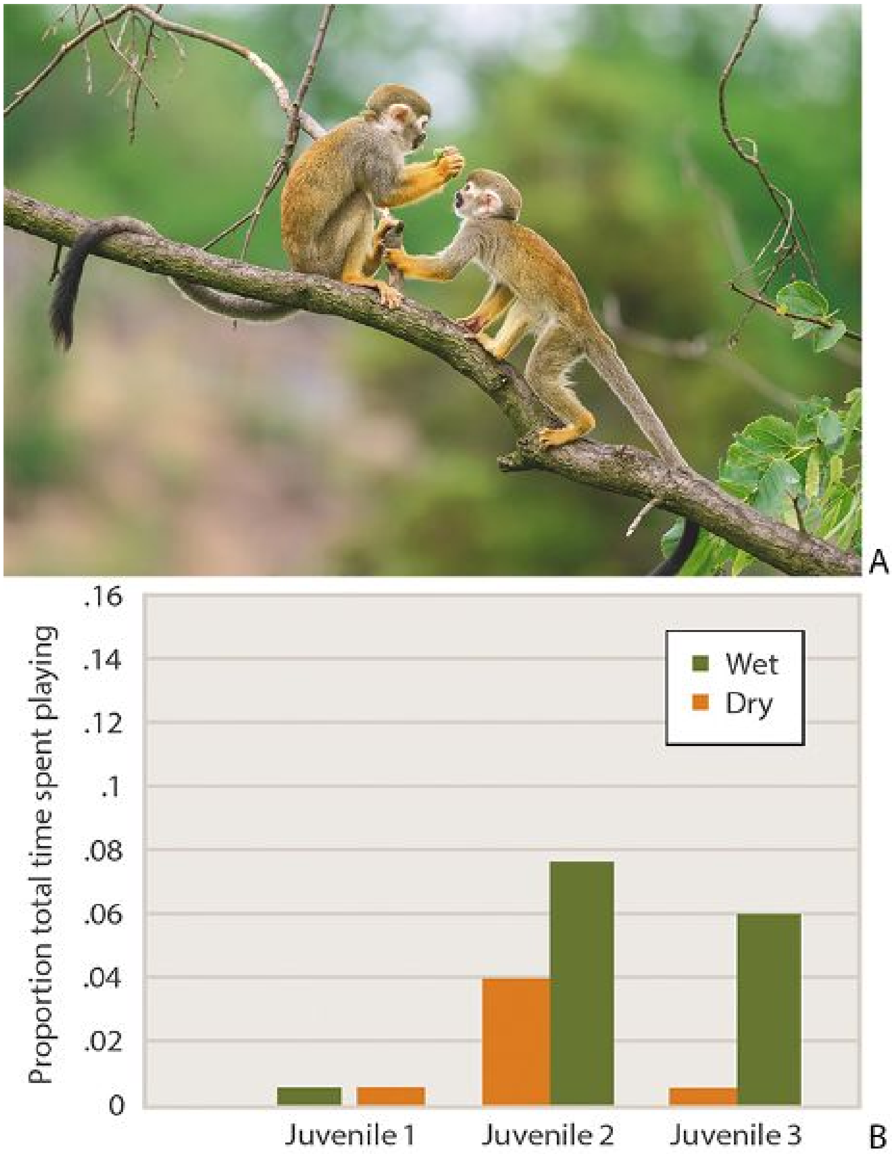


Figure 16.3. **Seasonality and play behavior.** (A) Juvenile squirrel monkeys. (B) The proportion of time spent in play decreased for most juvenile squirrel monkeys during the dry season in Brazil. Two of the three individuals shown on the graph reduced play behavior during the dry season, when fruit was scarce. *(Photo credit: Nick Fox / Shutterstock; graph from Stone, 2008)*

Stone's study suggests that a decrease in play in squirrel monkeys was linked to low food availability and low energy budgets. Other evidence suggests that decreased levels of play may indicate environmental stress in general, not just with respect to decreased food availability. Studies have found that when animals are stressed—by, for example, poor habitat quality, increased predation, and other threats—one of the first behaviors that drops from their repertoire is play behavior (Fraser and Duncan, 1998; Lawrence, 1987; Sarti Oliveira et al., 2010; Spinka et al., 2001), though the situation is often not so straightforward and requires future study (Held and Spinka, 2011).

Endocrinological and neurobiological studies are also being employed to understand the relationship between play and stress. Although comfort and pleasure are very difficult to measure in nonhumans, some work suggests that play and play-like behaviors may be associated with increased pleasure (Berridge, 2003; Dalgleish, 2004; M. S. Dawkins, 1990, 2008; Mendl, 2010; Paul, 2005; Vanderschuren, 2010). This type of work is still in its infancy, but such studies could, for example, examine whether areas of the brain associated with pleasure in other contexts, such as feeding and mating, are also active during play behavior.

All in all, changes in play may be a kind of behavioral bellwether that conservation biologists can use to measure whether environmental stressors are affecting individuals.

* * *

Play can take many forms. Evidence suggests that while not all species engage in play, it is common, particularly among young individuals. Young animals gently wrestle with each other; toss, kick, and push objects they find in their environment; chase one another for no apparent reason; jump; climb up and down trees over and over; and appear to practice hunting prey (Figure 16.2). Play is more common in large-brained vertebrates (such as primates) than in other species, but it is not limited to this group nor indeed is it even limited to vertebrates (some octopuses play: Kuba et al., 2006; Mather, 2008a,b; Table 16.2).

Figure 16.2. **Play.** Play behavior in (A) sea lions and (B) polar bears. *(Photo credits: iStock.com/Marketa Ebert; Gudkov Andrey/ Shutterstock)*

Table 16.2. Distribution of play. Play has been found across many, but not all, major vertebrate groups. *(Based on K. L. Graham and Burghardt, 2010)*

VERTEBRATE GROUP	EVIDENCE OF PLAY
Hagfishes	Play unknown in any
Lampreys	Play unknown in any
Sharks, rays, and skates	Play present in some

VERTEBRATE GROUP	EVIDENCE OF PLAY
Ray-finned fishes	Play present in some
Coelocanths	Play unknown in any
Lungfishes	Play unknown in any
Caecilians	Play unknown in any
Frogs and toads	Play present in some
Salamanders and newts	Play unknown in any
Turtles and tortoises	Play present in some
Birds	Play present in many
Crocodiles and relatives	Play present in some
Lizards, snakes, and relatives	Play present in some
Egg-laying mammals	Play present in some
Kangaroos and relatives	Play present in many
Placental mammals	Play present in many

At the Washington Zoo, an animal named Pigface played with whatever new objects (brown balls, orange balls, hoops, and so on) that zookeepers added to his otherwise bland environment (Burghardt, 1998). Pigface approached the new objects, followed them, pushed them around, and so on—he played with them.

Two things make Pigface's story particularly interesting. First, Pigface isn't a dog or a chimp; he's a turtle. Second, play had a profound effect on Pigface's health. Before objects were introduced into his environment, Pigface was clawing his own limbs and neck, causing infection and fungal growth. After the objects to play with were introduced, this self-destructive behavior decreased: once the bland environment Pigface lived in had potential play items added, he chose to play rather than self-mutilate.

Play is an understudied area in animal behavior (Burghardt, 2005; K. L. Graham and Burghardt, 2010). Why? One reason is that pet owners' and zookeepers' stories are usually anecdotal at best, and huge exaggerations at worst. Though play has been documented in many species, it had not been examined *experimentally* until relatively recently.

A second reason that play behavior was (and to some extent still is) relatively understudied is that animal behaviorists focus on behaviors that appear to have function. Function is sometimes very hard to determine for play. A third, related reason for the relative lack of controlled studies of play is tied to theory, or more precisely the lack of it. Others have suggested that a lack of *theory* for the function of play can explain why play research lagged behind other areas of interest in ethology (Fagen, 1981). A theoretical underpinning for play behavior has now begun to emerge, and we will examine this more throughout the chapter (Bekoff and Byers, 1998; Burghardt, 2005; Graham and Burghardt, 2010; Spinka et. al., 2001; Pellis et al., 2015).

The situation with respect to the study of play has certainly improved since 1975, when E. O. Wilson wrote that “no behavioral concept has proved more ill-defined, elusive, controversial and even unfashionable than play” (E. O. Wilson, 1975). There is now a sizable literature on many aspects of animal play (Bekoff and Byers, 1998; Bruner et al., 1976; Burghardt, 2005; Fagen, 1981; Power, 2000; Symons, 1978; see Box 16.1). In this chapter, we will examine:

- how play is defined,
- the different types of play behavior (object, locomotor, and social play) and their functions,
- the endocrinological and neurobiological bases of play, and
- the phylogeny of play.

Defining Play

In the animal behavioral literature there are many definitions of **play**. The most widely cited of these definitions is that of Marc Bekoff and John Byers, who propose the following:

> Play is all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing. If the activity is directed toward another living being it is called social play. (Bekoff and Byers, 1981, pp. 300–301)

One problem with this definition is that behaviors such as repetitive pacing—pacing back and forth for long periods of time in what appears to be a purposeless manner—meets the above criteria, but most researchers would argue that this is not really play behavior (Bekoff and

Allen, 1998). In addition, not only is it extremely difficult to determine when a behavior is purposeless, but behaviors that are apparently purposeless may be so for three very different reasons (Heinrich and Smokler, 1998): (1) Observers may simply fail to decipher what the immediate benefit of the play behavior is, (2) the purpose and potential benefit may not be accrued until long after play has occurred (Fagen and Fagen, 2004), and (3) the benefits may be multiple and confounding. The situation is actually more complex, because Bekoff and Byers's definition does not claim that play is purposeless, only that it appears to be so (Heinrich and Smokler, 1998).

Many ethologists argue that since experimental work on play lags behind controlled work in other areas of animal behavior, it is best to take a wait and see approach, while studying play in many species. The hope is that such work will eventually uncover certain commonalities in play behavior, and that such commonalities will then be used to construct a definition.

Types and Functions of Play

Animal behaviorists work on three different types of play—object, locomotor, and social play. We will examine each of these, looking at the functions of these three types of play.

OBJECT PLAY

Object play is play using inanimate objects such as sticks, rocks, leaves, feathers, fruit, and human-provided objects, and the pushing, throwing, tearing, or manipulating of such objects (S. Hall, 1998). For example, researchers examining videotapes of chimps in the Mahale Mountains of Tanzania found a behavior they labeled "leaf-pile pulling" (Figure 16.4). As chimps move down the slope of a mountain, an individual will sometimes stop and walk backward, pulling handfuls of leaves along with him as he proceeds. Then, the chimp stops and either walks or somersaults through the pile of the leaves that she created (Nishida and Inaba, 2009; Nishida and Wallauer, 2003; Nishida et al., 2009).

Figure 16.4. **Leaf play in chimpanzees.** “Leaf-pile pulling” is a type of play behavior seen in chimpanzees living in the Mahale Mountains of Tanzania. As they go down the slope of a mountain, individuals sometimes walk backward, pulling handfuls of leaves and then stopping and either walking or somersaulting through the pile of leaves. The photo shows a chimp as he gathers a leaf pile. *(Photo credit: © Toshisada Nishida / Japan Monkey Centre / Springer Japan)*

Object play has been documented in a wide array of taxa, and is particularly well studied in captive populations—such as zoo animals—where “toys” are given to animals to provide them with new items in an otherwise relatively constant environment (Fraser and Duncan, 1998; Sarti Oliveira et al., 2010). Object play has been distinguished from object exploration, with play often following exploration (Hutt, 1966; Wood-Gush and Vestergaard, 1991; Figure 16.5). In object exploration animals learn what an object is, while during object play the animal acts to determine what it can do with this object (Hutt, 1970; Power, 2000).

Figure 16.5. **Play or exploration?** Here a cheetah cub comes upon a novel object: bones. Exploring the bones may address the “What is it?” question, whereas play may address the “What can I do with this object?” question.

Object Play in Juvenile Ravens

From a functional perspective, object play in young animals is often associated with practice, where an animal learns something that will benefit it either in the short or long term—for example, young may use object play to practice hunting (B. Beck, 1980; Fagen, 1981; P. Martin and Caro, 1985; P. K. Smith, 1982).

Bernd Heinrich has described object play in ravens (Heinrich, 1999; Figure 16.6). Young ravens play with virtually every new kind of object they encounter—leaves, twigs, pebbles, bottle caps, seashells, glass fragments, and inedible berries (Heinrich and Bugnyar, 2007; Heinrich and Smokler, 1998). Heinrich, who has observed these birds for thousands of hours, writes of young birds’ seemingly obsessive drive to contact and manipulate any objects they encounter (Heinrich and Smokler, 1998). Ravens play with and display food items to others in their group, and some ethologists have suggested that such behaviors are an example of referential gestures in nonprimate species (Bugnyar et al., 2007; Pika and Bugnyar, 2011).

Figure 16.6. **Play in ravens.** Various “hanging games” Heinrich observed in ravens. *(Based on Heinrich, 1999, p. 289)*

Object play in young ravens affects what individuals fear, or don’t fear, when they mature (Heinrich, 1988a; Heinrich et al., 1996). Adult ravens still manipulate objects after they mature; but compared with how they react to items they played with when they were younger, they treat items they have never encountered before—including potential food sources—with heightened fear.

To examine the potential fitness benefit of object play, Heinrich examined object play in four young juvenile ravens raised by experimenters in a controlled experimental forest environment in Maine (Heinrich, 1995). Young ravens were observed in thirty-minute sessions for more than thirty days. During the first ten observation periods, Heinrich noted all the naturally occurring objects the birds encountered. Nine hundred and eighty naturally occurring items that fell into ninety-five different categories were encountered by the young birds during their first ten trials, and encounters often involved some combination of exploration and play.

After the first ten trials, Heinrich added forty-four “novel” items—objects the ravens had never seen before—to the birds’ environment and observed the manner in which juveniles interacted with these new objects. He found that exploration and play were directed at novel items. Novelty, per se, rather than other characteristics such as shininess, palatability, or conspicuousness, explained which items they chose. Yet while they did not choose items based on their palatability, they quickly treated inedible items as background material—they did not handle these items much after their initial encounters with them—

and edible novel items as their preferred foods. This suggests that juvenile play and exploration in ravens enable juvenile ravens to identify new food sources. Ravens are scavengers (as well as predators), and in an environment where many objects may be food, play and curiosity in ravens seem to be a means to decipher what is edible and what isn't (Heinrich, 1999; Heinrich and Bugnyar, 2007).

Object Play in Young Cheetahs

Tim Caro studied play in cheetah cubs in the Serengeti National Park in Tanzania, observing cubs for more than 2,600 hours, and documenting, among other things, many instances of object, social, and locomotor play (Caro, 1995b; Figure 16.7; Table 16.3). Caro was interested in the role of each type of play in shaping how cheetahs would learn to capture prey and what the costs associated with each type of play might be.

Figure 16.7. **Cheetah play.** Young cheetahs engage in social play often, including play fights. *(Photo credit: Gudkov Andrey / Shutterstock)*

Table 16.3. Types of cheetah play. Young cheetahs engage in many types of play activities in nature. *(From Caro, 1995b, p. 335)*

TYPE OF PLAY	BEHAVIOR PATTERN	RECIPIENT
Locomotor play	Bounding gait	No recipient
	Rushing around	
Contact social play	Patting Biting Kicking Grasping	Any family member
Object play	Patting Biting Kicking Carrying	Object
Noncontact social play	Stalking Crouching Chasing Fleeing Rearing up	Any family member

Caro set out to measure the costs associated with juvenile play (Figure 16.8). Estimating the cost of any behavior, particularly a behavior as complex and difficult to measure as play, is difficult, but evidence from a number of studies suggests that under certain conditions play may be very costly (W. Arnold and Trillmich, 1985; J. Berger, 1980; Douglas-Hamilton and Douglas-Hamilton, 1975; R. Harcourt, 1991; Lawick-Goodall, 1968). As an extreme case, while play accounted for just over 6 percent of young fur seals' time, twenty-two of the twenty-six pups that were killed over the course of long-term observations were engaged in some sort of play at the time they were killed (R. Harcourt, 1991).

Figure 16.8. **Play in cheetahs.** In cheetahs, play progressively disappears with age. *(From Caro, 1995b)*

To estimate the potential costs of play in young cheetahs, Caro gathereed data on the distance that a cub rushed around or chased during play as a measure of the energetic costs of play for cheetah cubs, and the distance cubs moved from their mothers during object, motor, and social play, as an estimate of predation or general injury costs associated with play: the farther the cub was from its mother, the greater was its risk of being harmed either during play or by a predator such as a lion or a spotted hyena. His data suggest that cheetah play—including object play such as patting, biting, kicking, and carrying—is a relatively low-cost activity. Cubs were never seriously injured during play. In addition, while young cheetah cubs that were involved in play were slightly farther from their mothers than cubs not playing, in all cases the cubs' mothers were so close that their cubs were not under any serious predation threat. Costs of play in juvenile cheetahs may still exist, but if such costs do exist, they are likely fairly minor.

In terms of benefits, increased play led cubs to display increased rates of patting, grasping, and biting live prey that their mother had just released. Such predatory-like behavior on the part of the cubs might make them more successful hunters when they mature (Box 16.2).

Box 16.2. SCIENCE AT WORK

What is the research question? What costs are associated with play?

Why is this an important question? To understand the evolution of play, a knowledge of the costs and benefits of social, object, and locomotor play are needed.

What approach was taken to address the research question? Researchers examined the distance of cheetah cubs from their mothers as cubs played (an indicator of increased threat of predation) and the amount of energy expended in play bouts.

What was discovered? The costs of play in young cheetahs, as measured in terms of predation threat and energy expended, are small.

What do the results mean? For young cheetahs, the benefits of play outweigh the costs of play.

LOCOMOTOR PLAY

In this section we will consider **locomotor play**, sometimes called locomotor-rotational play (Power, 2000). Fagan describes this type of play:

> The single most frequent and phylogenetically widespread locomotor act of play must surely be a leap upward. . . . Hops, springs, bounces and bucks are variations on the basic vertical leap. . . . Animals may somersault, roll, flip forward or backward, spin, whirl, pirouette, make handstands, chase their tails, rear and kick up their heels. . . . Often a vertical leap is decorated with body-twists, rear-kicks or head shakes. These acrobatics can be spectacular. (Fagen, 1981, pp. 287–291)

At least two, non–mutually exclusive hypotheses have been put forth for the function of locomotor play in animals and humans: 1) locomotor play provides exercise and training for specific motor skills needed later in life (J. Byers, 1984, 1998) and 2) locomotor play provides animals with a better understanding of where things are in relation to one another, and this may provide immediate benefits (Power, 2000; Stamps, 1995; Symons, 1978). Here we will focus on the exercise-related benefits, and we return to “the lay of the land” hypothesis later in the chapter.

