

Mental Health and Well-being in Animals

2nd Edition

Edited by Franklin D. McMillan



Mental Health and Well-being in Animals, 2nd Edition

Mental Health and Well-being in Animals, 2nd Edition

Franklin D. McMillan

Best Friends Animal Society



CABI is a trading name of CAB International

CABI Nosworthy Way Wallingford Oxfordshire OX10 8DE UK CABI 745 Atlantic Avenue 8th Floor Boston, MA 02111 USA

Tel: +44 (0)1491 832111 Fax: +44 (0)1491 833508 E-mail: info@cabi.org Website: www.cabi.org Tel: +1 (617)682-9015 E-mail: cabi-nao@cabi.org

© CAB International 2020. All rights reserved. No part of this publication may be reproduced in any form or by any means, electronically, mechanically, by photocopying, recording or otherwise, without the prior permission of the copyright owners.

A catalogue record for this book is available from the British Library, London, UK.

Library of Congress Cataloging-in-Publication Data

Names: McMillan, Franklin D, editor.

Title: Mental health and well-being in animals / edited by Franklin D. McMillan.

Description: Second edition. | Boston: CABI 2020. | Includes bibliographical references and index. | Summary: "The second edition is fully revised, expanded, and comprehensively updated with the most current knowledge about the full array of mental health issues seen in animals. Written by key opinion leaders, internationally-recognized experts and specialists, it is comprehensive covering basic principles to mental wellness, emotional distress, suffering and mental illness, through to measurement and treatment. With even more practical information and clinical pearls, this book remains invaluable to veterinary professionals, animal welfare researchers and advocates, and other animal caregivers"-- Provided by publisher.

Identifiers: LCCN 2019026055 | ISBN 9781786393401 (hardback) | ISBN 9781786393418 (epub) | ISBN 9781786393425 (ebook)

Subjects: LCSH: Animals--Diseases. | Animal health. | Mental health. | Veterinary medicine.

Classification: LCC SF745 .M46 2020 | DDC 636.089/6--dc23

LC record available at https://lccn.loc.gov/2019026055

ISBN-13: 9781786393401 (hardback) 9781786393425 (ePDF) 9781786393418 (ePub)

Commissioning Editor: Caroline Makepeace

Editorial Assistant: Lauren Davies Production Editor: Marta Patiño

Typeset by SPi, Pondicherry, India

Printed and bound in the UK by Severn, Gloucester

Contents

Cor	ntributors List	vii
Parı	t 1 Foundational Issues of Animal Mental Health and Well-being	
1	Mental Health in Animals: A Veterinary Behaviorist's View Debra F. Horwitz	1
2	The Problems with Well-Being Terminology Franklin D. McMillan and James W. Yeates	8
3	The Philosophical and Biological Evolution of Feelings in Well-being Ian J.H. Duncan	21
4	The Relationship Between Mental and Physical Health Melissa Bain and C.A. Tony Buffington	33
Part	t 2 The Pleasant Experiences: Mental Wellness	
5	Moving Beyond a Problem-based Focus on Poor Animal Welfare Toward Creating Opportunities to Have Positive Welfare Experiences David J. Mellor and Ngaio J. Beausoleil	50
6	The Mental Health and Well-being Benefits of Personal Control in Animals Franklin D. McMillan	67
7	Quality of Life of Animals in Veterinary Medical Practice James W. Yeates	82
8	The Mental Health and Well-being Benefits of Social Contact and Social Support in Animals Franklin D. McMillan	96
9	Subjective Well-being, Happiness, and Personality in Animals Alexander Weiss and Lauren M. Robinson	111
10	Fostering Mental and Behavioral Wellness During Upbringing and Throughout Life Daniel Q. Estep and Suzanne Hetts	123
Part	t 3 The Unpleasant Experiences: Distress, Suffering, and Mental Illness	
11	What Is Distress? A Complex Answer to a Simple Question Franklin D. McMillan	140
12	Suffering, Agency, and the Bayesian Mind Daniel M. Weary	156
13	Mental Illness in Animals: Diagnostic Considerations Using Selected Mental Disorders	167

14	Psychological Trauma and Posttraumatic Psychopathology in Animals Franklin D. McMillan	182
Part	4 Mental Health Issues in Special Populations	
15	Cognitive and Emotional Disorders in the Aging Pet Jacqueline Wilhelmy and Gary Landsberg	212
16	Mental Health Issues in Farm Animals: A Music Mixing Board Model of Behavioral Characteristics Using the Panksepp Emotional System Temple Grandin	231
17	Mental Health Issues in the Horse Daniel S. Mills, Claire Ricci-Bonot and Sophie S. Hall	242
18	Mental Health Issues in Shelter Animals Victoria Cussen and Pamela J. Reid	257
19	The Mental Health of Laboratory Animals Carine Elkhoraibi, Amy Robinson-Junker, Gina Alvino, and Larry Carbone	277
20	Mental Health Issues in Captive Birds Lynne M. Seibert	291
21	Psychological Well-being in Zoo Animals David Shepherdson and Kathy Carlstead	302
22	Mental Health Issues in Captive Cetaceans Lori Marino	315
Part	5 Assessment and Management of Emotional Distress and Disorders	
23	Assessing Affective States in Animals Michael Mendl and Elizabeth S. Paul	328
24	Treatment of Emotional Distress and Disorders – Nonpharmacologic Methods Pamela J. Reid	345
25	Treatment of Emotional Distress and Disorders – Pharmacologic Methods Sharon Crowell-Davis	364
Inde	ex.	377

vi

Contributors List

Gina Alvino, PhD

Institutional Animal Care and Use Program University of California, San Francisco San Francisco, California, USA

Melissa Bain, MS, DVM, Diplomate American College of Veterinary Behaviorists, Diplomate American College of Animal Welfare
Department of Medicine and Epidemiology
UC Davis School of Veterinary Medicine
Davis, California, USA

Ngaio J. Beausoleil, PhD

Animal Welfare Science and Bioethics Centre School of Veterinary Science Massey University Palmerston North New Zealand

C. A. Tony Buffington, DVM, PhD, Diplomate American College of Veterinary Nutrition (Emeritus) Department of Medicine and Epidemiology UC Davis School of Veterinary Medicine Davis, California, USA

Larry Carbone, DVM, PhD, Diplomate American College of Animal Welfare, Diplomate American College of Laboratory Animal Medicine
Institutional Animal Care and Use Program
University of California, San Francisco
San Francisco, California, USA

Kathy Carlstead, PhD

Research Associate, Center for Species Survival, Smithsonian Conservation Biology Institute Front Royal, Virginia, USA

Sharon Crowell-Davis, DVM, PhD, Diplomate American College of Veterinary Behaviorists Department of Veterinary Biosciences and Diagnostic Imaging College of Veterinary Medicine University of Georgia Athens, Georgia, USA

Victoria Cussen, PhD, CAAB

Anti-Cruelty Behavior Team American Society for the Prevention of Cruelty to Animals 424 E. 92nd St. New York, USA

Ian J.H. Duncan, PhD, Professor Emeritus, Emeritus Chair in Animal Welfare

Department of Animal Biosciences University of Guelph 50 Stone Road East Guelph, Ontario, Canada

Carine Elkhoraibi, MS, MA

Institutional Animal Care and Use Program University of California, San Francisco San Francisco, California, USA

Daniel Q. Estep, PhD, CAAB

Animal Behavior Associates, Inc. Sun City, Arizona, USA

Temple Grandin, PhD

Department of Animal Science Colorado State University Ft. Collins, Colorado, USA

Sophie S. Hall, BSc, PhD

Animal Behaviour Cognition and Welfare Group School of Life Sciences University of Lincoln Lincoln, UK

Suzanne Hetts, PhD, CAAB

Animal Behavior Associates, Inc.