Locomotor play has been studied primarily in rodents, primates, and ungulates, and it includes leaps, jumps, twists, shakes, whirls, and somersaults (Figure 16.9). In an attempt to quantify the possible benefits of locomotor play, Byers and Walker examined nineteen potential anatomical and physiological benefits associated with exercise and physical training in search of benefits that were available to individuals as juveniles (but not as adults), and that were long-lasting in their effects (J. Byers and Walker, 1995; Table 16.4). Only two of the nineteen possible benefits met their criteria.

Figure 16.9. **Pronghorn play.** Pronghorns undertake various forms of locomotor play, including (A) high-speed running and (B) stots (jumping with all four legs simultaneously off the ground). *(Photo credits: Johan Swanepoel / Alamy Stock Photo)*

Table 16.4. Physiological effects of elevated motor activity. In examining the potential benefits of locomotor play, Byers and Walker listed nineteen benefits that might be associated with elevated motor activity. *(Based on J. Byers and Walker, 1995)*

Specific effect	Presumed benefit	Effect available to juveniles?	Effect permanent?	Effect available to adults?

Specific effect	Presumed benefit	Effect available to juveniles?	Effect permanent?	Effect available to adults?
Increase in maximum oxygen reuptake	Greater endurance	Yes	No	Yes
Decrease in heart rate during exercise	Greater endurance	Yes	No	Yes
Decrease in blood lactate level during exercise	Greater endurance	Yes	No	Yes
Increased heart weight: body weight ratio	Greater endurance	Yes	No	Yes
Increased myoglobin	Greater endurance	Yes	No	Yes
Greater numbers and size of skeletal muscle mitochondria	Greater endurance	Yes	No	Yes
Increased muscle glycogen and triglyceride stores	Greater endurance	Yes	No	Yes
Greater capacity to oxidize fat	Greater endurance	Yes	No	Yes
Greater slow-twitch fiber area	Greater endurance	Yes	No	Yes
Greater total blood volume	Greater endurance	Yes	No	Yes
Greater muscle capillary density	Greater endurance	Yes	No	Yes
Greater maximal ventilation rate	Greater endurance	Yes	No	Yes
Increased maximal muscle blood flow	Greater endurance	Yes	No	Yes
Bone remodeling	Increased strength	Yes	No	Yes
Fast-twitch fiber hypertrophy	Increased strength	Yes	No	Yes
Increased recruitment of motor units	Increased strength	Yes	No	Yes
Modification of cortical areas involved in movement	Increased motor skill/ energetic economy of movement	Yes	No	Yes
Modification of muscle fiber type differentiation	Increased motor skill/ energetic economy of movement	Yes	Probably	Unlikely

Specific effect	Presumed benefit	Effect available to juveniles?	Effect permanent?	Effect available to adults?
Modification of cerebellar synapse distribution	Increased motor skill/ energetic economy of movement	Yes	Yes	Diminished

One potential benefit of locomotor play is an increase in the creation of synapses in the cerebellum. The cerebellum plays a critical role in limb coordination, movement, postural changes, eye-limb coordination, and many other aspects of movement in mammals. During development, more cerebellar synapses are created than are used in later life, and some of these synapses may be pruned as a function of experience (M. Brown et al., 1991; Greenough and Juraska, 1979; Jacobson, 1991; Purves and Lichtman, 1980; Pysh and Weiss, 1979).

Researchers have asked how play behavior maps onto cerebellar synapse formation and elimination. With respect to motor play in juvenile mice, the fit is good (Figure 16.10A). Mice start playing at about fifteen days of age and peak in their locomotor play activities at nineteen to twenty-five days, corresponding with a peak in cerebellar synapse formation. The same general pattern is found when examining locomotor and social play in rats (Figure 16.10B) and social play in cats (Figure 16.10C). A second major developmental change—the differentiation of muscle fibers that will be important for use in foraging and antipredator behaviors—also maps nicely onto the development of play (Close, 1972; Edgerton, 1978; Roy et al., 1988).

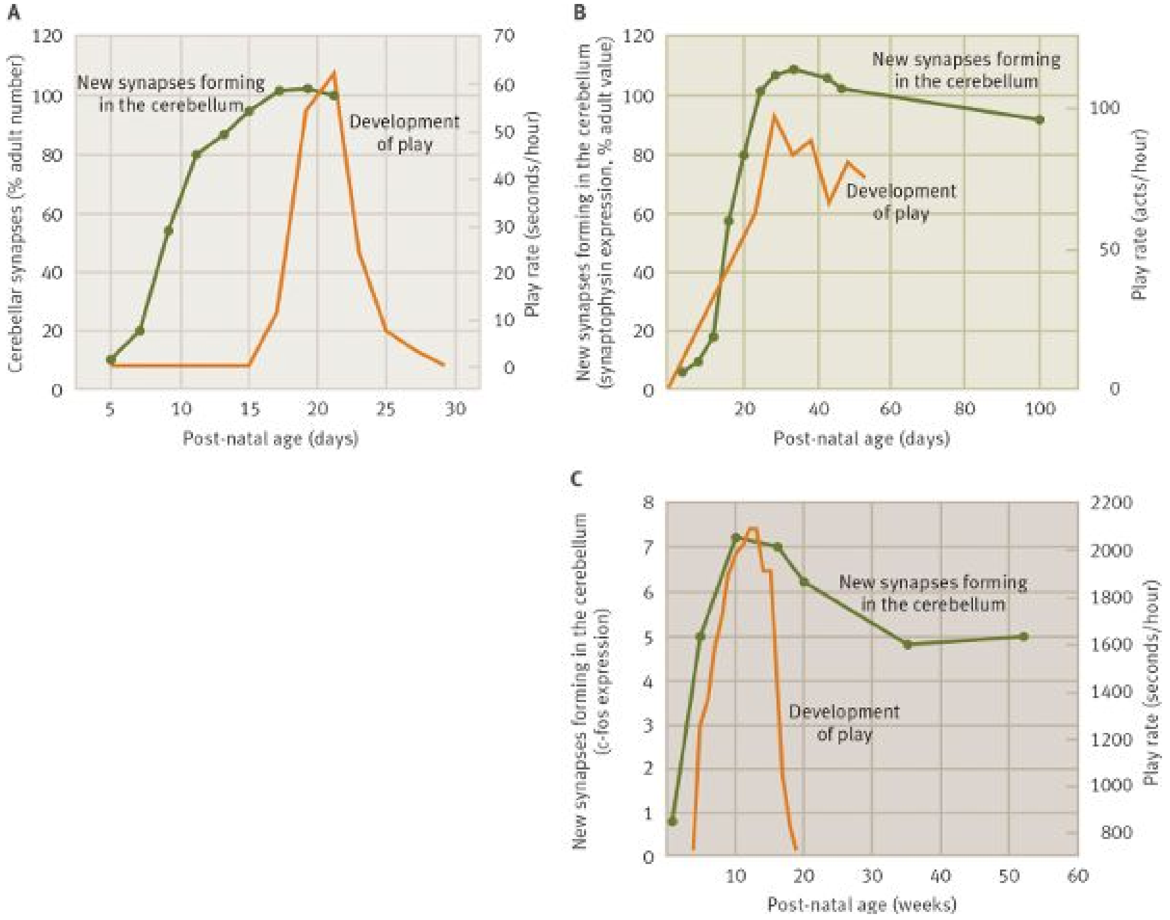


Figure 16.10. **Play and brain development.** New synapses forming in the cerebellum (green curve) is plotted along the development of play (orange curve) in (A) mice, (B) rats, and (C) cats. *(Based on J. Byers and Walker, 1995)*

It is important to note that this work is correlational. As Byers and Walker note in their study, we do not know if an increase in locomotor play causes an increase in cerebellar synapse formation, an increase in cerebellar synapse formation leads to an increase in locomotor play, or if some third variable is affecting both cerebellar synapse formation and play. Future work is needed to infer causation.

SOCIAL PLAY

Social play—playing with others—is the most well-studied type of play. A number of functions of social play have been proposed (K. L. Graham and Burghardt, 2010; K. V. Thompson, 1996). (1) Social play may lead to the forging of long-lasting social bonds (Carpenter, 1934). For example, male-male social play is very common among immature chimps in the Arnhem Zoo (in the Netherlands) (Mendozagranados and Sommer, 1995). A possible benefit of male-male social play sessions is to provide young males with coalition partners that may be important in their adult lives (de Waal, 1992; see chapter 10). (2) Social play may promote and fine-tune physical skills, such as those relating to fighting, hunting, and mating. (3) Social play may aid in the development of cognitive skills (Bekoff, 2000, 2004, 2007).

Play Fighting and Dominance in Later Life

One long-standing hypothesis for the function of social play among young individuals is that it positions them for rank acquisition in dominance hierarchies later in life. Some evidence has been found for this in chimpanzees and dogs, but these studies either have been of relatively short duration or involved a very low sample size (Paquette, 1994; Pal, 2010). The most comprehensive test of this hypothesis comes from a study of over 800 yellow-bellied marmots (*Marmota flaviventris*) living in a natural population in Colorado (USA). Blumstein and his colleagues gathered data on over 25,000 play fights among pups and true fights in yearling and adult (≥2 years old) marmots (Blumstein et al., 2013). Play fights contain many of the components of true fights, but pose no real danger of injury to pups. From the behavioral interactions recorded, Blumstein and his team constructed dominance hierarchies for play fights and true fights to test the hypothesis that rank in the former is positively correlated with rank in the latter. What they found was support for the hypothesis that rank in play fighting hierarchies did predict dominance ranks for yearlings but not adults (Figure 16.11; Box 16.3).

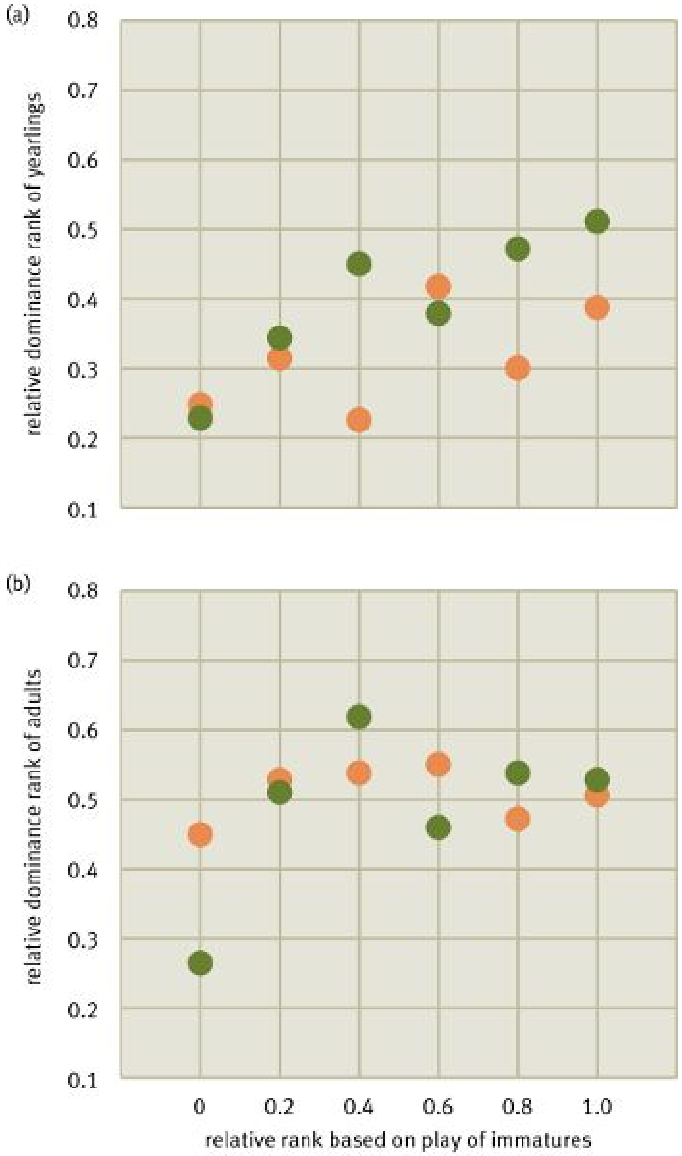


Figure 16.11. **Play in pups and subsequent rank in dominance hierarchy.** A pup's rank in a dominance hierarchy of play fights was positively correlated with dominance rank in yearlings but not adults in yellow-bellied marmots. By permission of the Royal Society. *(From Blumstein et al., 2013)*

Box 16.3. SCIENCE AT WORK

What is the research question? Does social play among young affect rank in subsequent dominance hierarchies?

Why is this an important question? Why animals play remains an unresolved question, in part because the function of play, including social play, remains understudied.

What approach was taken to address the research question? Researchers mapped hierarchies associated with play fighting in yellow-bellied marmots to subsequent hierarchies involving real fights in later life.

What was discovered? Rank in play fighting hierarchies predicted dominance ranks for yearlings but not adults.

What do the results mean? One function of social play in juveniles may be to prepare them for aggressive interactions as they mature.

Social Play and Cognition

Animals may use social play as a means to monitor their developmental progress as compared with others and to improve their self-assessment skills. For example, in young sable antelope (*Hippotragus niger*), individuals prefer same-age play partners, and Kaci Thompson hypothesized that in so doing, they are attempting to choose play partners that provide them with a reasonable comparison from which to gauge their own development (K. V. Thompson, 1996; Figure 16.12).

Figure 16.12. **Antelope play.** Young sable antelope like this pair often engage in play, particularly with same-age partners. *(Photo credits: Kaci Thompson)*

With respect to cognition skills and social play, one question that ethologists have addressed is, how do animals, especially young animals, know that they are engaged in play (Bekoff, 2000, 2004, 2007)? And, how do they communicate this information to each other? Since many of the behavior patterns seen during play are also common in other contexts—hunting, mating, dangerous aggressive interactions—how do animals know they are playing and not involved in the real activity? Marc Bekoff has proposed three possible solutions to this question (Bekoff, 2000).

One way that animals may distinguish play from related activities is that the order and frequency of behavioral components of play is often quite different from that of the equivalent real activity (N. Hill and Bekoff, 1977). When play behavior is compared with the adult functional behavior that it resembles, behavioral patterns during play are often exaggerated and misplaced. Young animals may be able to distinguish these exaggerations and misorderings of behavioral patterns by, for example, observing adults that are not involved in play.

A second, somewhat related, cue that animals may use to distinguish play from other activities is the placement of **play markers** (Bekoff, 1977, 1995; J. Berger, 1980; Pellis and Pellis, 2011; Petru et al., 2009; Palagi et al., 2016). **Play markers,** also known as play signals, can serve to initiate play, to indicate the desire to continue playing, and to warn adults that the young are playing and not in danger of injury. In canids, for example, biting and shaking are incorporated into the play behaviors of young canids, but are also used during dangerous activities such as fighting and predation. Bekoff found that play markers such as a bow often preceded biting and rapid side-to-side shaking of the head to indicate that they were not dangerous behaviors (and other work suggests that bows may reinitiate play sequences that are disrupted) (Bekoff, 1995; Byosiere et al., 2016; Figure 16.13). The bow may be a signal that this action should be viewed in a new context—that of play. Play markers can also be in the form of vocalizations—for example, chirping in a rat, whistling in a mongoose, panting in a wolf or a chimpanzee—before or during a play interaction.

Figure 16.13. **Play markers.** (A) Play signals and canine aggression. The dog on the right growls, while the dog on the left “paws.” Pawing is a play signal that can turn a potentially dangerous encounter into a playful one. (B) Play bows are also often used as signals that the bowing individual wants to play. The dog on the left is play bowing to another individual (not visible in the picture). *(Photo credits: Marc Bekoff)*

Play markers have been found in the lowland gorilla (Palagi et al., 2007; Waller and Cherry, 2012). Juvenile lowland gorillas play with each other often, and play ranges from what Elisabetta Palagi and her colleagues call “gentle play” to “rough play.” Palagi’s team discovered that when juvenile gorillas—particularly males—were involved with rough play, the play was often preceded by a facial gesture that the researchers call the “play face” (Figure 16.14). This facial gesture, which is not seen in other contexts, includes slightly lowered eyebrows and an open mouth (see Spinka et al., 2016, for work on play faces in Hanuman langurs, *Semnopithecus entellus*). In addition to using this facial gesture during rough play, juvenile gorillas also displayed it when a play session was in a place that made escape (leaving) difficult—another context in which it may be important to signal to others that “what is about to occur is play” (Box 16.4).

Figure 16.14. **Play face in gorillas.** Preceding bouts of aggressive play, juvenile gorillas use a facial gesture called a play face, which appears to signal play. *(Photo credit: William H. Calvin)*

Box 16.4. SCIENCE AT WORK

What is the research question? What are play markers and what is their function?

Why is this an important question? Many of the behaviors seen during play are also seen in other contexts, and ethologists have wondered how animals know they are playing and not involved in hunting, fighting, and so on. Play markers may be one means for doing so.

What approach was taken to address the research question? A play marker known as “the play face” (slightly lowered eyebrows and an open mouth) was studied in lowland gorillas.

What was discovered? Rough play, but not more gentle play, was often preceded by a play face.

What do the results mean? One way that animals might signal they want to play is through the placement of play markers before a bout of putative play.

A third way in which young animals may be able to distinguish play from related behaviors is by **role reversal**, or **self-handicapping**, on the part of their older playmates (Bekoff and Byers, 1998; Bekoff and Pierce, 2010; K. L. Graham and Burghardt, 2010). In role reversal and self-handicapping, older individuals either allow subordinate younger animals to act as if they are dominant during play, or the older animals perform some act (for example, an aggressive act) at an intensity below that of which they are capable. Either of these might provide younger playmates with the opportunity to recognize that they are involved in a play encounter.

Play Fighting and Role Reversal in Squirrel Monkeys

Squirrel monkeys (*Saimiri sciureus*) engage in play fighting from the age of five weeks, when infants start interacting with each other while still on their mothers’ backs (Baldwin, 1969, 1971; Biben, 1986; Dumond, 1968). Young squirrel monkeys prefer playing with same-sex partners, and role reversal occurs in male-male play bouts (Biben, 1986; Figure 16.15).

Figure 16.15. **Role reversal.** In play fighting between older and younger juvenile squirrel monkeys, role reversal sometimes occurs, wherein an older, larger playmate will allow a younger, smaller playmate to act as if it is dominant and to obtain the superior position when they wrestle.

Young male squirrel monkeys prefer to play with others lower in dominance rank (Biben, 1986; Boulton, 1991; Humphreys and Smith, 1987). Nonetheless, while their preference may be to play with those that are subordinate to them, squirrel monkeys play with individuals that are dominant to them. But why would subordinate individuals play with someone that is dominant to them (Altmann, 1962)? The answer appears to be that individuals that are clearly dominant *outside* the context of play often allow subordinates to take on the dominant role during play—that is, they engage in role reversal, wherein the subordinate does not defer to the dominant individual as he would outside the play situation, thus providing normally subordinate individuals with an incentive for playing.

Why are dominant males so quick to engage in role reversal when play fighting with same-sex partners? Part of the answer is that role reversal during play does not appear to influence the dominant/subordinate relationship *outside* of play, so the cost of role reversal is probably minimal. Yet, why bother with role reversal in the first place? It may be that without role reversal, dominant individuals would have few play partners, which could be costly, *if* play bouts provide individuals with benefits.

What might the benefits of play be for young male squirrel monkeys? One benefit might be that play fighting trains males for true aggressive behavior later in life. But, unlike the yellow-bellied marmots we discussed earlier, no evidence exists that those who play more win more fights later in life or those who win play fights win real fights. Maxeen Biben suggests three possible benefits to play fighting in squirrel monkeys (Biben, 1998):

1. Behavioral flexibility: Because play involves little in the way of costs to squirrel monkeys, it may be a means for individuals to learn how to be amenable to changing behaviors, and trying new options that they might not otherwise try.
2. Gauging the intentions of others: Real fighting in adult squirrel monkeys can be very dangerous. Play fighting might provide males with training in gauging the intentions of others in adult life.
3. Experience in both the subordinate and dominant roles: Males that end up as dominant in adult life must “work their way up” a dominance hierarchy. As they do, they will lose as well as win many encounters. Play fighting may teach males how to act both as a subordinate and as a dominant—roles they will encounter throughout life.

Which, if any, of these possible benefits drives play in the squirrel monkey system remains to be tested.

Box 16.5. COGNITIVE CONNECTION

Play and Brain Development

Fostering behavioral flexibility and complex cognitive processing may be among the functions of play in early life. Animal behaviorists have hypothesized that these putative functions of play might help explain why it is especially common in mammals, and in particular in primates (Byers, 1999; Fagen, 1981). But the role of brain development, a critical component of the cognitive processing that mediates play in primates, is less well understood. Although there is some evidence that the extent of play correlates with brain growth in adults, and that the size of some areas of the adult primate brain correlates with the degree of social play, very little is known about postnatal brain growth and the ontogeny of play in juvenile primates (Graham, 2011; Pellis and Iwaniuk, 2000).

Stephen Montgomery used comparative analyses to examine postnatal brain development in primates and its relationship to social, object, and locomotor play in juveniles (Montgomery, 2014). He used already published data on the percentage of an animal's time budget devoted to social play and nonsocial play, and employed a second unrelated database on brain development (adult size – size at birth = change in brain size) in these same species. Montgomery found a significant positive correlation between brain growth during ontogeny and the frequency of both social and nonsocial play (Figure 16.16).

Figure 16.16. **Play in primates.** Play has been studied in many species of primates, including baboons.

As we have discussed many times, correlation is not causation, but this study is a first step in studying how brain growth and juvenile play are linked.

A GENERAL THEORY FOR THE FUNCTION OF PLAY

Marek Spinka and his colleagues have hypothesized that the main function of play is to allow animals to develop the physical and psychological skills to handle unexpected events in which they experience a loss of control. They propose that “play functions to increase the versatility of movements used to recover from sudden shocks such as loss of balance and falling over, and to enhance the ability of animals to cope emotionally with unexpected stressful situations” (Spinka et al., 2001, p. 141). So, for example, the loss of control and balance associated with being chased by predators or losing an aggressive interaction may be dealt with more effectively if play allows animals to prepare for such events.

Spinka and his collaborators list twenty-four predictions that emerge from their hypothesis. Here we will touch on a few of these predictions. At the most general level, Spinka and his colleagues predict that the amount of play experienced will affect an animal's ability to handle unexpected events. While this prediction has not been directly tested, some correlational work in both humans and nonhumans supports it. In rats, for example, individuals deprived of social play often react more negatively to unexpected stimuli than those not deprived of play (Potegal and Einon, 1989). In humans, measures of rough-and-tumble play are sometimes correlated with scores on social problem-solving tests (Pellegrini, 1995; Saunders et al., 1999).

A second prediction is that self-handicapping, where dominant animals allow subordinates to defeat them during play fights, should be ubiquitous in species that play. Self-handicapping is thought to be an excellent means for preparing for the unexpected, as individuals put themselves in a position very different from that in which they normally find themselves. Evidence from many species supports the presence of self-handicapping in species that exhibit play.

During play, the brain must deal with sensory inputs that are different from the sensory inputs from other behaviors and with problems that must be solved by what Spinka and his group call "kinematic improvisation and emotional flexibility." As such, they predict that play should have measurable effects on an animal's somatosensory, motor, and emotion centers. In support of this prediction, rats that have been deprived of social play have long-term changes in opioid receptors, and they have permanently altered levels of dopamine and other neurotransmitters, all of which are important components of the stress response seen in these animals (Paul et al., 2005; Spinka et al., 2001; van den Berg et al., 1999).

One of the more obvious predictions from Spinka's general theory of play is that locomotor play should be most common in species that live in the most variable environments. If locomotor play allows one to experience loss of locomotor control, this effect might be most beneficial in environments that change most rapidly. More generally speaking, individuals that engage in play should be more prepared for the unexpected, which is more likely to occur where there is environmental change. Unfortunately, there is currently little evidence available to test this particular prediction.

Endocrinological and Neurobiological Bases of Play

So far we have focused our analysis primarily on ultimate questions about play behavior. In this section, we will take a more proximate perspective on play, by focusing on the endocrinological and neurobiological bases of play in rats and squirrels.

PLAY FIGHTING IN YOUNG MALE RODENTS

Male rats fight with one another from early on in development. While fights among adult males can be dangerous and can have significant effects on male reproductive success, aggression among younger rodents, including rats, often takes the form of much less dangerous play fighting (Figure 16.17). Here we will examine some work on the endocrinology and neurobiology of play fighting behavior in young male rodents.

Figure 16.17. **Play fighting in rodents.** (A) Djungarian hamsters (*Phodopus campbelli*); (B) fat sand jirds (*Psammomys obesus*); (C) Syrian golden hamsters (*Mesocricetus auratus*). *(Photo credit: © Serge Pellis)*

Testosterone and Play Fighting

Testosterone has long been linked to male aggression and much of the work on the endocrinology of play has focused on this hormone (R. Nelson, 2005). As discussed in earlier chapters, when examining the relationship between testosterone and aggression, it can often be difficult to assign cause and effect. For example, suppose you hypothesize that young male rats with high levels of testosterone are more likely to win play fights than males with lower levels of testosterone. If you took testosterone measures after a fight and found that males with higher levels of testosterone won more aggressive encounters, you would not be able to distinguish cause and effect—winning may be a result of high levels of testosterone, high testosterone levels may be a result of winning, or both. Even if you had been able to measure testosterone levels in males before they fought, and victors had high levels of prefight testosterone, determining cause and effect would still be difficult, as other factors may have caused an increase in both testosterone and the probability of victory—that is, testosterone level per se may not have caused an increased probability of winning play fights.

To see how experimental work can distinguish between cause and effect with respect to hormones and play fighting, let us examine the work of Serge Pellis and his colleagues on play fighting and testosterone in rats (Pellis, 2002; Pellis, Pellis, and Kolb, 1992). Play fighting in rodents typically involves attack and defense of the nape area around the neck, and males engage in this sort of activity significantly more often than do females. Early work suggested that sex differences in play fighting were related to testosterone levels, as males that were castrated at birth reduced their play fighting to levels typically seen in juvenile females, and young females whose levels of testosterone were experimentally increased were involved in more play fights (Beatty et al., 1981; Olioff and Stewart, 1978).

To experimentally examine the effect of testosterone levels on play fighting, Pellis and his team injected neonatal male rats with either testosterone propionate (TP) or oil as a control (Pellis, Pellis, and Kolb, 1992). They then compared play fighting of TP-treated and control rats between days thirty and thirty-six. Pellis and his team found that the rate of initiating playful attacks was significantly greater for TP-treated rats.

Evelyn Field, Pellis, and their colleagues next examined whether it was the presence of testosterone or the transformation of testosterone into other substances that affected play fighting in rats. To do so, they worked with a unique strain of rats, called the *tfm* strain (E. F. Field et al., 2006). Male *tfm* rats have testes that secrete normal levels of testosterone, but they lack the gene associated with the production of testosterone receptors, and their appearance is feminized (Purvis et al., 1977; Yarbrough et al., 1990). Because they lack this gene, the typical process in which some testosterone is transformed into estrogen by the aromatase enzyme in the liver does not occur in male *tfm* rats (McCarthy, 1994; Olesen et al., 2005; K. L. Olsen and Whalen, 1982). Pellis and his team reasoned that work with *tfm* males would allow them to determine whether it was the presence of testosterone or the transformation of testosterone into estrogen that was most important in the development of male play fighting. Their results suggest that both the production of testosterone and its transformation (called aromatization) to estrogen are important in the development of play fighting in males, though some components of play fighting are more tightly tied to the former, and other components are linked more closely to the latter (E. F. Field et al., 2006).

Neurobiological Approaches to the Study of Play

Ethologists have also examined the neurobiology and neurochemistry of play (Siviy and Panksepp, 2011; Siviy, 2016; Palagi and Fouts, 2016). Broadly speaking, neuroethologists use one of two techniques to study play behavior. In the first, neurotransmitters are targeted to examine their role in play (inhibition, stimulation, and so on), and in the second, the neural pathways involved with a particular form of play are targeted, either by making surgical lesions or by some pharmacological means that activate a neural pathway (Auger and Olesen, 2009; Siviy and Panksepp, 2011; van Kerkhof et al., 2013).

When examining neurotransmitters and their role in social play, researchers systemically administer a compound that either blocks or enhances a particular neurotransmitter (Auger and Olesen, 2009; Siviy, 2016; Kerkhof et al., 2013). If they do so with enough neurotransmitters, a broad picture of the neurochemistry of play emerges. For example, three neurotransmitters, dopamine, norepinephrine, and serotonin, seem to be involved in rat play fighting.

Dopamine inhibitors typically reduce play (Beatty et al., 1984; Holloway and Thor, 1985; Niesink and Van Ree, 1989; Siviy et al., 2011). Rather than looking at dopamine in terms of increasing or decreasing play activities, however, a number of researchers have argued that dopamine's most important function may be to invigorate or prime an animal to prepare for play (Blackburn et al., 1992; Salamone, 1994; Siviy, 1998).

Because rats can be trained to anticipate play, it is possible to directly test whether anticipation of play is linked to changes in dopamine levels (Humphreys and Einon, 1981; Normansell and Panksepp, 1990). Stephen Siviy constructed an experimental apparatus that consisted of two chambers connected by a tube, and counted the number of times that rats crossed the tube each day (Siviy, 1998; Figure 16.18). Two groups of rats were tested. Those in the play treatment were allowed to play with another rat in the experimental apparatus for five minutes each day. Those in the control treatment had five minutes in the apparatus, but no other individual was present, and so no social play occurred. Rats in the play treatment crossed back and forth in the tube *before* their partner was placed in the experimental apparatus much more than did rats in the control condition at the same point in time.

Figure 16.18. **Experimental device for studying play.** This experimental apparatus was used to study the role of neurotransmitters in rat play behavior. *(Photo credit: Steven Siviy)*

One interpretation of Siviy's experiment is that rats in the play treatment anticipated the opportunity for play and searched for it, increasing their number of crossings. To further examine this possibility, half the rats were given a dopamine inhibitor drug. These rats reduced their tunnel crossings significantly, but their play behavior, once a partner was present, remained level, providing support for the idea that dopamine acts to increase the anticipation of play (Figure 16.19). Dopamine may also be involved in the increase in the "chirping" sound that is often heard during rat play but not at other times (Panksepp, 2005; Panksepp and Burgdorf, 2003). By neurochemically stimulating dopamine receptors in the rat brain, researchers have increased the rate of chirping, and behavioral geneticists have even bred strains of rats that chirp excessively during play (Burgdorf et al., 2005).

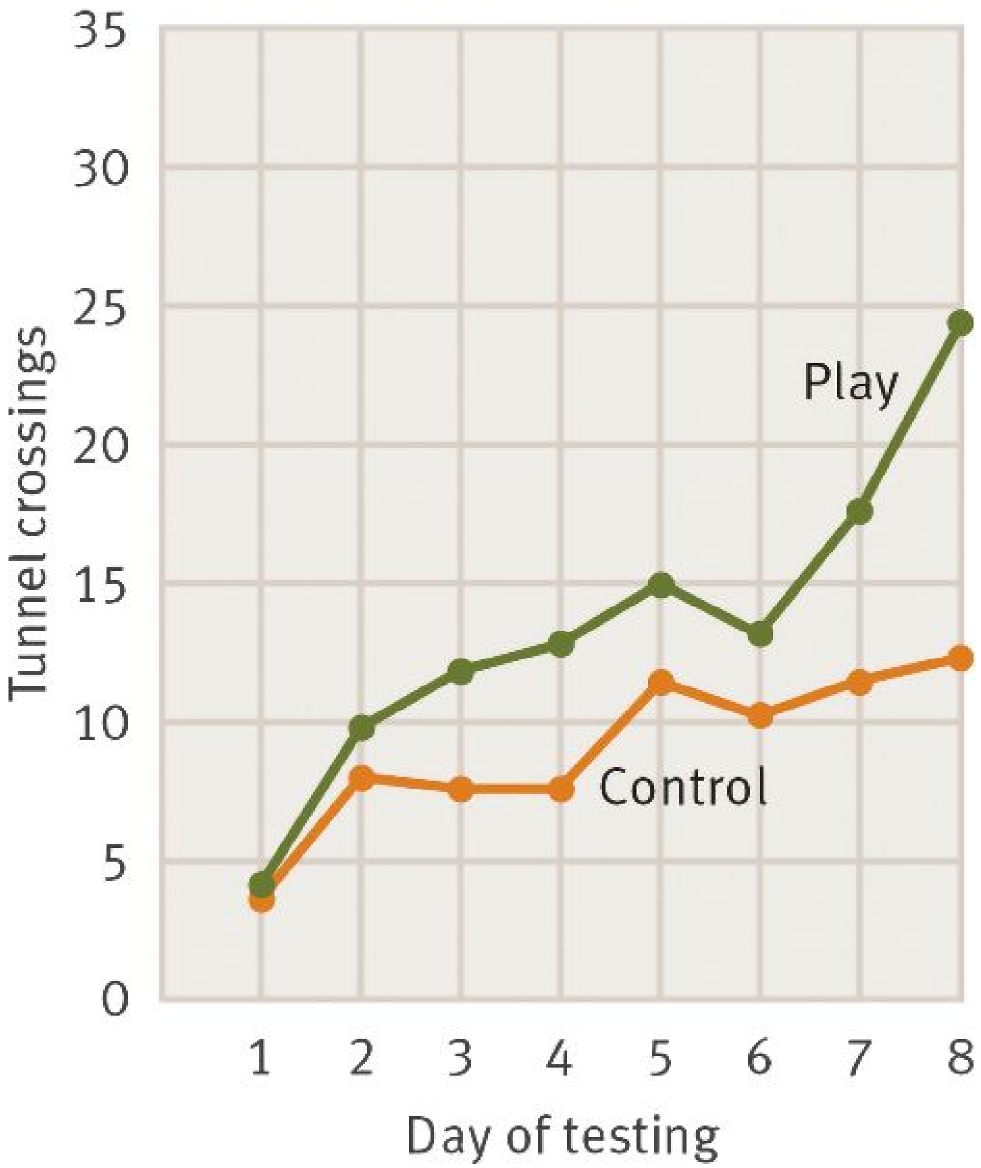


Figure 16.19. **Anticipating play.** Mean number of tunnel crossings in rats. Rats in the play treatment were given a five-minute opportunity to play with a same-age partner in an apparatus right before the test. Control animals had no such opportunity. *(Based on Siviy, 1998, p. 229)*

A Phylogenetic Approach to Play

Muroid rodents have been the subject of many ethological studies of play. The phylogeny of this family of rodents is fairly well established and a wide range in the complexity of play has been observed in this family (Jansa and Weksler, 2004; Pellis and Iwaniuk, 1999). Serge Pellis and Andrew Iwaniuk examined this range of complexity in a phylogenetic context and tested whether species with relatively complex play share a common ancestor, and whether species with simpler play repertoires share a different common ancestor that displayed simpler forms of play.

To begin their analysis, Pellis and Iwaniuk developed a composite score for play “complexity” for each of the thirteen muroid rodent species they examined. These composite scores—ranging from 0 to 1—were based on seven different measurements of play seen in rodents. Higher scores indicate greater play complexity. Values for this complexity measure varied from 0 in *Pseudomys shortridgei* to 0.94 in *Rattus norvegicus*. The researchers tested whether similarities in complexity scores were, in part, the result of common ancestry (Maddison and Maddison, 1992; Pellis and Iwaniuk, 1999). None of the aspects of play fighting that were examined could be explained by phylogenetic history per se; closely related species of rodents were no more likely to share similar play complexity scores than were species that were much more distantly related.

Pellis and Iwaniuk’s phylogenetic analysis suggests that the ancestral state of play in muroids was moderately complex (Figure 16.20). From this state of moderate complexity, species independently evolved either more complex or less complex play-fighting repertoires. This hypothesis remains to be tested, but if future works is in line with its predictions, it will reshape the way play evolution is conceptualized, in that ethologists would need to understand what selective forces act to make play more complex in some lineages, but less complex in others.

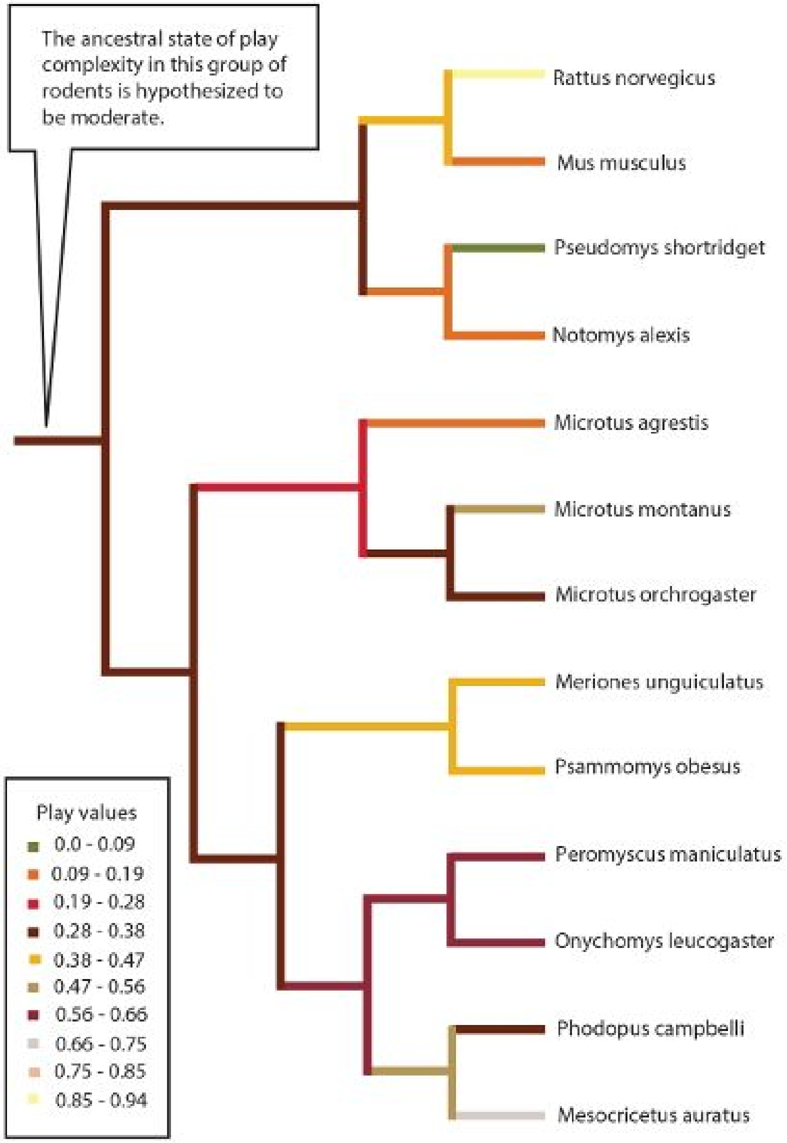


Figure 16.20. **The phylogeny of play in rodents.** The pattern of play complexity was mapped onto a phylogeny of muroid rodents. An analysis of the distribution of play complexity suggests that a moderate level of play (0.28–.38 on a scale of 1) was the ancestral state in this group. Reprinted by permission of Elsevier Ltd. © 1999. *(From Pellis and Iwaniuk, 1999)*

Interview with Dr. Marc Bekoff

What do researchers have to document before they feel comfortable calling some behavior "play"?