Sun City, Arizona, USA

Debra F. Horwitz, DVM, Diplomate American College of Veterinary Behaviorists

Veterinary Behavior Consultations

St. Louis, Missouri, USA

Gary Landsberg, BSc, DVM, Diplomate American College of Veterinary Behaviorists, Diplomate

European College of Animal Welfare and Behavioural Medicine

Head, Fear Free Research

Vice President, CanCog Technologies

Fergus, Ontario, Canada

Lori Marino, PhD

The Kimmela Center for Animal Advocacy and President, The Whale Sanctuary Project Kanab, Utah, USA

Franklin D. McMillan, DVM, Diplomate American College of Animal Welfare

Best Friends Animal Society

Kanab, Utah, USA

David J. Mellor, PhD

Animal Welfare Science and Bioethics Centre School of Veterinary Science Massey University New Zealand

viii Contributors List

Michael Mendl, PhD

Bristol Veterinary School University of Bristol Langford House, Langford Bristol, UK

Daniel S. Mills, BVSc, PhD, CBiol, FRSB, FHEA, CCAB, Diplomate European College of Animal Welfare and Behavioural Medicine (Behavioural Medicine), Fellow of the Royal College of Veterinary Surgeons, European and Royal College of Veterinary Surgeons Recognised Specialist in Veterinary Behavioural Medicine Animal Behaviour Cognition and Welfare Group

School of Life Sciences University of Lincoln Lincoln, UK

Karen L. Overall, MA, VMD, PhD, Diplomate American College of Veterinary Behaviorists

Biology Department University of Pennsylvania Philadelphia, Pennsylvania, USA Atlantic Veterinary College University of Prince Edward Island Charlottetown, Prince Edward Island, Canada

Elizabeth S. Paul, PhD

Bristol Veterinary School University of Bristol Bristol, UK

Pamela J. Reid, PhD, CAAB

Anti-Cruelty Behavior Team
American Society for the Prevention of Cruelty to Animals
424 E. 92nd St.
New York, USA

Claire Ricci-Bonot, BSc, MSc

Animal Behaviour Cognition and Welfare Group School of Life Sciences University of Lincoln Lincoln, UK

Lauren M. Robinson, PhD

Domestication Lab Konrad Lorenz Institute of Ethology University of Veterinary Medicine Vienna Vienna, Austria Language Research Center Georgia State University Atlanta, Georgia, USA

Amy Robinson-Junker, MS

Laboratory Animal Resource Center University of California, San Francisco San Francisco, California, USA

Contributors List ix

Lynne M. Seibert, DVM, MS, PhD, Diplomate American College of Veterinary Behaviorists Veterinary Behavior Consultants LLC Roswell, Georgia, USA

David Shepherdson, PhD Oregon Zoo Portland, Oregon, USA

Daniel M. Weary, BSc, MSc, D.Phil. Professor and NSERC Industrial Research Chair University of British Columbia Animal Welfare Program Faculty of Land and Food Systems Vancouver, British Columbia, Canada

Alexander Weiss, PhD
Department of Psychology
University of Edinburgh
Edinburgh, UK
Scottish Primate Research Group

Jacqueline Wilhelmy, MS, VMD, Diplomate American College of Veterinary Behaviorists Delaware Valley Veterinary Behavior Quakertown, Pennsylvania, USA

James W. Yeates, BSc, BVSc, DWEL, MBA, PhD, FRCVS, Diplomate European College of Animal Welfare and Behavioural Medicine
Cats Protection
Haywards Heath
East Sussex, UK

x Contributors List

1

Mental Health in Animals: A Veterinary Behaviorist's View

Debra F. Horwitz

Veterinary Behavior Consultations, St. Louis, Missouri, USA

1.1 Introduction

The concept of mental health in animals has not necessarily been an important variable in understanding the animals we interact with and in establishing their overall welfare and well-being. Early studies of the behavior of differing species focused on how certain traits were passed along to offspring and Darwin was the first to correctly posit that the desire for reproductive success, i.e., putting one's genes into the next generation, drove many changes in both form (how the organism looked) and function (what the animal did). Further studies discovered that certain behaviors were not affected by environmental circumstances and occurred regularly in response to very specific cues. These were termed instincts, which refers to behaviors that appears in a fully functioning form the first time they are performed – where no learning is required (Alcock, 1993). However, other behaviors are the result of learning: the modification of behavior in response to specific circumstances and information from other individuals and the environment. Over time and further study this came to be formulated into 'learning theory', which comprised definitions and examples of how individuals (both people and animals) learn new tasks (Schwartz and Robbins, 1995). Finally, there are behaviors that occur because they are a normal part of the animals' behavioral repertoire. For example, obtaining food may occur due to information from scent or sight, determining where the food is readily available, and so on. Given that so many companion animals live in our homes, their mental health has taken on a greater meaning.

1.2 What is Behavior and What is Mental Health?

1.2.1 Behavior

Behavior can be broadly defined as what an animal or person does and how they function within their environment. One's behavior is influenced and affected by the individual's genetics, environment, early experiences, social experiences, and encounters with animate and inanimate objects. The accumulating knowledge in this area led to the creation of the field of ethology, which seeks to understand the adaptive function of animal behavior and behavioral characteristics. Ethological studies now widely utilize the ethogram – a catalog of individual or species behaviors that may include the frequency and duration of each behavior.

Ongoing behavior is usually influenced by its consequences: if the outcome is one that the animal finds favorable the behavior is likely to occur again, and, conversely, if the outcome is something less than favorable or even adverse then the behavior is less likely to occur in the future (at least in that circumstance). This is all controlled by learning, whether through interactions with the environment or with other individuals. Some behaviors are more highly motivated and thus more likely than others to occur; these behaviors are more important to the animal's normal behavioral patterns and may be difficult to deter. Additionally, changes in the environment, social organization, illness, anxiety, and stress can result in the animal showing alterations in their behavior.

1.2.2 Mental health

Assessing the mental health of animals is a relatively recent development and has been utilized more consistently in the past 20 years in companion animals. Prior to that time, what was discussed was the welfare of those animals in human care. The most commonly used method – originally developed for use in farm animals – is known as the Five Freedoms (Farm Animal Welfare Council, 2009) and includes the following:

- 1. Freedom from hunger and thirst by ready access to fresh water and a diet to maintain full health and vigor.
- **2. Freedom from discomfort** by providing an appropriate environment including shelter and a comfortable resting area.
- 3. Freedom from pain, injury, or disease by prevention or rapid diagnosis and treatment.
- 4. Freedom to express normal behavior by providing sufficient space, proper facilities, and company of the animals' own kind.
- 5. Freedom from fear and distress by ensuring conditions and treatment which avoid mental suffering.

Another measure is the United States Department of Agriculture's Six Elements to Psychological Wellbeing in Captive Animals (Kulpa-Eddy et al., 2005), which has recently been clarified and updated. Additional approaches include quality-of-life (QOL) assessments and mental health wellness as described by McMillan (2002), which focus on a balanced QOL by recognizing both pleasant and unpleasant feelings in the areas of social relationships, mental stimulation, health, food, stress, and control/predictability while incorporating differences in personal preferences. Others define QOL as the combinations of the animal's feelings, physical state, and its ability to satisfy its nature (Wojciechowska and Hewson, 2005).

Merriam-Webster (2019) defines mental health as

the condition of being sound mentally and emotionally that is characterized by the absence of *mental illness* and by adequate adjustment especially as reflected in feeling comfortable about oneself, positive feelings about others, and the ability to meet the demands of daily life.

As can be seen, this definition takes in most of the items discussed in the Five Freedoms and QOL definitions.

1.2.3 How do stress and anxiety factor into mental health and behavior?

At its simplest, anxiety is the anticipation of danger or threat. Sources of anxiety in companion animals can be anything from being left home alone for long periods of time, uncertain social interactions with other animals or humans, the inability to engage in normal species-specific behaviors, and lack of control and predictability in daily life. However, in many cases the source of anxiety may not be readily identifiable.

Anxiety can cause stress, which is a protective mechanism. When an organism perceives a threat – a stressor – activation of the hypothalamic–pituitary– adrenal (HPA) axis and sympathetic nervous system occurs, engaging the body's 'fight-or-flight' response (Mills et al., 2013). This stress response has physiological, behavioral, and psychological components and enhances the animal's ability to perceive, evaluate, and choose the correct response to alleviate and recover from the threat. Not all stress is problematic if it is short term and the animal is able to return to normal baseline functioning. If this is not possible, the animal is experiencing 'distress', the mental state that occurs when the circumstances overwhelm the animal's ability to cope with the situation (see also Chapter 11, this volume). Distress is highly individual: that which is distressing to one animal may not be distressing to another. Chronic distress can occur with frequent exposure to stressors or unrelenting exposure to a stressor that never abates and acts over an extended period of time. This can cause chronic dysregulation of the HPA axis and excessive corticosteroid exposure, which may then lead to changes in learning and memory and adversely affect the animal's overall health. Chronic stress can be due to a health issue, social conflict with other animals in the home, social isolation, and many other causes.

On its own, anxiety and its accompanying physiological changes are probably not pathological when short-lived, but chronic anxiety can lead to chronic stress. Anxiety, like stress, can become a chronic state and compromise the health, welfare, and lifespan of the individual (Dreschel, 2010). Responses to anxiety-provoking stimuli are likely influenced by early learning, negative experiences during development, and the individual's genetics (Mertens and Dodman, 1998). If the same experience is repeatedly encountered, anxiety and apprehension may occur through sensitization, potentially resulting in

D.F. Horwitz

enhanced responses. Stimulus intensity and frequency of encounters may compound the response and various associative processes may accelerate acquisition of responses (Levine, 2009). Because of this, we must acknowledge and accept that animals can and often will refuse to perform behaviors that cause them distress, fear, or pain, and forcing animals to do these things is unacceptable. Therefore, to provide optimum health and welfare for all pets we should include anxiety and stress as adverse states that can affect the mental health of companion animals.