This is a very good question, but I think that it's difficult to know that a behavioral interaction is play until it actually begins. In canids, for example, one would look for a play signal, such as the "bow," to know that at least one of two dogs, coyotes, or wolves wants to play and is saying "I want to play with you, not fight, mate, or eat you," and then see what the recipient of the bow or other signal does. Then, as the interaction ensues one would look for a variety of actions used in sequence and perhaps a bow or other play signal being used to punctuate the interaction to make sure that play remains "the name of the game." When bows, for example, are used during an encounter the message is "I still want to play with you" or "I'm sorry I bit you too hard, let's keep playing." Cooperation, apology, and forgiveness are part of the interaction and our data on dogs, coyotes, and wolves shows this to be so. Of course some play interactions begin spontaneously, especially between animals who know one another, but even then it's most usual to see some sort of play signal. So, it's the presence of a play signal at the beginning and then seeing them used from time to time during an encounter that helps one reliably say this is play.

How do you avoid anthropomorphism—attributing human emotions to nonhumans—when studying play?

Of course it's impossible not to use words that describe human emotions to describe, interpret, and explain the behavior of nonhuman animals so this isn't unique to play. Using solid evolutionary theory about evolutionary continuity as argued by Charles Darwin, it's safe to say that "if we have something, 'they' (other animals) have it too." The differences among animals are differences in degree, not kind. With respect to play, it's clear by watching and very carefully describing what the animals are doing, that they feel safe and secure and are comfortable letting another animal bite or mount them. They trust their play partner that play is the name of the game. It's also clear that animals enjoy playing—it's a voluntary activity and animals can be unrelenting in trying to get another animal to play. Play is also contagious and it's common to see play spread among a group of animals after some begin playing. All mammals, for example, share the same structures in the limbic system that are important for processing emotions so in fact, the "problem" of anthropomorphism actually disappears *because we're not inserting something human into other animals that they don't already have*. I've written about what I call "biocentric anthropomorphism," which simply means that we need to take into account the nature of the animals about which we're talking and be very careful about the words we use.

Is it possible to experimentally examine whether animals enjoy play?

I think so, but perhaps right now we don't have the ability to do so in a noninvasive way that doesn't change the behavior of the animals involved. One way could involve somehow taking blood from the animals who are "on the run," and other than a pin prick it wouldn't involve any pain. And, when animals are playing I expect they wouldn't feel a pin prick. Another would be to do some brain imaging as the animals are playing to see what areas of the brain light up. However, I think that we already know that there is something very enjoyable about play because it's voluntary, animals seek it out, and they wouldn't seek out something that's not enjoyable, and also because across species we see that clear and unambiguous signals have evolved that allow play to continue without escalating into a fight or attempt to mate. Arguments from analogy appealing to evolutionary continuity go a long way here but I'm optimistic that in the future we will be able to do some really neat noninvasive neural imaging that will clearly show that animals truly enjoy playing.

What is the most unexpected thing you've learned from your own work on play behavior?

When I first began studying play decades ago I was told it was a waste of time—that animals didn't play, that the category of play didn't exist, or that it was so complex it was impossible to study. A small number of people told me that play was a wastebasket category of behavior and when someone didn't really understand what animals were doing they called it "play." I persisted and am thrilled that I did because not only did I learn that variations in play style are related to the life history patterns of various species, in my case members of the dog family, but also that we could learn a lot about the evolution of social communication. I suppose that the most unexpected thing that I've learned is how play is very carefully negotiated to make sure that it remains fair, and that among coyotes, at least, playing fair appears to be related to individual fitness. These data emerged after years of study and thousands of hours of observation but it seems that coyotes who don't play fair don't form strong social bonds with other group members and they often leave their group of their own accord, rather than being forced out. Other coyotes ignore them and they leave, and individuals who leave their group suffer as much as four times higher mortality than those who remain with their group. Of course, that playing fair has a fitness component isn't all that surprising if one understands how natural selection operates.

What do you see as the next frontier in play research?

It's clear that we need the nitty-gritty details of what animals do when they play. There's no substitute for watching animals play by studying videos of what they do when they're on the run—how they ask another individual to play and how they maintain the play mood. From our own work on play it's clear that play is important in the development of knowing what's right and what's wrong, moral sentiments if you will, what I call “wild justice.” I see the next frontier as learning much more about how play is related to the ways in which individuals learn species-specific rules of social engagement. It’s clear from our own and others’ research that play is related to moral development and is the way in which individuals acquire the social skills that are needed to interact fairly and cooperatively, and that this ability is important for maintaining the integrity and stability of social groups such as wolf packs. What’s really exciting is how what we’re learning about the development of play and what’s right and what’s wrong in nonhuman animals is very related to what we’re learning about the development of play and moral development in young humans.

Dr. Marc Bekoff is emeritus professor at the University of Colorado. He is well known for his pioneering work on animal play behavior and animal rights.

SUMMARY

1. The most widely accepted definition of play is “all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing. If the activity is directed toward another living being, it is called social play” (Bekoff and Byers, 1981).
2. Ethologists studying play behavior generally delineate three types of play: object, locomotor, and social play.
3. From a functional perspective, object play in young animals tends to be associated with practice that will benefit the animal either in the short or long term and is tied to learning.
4. One hypothesis for the function of locomotor play in animals and humans is that it both provides general exercise and trains specific motor skills needed later in life.
5. The benefits of social play include forging long-lasting social bonds; honing physical skills, such as those relating to fighting, hunting, and mating; and aiding in the development of cognitive skills.
6. One general theory of play hypothesizes that play allows animals to develop the physical and psychological skills to handle unexpected events in which they experience a loss of control.
7. Neuroethologists often use two techniques to study play behavior. In one, certain neurotransmitters are targeted and either inhibited or stimulated to examine their role in play. In another, the neural pathways involved with a particular form of play are targeted and studied by making surgical lesions or using some pharmacological means to activate a neural pathway to determine what brain areas are affected, what gene products are involved, and what changes are occurring in neurons.
8. Play has been studied extensively across many species of rodents, and phylogenetic analysis of play in this group suggests that a moderate level of play is the ancestral state of rodent play in this group.

DISCUSSION QUESTIONS

1. Based on what you have learned in this chapter, try to construct a definition of play. After you have done so, answer the following questions: Does your definition cover all cases of play? Does it cover behaviors that you don't consider to be play?
2. It is very difficult to study whether play is enjoyable to nonhumans. Can you construct an argument that it is, at least in principle, possible to know the answer to this question? If so, what would your argument be? If not, can you give other reasons why you believe we can't know whether animals enjoy play?
3. Recall from the start of the chapter Gordon Burghardt's work with play in turtles. How could this sort of study help in the design of animal habitats in zoos?
4. Think about play in young children. Does reading a book for pleasure count as play? Does watching a movie or television show or playing a video game count as play? If they are considered play, how might these activities fit into Spinka's hypotheses about play?
5. Some researchers have suggested that play facilitates creativity. After constructing your own definition of creativity, how would you test this hypothesis? Can you construct tests that measure both the behavioral and neurobiological/endocrinological correlates of play as they relate to creativity?

SUGGESTED READING

Burghardt, G. (2005). *The genesis of animal play: Testing the limits*. Cambridge, MA: MIT Press. A thought-provoking book on ethology and play.

Graham, K. L., & Burghardt, G. M. (2010). Current perspectives on the biological study of play: Signs of progress. *Quarterly Review of Biology*, *85*, 393–418. An overview and synthesis of work on animal play.

Held, S. D. E., & Spinka, M. (2011). Animal play and animal welfare. *Animal Behaviour*, *81*, 891–899. An examination of ways the study of animal play can inform work on animal welfare.

Palagi, E., & Fouts, H. N. 2016. Motivation of play: From ethological to neurological perspectives. *Behaviour*, *153*, 655–662. A review of motivational aspects of play behavior.

Spinka, M., Newberry, R., & Bekoff, M. (2001). Mammalian play: Training for the unexpected. *Quarterly Review of Biology*, *76*, 141–168. Lays out the argument that training for unexpected events is central to understanding both the proximate and ultimate underpinnings of play behavior.

17

Animal Personalities

Individuals living in a colony of the social spider *Anelosimus studiosus* show none of the dramatic morphological differences seen within colonies of social insects, and there are no castes (foragers, guards, and so on). But work on *A. studiosus* has found that females tend to have one of two different personality types: they are either “docile” or “aggressive” (Wright et al., 2014, 2016; Grinsted and Bacon, 2014). Aggressive females, as per their moniker, act aggressively in defending the colony from predators, but are also aggressive toward other females and toward their own mates. Docile females are less aggressive and devote more time and energy toward parental care than do aggressive females (Figure 17.1). Similar personality types have been found in other social spider species (Lichtenstein and Pruitt, 2015; Modlmeier et al., 2015).

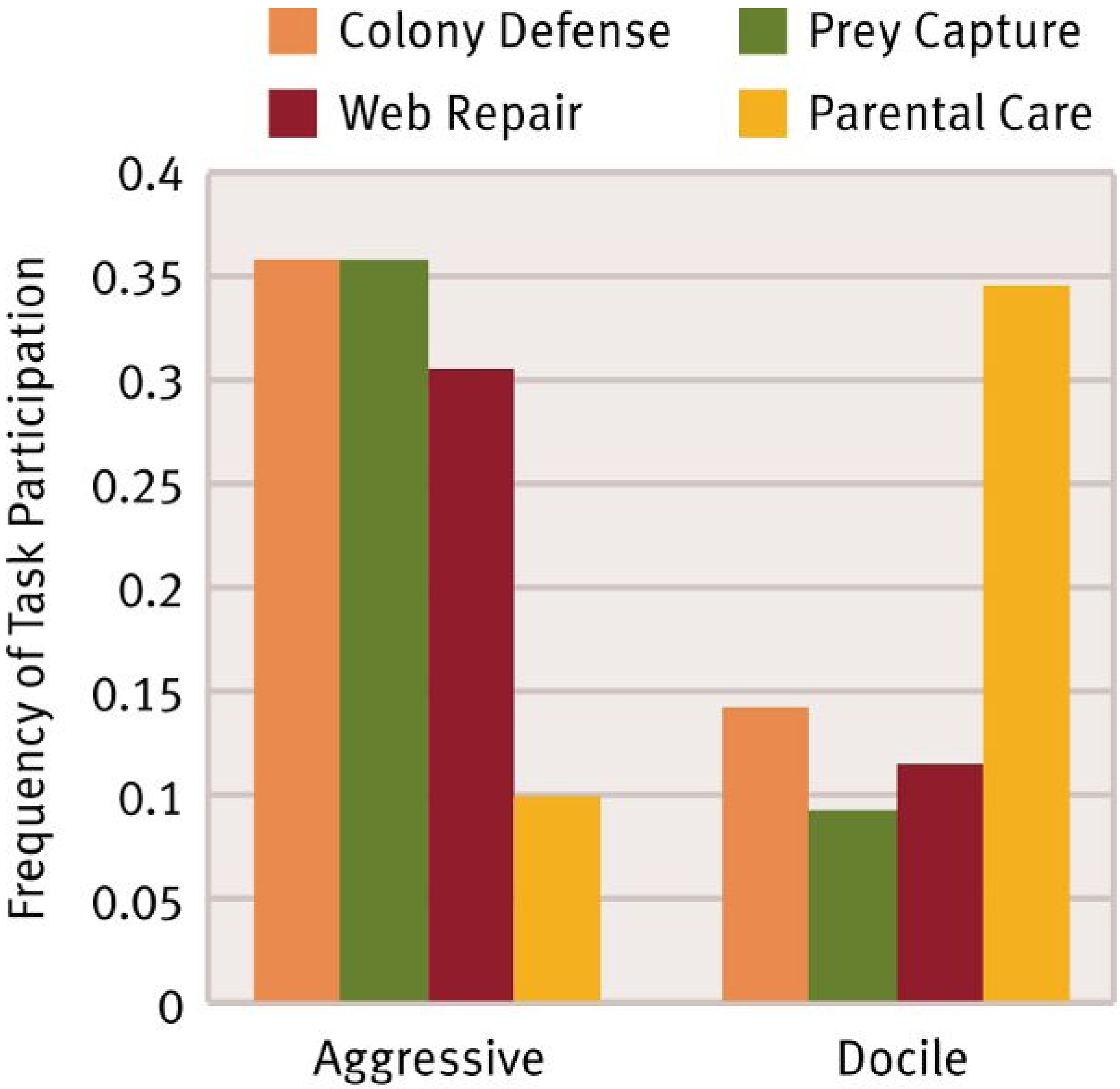


Figure 17.1. **Specialization and spider personality types in *Anelosimus studiosus***. Aggressive and docile females specialize on different subsets of behavior within a colony (n = 15 colonies). *(From C. M. Wright et al., 2014)*

Because other work had found that females are either consistently docile or consistently aggressive throughout their lives, Colin Wright and his colleagues used experimental colonies to test how efficient docile and aggressive females were at the tasks at which they specialized. Aggressive females were more than twice as efficient at capturing prey than docile females, and built webs that lasted longer than those built by docile females. Docile females were better at raising young than aggressive females (who sometimes attacked or even cannibalized their young), with docile females' spiderlings having a significantly higher probability of survival through the fourth instar stage when clutch size was high (Figure 17.2).

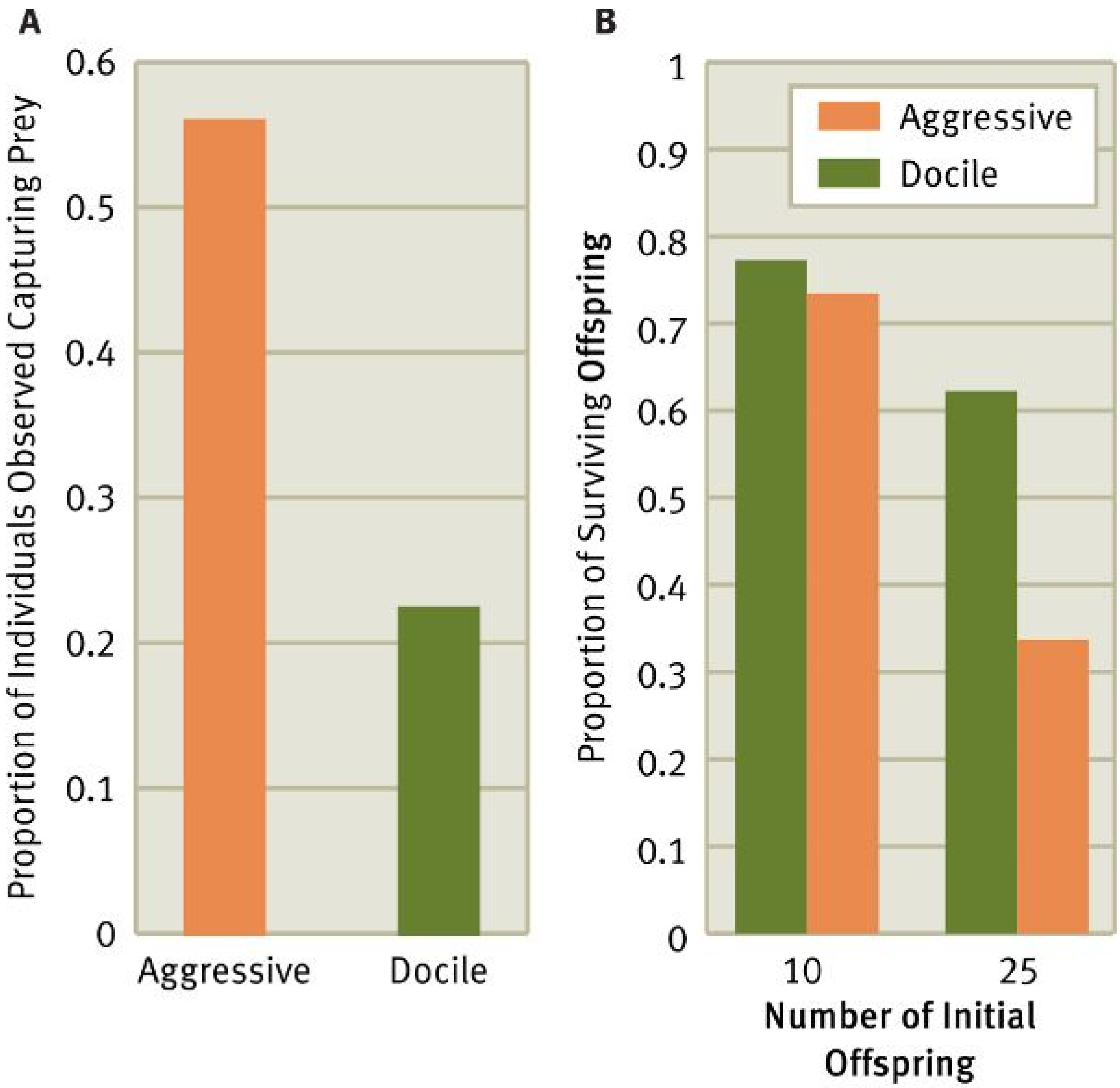


Figure 17.2. **Spider personality and efficiency on different task types.** Aggressive *Anelosimus studiosus* females were better than docile females at capturing individual prey (A), but a significantly greater proportion of docile females' offspring survived through the fourth instar stage (B). *(From C. M. Wright et al., 2014)*

How much of the differences in task efficiency across personality types is due to learning versus innate differences is not yet known, nor is it clear how both types remain in populations over evolutionary time, but the *A. studiosus* system is ripe for answering this and other questions about animal personalities.