1.3 The Intersection of Mental Health and Behavior

If behavior is what the animal does, then mental health is how the animal 'feels'. However, the behavior displayed may or may not accurately represent emotional states or the animal's mental health. The meaning of the behavior is based on the animal itself and its early experiences, socialization, genetics, training, and traumatic events (see Chapter 14, this volume).

The disciplines of veterinary behavior and mental health care in animals overlap at many points. Both are concerned with the ability of animals to experience fulfilling and clear social relationships, perform and engage in normal species behaviors, have appropriate outlets for mental stimulation, be provided with appropriate and timely physical health care, and receive a diet that meets their needs. Additionally, both disciplines recognize that all animals need some control and predictability to feel behaviorally and mentally healthy (see Chapter 6, this volume). Animals should be allowed to say 'no'; behaviorists and mental health practitioners agree that animal caregivers must respect an animal's decision not to engage in a particular behavior or activity and help the animal learn and understand why, when the behavior is necessary, it must be performed. Furthermore, the disciplines of behavior and mental health care also intersect with regard to the animal's response to and ability to function when the environment or some other aspect of life is stressful.

The point where the two disciplines can seem to work in opposing directions often depends on the how a pet owner interprets specific behaviors – as good or bad – and attaches importance to the animal's mental health. Consider a dog whom the owner wants to take running with them every day. After

several months the dog begins to hide when it is time to go running. The owner could be upset since she feels that taking the dog on a daily run provides the exercise and mental stimulation essential for the animal's good mental health. However, the dog may find running unpleasant, perhaps because of such things as stress when encountering other dogs, frustration from the inability to explore and sniff the environment, or pain from osteoarthritis or other physical disorders. It is entirely possible that in this example something that the owner sees as an improper behavioral response to her efforts to benefit her dog's mental well-being is actually the dog's attempt to protect itself from things which can harm this well-being.

Another example is a cat who is friendly to family members but runs and hides whenever company comes to the house. The family may see this as undesirable behavior: being friendly to them but unfriendly to others may be insulting and upsetting to owners who expect the cat to behave differently. However, the cat may not have been sufficiently socialized to people early in life and now finds strangers frightening and stressful. By seeking a safe hiding place stress and anxiety is alleviated, which is beneficial to the cat's mental health. The owner must respect this need to escape; after all, we do not expect every person to be comfortable around every other person.

The divergence of the two disciplines is perhaps clearest in cases where an animal with excellent mental health is performing a normal and natural behavior that the owner finds unacceptable. It must be kept in mind that the evolutionary history of companion animals spans tens of thousands of years, and keeping pets inside human homes is, relatively speaking, a very recent development. It is no surprise, then, that there are numerous normal behaviors which companion animals perform that may not be suitable for the household, and are unwanted by caregivers. These include marking with urine or claws, exploratory chewing, climbing, and rambunctious activities that result in damage to the owner or her possessions. These behaviors are commonly unaccompanied by impaired mental health and are often presented to both veterinary behaviorists and trainers as behavior problems when in reality they might just be a result of insufficient outlets for normal species-specific behaviors, inadequate attention to normal animal needs, or unrealistic expectations. In other cases, the animal may be frustrated by the inability to meet its daily need for mental stimulation, social interaction, safety, and control and predictability, and once these needs are provided for and the animal is shown how to properly meet those needs, the undesired behavior may cease. So, to illustrate the point of divergence of behavior care and mental health care, consider the example of the cat who is destroying the furniture by clawing. Here, addressing the behavior is essential, but the cat's mental health does not need help. Conversely, a pet with greatly impaired mental health may show no behaviors that the owner feels need correction. For example, a dog experiencing extreme loneliness may simply 'suffer in silence', or another dog with the same emotional distress may exhibit behavior that is an effort to cope with the stress but does not bother the pet's owner, such as relentless digging in a large yard behind the house. Here, addressing the animal's mental health is essential, even when there is no 'behavior problem' needing correction.

1.3.1 Systemic signs of poor mental health

One challenge in assessing behavior and mental health is that many of the signs may be attributable to mental disorders, physical disorders, or both (see Table 1.1). This crossover in causes means that the first step in the evaluation of these signs should be a veterinary visit with a physical examination and appropriate diagnostic testing to rule out physical health causes. Importantly, however, because it is possible for both a mental health issue and a physical issue to exist at the same time, identifying a physical disorder does not necessary exclude a mental problem. In cases where both co-exist, treating one or the other may or may not create a change in the behavior; it is usually necessary to treat both.

1.3.2 When does a change in behavior or mental state require intervention?

The answer to this question will vary from animal to animal and household to household. Some homes will have a very low tolerance for unwanted house soiling, destruction, and rambunctious behavior. In most cases these situations do not impair the pet's ability to live a normal life, but without appropriate input some caregivers may become frustrated to the point of severing their bond with the pet and relinquishing the animal to a shelter or rescue. Others may not care as much, believing the pet will 'grow

out' of the problem. Still others will seek assistance from inappropriate sources (e.g., the internet, friends, or unqualified animal 'trainers'), which either fails to help, makes the problem worse, or increases caregiver frustration and decreases willingness to keep the pet. Fortunately, prompt and appropriate intervention by qualified experts can often control these behaviors and help pets stay in their homes.

Crucially, when behavioral changes accompany severe changes in mental health (see Table 1.1), immediate intervention is required. These are behavior changes and behavior patterns that are not normally part of the daily behavioral repertoire, or are normal behaviors performed excessively and that interfere with the normal functioning of that pet. In these cases, specialists in behavioral diagnosis and treatment should be consulted. Board-certified veterinary behaviorists can be found at https://www.dacvb.org.

1.3.3 How can we protect our pets from behavioral or mental health problems?

The first thing we can do is educate ourselves about normal dog (Horwitz et al., 2014) and cat behavior so that we understand that unwanted behaviors are often attempts to meet species-specific needs for mental stimulation, social engagement, exercise, and a more controllable and predictable environment. We also must treat our pets with kindness and understanding and realize that they do not speak our language. Training is the language by which we impart the information needed for the pet to understand and carry out desired behaviors, which not only ensures that the pet will function well in the human world, but will acquire the ability to *flour*ish. All training and interactions should be based on the principles of positive reinforcement (i.e., rewarding desired behaviors). Finally, we can help our pets develop resilience and flexibility by controlling what they are exposed to and minimizing threats when the pet shows signs of discomfort, anxiety, or fear. In this way pets learn that we will protect them and that we care about their wellbeing. Often, once they learn they are protected they gain the ability to face new challenges with increased boldness, confidence, and resilience – all contributing to their greater happiness.

1.4 Concluding Remarks

Changes in mental health and behavior are often the first signs of a medical disorder and all abrupt

D.F. Horwitz

Table 1.1. Behavioral signs and possible causes: physical disorders versus mental health and/or behavioral disorders.

Type of systemic change	Behavioral change	Possible physical causes ^a	Behavioral and/or mental health causes
Self-care	Excessive self-grooming (Amat et al., 2016), chewing and licking skin and fur Licking inanimate objects or household items (Bécuwe-Bonnet et al., 2012) Changes in sleep – less sleep or sleeping more	Dermatological problems Nausea, gastrointestinal upset Illness or pain Food allergies	Anxiety (Ohl et al., 2008) or stress Displacement behavior Compulsive disorders Depression or cognitive decline (Landsberg et al., 2011)
Alimentary	Increased or decreased appetite, especially a loss of appetite Vomiting, diarrhea, or constipation	Infectious illness Irritation from food intake Gastritis or colon issues Food allergies	Anxiety or stress Competition from other animals while eating Inability to safely access the elimination location
Social behaviors	Avoiding social interactions and hiding from people or other animals (Fureix and Meagher, 2015) Excessive attention seeking behaviors Increase in aggressive signaling and responses; growling, snapping, biting at other animals	Illness Pain	Fear of interactions Threats from household pets Unclear interactions with caregivers
Locomotor	Circling behaviors, spinning Light chasing Pacing or tremors Excessive licking	Injury Pain Neurologic problem Brain tumor	Displacement behaviors Compulsive disorders Tremors due to fear Anxiety Pain Cognitive changes
Vocalization	Increased barking or meowing Increased aggressive signaling Whining	Injury Pain Neurologic disorder Brain tumor	Compulsive disorder (Bain, 2018) Cognitive decline Separation anxiety or distress (Ogata, 2016) Attention seeking Fear Social signaling
Destructiveness	Destructive behavior toward household objects and structures	Pain	Separation anxiety or distress (Ogata, 2016) Noise phobias Storm phobia
Elimination	Elimination of urine (Pryor <i>et al.</i> , 2001) or stool in unwanted locations	Metabolic dysfunction Infection bladder or bowel	Separation anxiety or distress (Storengen et al., 2014) Noise or storm phobias Inability or unwillingness to access correct area Cognitive changes Social issues between animals

^aPhysical and behavioral problems may exist concurrently. In such cases treatment often must focus on both the underlying medical issues and the outward behavior as well as the triggers for the behavior.

changes should be investigated by a veterinarian for medical disorders that may be contributory. In many cases the changes in behavior will diminish or resolve if the animal feels better. However, in cases where there is no medical issue or a medical issue has been resolved, behavioral changes and/or associated mental health issues might remain. This may occur for two reasons: the animal has learned that the performance of the behavior is reinforcing and enjoyable, or the environment (both social and experiential) are still creating stress or untenable choices for the animal.

As caregivers of our animals we are responsible for their physical, mental, and behavioral health. This requires that we always consider what our animals need and that we look at the world through their eyes. One can begin with the Five Freedoms discussed in Section 1.2.2. Most importantly, we must always remember that as sentient beings the animals also deserve consideration as thinking and feeling animals. We must realize and provide for a good social environment that meets their needs for exploration, mental stimulation, and safety from harm. We must realize that animals have the right to 'say no' to something we want them to do – without reprisals. It is our job to figure out why what we ask is not possible for the animal at that time and devise a way to either change what we want or teach them why our request is not dangerous or harmful. At other times our pets are provided with all the things that they appear to need and still seem to have mental health and/or behavioral problems. That is when it is important to seek help from a veterinarian and/or veterinary behavior specialist for intensive treatment.

1.5 References

- Alcock, J. (1993) Animal Behavior, 5th edn. Sinauer Associates, Sunderland, Massachusetts, USA.
- Amat, M., Camps, T., Manteca, X. (2016) Stress in owned cats: Behavioural changes and welfare implications. *Journal of Feline Medicine and Surgery* 18, 577–586. http://dx.doi.org/10.1177/1098612X15590867.
- Bain, M. (2018) Compulsive and repetitive disorders overview. In: Horwitz, D, (ed.) Blackwell's Five-Minute Veterinary Consult Clinical Companion: Canine and Feline Behavior, 2nd edn. Wiley Blackwell, Hoboken, New Jersey, USA, pp. 391–403.
- Bécuwe-Bonnet, V., Bélanger, M.C., Hélie, P. (2012) Gastrointestinal disorders in dogs with excessive licking of surfaces. *Journal of Veterinary Behavior: Clinical*

- Applications and Research 7, 194–204. http://dx.doi.org/10.1016/j.jveb.2011.07.003.
- Dreschel, N.A. (2010) The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science* 125, 157–162. http://dx.doi.org/10.1016/j.applanim.2010.04.003.
- Farm Animal Welfare Council. (2009) Farm animal welfare in Great Britain: Past, present and future. Available at: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/319292/Farm_Animal_Welfare_in_Great_Britain_-_Past__Present_and_Future.pdf (accessed 14 Jan 2019).
- Fureix, C. and Meagher, R.K. (2015) What can inactivity (in its various forms) reveal about affective states in non-human animals? A review. Applied Animal Behaviour Science 171, 8–24. http://dx.doi.org/ 10.1016/j.applanim.2015.08.036.
- Horwitz, D.F., Ciribassi, J.C., Dale, S. (2014) Decoding Your Dog. Houghton Mifflin, Harcourt, Boston, Massachusetts, USA.
- Kulpa-Eddy, J.A., Taylor, S., Adams, K.M. (2005) USDA perspective on environmental enrichment for animals. *ILAR Journal* 46, 83–94. http://dx.doi.org/10.1093/ilar.46.2.83.
- Landsberg, G.M., DePorter, T., Araujo, J.A. (2011) Clinical signs and management of anxiety, sleeplessness, and cognitive dysfunction in the senior pet. Veterinary Clinics: Small Animal Practice 41, 565–590.
- Levine, E.D. (2009) Sound sensitivities. In: Horwitz, D.F. and Mills, D.M. (eds.) BSAVA Manual of Canine and Feline Behavioural Medicine, 2nd edn. BSAVA, Gloucester, UK, pp. 159–168. http://dx.doi.org/ 10.22233/9781905319879.15.
- McMillan, F.D. (2002) Development of a mental wellness program for animals. *Journal of the American Veterinary Medical Association* 220, 965–971. http://dx.doi. org/10.2460/javma.2002.220.965.
- Merriam-Webster. (2019) Mental health. Available at: www. merriam-webster.com/dictionary/mental%20health (accessed 14 Jan 2019).
- Mertens, P.A. and Dodman, N.H. (1998) Pharmacologic treatment of fear and anxiety in animals. In: Dodman, N.H. and Shuster, L. (eds.) Psychopharmacology of Animal Behavior Disorders. Blackwell Science, Malden, Massachusetts, USA, pp. 135–137.
- Mills, D., Dube, M.B., Zulch, H. (2013) Stress and Pheromonatherapy in Small Animal Clinical Behaviour. John Wiley and Sons, Chichester, UK.
- Ogata, N. (2016) Separation anxiety in dogs: What progress has been made in our understanding of the most common behavioral problems in dogs? *Journal of Veterinary Behavior: Clinical Applications and Research* 16, 28–35. http://dx.doi.org/10.1016/j.jveb.2016.02.005.
- Ohl, F., Arndt, S.S., van der Staay, F.J. (2008) Pathological anxiety in animals. *The Veterinary Journal* 175, 18–26. http://dx.doi.org/10.1016/j.tvjl.2006.12.013.
- Pryor, P.A., Hart, B.L., Cliff, K.D. (2001) Causes of urine marking in cats and effects of environmental

6 D.F. Horwitz

- management on frequency of marking. *Journal of the American Veterinary Medical Association* 219, 1709–1713. http://dx.doi.org/10.2460/javma.2001.219.1709.
- Schwartz, B. and Robbins, S.J. (1995) *Psychology of Learning and Behavior*, 4th edn. W.W. Norton Company, New York, USA.
- Storengen, L.M., Boge, S.C.K., Lingaas, F. (2014) A descriptive study of 215 dogs diagnosed with
- separation anxiety. *Applied Animal Behaviour Science* 159, 82–89. http://dx.doi.org/10.1016/j.applanim.2014.07.006.
- Wojciechowska, J.I. and Hewson, C.J. (2005) Quality-of-life assessment in pet dogs. *Journal of the American Veterinary Medical Association* 226, 722–728. http://dx.doi.org/10.2460/javma.2005.226. 722.

The Problems with Well-being Terminology

FRANKLIN D. McMILLAN AND JAMES W. YEATES

Best Friends Animal Society, Kanab, Utah, USA; Cats Protection, Haywards Heath, UK

2.1 Introduction

Suppose you were given the task of looking at one nonhuman animal (hereafter animal) and measuring that animal's welfare, well-being, quality of life (QOL), and happiness. But time and funding constraints allow you to measure only one of these. If you pick one, would there be anything important to the animal that you would miss by not being able to measure the others? Would your answer be the same no matter which concept you chose to measure? If you wanted that animal to have the best life, would any of the four concepts be the best one to look at?

An individual's judgment of how their own life is faring can vary widely in the cognitive complexity of that evaluation. We aren't certain whether and how such judgments are made by different animals, or by humans - particularly those lacking verbal capacity to convey their thoughts. For many, it may be that such judgments consist simply of feelings based on time frames as short as each moment, or possibly based on the animal's experiences over several hours or even days prior to the judgment. At the other end of the cognitive spectrum, judgments of how one's life is faring can involve not just feeling states but also complex cognitive appraisals (e.g., comparisons with others, having meaning or purpose in one's life, and a sense of personal accomplishments) and incorporate an extensive time frame dating back decades and a vision forward to one's life goals. Furthermore, in terms of complexity of emotional processing, some animals might experience relatively simple feelings of momentary enjoyment and suffering, while others' assessments may be based, at least partly, on more complex emotions such as relief, hope, jealousy, achievement, and self-worth.

We are far from being able to determine where individual humans and animals fall on these scales of complexity in their evaluations of how things are going for them, but evidence suggests that all conscious beings have some conceptualization of judging how their lives are faring - by affective and cognitive processes - as going well or not so well, whether the 'life' is this moment or over the last several years. For example, Kahneman and Riis (2005) suggested that a measure of momentary well-being in humans could consist of asking the person to indicate whether they feel impatient for their current situation to end, or would prefer for it to continue. When this measure is repeated over a period of time, the average summing of the momentary preference for continuing or stopping 'identifies well-being with the extent to which individuals live their lives in a state of wishing for the present to extend, as against wishing they were somewhere else—or not caring one way or the other' (p. 292). Behavioral research, in particular preference and aversion studies, have indicated that the capacity to signal a desire for one's current situation to continue or end is exhibited in a wide range of animal species (Kirkden and Pajor, 2006).