* * *

In ethology a **personality type** is defined as a suite of behaviors that show consistent, long-term differences between individuals (A. M. Bell, 2007; Caro and Bateson, 1986; Carere and Maestripieri, 2013; A. B. Clark and Ehlinger, 1987; Dingemanse and Reale, 2005; Pervin and John, 1997; Stamps, 2007; M. M. Webster and Ward, 2011; A. M. Bell and Aubin-Horth, 2010; David and Dall, 2016; Garamszegi et al., 2012). Personality traits may be heritable (Dingemanse and Reale, 2005; Dochtermann et al., 2015; Monceau, 2015). In addition, individual learning and social learning, especially when such learning occurs early in development, can have long-term effects on personality development. Synonyms for personality in the animal behavior literature include **coping style**, behavioral syndrome, and temperament.

Watch a group of animals, chimpanzees, for example, long enough, and you will notice consistent, individual differences among group members. Once you get to know a chimp's personality, you can even predict, in a general fashion, how it will act when placed in a new behavioral scenario. The same is true for many animals, most of whom are not nearly as closely related to humans as chimps are. In the sticklebacks that we discussed numerous times throughout this book, there are "bold" and "inhibited" fish. If we test a series of sticklebacks over and over again in the presence of danger, we end up with very distinct behavioral types. Some fish are willing to take risks and inspect the source of this danger, and others aren't.

As one example of how ethologists study personality, let's look at Alexander Weiss and his colleagues' study of orangutans. For many years, psychologists have used subjective well-being scales as one way to measure personality traits. Observers are asked to rate a person on a scale (from 1 to 7) with respect to such behaviors as positive versus negative mood, pleasure derived from social interactions, and ability of the individual to achieve his or her goals. These scales have been modified to measure well-being in nonhuman primates (King and Landau, 2003; King et al., 2005; Uher, 2008; Uher and Asendorph, 2008; A. Weiss et al., 2012), and Weiss and his team measured subjective well-being in 172 orangutans housed in zoos (M. J. Adams et al., 2012; A. Weiss et al., 2006, 2011).

Data from seven years of observation found that some orangutans scored high on subjective well-being and that those orangutans showed low rates of neurotic behavior and high levels of extraversion and were generally agreeable in interactions with other orangutans and with their zookeepers. Other orangutans showed the opposite set of traits: two very different personality types exist in this population of orangutans. When Weiss and his team looked at mortality data on these animals, they found something remarkable: Orangutans that were rated as scoring high on subjective well-being measures—animals that appeared subjectively happier—lived longer than those that scored lower on subjective well-being. The difference between one standard deviation above and one standard deviation below average scores on subjective well-being translated into an orangutan living an average of 11.34 years longer (A. Weiss et al., 2011; Figure 17.3).

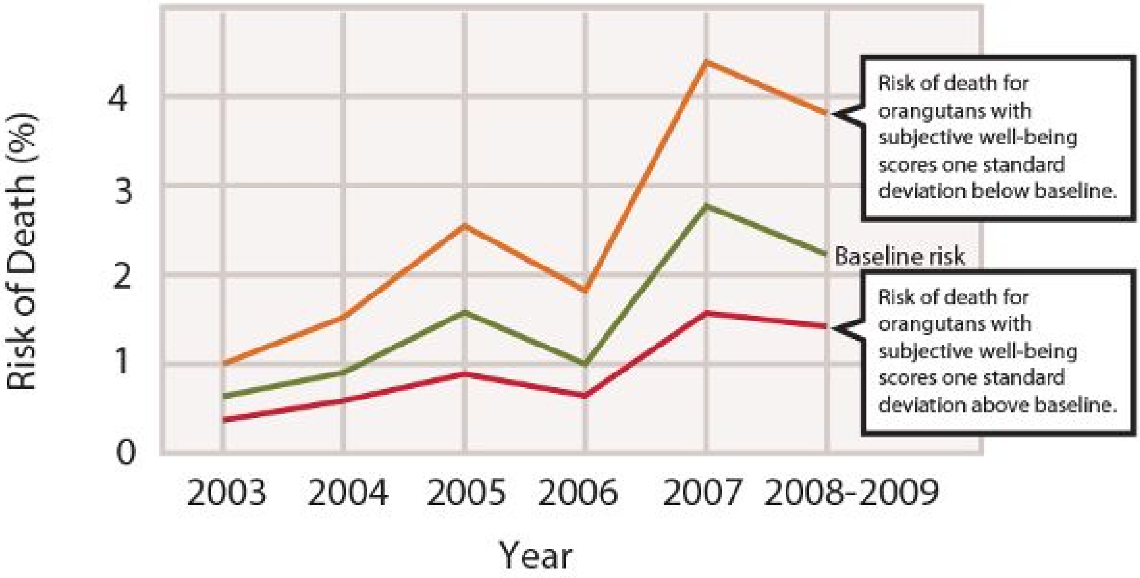


Figure 17.3. **Subjective well-being and mortality.** Orangutans that score high on subjective well-being measures live longer than baseline value; those that score low on subjective well-being measures live shorter than baseline values. The difference between one standard deviation above and one standard deviation below average scores on subjective well-being translated into living an average of 11.34 years longer. Reprinted by permission of The Royal Society. © 2011. *(From A. Weiss et al., 2011)*

We can cast our discussion of animal personalities in a theoretical mold by viewing individual differences in the language of evolutionary game theory (A. M. Bell, 2007; Dall et al., 2004; Dingemanse and Reale, 2005; Reale et al., 2007; Sih et al., 2004a,b.) Recall that game theory models often produce a solution that contains more than one behavioral strategy—for example, hawks and doves, or cooperators and defectors (chapters 10 and 15). If individuals adopt strategies for long periods of time, such strategies can be thought of as personality traits. To see how this might work, let's return to the producers and scroungers discussed in chapter 11. When foraging in groups, animals sometimes adopt one of two very different strategies. Producers search for food, so they accrue the costs associated with uncovering new food patches. Scroungers watch producers, and learn where new food patches are by parasitizing the work of producers.

Barnard and Sibly constructed a game theory model of the producer-scrounger scenario that we can use as a baseline model of personality types (Barnard and Sibly, 1981; Figure 17.4). The solution to this game is some combination of both producers and scroungers, and the equilibrium frequency of each strategy depends on the exact costs and benefits associated with producing and scrounging. In any game theory model, solutions that contain more than one behavioral strategy can be conceptualized in at least two ways. Imagine that the equilibrium frequency of producers is 50 percent, and the equilibrium frequency of scroungers is 50 percent. This might translate into each individual in a group using the producer strategy 50 percent of the time and the scrounger strategy the remaining 50 percent of the time. Alternatively, we might see 50 percent of the individuals in a group consistently adopting the producer strategy and 50 percent of the individuals adopting the scrounger strategy (Figure 17.5). When the latter is true—and it often is—the producer-scrounger game can be thought of in terms of personality traits (Giraldeau and Caraco, 2000).

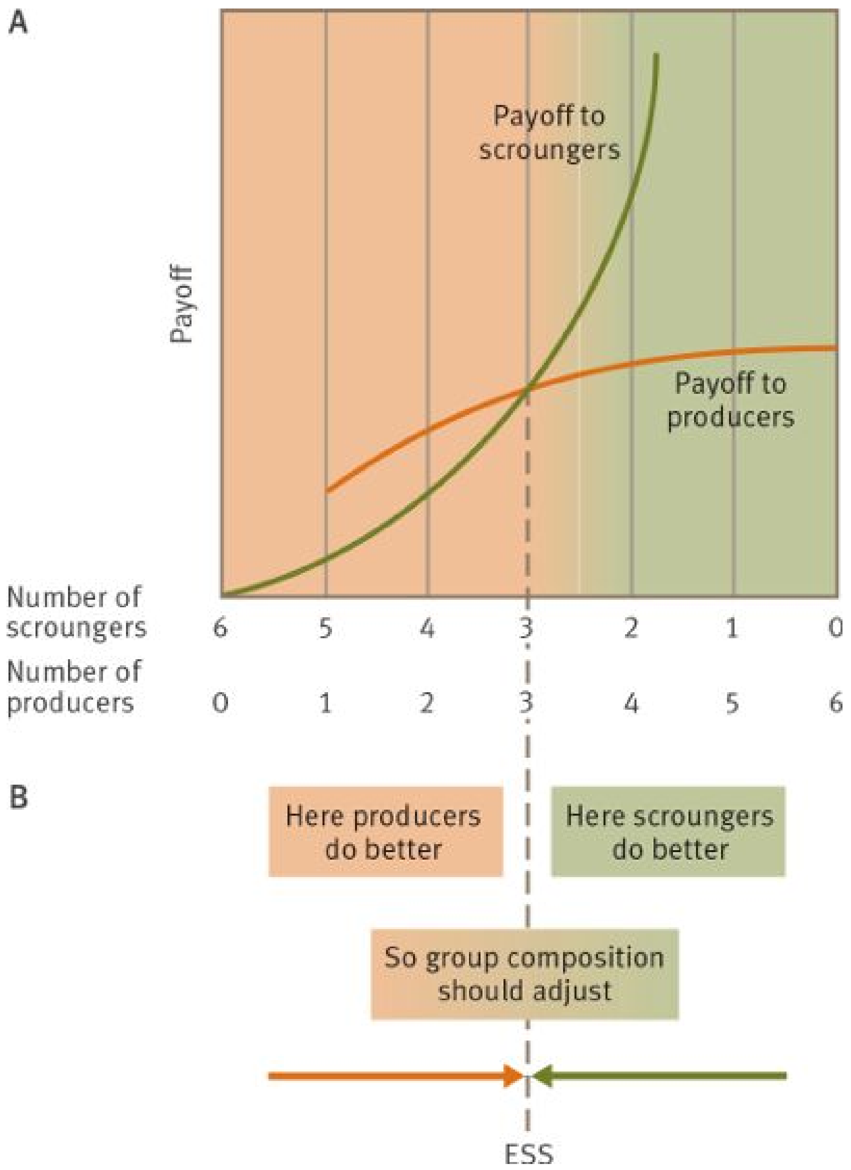


Figure 17.4. **Producers and scroungers.** (A) Hypothetical payoff to producers and scroungers as a function of group composition, and (B) the evolutionarily stable strategy, given the payoffs in panel A. *(From Barnard and Sibly, 1981)*

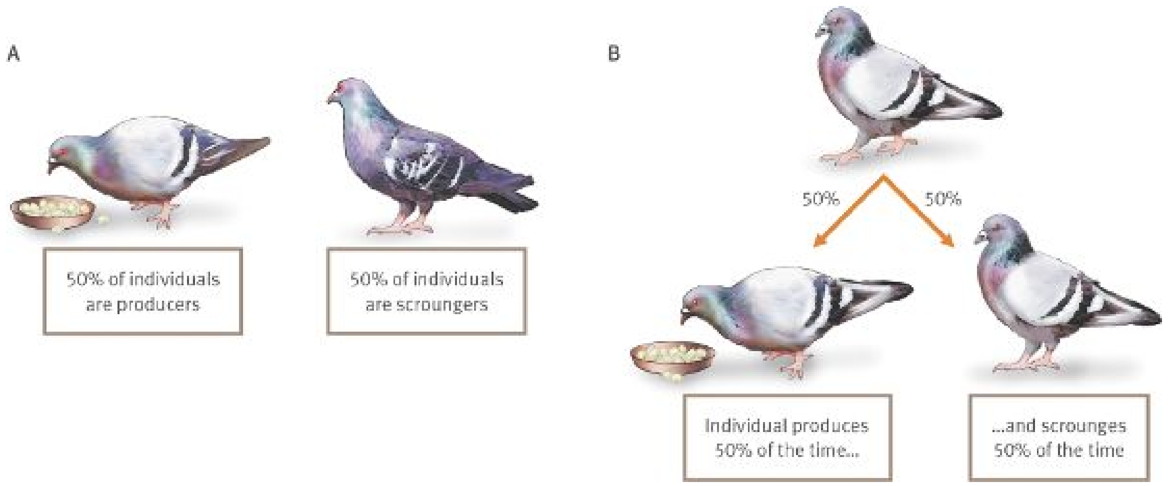


Figure 17.5 Behavioral strategies. Suppose a producer/scrounger model predicts an equilibrium of 50 percent producers and 50 percent scroungers. This can occur by either (A) having 50 percent of the individuals play producer and 50 percent of the individuals play scrounger, or (B) having individuals act as producers 50 percent of the time and as scroungers 50 percent of the time.

The producer-scrounger game helps us cast the evolution of personality types in a theoretical framework. This model applies not only to food producers and scroungers per se, but for any situation in which there are personality types with the same kinds of costs and benefits associated with producers and scroungers. For example, in many group-living species, some individuals take on the role of leaders, directing the orientation and movement of a group, and others are followers. Recent work in groups of barnacle geese (*Branta leucopsis*) has found consistent leaders, who tended to be bold risk takers, and followers, who tended to be less bold than leaders (Kurvers et al., 2009, 2011; Liste et al., 2014; Figure 17.6). A leader is likely to have first access to new resources but may pay various costs—predation, parasitism—that followers do not. In that sense, the payoffs to leaders and followers are similar, but not identical, to those for producers and scroungers, and so we can apply the game theory to a different set of personality traits: leader and follower (Box 17.1).

Figure 17.6. **Leadership and novel objects.** In barnacle geese, birds that were leaders—directing the orientation and movement of their groups—were also more willing to explore novel objects than were follower geese. Reprinted with permission of Elsevier Ltd. © 2009. *(From Kurvers et al., 2009)*

Box 17.1. SCIENCE AT WORK

What is the research question? How can game theory models be used to study personality?

Why is this an important question? Work on animal personality lacks a strong theoretical underpinning, and game theory models may provide such a framework.

What approach was taken to address the research question? Ethologists applied the producer-scrounger game to the evolution of personality types.

What was discovered? The producer-scrounger game predicts a mix of personality types. The model can be applied to other situations in which the costs and benefits are similar to these in the producer-scrounger game.

What do the results mean? Game theory models of social behavior can be used to address questions with respect to the evolution of personality.

Producers and scroungers and leaders and followers are only two ways in which personality traits manifest themselves in animals. In this chapter, we will examine

- bold and inhibited personality types,
- case studies of personality across an array of species and ecological conditions,
- differences in coping styles

Boldness and Shyness

Psychologists have found that where a person falls on the continuum from very shy to very bold behavior is one of the most stable personality variables in humans. If you are shy when you are young, chances are very good that you will be shy when you get older (Kagan, 1994; Kagan et al., 1987, 1988, 1989). While definitions of shyness and boldness vary considerably, **boldness** usually refers to the tendency to take risks in both familiar and unfamiliar situations, while **shyness** refers to the reluctance to take such risks, or even a reluctance to engage in unfamiliar activity at all. In the language of psychology, shyness is similar to behavioral inhibition, while boldness is similar to sensation seeking (M. Zuckerman, 1979, 1994).

While a great deal of work has been undertaken to examine both inhibition and boldness from psychological, psychiatric, and physiological perspectives, until recently little in the way of controlled experimental work examined the *costs and benefits* of inhibition and boldness. From an ethological perspective, this omission is striking, as a thorough understanding of the evolution of inhibition and boldness is only possible when we understand the costs and benefits associated with these traits.

BOLD AND SHY PUMPKINSEEDS

David Sloan Wilson and his colleagues have studied shyness and boldness in pumpkinseed sunfish (*Lepomis gibbosus*; Figure 17.7). They used two trapping methods that allowed them to segregate shy and bold fish in natural populations (D. S. Wilson et al., 1993; Figure 17.8). The first technique was to place traps in the water. In effect, these underwater traps were meant to mimic the “novel object” test that psychologists use to classify humans along the shy-bold continuum. The traps were designed so that a pumpkinseed fish would have to actively swim into them to be collected, but once a fish was inside, the construction of the trap was such that it was very difficult for the fish to get out: traps would primarily capture bold sunfish, who would be the ones willing to enter the trap in the first place.

Figure 17.7. **Bold and shy fish.** Pumpkinseed sunfish have been studied extensively in order to understand the evolution of boldness and shyness. *(Photo credit: Rostislav Stefanek / Shutterstock)*

Figure 17.8. **Experimental setup to study bold and shy fish.** Two experimental techniques were used to examine boldness and shyness in pumpkinseed sunfish: in one, a large seine was dragged through a pond; in the other, underwater traps were used to capture fish.

The second technique for capturing fish involved dragging a large net called a seine through the pond. Seining occurred immediately after all underwater traps were collected, and it was done in such a manner as to capture as many sunfish in the vicinity of the traps as possible. Seining, then, should capture a combination of both inhibited and bold fish, while the trapping method should have captured, on average, bolder fish than the seining method. In addition, the researchers ran a control in which trapped fish were placed in a seine and run through the pond for thirty seconds (approximately how long it takes to run the seine through a pond). This was done to test whether the seining process itself was more traumatic than the trapping process, and hence might account for any differences found between seined and trapped fish. The results indicated that it was not.

Wilson and his colleagues next examined the diets of trapped and seined fish, their parasite loads, and their growth rates. In addition, they tagged and released fish back into the pond, and then made detailed observations of these marked fish. In one experiment in which both trapped and seined fish were tagged and released back into their pond, behavioral observations indicated that trapped fish were less likely than seined fish to flee from human observers, as might be expected from bolder fish, and in general, the behavioral observations of pumpkinseeds in their natural habitat suggest that the researchers indeed collected different proportions of bold and inhibited fish using the two techniques.

In ponds, trapped (bolder) fish were more likely to forage away from other fish, and their diet contained three times as many copepods—small crustaceans that are the usual food of pumpkinseeds—as did the diet of seined (shier) fish (Ehlinger and Wilson, 1988; D. S. Wilson et al., 1996). In addition, trapped and seined fish differed in terms of the parasites they carried, suggesting different habitat use based on personality types. The diet and parasite data in conjunction with the behavioral observations suggest that bold and shy fish, though caught in the same pond, behave quite differently in nature, though behavioral observations suggest that bold and shy fish were not segregating into distinct groups.

Once seined and trapped fish were brought into the laboratory, Wilson and his colleagues ran a suite of behavioral and physiological tests on them over the course of approximately three months (D. S. Wilson et al., 1993). They found no differences between trapped and seined fish with respect to age or sex (close to a 1:1 ratio was found in both groups). They did find that trapped fish acclimated to feeding in the lab more quickly than did seined fish, as might be expected if in fact trapped fish were bolder (Figure 17.9).