How an individual perceives his or her own life to be faring, on a scale of good to bad, is currently described by an indistinct and confusing number of terms. In the human and animal literature alike, limited agreement has been reached about the meaning of well-being, welfare, quality of life, happiness, and subjective well-being (SWB) (Novak and Suomi, 1988; Clark et al., 1997; Hetts et al., 2005; Nordenfelt, 2006; Green and Mellor, 2011). While all of these concepts refer in some way to how much one likes the life one is leading, at present authors

frequently – but in different ways – equate or differentiate terms, use terms interchangeably, and define terms by using other similar ill-defined terms. Different studies often use the same terms to refer to different phenomena or different terms to refer to the same or very similar phenomena. Factors as immaterial as geographical preferences contribute to the confusion, as, for instance, in the animal literature where 'welfare' is the European term for the North American 'well-being' (Jones, 2004; Nordenfelt, 2006). Moreover, certain languages may not contain terms for concepts which bear different terms in other languages (e.g., French uses *bien-être* with no obvious equivalent for 'welfare').

To illustrate the terminology problem, Table 2.1 presents reference citations from the animal literature in which different terms have been equated (stated explicitly as equals or used interchangeably as synonyms). The human literature is equally if not more problematic while also including additional terms such as *emotional well-being* (Diener and Lucas, 2000) and *life satisfaction* (Lyubomirsky *et al.*, 2005).

The first challenge in scrutinizing this field is deciding on a term to use to refer collectively to these similar concepts - that is, to give a name to the overall topic under discussion. To date no single agreed-upon term (or conceptualization) has emerged to describe the different evaluations individuals (human and nonhuman) make regarding their lives, the events happening to them, their bodies and minds, and the circumstances in which they live – in short, how much one views his/her own life as 'the good life' (Diener, 2006; Brülde, 2007; Yeates, 2017). For the purposes of the present chapter this umbrella term will be Well-being¹ - capitalized to distinguish it from the use of 'well-being' as an individual concept - and 'Well-being concepts' will refer collectively to the terms welfare, well-being, QOL, happiness, and SWB.

As we will see, some interpretative discrepancies among these terms are difficult to reconcile. One of the most important reasons for this challenge is rooted in a fundamental difference regarding what the terms are referring to. The Well-being concepts may be about (i) the quality of one's *life conditions*, or (ii) the quality of one's *life experiences*. The former include *physical health*, *biological functioning*, and *environmental factors*; the latter include only conscious experiences. The two can be strongly linked, as when an individual is being chased by a predator, or they may be uncoupled from one

another, as when an individual has an undetected cancer. Adaptation can also disconnect life conditions and life experiences such as after one loses their vision or the use of one or more limbs; in these cases disability causes permanent functional impairment but after adaptation the individual often regains very high levels of Well-being with positive life experiences (humans: Duggan and Dijkers, 2001; Diener *et al.*, 2006; animals: Bauer *et al.*, 1992; Dickerson *et al.*, 2015). We will return to this conundrum later.

2.2 Similarities and Differences Between Well-being Concepts in Animals

On the basis of their usage in the scientific literature, the different Well-being concepts can be found to have extensive similarities as well as some dissimilarities. This approach provides an important starting point in understanding the entanglement that has evolved between these terms. However, no matter how meticulously we analyze the terms, they will not come out at the other end as clearly the same or clearly distinct. The following discussion will focus primarily on the animal literature while including relevant information from human literature where it can help provide some explanatory clarification.

2.2.1 Common attributes among Well-being concepts in animals

Represents the individual's perspective and perception

The first feature shared broadly among Well-being concepts is that it is, at the minimum, based largely if not solely on a view from within, of how the individual perceives and appraises aspects of his/her own life. This means it is not something given to the individual (Broom, 1996). One could bestow the same exact objectively described living conditions to ten different humans or animals - e.g., shelter, food, social companionship, stimulation/entertainment, and even health - and because of vast differences in preferences, likes, dislikes, etc., the result could be ten different levels of Well-being, from very low to very high. The individual's perspective and perception has been described in the literature in animals for welfare (Sandem et al., 2002; Bracke, 2007; Green and Mellor, 2011) and QOL (Wiseman-Orr et al., 2006; Bracke, 2007; Scott et al., 2007; Taylor and Mills, 2007), and in humans for QOL (Diener, 2006; Peterson, 2006; Scott et al., 2007; Taylor and

Table 2.1. Terms equated (explicitly or used as synonyms) in the animal literature.

	Well-being	Subjective well-being	Welfare	Quality of life
Subjective well-being	Boissy et al., 2007			
Welfare Quality of life	Appleby and Sandøe, 2002 Christiansen and Forkman, 2007 DeGrazia, 1998 Fraser and Weary, 2004 Hurnik et al., 1995 Jones, 2004 Mason, 1991 Mench, 1998 Morton, 2000 Scott et al., 2007 Stafford, 2006 Vitale, 2004 Wojciechowska and Hewson, 2005 Appleby and Sandøe, 2002	Nordenfelt, 2006 Robinson et al., 2017 Weiss et al., 2009	Anniehy and Sandae	
Quality of life	Appleby and Sandøe, 2002 Boissy et al., 2007 Christiansen and Forkman, 2007 DeGrazia, 1998 Fraser, 2004 Hurnik et al., 1995 Mench, 1998 Nordenfelt, 2006 Sandøe, 1999 Stafford, 2006 Vitale, 2004 Wojciechowska and Hewson, 2005	Nordenfelt, 2006	Appleby and Sandøe, 2002 Bracke, 2007 Broom, 2007 Christiansen and Forkman, 2007 DeGrazia, 1998 Fraser, 2004 Green and Mellor, 2011 Hewson, 2003a Hurnik et al., 1995 Mench, 1998 Mullan, 2015 Nordenfelt, 2006 Sandøe, 1999 Vitale, 2004 Whay et al., 2003 Wojciechowska and Hewson, 2005	
Happiness		Robinson et al., 2016 Robinson et al., 2017 Weiss et al., 2006 Weiss et al., 2009 Weiss et al., 2011a	Carbone, 2004 Nordenfelt, 2006 Robinson et al., 2016 Robinson et al., 2017 Webb et al., 2019 Weiss et al., 2009	Belshaw, 2018 Nordenfelt, 2006

Mills, 2007), well-being (Kahneman and Riis, 2005), and SWB (Diener, 2006; Peterson, 2006).

Based on the same philosophical frameworks

In discussions of definitions and principles of Wellbeing concepts in animals, welfare, well-being, and QOL often share the same (or at least seemingly similar) philosophical bases. One approach has been to categorize welfare definitions (Barnard and Hurst,

1996; Duncan and Fraser, 1997) or concepts (Appleby and Stokes, 2008) into three types: (i) functioning-and health-based; (ii) feelings-based; and (iii) natural living-based. Another approach has been to separate QOL (Duncan and Fraser, 1997; Fraser *et al.*, 1997; Sandøe, 1999; Taylor and Mills, 2007), well-being (Appleby and Sandøe, 2002), and welfare (Appleby and Sandøe, 2002) into three theoretical foundations, the first one being solely objective, the second one containing both objective and subjective elements,

and the third one being solely subjective: (i) perfectionism and other forms of objective list theories, which hold that there are things that are objectively good for an individual whether or not he/she realizes it and focus on objectively measurable factors, such as health, biological functioning, basic resources, and living conditions; (ii) desire or preference satisfaction, which holds that satisfying one's preferences or desires is what improves one's Wellbeing; and (iii) hedonism, in which Well-being is based on pleasant and unpleasant affective states.

Based on a balance of pleasant versus unpleasant affect

Notwithstanding some of the philosophical approaches above that do not focus on feelings (e.g., objective list theory), a large body of literature on Well-being concepts emphasizes the role of affective states in animal Well-being. More specifically, it has been suggested by many authors that it is the balance of pleasant feelings over unpleasant that corresponds to the level of welfare (Dawkins, 1990, 2006; Mench, 1998; Sandem et al., 2002; King and Landau, 2003; Broom, 2007; Kirkwood, 2007; Robinson et al., 2016), QOL (Mench, 1998; Broom, 2007; Kendrick, 2007; Taylor and Mills, 2007; Green and Mellor, 2011; Yeates, 2011), well-being (Mench, 1998), SWB (King and Landau, 2003; Gartner and Weiss, 2013; Robinson et al., 2016), and happiness (King and Landau, 2003; Robinson et al., 2016).

The Affect Balance Model was first proposed by Bradburn (1969) to explain psychological well-being in humans. Since then, the model has been applied to other Well-being concepts in humans, including most recently to happiness. Lyubomirsky et al. (2005) concluded that 'happiness is best regarded as a state in which people feel a preponderance of positive emotions most of the time'. Happy people, said the researchers, do not experience

positive affect 100% of the time, rather, they also experience infrequent – though not absent – negative emotions, such as sadness, anxiety, and anger. Current evidence suggests that in both animals and humans, an increase in the positivity of the affect balance is linked to increases in all Well-being concepts (Fig. 2.1).

A bipolar continuum phenomenon

The nature of biological and psychological phenomena may be dichotomous or a continuum. The dichotomous structure works as an all-or-nothing process using a threshold above which the individual 'has' the condition; for the continuum the individual experiences progressive degrees of the condition. It is not uncommon to encounter language in the literature that implies Well-being concepts are threshold phenomena, such as to 'not have quality of life', 'for welfare to exist', 'to reach quality of life', and 'preserving or ensuring well-being'. However, because there now appears to be a consensus that all Wellbeing concepts exist on a continuum (Nordenfelt, 2006; Broom, 2007), it appears the language implying Well-being concepts to be a threshold phenomenon is likely nothing more than a bit of careless locution.

But why, then, would it be correct to say that one can 'achieve' happiness? A key problem involved with the continuum-threshold question becomes evident when the issue of polarity is added in. If it is agreed that Well-being concepts are continuum phenomena, then it needs to be clarified whether the continuum is unipolar (all positive or all negative) or bipolar (both positive and negative). Empirically as well as intuitively, judgments of one's own life can range from very good to very poor (Galtung, 2005; Diener, 2006; Broom, 2007), constituting a bipolar nature. The problem is one of terminology, and the clearest example is the term happiness (see Fig. 2.2). The

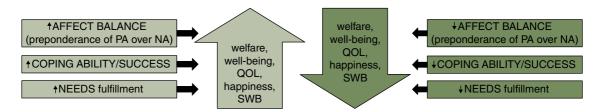


Fig. 2.1. Effects on Well-being. Changes in these factors will cause all Well-being concepts to vary in the same direction: when any of the factors is increased, all Well-being concepts increase; when any are decreased, Well-being concepts decrease. PA, positive affect; NA, negative affect; QOL, quality of life; SWB, subjective well-being.

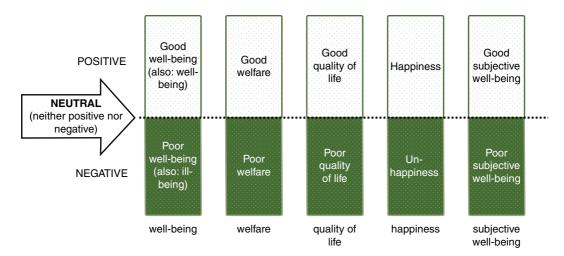


Fig. 2.2. Different terminology for positive and negative aspects of Well-being states.

word happiness refers to a positive state, so the only way to conceive a bipolar continuum for the happiness concept is to create a separate term to represent the negative counterpart of happiness, i.e., unhappiness, which includes such affects as sadness, misery, and the like. Less commonly, the same has occurred in the human literature for well-being, where 'illbeing' has been used as the negative counterpart (Galtung, 2005; Diener, 2006; Nordenfelt, 2006). In contrast, welfare has no separate term for the negative side of the continuum and has a history of different emphases. Prior to the twentieth century, welfare referred primarily to the positive side of the continuum (Merriam-Webster, 2018), then during the twentieth century it reflected more the negative side (Nordenfelt, 2006), and presently it is viewed as balanced between the two sides. For example, Nordenfelt (2006) noted that 'welfare covers the whole area of positive human and animal experiences'. The reason at least some of the Well-being concepts can seem to be both a bipolar continuum (e.g., happiness to unhappiness) and a unipolar threshold phenomenon (e.g., one can 'reach' happiness) can be attributed to the ambiguous terminology.

Coping ability

In animals, the individual's ability to cope successfully with challenges (internal as well as external) has been connected to welfare (Broom, 1986; Hubrecht, 1995; King and Landau, 2003; Broom, 2007; Green and Mellor, 2011; Robinson *et al.*, 2016), QOL (Wojciechowska and Hewson, 2005; Broom, 2007),

SWB (King and Landau, 2003), and happiness (King and Landau, 2003). For example, Hubrecht (1995) states that welfare problems arise when coping ability is exceeded. Coping refers to the animal's ability to lessen the negative psychological impact of a stressful stimulus; the degree of success thereby dictates the level of psychological discomfort experienced. Evidence suggests that Well-being is promoted by successfully coping with life's problems, not from experiencing no problems that demand coping behavior (Boissy *et al.*, 2007). This is consistent with the research mentioned earlier that people who report being the happiest do occasionally experience negative emotions (Lyubomirsky *et al.*, 2005).

Coping has been considered so important to Wellbeing that some researchers regard it to be the central determinant of Well-being concepts, such as Broom's (1986, p.524) definition that 'the welfare of an animal is its state as regards its attempts to cope with its environment'. As shown in Fig. 2.1, all Well-being concepts rise and fall with, respectively, improvement and deterioration in the individual's ability to cope (Hubrecht, 1995; King and Landau, 2003; Broom, 2007; Green and Mellor, 2011).

Meeting of needs

Another common feature shared by the range of Well-being concepts was touched on briefly in the section above on philosophical frameworks, and that is the meeting of needs. Broom (2007) notes the connection between needs and feelings (unpleasant feelings are often associated with unsatisfied needs,

12 F.D. McMillan and J.W. Yeates

whereas pleasant feelings occur when needs are satisfied). He further suggests that when needs are not satisfied, welfare (and QOL, which he considers the same) will be poorer than when they are satisfied (see Fig. 2.1). Taylor and Mills (2007) include the fulfillment of health, social, and environmental needs in their definition of QOL.

Methods of measurement

The measurement of Well-being concepts in humans and animals is far from perfected. In animals, many literature reports have described methods for measuring aspects of the various Well-being concepts: welfare (Mendl, 1991; Mason and Mendl, 1993; Wojciechowska and Hewson, 2005; Broom, 2007; Robinson et al., 2017), QOL (Wojciechowska and Hewson, 2005; Broom, 2007; Hewson et al., 2007; Taylor and Mills, 2007; Timmins et al., 2007), SWB (Weiss et al., 2011b), and happiness (Robinson et al., 2017). Importantly, the overlap of these methods across the Well-being concepts is extensive. Lists of the factors being assessed include physiologic measures (e.g., concentrations of glucocorticoid levels, leukocyte count, and heart and respiratory rates), health parameters, level of physical and social functioning, and behavioral indices (e.g., documentation of abnormal behavior such as stereotypies, subjective mood assessment, preference and motivation testing, operant tests, aversion techniques, cognitive bias testing, consumer demand theory tests, and success in achieving goals). Furthermore, it is widely accepted that for all Well-being concepts none of these methods of measurement is sufficient by themselves; measurement should be performed using a combination of different methods. In all, the resemblance of assessment methods across Well-being concepts is such that if one were to be given only a description of the factors being measured but not which Wellbeing concept is entailed, it would be exceptionally difficult to deduce which concept is being measured.

General descriptions

While less scientific, general descriptions of 'the good life' (Yeates, 2017) in animals are, in general, equally appropriate for all Well-being concepts. Consider, for example, the following description of an animal faring well:

The animal is free from distress most of the time, is in good physical health, exhibits a substantial range of species-typical behaviors, and is able to deal effectively

with environmental challenges. There are few, or brief, unpleasant feelings, and a predominance of pleasant feelings.

(Modified from McMillan, 2004, p.1143)

Is it possible to know what Well-being concept this is describing? As is the case with methods of measurement, this description alone will leave the reader very hard pressed to correctly name the concept being depicted. Numerous additional examples can be found. Consider this edited quotation by Webster et al. (2004, p.S93): 'Our operational definition of animal [blank] is encapsulated by the following minimalist statement: "Fit and Feeling Good"'. It seems likely that if a group of animal welfare scientists and veterinarians were asked to fill in the blank, the answers would include a variety of Well-being concepts. (The actual answer is welfare. The previous description was for psychological well-being.) Another description of a Well-being concept is 'high level of biological functioning, freedom from suffering, and positive experiences' (Mench, 1998, pp.94-95). And when Duncan and Dawkins (1983, p.13) reviewed the literature on animal welfare to identify any common threads among the different descriptions they found that a broad working description of welfare would be one that encompassed the notions of 'the animal in complete mental and physical health, the animal in harmony with its environment, the animal able to adapt to an artificial environment provided by human beings without suffering, with the animal's feelings, somehow, taken into account'. Finally, the OIE Terrestrial Animal Health Code (2018) describes an animal as having good welfare if it is 'healthy, comfortable, well nourished, safe, is not suffering from unpleasant states such as pain, fear and distress, and is able to express behaviours that are important for its physical and mental state'. Based on current knowledge, none of these descriptions for welfare would differ appreciably if used for QOL, well-being, SWB, or happiness.