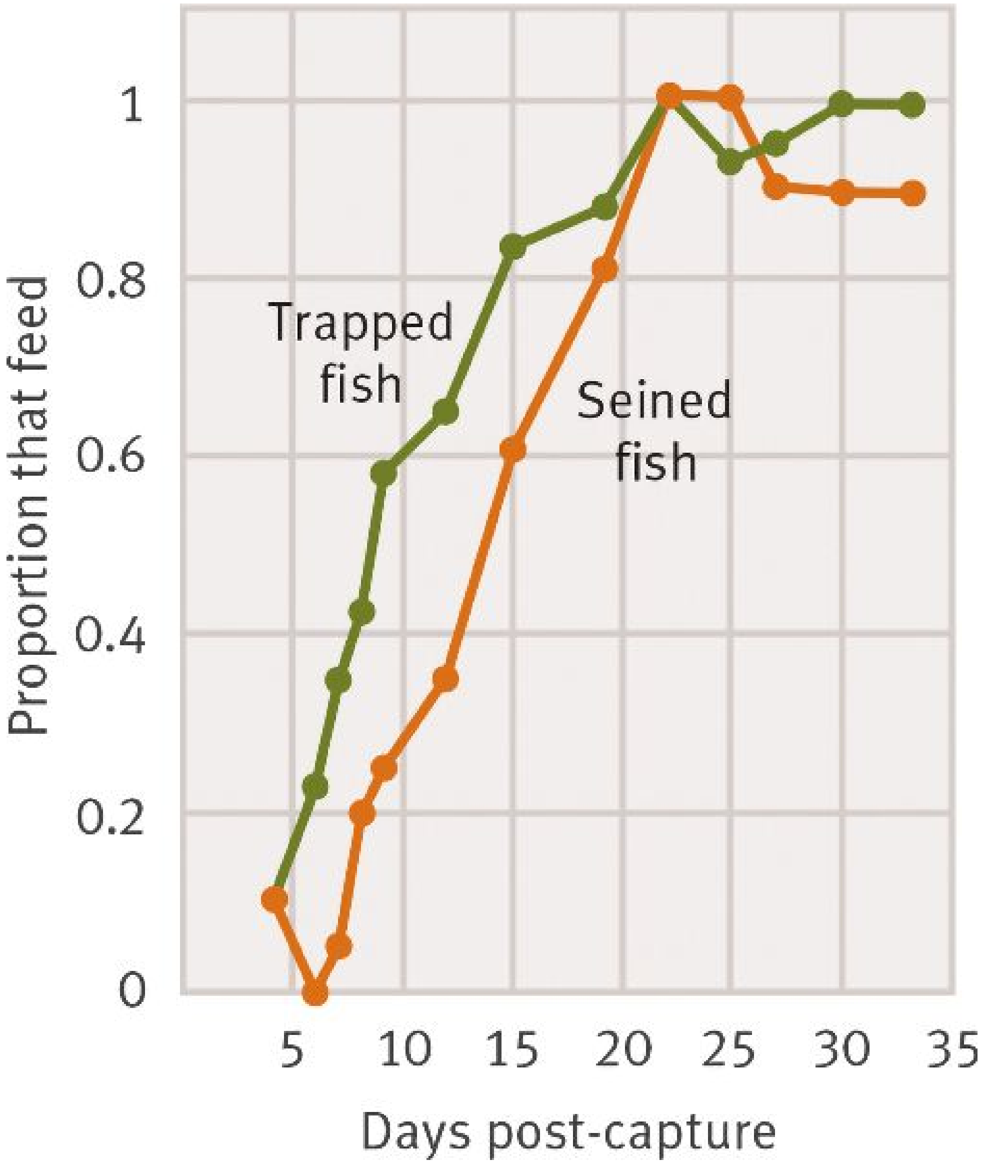


Figure 17.9. **Feeding and boldness.** Trapping caught the boldest fish, and seining caught a mixture of bold and shy pumpkinseed sunfish. Once brought into the lab, trapped fish acclimated to feeding more quickly than seined fish (this effect disappeared with time). *(Based on D. Wilson et al., 1993)*

Twenty-five days after fish were captured, the researchers ran a series of behavioral and physiological post-acclimation tests of the trapped and seined fish. These tests included a “response to handling” test, a novel object test, aggressive contests between seined and trapped fish, and physiological tests of stress. In no case did the trapped and seined fish differ from each other in any of these treatments; indeed after thirty days of social and ecological isolation in the laboratory, all the differences between trapped and seined fish disappeared.

While there are numerous possible explanations for the disappearance of differences across samples over time in the laboratory, D.S. Wilson and his colleagues hypothesize that ecologically and socially relevant cues may solidify the differences between bold and inhibited pumpkinseed fish and that, in the laboratory, where such cues may be absent, differences in boldness and inhibition may either disappear or become too small to notice.

Some Case Studies

In this section, we will look at a number of case studies to better understand the dynamics of animal personality.

HYENA PERSONALITIES

Samuel Gosling (1998) studied personality in spotted hyenas (*Crocuta crocuta*), a species that is native to African savannas and lives in stable clans that often engage in cooperative hunting (Figure 17.10). Females hold the alpha (top-ranked) status in groups and dominance rank is inherited maternally (Engh et al., 2000; Frank, 1986a,b; Gosling, 1998; Holekamp and Dloniak, 2010; H. E. Watts et al., 2010; Zabel et al., 1992)

Figure 17.10. **Hyena personalities.** Forty-four personality traits were studied in spotted hyenas. Assertiveness, excitability, human-directed agreeableness, sociability, and curiosity are all components of personality in hyenas. *(Photo credit: Chris Stenger/ Buiten-beeld / Minden Pictures)*

Gosling studied thirty-four hyenas to determine whether personality could be distilled down to a few key variables in this group. As far as animal behavior studies go, Gosling's work on hyenas began in a somewhat unconventional manner. At the start of this work, three experts on hyena behavior were provided with a list of more than forty traits that had been used in other studies of animal personality, and they were asked which traits they believed would apply to hyenas. Then these experts were provided with a list of forty traits used in human personality work, and they were asked which applied to hyenas. From this, Gosling amassed a list of sixty personality traits. Finally, two other hyena experts were asked to go through this master list and to remove any redundancies (for example, fearful and apprehensive covered the same trait), and forty-four traits remained after this final culling process.

Four observers then used these traits to score the behavior of thirty-four hyenas and Gosling ran an analysis to determine whether certain traits grouped together. Results of this analysis suggest that hyena personalities were an aggregate of five clusters of traits—assertiveness (which incorporated fifteen of the original forty-four traits), excitability (twelve of the original traits), human-directed agreeableness (seven of the original traits), sociability (four of the original traits), and curiosity (six of the original traits). Gosling examined whether any of these aggregate personality traits correlated with an individual’s sex, age, or rank in the hierarchy. Neither age nor dominance rank correlated with these aggregate traits. Females were more assertive than males, however, as might be expected in a social system with matriarchal dominance hierarchies. To get a broader picture of what the hyena work meant for personality research in animals, Gosling compared the five aggregate traits that he uncovered in hyenas with major traits found in two studies of rhesus monkeys and in one study of gorillas (Bolig et al., 1992; Gold and Maple, 1994; Stevenson-Hinde and Zunz, 1978; Stevenson-Hinde et al., 1980). Except for “human-directed agreeableness,” which was not measured in the primate studies, hyenas and nonhuman primates shared major personality traits, suggesting some cross-species commonalities.

OCTOPUS AND SQUID PERSONALITIES

Most work on animal personality has been done on vertebrates. This may reflect an inherent bias in the way we think about the complex nature of personality, but whatever the reason, the result is that a large portion of the animal world—the invertebrates—has largely been ignored (Kralj-Fiser and W. Schuett, 2014).

A comparative approach to personality in vertebrates and invertebrates may lead us to new insights on the evolution of personality. Jennifer Mather and her colleagues have proposed that because cephalopods, such as octopuses, squids, and cuttlefish, display an array of complex behaviors, they are ideal subjects for personality studies in invertebrates (Mather, 1995, 2008; Mather and Anderson, 1993, 1999; Carere et al., 2015).

Mather and Anderson tested the response of one-year-old *Octopus rubescens* to three treatments that were labeled alert, threat, and feed (Mather and Anderson, 1993). In the “alert” treatment, an experimenter opened the lid to an octopus tank and brought her head down to where the octopus could see it. The "threat" treatment involved using a brush to touch, and presumably frighten, an octopus, and the "food" treatment recorded an octopus's response when a food item (a shore crab) was put into its tank. The nineteen octopus behaviors displayed across these three treatments were analyzed, and octopuses differed on three aspects of personality—active versus inactive, anxious versus calm, and bold versus inhibited (Table 17.1). Individual octopuses were consistent with respect to these three personality traits, and these traits accounted for 45 percent of all the behavioral variance uncovered in the experimental treatments (Mather, 1991; Mather and Anderson, 1993; Figure 17.11).

Table 17.1. Octopus personality traits. Three components of personality uncovered in Mather and Anderson's work on personality in *Octopus rubescens*. *(Based on Mather and Anderson, 1993)*

Dimension	Predictor Behavior
Factor 1: Activity (active/inactive)	In den[a]
	At rest[a]
	Grasp[b]
Factor 2: Reactivity (anxious/calm)	Squirt[b]
	Shrink[b]
	Swim[b]
	Crawl[b]
Factor 3: Avoidance (bold/inhibited)	In den[b]
	In den[c]
	Color change[a]
	Ink[b]
	Alert[c]

[a] During alert test. [b] During threat test. [c] During feeding test.

Figure 17.11. **Octopus personalities.** Studies on personality in the red octopus (*Octopus rubescens*) represent some of the work on invertebrates done in this field. *(Photo credit: © Visual&Written SL / Alamy Stock Photo)*

Personality traits have also been studied in dumpling squids (*Euprymna tasmanica*). Sinn and his colleagues examined the behavior of these squid in two contexts—threat situations and feeding situations (Sinn and Moltschaniwskyj, 2005; Sinn et al., 2006, 2008, 2010). Each squid was tested four times in each context, and the researchers examined whether any consistent personality traits could be detected. As in the red octopus, shy versus bold and active versus inactive emerged as two personality types in the dumpling squid. Subsequent work showed that these traits were heritable (Sinn et al., 2006).

NATURAL SELECTION AND PERSONALITY IN GREAT TITS

In a long-term study of exploratory behavior and reaction to novel objects in great tits (*Parus major*), Pieter Drent and his colleagues have uncovered different personality types in these birds (Verbeek et al., 1994; Figure 17.12). “Fast” birds quickly approach novel objects and explore new environments rapidly, spending relatively short periods in any particular area. Fast birds are also aggressive—though they have low testosterone levels (chapter 3)—and once they develop a food-searching pattern, they are unlikely to change that pattern (Dingemanse et al., 2012; van Oers et al., 2011; Verbeek et al., 1996, 1999). On the other end of the behavioral spectrum, “slow” birds are reluctant to approach novel objects, vary their foraging routine often, are not physically aggressive (though they have high testosterone levels), and are slow to approach members of the opposite sex (Figure 17.13).

Figure 17.12. **Personality types in great tit birds.** Personality type has been studied in the great tit (*Parus major*). *(Photo credit: © Bachkova Natalia / Shutterstock)*

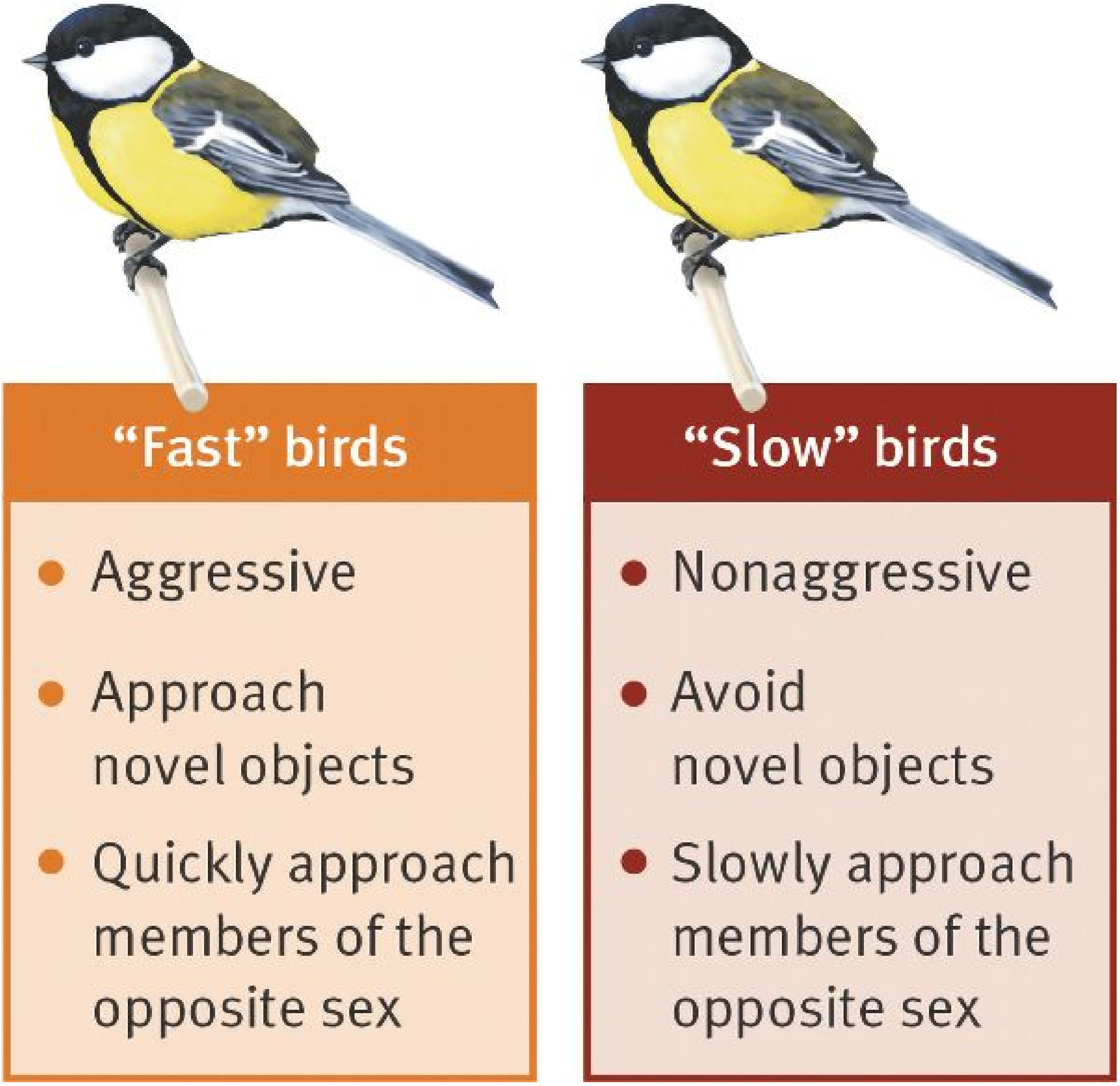


Figure 17.13. **Fast and slow birds.** An overview of "fast" and "slow" great tit birds.

Researchers have measured the reproductive success of slow and fast birds in a number of types of environments (Both et al., 2005). Using detailed measurements of marked birds in a natural population of great tits in the Netherlands, they found that reproductive success was greatest when pairs of birds had similar personalities; slow-slow and fast-fast pairings led to production of the healthiest chicks. When they looked at extrapair matings, they found that females paired with males that had a personality type similar to their own (fast-fast or slow-slow) had the highest rates of extrapair matings. One possible benefit of such extrapair partner choice is to increase behavioral variation among offspring (van Oers et al., 2011). Other work by Drent, Kees van Oers, Arie van Noordwijk, and Neils Dingemanse has shown that, in addition to having fitness consequences, personality in the great tit is also a heritable trait (Dingemanse et al., 2002; Drent et al., 2002; van Oers, Drent, de Jong, et al., 2004; van Oers, Drent, de Goece, et al., 2004).

Drent's team has also examined personality in the context of learning. Slow birds, while taking longer to explore an environment, also spend more time learning about each aspect of a new environment. To better understand whether other aspects of tit behavior correlate with fast-slow personality types, Marchetti and Drent examined whether birds could learn about changes in their foraging environment from watching a demonstrator bird (Marchetti and Drent, 2000). After giving both slow and fast birds the opportunity to see a demonstrator bird forage, they found that although slow birds change feeders often when alone, they do not use the information on new food sources provided by tutors (Marchetti and Drent, 2000). Conversely, fast birds, though reluctant to change feeders once they have established a routine of their own, are quick to change their foraging habits when paired with tutors that provide them with information about new food sources: slow tits behave like producers, whereas fast birds act more like scroungers.

Coping Styles

How animals cope with stressors can have impacts on health, and hence reproductive success (Bartolomucci, 2007; Cavigelli, 2005; Koolhaas et al., 2007; Overli et al., 2007). In their review of the literature on personality, stress, and coping, Jaap Koolhaas and his colleagues found two coping styles that they labeled **proactive** (sometimes called the active response) and **reactive** (also known as the conservation-withdrawal response; Cannon, 1915; Coppens et al., 2010; Engel and Schmale, 1972; Henry and Stephens, 1977; Koolhaas et al., 1999, 2007, 2010). The proactive personality type is characterized by territorial control and aggression, while the reactive style is characterized by immobility and low levels of aggression (Koolhaas et al., 1999; Table 17.2).

Table 17.2. Proactive and reactive coping styles. A summary of the behavioral differences between proactive and reactive male rats and mice. *(Based on Koolhaas et al., 1999)*

Behavioral characteristics	**Proactive**	**Reactive**
Attack latency	Low	High
Defensive burying	High	Low
Nest-building	High	Low
Routine formation	High	Low
Cue dependency	Low	High
Conditioned immobility	Low	High
Flexibility	Low	High

Proactive animals are also more likely to remove negative stimuli from their environment, whereas reactive animals are more likely to hide from any new negative stimulus. Frans Sluyter studied different strains of rats that had been selected for proactive or reactive coping styles (Sluyter et al., 1995). Male rats were exposed to an intruder in an experiment in which another male was placed in an individual's home cage. Proactive rats were very aggressive toward intruders, while reactive rats tended to hide from such intruders (Figure 17.14). The rats were next tested in a "defensive burying" experiment. In this experiment, a small electric prod was placed in a male's cage, and if the male investigated the prod and touched it, he received a mild shock. Once shocked, a rat had two ways to avoid future shock: he could either bury the prod under his bedding or curtail his movements. The researchers found that individuals from the proactive strain of mice were much more likely to bury the prod than were mice from the reactive strain.