2.2.2 Distinctions between Well-being concepts

As is now evident, the extensive overlapping of attributes of the main Well-being concepts of welfare, well-being, QOL, happiness, and SWB strongly suggests that several, if not all, of these concepts are the same phenomena. However, some distinctive elements have been described in the literature that appear to maintain some difference between the concepts. Some observations regarding the use of Well-being terms in humans are offered first.

Distinctions in the human literature

The terms welfare and well-being have been compared in humans. The term 'well-being' in humans typically refers to the subjective experiences of the individual - the overview of how good one's own life is (Nordenfelt, 2006). In contrast, as briefly mentioned earlier, the meaning of 'welfare' in humans has undergone a substantial change in meaning over the past 100 or so years. The term derives from the Middle English phrase wel faren, meaning to fare well (Merriam-Webster, 2018). The first known use of the term was in the fourteenth century, at which time it meant 'the state of doing well especially in respect to good fortune, happiness, well-being, or prosperity' (Merriam-Webster, 2018). While the timing is unclear, a second meaning for welfare arose: aid in the form of money or necessities for those in need. Developments during the twentieth century placed increasing emphasis on this second meaning, in particular the establishment of a welfare system in the 1930s in the United States. Since then, welfare has taken a central place in sociological theory, where it is almost universally used in humans as a term referring to social resources such as institutions, financial assistance, housing, food resources, and the like (Nordenfelt, 2006) (with some clear exceptions, such as 'child welfare', which refers to resource provisions but also to the child's physical and psychological well-being). Welfare is now rarely used today in the human healthcare sector (Nordenfelt, 2006). In animals, welfare has fully retained the original meaning of faring well.

At first glance it seems that QOL differs from SWB and happiness in humans, but on closer consideration this appears to be attributable to the separate contexts of their use. Whereas QOL is used predominantly in the health field, SWB and happiness are much more common in the psychological fields (Nordenfelt, 2006). However, any actual distinction between the terms is very difficult to discern. Diener (1984, 2006) has contrasted QOL with SWB (which he equates to happiness) in humans and offers the explanation that QOL usually refers to the desirability of one's life, and often emphasizes external elements of that life, such as environmental factors and income. Accordingly, QOL describes more the circumstances of a person's life than the person's reaction to those circumstances, and, as a result, appears to be more 'objective'. This is in contrast to SWB, which is based on subjective experience. The problem with this apparent distinction, however, is that SWB/happiness also refers to the desirability of one's life (King and Napa, 1998). Moreover, as Diener (2006) notes, some scholars use a broader definition of QOL which includes the individual's reactions to the objective life circumstances, further heightening the resemblance of QOL to SWB/happiness. Finally, evidence in humans and animals strongly suggests that QOL cannot be, at least solely, the conditions of one's life. The clearest demonstration of this is the scenario mentioned earlier that if many different individuals (human or animal) were provided with the same objective life conditions the result would be a range of levels of QOL. For instance, if the same house, food, human companionship, playtime, and physical health were to be provided to an extremely pampered dog, an average middle-class American pet dog, and a starving dog from the streets of El Salvador, we could expect QOL levels of, respectively, low, satisfactory to good, and exceptionally high.

Distinctions in the animal literature

TEMPORALITY A longstanding question surrounding Well-being concepts involves time, specifically, what duration of an experience – good or bad – is necessary before it can be said that that experience affects the individual's overall Well-being experience? Is an individual's OOL affected by being in fear for 5 minutes? What about 5 hours, or 5 weeks, or 5 months? Nicol (2011) wrote that in transporting sheep, the care on loading and unloading will have a major impact on sheep welfare. What about their QOL, or happiness? Some authors have viewed this question as a source of differentiation between some of the Well-being concepts. For example, Broom (2007, p.46) has written that, 'We do not talk about poor QoL when the experience is of pain or fear for just a few minutes; neither do we refer to better OoL because of a moment of pleasure'. This differs from welfare, says Broom, which applies to momentary as well as long-term experiences. Time, in fact, is the sole distinguishing feature: 'QoL is welfare, except that it does not refer to short timescales' (Broom, 2007, p.51). Yeates (2011) agrees with this view, stating that QOL, unlike welfare, is explicitly considered over time.

But is this a true distinction between Well-being concepts? Note that in this view the terminology difference refers to the same concept, just different in their duration. This is a distinction without a

meaningful difference – what Yeates (2016) has referred to as a 'false distinction'.

PHYSICAL, PSYCHOLOGICAL, OR BOTH (FIG. 2.3) The variety of Well-being concepts encompass states of both body and mind (Hewson, 2003b; Morton, 2004). However, on closer examination of this notion we can see potential lines emerge between some of the Well-being concepts. Several researchers have stated that in humans and animals there is a physical well-being (and welfare) and mental well-being (and welfare) (Dawkins, 1998; Webster, 2001; Hewson, 2003b; Stafford, 2006). Indeed, it is for this reason that researchers in the human field have preferred the term subjective well-being - to avoid any confusion with solely physical changes. In contrast, there appear to be no claims that either QOL or happiness have a purely, standalone physical form.

The central point of contention here is the question of whether conscious experience is required for the different Well-being concepts to apply to an animal. The question as to whether Well-being can exist, and be altered, without the individual's conscious awareness is not new (Mason and Mendl,

1993; Appleby and Sandøe, 2002; Duncan, 2004; Nordenfelt, 2006; Broom, 2007). Is a badly injured animal's Well-being poor even if anesthesia or a comatose state prevent the animal from suffering (Mason and Mendl, 1993) (Fig. 2.4)? Does an animal (or person) with an early and as yet asymptomatic malignant cancer have a diminished Well-being?

Some researchers argue that consciousness is not necessary for Well-being concepts to apply. Broom (2007) says that welfare applies to all - not just sentient - animals. Similarly, Dawkins (2015) argues that consciousness is irrelevant to much of what is done to improve the welfare of animals in zoos, farms, and laboratories, where the focus is on improving the physical health of the animals by changing the conditions in which they live. Other researchers say yes, consciousness is necessary for Well-being. Some contend that Well-being concepts are solely about feelings – i.e., conscious experience (Appleby and Sandøe, 2002; Carenzi and Verga, 2009). Others imply that conscious experience is only part of what is important for animals, combining experiential and physical aspects. Examples include Dawkins's (2008) view that welfare is about the animals being healthy and getting what they want, and Webster et al.'s (2004)

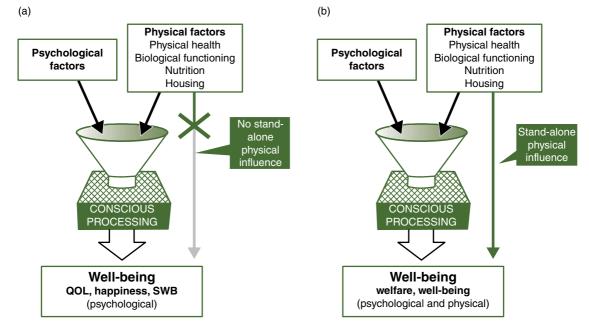


Fig. 2.3. Apparent differences in the routes by which inputs influence quality of life (QOL), happiness, and subjective well-being (SWB) (a) as compared to the routes by which inputs influence well-being and welfare (b). (a) All factors exert their effect through conscious processing. Without consciousness, nothing 'gets through' to alter Well-being. (b) With a stand-alone physical form, Well-being can be affected without requiring conscious processing.



Fig. 2.4. Can this animal's QOL change while under anesthesia? If something very detrimental to the animal's health occurred under anesthesia but the animal died before regaining consciousness, did QOL go down? If during surgery a health problem was corrected (e.g., a brain tumor was removed), when does the animal's QOL increase – when the tumor is removed before regaining consciousness, when consciousness is regained, or only after consciousness is regained and the results show improvement in the animal's life? What if the same questions were asked about well-being, welfare, or happiness? (Image used under license from Shutterstock.com.)

synopsis of animals being fit and feeling good. A disadvantage of this approach is the practicality of knowing (and agreeing) which, when, and how animals are conscious (not to mention the more detailed question of how their situations affect their Well-being). We might theoretically limit the scope of application of Well-being concepts, but that does not help us find the dividing lines between animals who can and cannot be said to experience Well-being. Absent a requirement of sentience, Well-being concepts would seem to apply to corals, plants, bacteria, and, arguably, non-living systems.