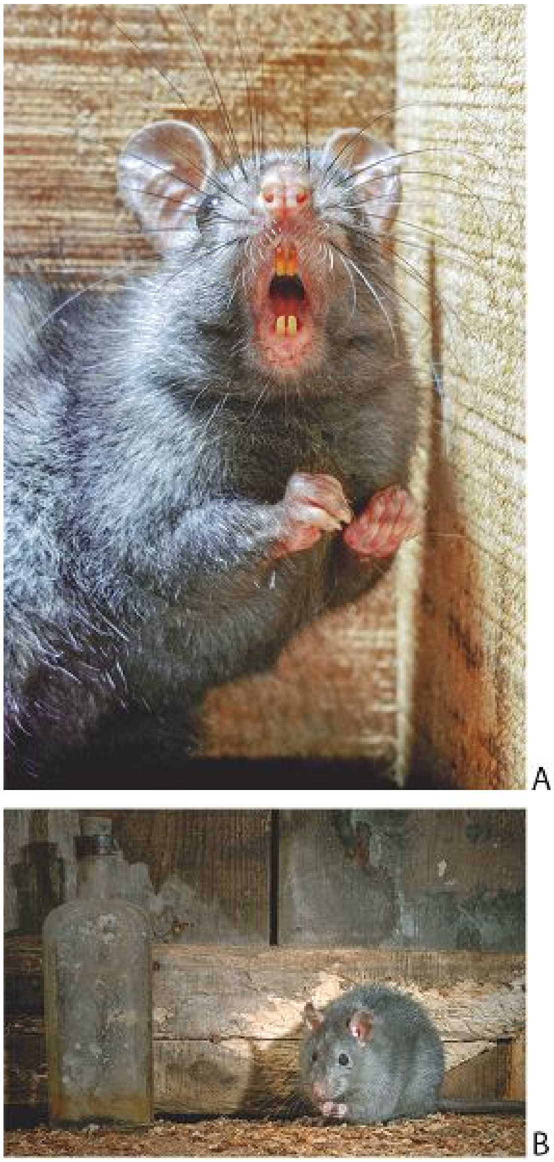


Figure 17.14. **Proactive and reactive rats.** (A) Proactive mice and rats tend to be territorial and aggressive, whereas (B) reactive mice and rats tend to be timid and become immobile or hide when threatened. *(Photo credits: Tom McHugh/Photo Researchers, Inc.; Arterra Picture Library / Alamy Stock Photo)*

The underlying proximate mechanisms associated with proactive and reactive strains have also been examined (Sluyter et al., 1995). Proactive and reactive mice were exposed to two different stressors—a five-minute forced swim or long-term stress associated with frequent handling. Alexa Veenema and her colleagues took a series of neuroendocrinological measurements of mice in the proactive and reactive strains, both before and after exposure to stress (Veenema et al., 2004, 2007).

Before exposure to stress conditions, corticosterone levels were fairly stable in reactive mice, but the levels fluctuated in proactive mice. Once they were stressed, reactive mice showed a dramatic increase in corticosterone levels, compared with proactive mice. The “freeze response” and reduced aggression in reactive mice might be linked to such increases in corticosterone. Compared with proactive mice, reactive mice also showed reduced cell growth in the hippocampal region of the brain, suggesting that the proximate differences between coping styles may also affect learning and memory (Veenema et al., 2004, 2007).

Proactive and reactive personalities have been found not only in laboratory and natural populations of animals, but also in domesticated animals such as pigs and cows (Hopster, 1998; Prelle et al., 2004; Spoolder et al., 1996; D. Weiss et al., 2004). While data on the costs and benefits of these two coping styles are scant, there is some evidence that proactive and reactive animals differ in their susceptibility to diseases such as hypertension, atherosclerosis, gastric ulcers, and immunosuppressive capabilities (Ely, 1981; Henry et al., 1993; Hessing et al., 1994; Sgoifo et al., 2005; J. Weiss, 1972; Koolhaas and van Reenen, 2016) (Box 17.3).

Box 17.2. COGNITIVE CONNECTION

Brain Size and the Proactive-Reactive Personality Continuum

Proactive animals habituate more quickly to new environments and are quicker to learn new tasks than their reactive counterparts. But, reactive animals are more flexible learners, in that they often do better than proactive animals on reversal learning tests. These findings beg a better understanding of the brain science of personality. One step in that direction was taken in a study on the relationship between brain size and the proactive-reactive personality continuum in guppy populations (Kotrschal et al., 2014).

Alex Kotrschal and colleagues tested guppies from two groups: one group had been artificially selected for large brain size, and the other for small brain size (Kotrschal et al., 2012, 2013,a,b). Prior work in these lines had shown that larger-brained females outperform smaller-brained females on numerical learning tasks, and larger-brained males outperform smaller-brained males on spatial learning tasks. What Kotrschal's team wanted to know was whether brain size per se was linked to personality differences on the proactive-reactive continuum.

To test for differences in boldness and exploration, the researchers tested fish from these two lines in an open field test, where proactive fish tend to spend more time in the central, less protected, area of the arena than reactive fish. To measure how the fish respond to stress, they assayed cortisol levels when fish were placed alone in a beaker that was under a bright light; and to examine behavioral flexibility, they measured responses to a novel foraging task (feeding from time-released food tablets on the substrate) after fish had experienced a different feeding protocol (feeding from the water column or from the surface). On all three measures, large-brained fish showed signs of proactive personalities: they displayed more exploratory behavior than small-brained fish in the open field test, produced less cortisol when stressed, but when faced with a novel foraging task that required learning a new set of skills, performed worse than smaller-brained fish (Figure 17.15)

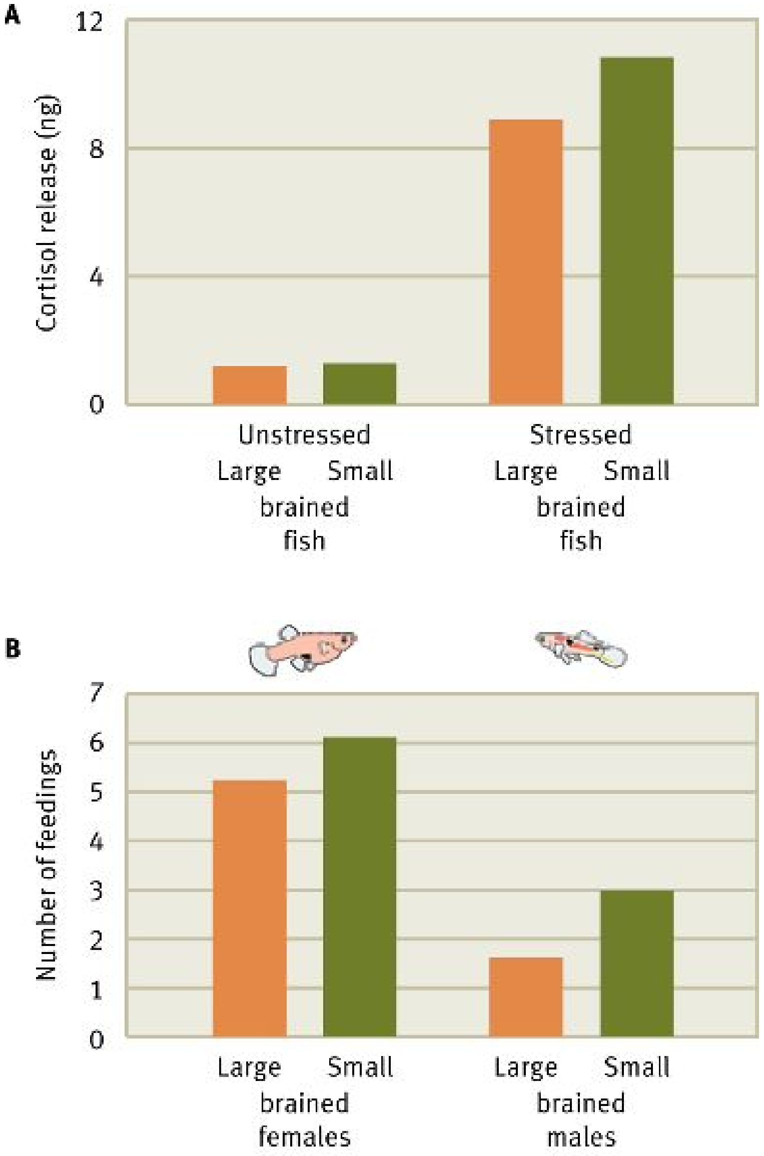


Figure 17.15. **Brain size and personality.** (A) Under stressful conditions, large-brained guppies produced less cortisol than small-brained fish. (B) Small-brained males outperformed large-brained males when learning a new foraging task that required learning a new set of skills. *(From Kotrschal et al., 2014)*

Selection on brain size per se seems to have led to personality differences in these artificially selected lines of guppies, though the mechanisms underlying the relationship between brain size and personality are not yet understood.

Box 17.3. SCIENCE AT WORK

What is the research question? How does brain size affect personality?

Why is this an important question? Studies are now examining the cognitive aspects of personality, but little is known about how brain size per se affects personality.

What approach was taken to address the research question? The personality of guppies from an artificial selection experiment, which had a line of large-brained and a line of small-brained fish, was examined.

What was discovered? Large-brained fish explored more than small-brained fish and produced less cortisol when stressed. Small-brained fish performed better when presented with a new foraging task.

What do the results mean? Brain size per se affects personality development, though the mechanisms involved require more study.

Personality and Dispersal Behavior

Animal behaviorists, ecologists, and biogeographers have examined whether personality differences *within* populations might have consequences for large-scale dispersal patterns in nature (Canestrelli et al., 2016): bolder individuals may be more likely to disperse to new environments, founding and initiating new populations there (Fraser et al., 2001; Dingemanse et al., 2003; Duckworth and Badyaev, 2007; Krackow, 2003).

To test this idea, Brodin and colleagues sampled eggs from four mainland populations of the common frog (*Rana temporaria*) near Umea, Sweden, and eggs from four close-by island populations of *R. temporaria* (Brodin et al., 2013). They hypothesized that if bolder individuals were more likely to disperse and start new populations, then frogs from the four island populations would be bolder than those from the mainland population, both because the ancestors of such individuals would have been more likely to disperse to such islands, and because selection pressure today might still favor boldness on islands.

All eggs from the island and mainland populations were raised in a controlled laboratory environment. When the frogs reached the tadpole stage, and then again when they reached the froglet stage, they were placed in a gray opaque covered refuge chamber, which had an opening (initially covered by a lid) that led to the center of the tank in which the chamber rested. The lid was opened and boldness was measured as the latency to leave the refuge, and exploratory behavior was calculated based on how the frog swam around over the next five minutes.

Brodin's team found that tadpoles from the island populations were bolder and explored more than their mainland counterparts, and that at the froglet stage, island frogs were bolder than mainland frogs (no differences in exploration were found at this stage in ontogeny; Figure 17.17). These results suggest that an understanding of animal personality not only informs ethology, but has implications for broad scale questions about dispersal and biogeography, including, perhaps, human dispersal patterns over evolutionary time. For example, a number of studies of novelty seeking behavior in contemporary populations, combined with molecular genetic analyses of late Pleistocene human populations, suggest that variation in novelty seeking sheds light on human dispersal patterns in our evolutionary past (Chen et al., 1999; Matthews and Butler, 2011; Box 17.5).

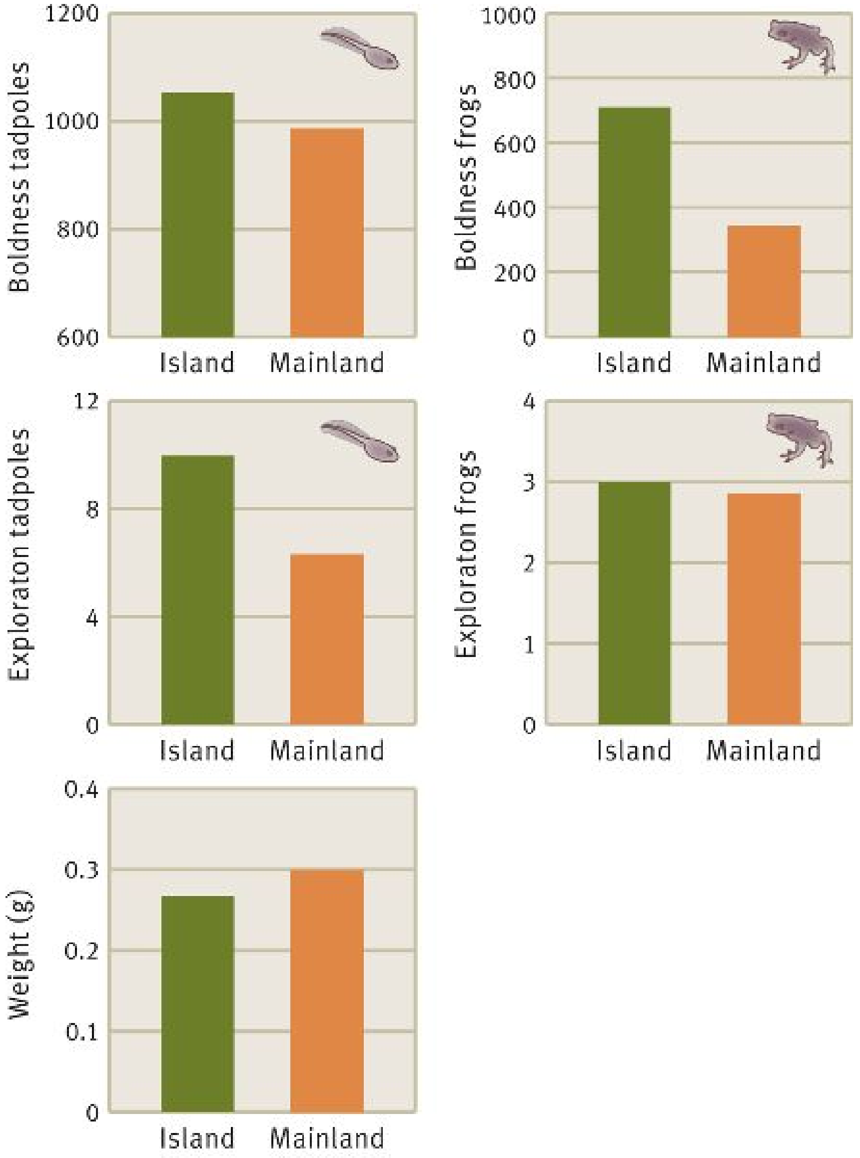


Figure 17.17. **Boldness, exploration and dispersal.** Tadpoles from island populations were bolder and explored more than tadpoles from mainland populations, and froglets from island populations were bolder than those from mainland populations. *(From Brodin et al., 2013)*

Box 17.4. CONSERVATION CONNECTION

Using Personality to Reduce Human-Animal Conflicts

As a result of species recovery and conservation plans, a number of large carnivores have been successfully reintroduced into the wild or have had their natural population numbers increase dramatically over the last few decades. The downside of this conservation success has been the rekindling of an old rivalry between ranchers and large carnivores that feed on their animals (Blanco et al., 1992; Cozza et al., 1996; Kaczensky, 1996; Oli et al., 1994; Quigley and Cragshaw, 1992). For example, problems arose when wolf populations began to increase in many parts of Europe and began attacking local livestock, and a similar sort of problem emerged when it was discovered that a small proportion of seal populations that have been the subject of conservation efforts were consuming economically valuable fish like salmon (I. M. Graham et al., 2011; Figure 17.16). The reduction of such conflicts may be possible with an understanding of the carnivore personality.

Figure 17.16. **Seal personality and conservation.** (A) A harbor seal (*Phoca vitulina*) and (B) a grey seal (*Halichoerus grypus*). In both harbor and grey seals, a few bold individuals are found in rivers and eat economically valuable fish like salmon. These animals (on the right side of each graph) were captured and recaptured many times. Understanding boldness in seals could help reduce conflict between the seals and the people who rely on the salmon that bold seals consume. *(Photo credits: © Karel Bartik / Shutterstock; © Ondrej Prosicky / Shutterstock)*

Because there is widespread opposition to large-scale killing of carnivores, one way that carnivores feeding on livestock has been tackled is to focus on “problem individuals”—carnivore individuals that repeatedly attack and kill ranchers’ livestock. The data on specific aspects of the hunting behavior of large carnivores preying on domestic prey are difficult to obtain, but studies of hunting behavior in wolves, cougars, leopards, seals, lions, tigers, bears, and many other species suggest that certain individuals are more likely to prey on domesticated animals (Dickman, 2010; Karlsson and Johansson, 2010; Linnell, 2011; Treves, 2009; Treves and Karanth, 2003).

Attacking ranchers’ livestock is a risky endeavor for a carnivore. The predator must circumvent any fencing or other defensive measures put into place and then risk being killed by humans defending their livestock. Carnivores that consistently attempt to attack such livestock—the so-called problem individuals—display many of the personality traits associated with boldness.

Exactly how to use the information on personality differences and problem individuals is still a matter of debate. One possibility would be to use the growing ethological understanding of bold predators to design new traps specifically for these sorts of individuals. For example, bold predators might use specific hunting strategies that differ from the strategies of others in the population—they may use different paths to reach prey, hunt at different times, or be more or less attracted to certain stimuli. Traps could then be constructed that were designed with these hunting strategies of bold predators in mind.

Box 17.5. SCIENCE AT WORK

What is the research question? How does personality affect dispersal behavior?

Why is this an important question? An understanding of how personality affects dispersal behavior will link together work in ethology, ecology, and biogeography.

What approach was taken to address the research question? To test the hypothesis that island populations might have bolder individuals, eggs from four island and four mainland populations of *Rana temporaria* were raised in a common environment to test where personality differences across island and mainland populations could be detected as the frogs matured.

What was discovered? Tadpoles from the island populations were bolder and more exploratory than mainland tadpoles. At the froglet stage, island frogs were bolder than mainland frogs.

What do the results mean? Personality affects not just behavioral interactions within groups, but dispersal behavior, and perhaps the founding of new populations.

Interview with Dr. Sam Gosling

Why study animal personality?

I think there are three main reasons to study animal personality: (1) Using animal models to learn about humans: Animal studies have long been used to inform discoveries in human psychology (in the domains of learning, problem solving, language, brain function, sensation, perception, etc.). Now that we have established that animals have personalities and animal personality can be measured reliably, we can also use animal studies to learn a lot about personality more broadly. Animal studies are particularly well poised to offer insights that would be difficult to gain using human research alone; this is because animal studies afford high levels of experimental control, permit measurement and manipulation of a wide range of biological and environmental parameters, can be combined with emerging genetic techniques (such as cloning and transgenic methods), and provide opportunities to follow animals longitudinally in a time frame that is considerably accelerated compared to that for humans. As in all animal research, many of these studies may raise ethical considerations that must be handled responsibly.

(2) Applied contexts: Some humans are better cut out to be librarians and others are better suited to work in sales or be lawyers, and some individual animals are better suited than others to perform the tasks assigned to them (finding explosives, guiding the visually impaired, etc.). Assessments of animal personality can help match individual animals to the tasks for which they are well suited. In addition, knowing about an animal's personality can help promote the welfare of captive animals (for example, by shaping housing conditions to match the personalities of captive animals), can match humans to appropriate animal companions (for example, in animal shelters), and can be used to select animals suitable for relocation in conservation work.

(3) Understanding the forces that drive and maintain individual differences: For too long, individual differences among animals were treated as meaningless variation that could be controlled statistically by averaging findings across numerous individuals. However, in the last decade or so, researchers and theorists have come to realize that variation among individuals is something that needs to be understood, not swept under the rug. Behavioral ecologists trained in evolutionary theory and ethological methods are particularly well positioned to understand the distal and proximal mechanisms that drive individual differences. So research on animal personality is vital to understanding the constraints that help determine how animals behave and, more generally, how variation among animals is maintained.

Why is it important to study animal personality from a comparative perspective?

A comparative perspective on personality can help identify common solutions that different species have taken to solve common problems. Without taking a comparative—and phylogenetically informed—perspective, it is difficult to determine the origin of personality differences and the forces that shaped them.

Darwin wrote *The Expression of Emotions in Man and Animals* more than 125 years ago. Why did it take so long for the

experimental study of animal personality to emerge?

In my classes I often ask the students whether they think cows have personality. Those students who grew up in cities generally think it is obvious that cows don’t have personality, and those people who grew up on farms generally think it is obvious that cows do have personality. When I first started studying animal personality, I noticed that many animal researchers would often hold both of these positions but at different times. When chatting to one another casually on their tea breaks, the researchers would happily talk about how one animal was friendly or anxious or calm or curious, but when the break was over they would put on their white coats and avoid talking about the animals using such anthropomorphic terms. So there has long been a sense among scientists that personality did not offer a legitimate way to characterize animals. As animal behaviorists strove to establish themselves as scientists, they tended to distance themselves from anything that had an aura of anthropomorphism or subjectivity, with personality and emotion being prime examples. At the same time, human personality researchers came from a tradition that, in addition to behavioral traits, incorporated constructs such as identity, values, and motives, which were not such an obvious fit in the animal domain. So both the animal researchers and the personality researchers had their own reasons for not being open to the idea of personality in animals. But I think the research that we did summarizing and synthesizing all the isolated studies of animal personality, along with the work done by Andy Sih and Alison Bell sketching out some of the evolutionary and ecological implications, gave the topic enough legitimacy for people to start thinking about it seriously. Once they did that, the benefits of studying personality quickly became clear.

What is the most unexpected thing you’ve learned from your own work on animal personality?

It sounds odd to say now, but when I started this research I really didn’t know if it would be possible to measure personality reliably or that personality assessments would predict behavior. So the biggest surprise was discovering that measures of animal personality typically meet or exceed the standards met by measures of human personality.

What do you see as the next frontier in research on animal personality?

I think the next frontier will be discovering the biological mechanisms underlying personality traits and extending these findings to the human domain.

Dr. Sam Gosling is a professor in the Department of Psychology at the University of Texas. Among his many research interests are ultimate and proximate questions centering on animal personality. Dr. Gosling is the author of *Snoop: What Your Stuff Says about You* (Basic Books, 2008).

SUMMARY

1. Personality differences can be conceptualized as consistent long-term behavioral differences among individuals.
2. Boldness/shyness is one of the most stable personality variables.
3. How an animal copes with stressors can impact its health. Two general coping styles emerge from studies across a wide variety of animals: proactive and reactive. The proactive coping style entails territorial control and aggression, whereas the reactive coping style is characterized by immobility and low levels of aggression.
4. The study of animal personality has potential practical implications for conservation biology, human-animal interactions, and many other areas.

DISCUSSION QUESTIONS

1. Go to the monkey exhibit at your local zoo and pick four individual monkeys to observe for at least four hours. Or go to a working farm and pick four individual cows or horses. Record all the information you can on each individual (“grooms,” “eats,” “attacks,” “retreats,” “sleeps,” “plays,” and so on), and if possible, note the proximity of the animals you are studying to others in the group. From your observations, can you suggest a list of behaviors that you might focus on during a longer, more controlled, study of personality in the population you are observing?
2. How would you construct an experiment to examine whether boldness and/or behavioral inhibition are heritable traits?
3. Besides the ones mentioned in this chapter, what general costs and benefits might you associate with being bold or inhibited? Pick a particular species you are familiar with and create a list of the potential costs and benefits of boldness and shyness in that species.
4. Pick up a few recent issues of the journal *Animal Behaviour* and scan the titles for anything on “alternative strategies.” Once you have found one or two such articles, read them—is there any mention of personality in these papers? If not, how might you reanalyze the data to see whether the alternative strategies could be construed in light of the work on animal personalities? What other sorts of data could you collect to better understand whether the alternative strategies studied represent personality types?
5. Can you think of any other practical applications of personality work in animals? How might you construct some experiments to better understand whether the

applications you suggest are feasible?

SUGGESTED READING

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Glossary

adaptation A trait that results in the highest fitness among a specified set of behaviors in a particular environment. Adaptations are typically the result of the process of natural selection.

allele A gene variant; one of two or more alternative forms of a gene.

alliance A long-term coalition. *See also* coalition.

allogrooming The grooming of another individual, usually by scratching or licking an area of skin, often to remove parasites. Also known as social grooming.

analogous traits (analogies) Traits that are similar as a result of similar natural selection pressures rather than common descent.

appetitive stimulus Any stimulus that is considered positive, pleasant, or rewarding.

arena mating *See* leks.

artificial selection Selection in which humans are the selective agent and choose certain varieties of an organism over others for breeding. *See also* natural selection.

audience effect When individuals involved in social interactions change their behavior as a function of being watched by others.

aversive stimulus Any stimulus that is associated with an unpleasant experience.

axons Nerve cell fibers that transmit electrical information from one nerve cell to another.

Bateman's principle The hypothesis that, since eggs require greater energy to produce than sperm, females should be the choosier sex and this should result in greater variance in the reproductive success of males.

behavioral genetics The study of the genetic variance associated with behavior.

blocking When an association between an unconditioned stimulus (US1) and a response prevents an individual from responding to another stimulus (US2) or causes the individual to respond less strongly to the US2.

boldness The tendency to take risks.

byproduct mutualism A type of cooperation in which an individual pays an immediate cost or penalty for not acting cooperatively, such that the immediate net benefit of cooperating outweighs that of not cooperating.

bystander effect When observers of an interaction between other individuals change their estimation of the fighting ability of those they are watching as a function of what they observe.

classical conditioning *See* Pavlovian conditioning.

coalition Cooperative action taken by at least two individuals or groups against another individual or group. *See also* cooperation.

communication The transfer of information from a signaler to a receiver.

conceptual approach An approach that usually entails integrating ideas generated in different disciplines and combining them in a new, cohesive way.

conditioned response (CR) The learned response to a conditioned stimulus.

conditioned stimulus (CS) A stimulus that initially fails to elicit a particular response, but comes to do so when it is associated with a second (unconditioned) stimulus.

convergent evolution The process whereby different populations or species converge on the same phenotypic characteristics as a result of similar natural selection pressures.

cooperation An outcome that, despite possible costs to the individual, provides some benefits to others. “To cooperate” means to behave in a way that makes cooperation possible.

coping style A set of behavioral and related stress responses that are consistent over time.

copying Behavior that occurs when an observer repeats the actions of a demonstrator.

cross-fostering experiment An experiment measuring the relative contributions of genetic and environmental variation on the expression of behavioral traits. Often involves removing young individuals from their parent(s), and having them raised by adults that are not their genetic relatives.

cryptic Hidden through camouflage, and blending into the environment.

cryptic mate choice Females affect which sperm transferred during copulation are used in actual fertilization.

cultural transmission The transfer of information from individual to individual through teaching or social learning. *See also* social learning; teaching.

dendrites Nerve cell fibers that receive electrical information from other cells.

DNA fingerprint A molecular genetic technique used to examine the genetic relatedness among individuals.

dominance hierarchy The relationship between individuals in a group as a result of aggressive behaviors and the response to aggressive behaviors.

dominant allele An allele that is expressed in heterozygote individuals. Allele A is dominant to allele a if the Aa genotype is identical to the AA genotype. *See also* allele.

dyadic interactions Interactions involving two individuals.

ecology The study of the interaction of organisms with their environment.

empirical approach An approach that entails gathering data in one form or another and drawing inferences from that data. Empirical work in ethology can take many forms, but most often it is either observational or experimental.

endocrine system A communication network of ductless glands that secrete chemical messengers called hormones.

ethology The scientific study of animal behavior.

eusociality An extreme form of sociality in which there is cooperative brood care, division of labor, and overlapping generations.

evolutionarily stable strategy (ESS) A strategy that, if used by almost all individuals in a population, will not decrease in frequency when new, mutant strategies arise.

excitatory conditioning When a conditioned stimulus leads to an action.

extinction curves Graphs that depict how long an animal will remember some paired association once the pairing itself has stopped.

extrapair copulations Copulations that occur outside the context of a pair bond.

female defense polygyny A mating system in which males aggressively guard females that are found in spatial clusters.

fitness Lifetime reproductive success—usually measured in relative terms.

flight initiation distance The distance at which prey begin to flee from a predator.

foraging Feeding and all behaviors associated with feeding.

genetic recombination A recombination of genes during cell division in sexually reproducing organisms that involves sections of one chromosome crossing over and swapping positions with sections of the homologous chromosome.

genetic variation Variation caused by genetic differences.

genotype The genetic makeup of an individual.

goal-directed learning *See* instrumental conditioning.

good genes model A model of sexual selection in which females choose to mate with males that possess traits that are indicators of good health and vigor.

group selection A hierarchical model in which natural selection operates at two levels: within-group selection and between-group selection.

habitat choice How animals distribute themselves in space and time with respect to some resource in their environment.

habituation Becoming less sensitive to stimuli over time.

hawk-dove game A game theory model of aggression. Hawk is a strategy in which the individual escalates and continues to escalate until either it is injured or its opponent concedes, and dove is a strategy in which the individual bluffs, initially displaying as if it will escalate, but retreating and ceding the resource if its opponent escalates.

heritability The proportion of variance in a trait that is due to genetic variance.

home range A delineated, undefended area in which an animal spends most of its time.

homologous traits (or homologies) Traits that are shared by two or more species as a result of common descent.

homoplasy A trait that is present in two or more species but that is not due to common descent but rather from natural selection acting independently on each species. *See also* analogous traits.

honest indicators Traits that are costly to produce and difficult to fake. Honest indicators are hypothesized to signal the genetic quality of an individual.

horizontal cultural transmission Cultural transmission in which information is passed across individuals of the same age or peer group. *See also* cultural transmission.

ideal free distribution (IFD) A mathematical model used to predict how animals will distribute themselves among habitats.

imitation The acquisition of a topographically novel response through observation of a demonstrator making that response.

inclusive fitness A measure of fitness that takes into account not only the effect an allele has on its bearer, but also the effect it has on the reproductive success of its genetic relatives.

individual learning A relatively permanent change in behavior as a result of experience. Individual learning differs from social learning in that it does not involve learning from others.

inhibitory conditioning When a conditioned stimulus suppresses or inhibits behavior.

instrumental conditioning Learning that occurs when a response made by an animal is reinforced by reward or punishment. An animal must undertake some action or response in order for the conditioning process to produce learning.

intersexual selection A form of sexual selection in which individuals of one sex choose which individuals of the other sex to take as mates. *See also* sexual selection.

intrasexual selection A form of sexual selection whereby members of one sex compete with each other for access to the other sex. *See also* sexual selection.

kamikaze sperm hypothesis The hypothesis that natural selection favors sperm that are designed to kill (or otherwise incapacitate) other males' sperm rather than to fertilize eggs.

kin recognition matching models Models in which internal templates are used to gauge genetic relatedness to others.

kin selection *See* inclusive fitness.

law of effect If a response in the presence of a stimulus is followed by a satisfying event, the association between the stimulus and the response will be strengthened.

leks Areas in which groups of males set up and defend small, temporary territorial patches and in which they display to females. The result is called lekking and arena mating.

local enhancement When an individual is drawn to a particular area because it observed another individual in that location.

locomotor play Play behaviors in which animals leap, jump, twist, shake, whirl, somersault, roll, or chase their tails. Also known as locomotor rotational play.

loser effect The increased probability of losing a fight at time T, based on losing at time T-1, T-2, and so on.

marginal value theorem A mathematical model developed to predict how long a forager will spend in a patch of food before moving on to new patches.

mate-choice copying The act of copying the mate choice of others.

migration The movement of organisms over long distances.

mobbing A type of antipredator behavior in which groups of prey join together, approach a predator, and aggressively attempt to chase it away.

monogamous mating system A mating system in which a male and female mate only with one another during a breeding season.

mushroom bodies A cluster of small neurons located at the front of the brain of some invertebrates and associated with spatial navigation.

mutation A change in genetic structure.

mutualism An interaction that benefits all parties involved. Interspecies cooperation is often referred to as a mutualism.

natural selection A process that occurs when variants of a trait that best suit an organism to its environment, and that are heritable, increase in frequency over evolutionary time. This process requires variation, fitness differences, and heritability.

neuroeconomics A collaborative research effort between economists, neurobiologists, and evolutionary biologists that uses brain-imaging technology to understand questions regarding behavior.

neurohormones Hormones that are secreted directly into the bloodstream by nerve cells.

nomads Individuals that lack a home range or a territory and who rarely frequent the same area over time. Occasionally, reference is made to a nomadic species.

nuptial gifts Prey presented by members of one sex to members of the other sex during courtship.

object play Play involving inanimate objects such as sticks, rocks, leaves, feathers, fruit, and human-provided objects, and the pushing, throwing, tearing, or manipulating of such objects.

oblique cultural transmission Cultural transmission in which information is passed across generations, but not from parent to offspring.

operant learning *See* instrumental conditioning.

operant response A learned action that an animal makes to change its environment.

optimal foraging theory (OFT) A family of mathematical models developed to predict animal foraging behavior.

optimal skew theory A family of models that predicts the distribution of breeding within a group, as well as the degree of cooperation or conflict over reproductive activities.

overshadowing When the learned response to an unconditioned stimulus (US1) is stronger if it is presented alone versus when it is paired with a second unconditioned stimulus (US2).

parental investment The amount of energy parents invest in raising their offspring.

parent-offspring conflict A zone of conflict between parents and offspring regarding the optimal allocation of parental resources.

parent-offspring regression A statistical technique for measuring heritability that involves comparing a trait in parents and offspring.

parsimony analysis A technique for choosing among alternative phylogenetic trees by selecting the tree that requires the fewest character changes.

Pavlovian conditioning The experimental pairing of a conditioned and unconditioned stimulus. *See also* conditioned stimulus; unconditioned stimulus.

personality differences Consistent long-term phenotypic behavioral differences among individuals.

phenotype The observable characteristics of an organism.

phenotypic plasticity The ability of an organism to produce different phenotypes depending on environmental conditions.

phylogenetic tree The depiction of phylogeny by using branching, tree-like diagrams.

phylogeny Evolutionary history via common descent.

play Motor activity performed during development that appears to be purposeless.

play markers Behavioral indicators that denote that an action that is about to be undertaken should be considered playful, not dangerous. Also known as play signals, they may serve to initiate play or to indicate the desire to keep playing.

polyadic interactions Interactions involving more than two individuals.

polyandry A mating system wherein females mate with more than one male per breeding season.

polygamy A mating system in which either males or females have multiple mates during a given breeding season.

polygenic Caused by the action of more than one gene.

polygynandry A mating system wherein several males form pair bonds with several females simultaneously.

polygyny A mating system in which males mate with more than one female per breeding season.

polygyny threshold model A model that predicts the conditions under which a mating system will move from monogamy to polygyny (or vice versa).

predator inspection An antipredator behavior in which one to a few individuals break away from a group and slowly approach a potential predator to obtain various sorts of information.

preexisting bias *See* sensory exploitation.

prisoner's dilemma A game theory payoff model that is used to study the evolution of cooperation.

proactive coping style A personality type characterized by territorial behavior and various forms of aggression. This style is sometimes referred to as the active response.

producers Individuals that find and procure some resource.

promiscuity A type of mating system in which both polyandry and polygyny are occurring. In one form of promiscuity, both males and females mate with many partners and no pair bonds are formed. In the second type of promiscuous breeding system, called polygynandry, several males form pair bonds with several females simultaneously. *See also* polyandry; polygynandry; polygyny.

proximate analysis Analysis based on asking questions that focus on immediate causation.

reactive coping style A personality type characterized by immobility and low levels of aggression. Also known as the conservation-withdrawal response.

recessive allele An allele in heterozygote individuals that is not expressed when combined with a dominant allele.

reciprocal altruism The exchange of altruistic acts.

resource holding power A measure of an animal's fighting ability.

risk-sensitive optimal foraging models A family of mathematical models that examines how variance in food supplies affects foraging behavior.

role reversal Behavior in which older individuals allow subordinate, younger animals to take on the dominant role during play, or in which older individuals perform some act that is at a level below that of which the older individual is capable. Also known as self-handicapping.

runaway sexual selection A model of sexual selection in which the genes for mate choice in the female and the genes for preferred traits in males become genetically linked.

scroungers Individuals that obtain a portion of their diet by parasitizing the resources that others (producers) have uncovered. *See also* producers.

search image A representation of prey that predators form over time.

self-handicapping *See* role reversal.

sensitization Becoming more sensitive to stimuli over time.

sensory bias *See* sensory exploitation.

sensory exploitation A theory of sexual selection that hypothesizes that females prefer male traits that elicit the greatest amount of stimulation from their sensory systems. Also known as sensory exploitation, sensory drive, or preexisting bias.

sequential assessment model A model of fighting in which an individual assesses its opponent's fighting ability during different stages of an aggressive interaction, and decides whether to continue in such an interaction based on the assessment it has made.

sexual selection A form of natural selection that, according to Darwin (1871), involves "a struggle between the individuals of one sex, generally the males, for the possession of the other sex."

sexy-son hypothesis A hypothesis that females select among males based on genetic traits in the males that will lead to the production of sons that are attractive to the opposite sex.

shyness The reluctance to take risks or to engage in unfamiliar activity.

sibling rivalry Aggressive interactions among siblings.

social facilitation When the presence of a model, regardless of what it does, facilitates learning on the part of an observer.

social grooming *See* allogrooming.

social learning Learning by observing others.

social play Playing with others.

sperm competition A form of sexual selection that occurs directly between sperm after insemination.

teaching A behavior that occurs when one individual serves as an instructor and at least one other individual acts as a student that learns from the instructor.

territory A delineated, defended area.

theoretical approach Generating models, most often mathematical models, to study some phenomenon.

tit for tat (TFT) A behavioral strategy in which a player initially cooperates with a new partner, and subsequently does whatever that partner does.

truncation selection experiment An experimental procedure that measures heritability by allowing only those with extreme forms of a trait to breed and then tracking changes in that trait across generations.

ultimate analysis An analysis relating to the evolution of a trait.

unconditioned stimulus (US) A stimulus that elicits a vigorous response in the absence of training.

vertical cultural transmission Cultural transmission in which information is passed directly from parent(s) to offspring. *See also* cultural transmission.

waggle dance A dance performed by forager bees on the return to the hive. The waggle dance provides information on the spatial location of food located at some distance from the hive.

war of attrition model A model of fighting in which animals display aggressively to one another without actually fighting, and the winner of the encounter is the individual that displays the longest.

winner effect The increased probability of winning a fight at time T, based on victories at times T-1, T-2, and so on.

worker policing Behavior that involves workers in a social insect species destroying the eggs laid by other workers.

xenophobia The fear of strangers or those from outside one's group.

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