The deciding factor is this: having stand-alone physical criteria, as is widely claimed for welfare and well-being, means that even in the absence of consciousness the individual's welfare and well-being exist and can increase or decrease (see Fig. 2.3). On the other hand, lacking a stand-alone physical form means that factors related to the physical body exert their effects on or through conscious experience, and that without consciousness the physical factors are irrelevant as there is no experience of Well-being (at least at the time when an animal is unconscious) to influence. Perhaps based on the above considerations, we might distingush wholly subjective concepts of happiness and QOL from the

combined objective-subjective concepts of welfare and well-being. It seems reasonable to see that an injured animal (or person) in a coma has reduced welfare and well-being (both having physical as well as psychological forms), but it is much more difficult to argue that such an individual has a poor QOL or unhappiness (both lacking a purely physical form).

But does this truly distinguish these Well-being concepts from one another? An answer can be found in the notion raised earlier: Well-being concepts may be about the quality of one's *life conditions* or one's *life experiences*. Those concepts focusing on the former will exist in conscious and unconscious animals, and in those aware of the influencing stimuli within or without the physical body. In contrast, those Wellbeing concepts focusing exclusively on the quality of *life experiences* will exist only in conscious animals and those aware of the influencing stimuli.

PREDISPOSITIONS, RISKS, AND ENDANGERMENT Related to the issue of consciousness and asymptomatic disease is how we should regard the Well-being effects of predispositions, risks, and endangerment. Consider, for example, an individual with an inherited predisposition to developing a particular disease. Or suppose an individual were to be endangered by a caregiver, such as a parent dangling their infant over the ledge of a fourth floor balcony. Similarly, think of a dog riding unrestrained on the back of a flat-bed truck. In these cases, the individual may be completely unaware of the danger involved, but clearly the risk of that individual being harmed is increased. The question, then, is what happens to this individual's welfare, well-being, QOL, and happiness? Are they equally affected (or unaffected)? For the endangered child, would we say that this child's welfare is impaired, or *potentially* impaired? If the latter, does that mean his welfare is, right now, unaffected and thus no different than a non-endangered child? The point here is not that the questions lack simple answers, but that the questions only make sense for welfare and well-being, and not QOL and happiness. There is no possibility of one's happiness or QOL being lessened by being at risk but having no awareness of it. In fact, it is entirely possible that the dog riding freely on the back of a truck, although endangered, experiences an *increase* in happiness and QOL.

OBJECTIVITY Timmins *et al.* (2007) have written that whereas welfare usually refers to the observable and measurable experiences of an animal, QOL is related

to the animal's mental state, which is determined by feelings and emotions. Broom (2007) holds a similar view, suggesting that welfare is more scientifically quantifiable than QOL. It is interesting to note that these views connote the opposite of those of some researchers in the human field, such as Diener's (1984, 2006) position that QOL is more objective than SWB.

2.3 Summary View of the Terminology in Animals

Given the current use of Well-being terms in the animal literature, there seem to be good reasons for equating welfare and well-being (e.g., Mason, 1991; Wojciechowska and Hewson, 2005). There are also good reasons for considering QOL to be closely related to welfare and well-being (e.g., Appleby and Sandøe, 2002), with the distinguishing point that welfare and well-being do, and QOL does not, have a purely stand-alone physical form as well as a psychological form. Indeed, we might argue that QOL represents the experiential aspects of welfare/well-being.

Happiness (including unhappiness) and SWB have been explicitly equated in the human literature (Diener and Lucas, 2000) and because their recent entry into the animal literature was based on the human usage, the two terms are considered equals for animals (Robinson et al., 2016). Because happiness and SWB also lack a stand-alone physical form, they, like OOL, retain a degree of distinction from welfare and well-being. However, in humans (Diener and Lucas, 2000) and animals (Boissy et al., 2007), SWB has been equated with well-being, which creates a logical contradiction with the above summation: since because SWB equals happiness but happiness does not equal welfare, and well-being equals welfare, we are led to the conclusion that well-being both is and isn't equal to welfare.

There are other ways to examine the comparability of the terms. One is by using the thought experiment that opened this chapter. Another is to see what occurs when one Well-being term is used in the evaluation of another. For example, one QOL questionnaire popular among US veterinarians (though not validated) is Villalobos's (2004) 'HHHHHHMM' scale, in which seven factors – hurt, hunger, hydration hygiene happiness, mobility, and more good days than bad – are each scored and then summed to a single score. Consider the factor 'happiness'. If the animal receives a score for this factor, are any of the other scores necessary? Or does happiness tell us all we need to know? These types of questions

offer informative perspectives and insights as to how the various Well-being terms compare and contrast.

2.4 Is There a Solution?

The reasons for the confusion in Well-being terminology cannot be fully explained by conceptual analysis, as they vary in accordance with personal preference, geographical differences in language development, and separate literatures and research. Of particular importance is the differing uses of terms for addressing quality of one's *life conditions* versus quality of one's *life experiences*. Other causes may also have contributed to the ambiguity. Is there a solution?

The situation at present is not promising. For example, Broom (2007, p.51) wrote 'it is generally better to use the term "welfare" rather than "quality of life"... in scientific publications'. However, Taylor and Mills (2007, in the same issue of the same journal) wrote that because of its 'individualcentered approach', QOL may be preferable to welfare. Another example is that in the field of veterinary medicine, the preferred term for animal Well-being among companion animal veterinarians (and pet owners) is quality of life whereas for large animal (farm) veterinarians it is welfare. The ideal objective for rectifying the terminology inconsistencies in animals can be seen as twofold: (i) unifying the like concepts under a single term; and (ii) clarifying the difference(s) between the unlike terms. Numerous impediments stand in the way of achieving these outcomes. Foremost may be simply the comfort level people feel in using particular terms. The use of quality of life, for example, is so entrenched in the fields of human as well as small animal medicine that it would seem unrealistic to expect any receptiveness to the entire field abandoning the term. Rather than attempting drastic changes to terminology a more reasonable goal would be to work toward eliminating the separate literatures that have developed by merging the different Wellbeing concepts into a single field - even if a single name cannot (yet) be agreed upon. This can begin with the minimalist step of making certain that any publications on Well-being topics be assigned the keywords of all current Well-being terms. This will assure that, at the least, literature searches will capture all the relevant work published under the different names. Authors can then strive to be clear on what they mean by the terms they use, in particular whether the focus is on life conditions, life experiences, or a combination of the two.

Can we work with different terms for the same thing, that is, agree to disagree? It looks like, for at least the time being, we will have to.

Notes

¹ It is worth pointing out that this choice reflects a North American bias just as the equally suitable choice of 'Welfare' as the umbrella term would reflect a European bias. However, introducing a new term altogether simply adds to the list of overlapping terms, and as will be made clear by the end of the chapter a key objective is to decrease, not increase, the number of terms used in this area of study.

2.4 References

- Appleby, M.C. and Sandøe, P. (2002) Philosophical debate on the nature of well-being: Implications for animal welfare. *Animal Welfare* 11, 283–294.
- Appleby, M.C. and Stokes, T. (2008) Why should we care about nonhuman animals during times of crisis? *Journal* of Applied Animal Welfare Science 11, 90–97. http:// dx.doi.org/10.1080/10888700801925612.
- Barnard, C.J. and Hurst, J.L. (1996) Welfare by design: The natural selection of welfare criteria. *Animal Welfare* 5, 405–433.
- Bauer, M., Glickman, N., Glickman, L., Toombs, J., Golden, S., et al. (1992) Follow-up study of owner attitudes toward home care of paraplegic dogs. *Journal* of the American Veterinary Medical Association 200, 1809–1816.
- Belshaw, Z. (2018) Quality of life assessment in companion animals: What, why, who, when and how. Companion Animal 23, 264–268. http://dx.doi.org/10.12968/ coan.2018.23.5.264.
- Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., et al. (2007) Assessment of positive emotions in animals to improve their welfare. *Physiology* and Behavior 92, 375–397. http://dx.doi.org/10.1016/j. physbeh.2007.02.003.
- Bracke, M.B.M. (2007) Animal-based parameters are no panacea for on-farm monitoring of animal welfare. *Animal Welfare* 16, 229–231.
- Bradburn, N.M. (1969) *The Structure of Psychological Well-Being*. Aldine Publishing Company, Chicago, Illinois, USA.
- Broom, D.M. (1986) Indicators of poor welfare. *British Veterinary Journal* 142, 524–526. http://dx.doi.org/10.1016/0007-1935(86)90109-0.
- Broom, D.M. (1996) Animal welfare defined in terms of attempts to cope with the environment. Acta Agriculturae Scandinavica, Section A — Animal Science 27 (Suppl), 22–28.
- Broom, D.M. (2007) Quality of life means welfare: How is it related to other concepts and assessed? *Animal Welfare* 16(S), 45–53.

- Brülde, B. (2007) Happiness theories of the good life. Journal of Happiness Studies 8, 15–49. http://dx.doi. org/10.1007/s10902-006-9003-8.
- Carbone, L. (2004) What Animals Want: Expertise and Advocacy in Laboratory Animal Welfare Policy. Oxford University Press, Oxford, UK.
- Carenzi, C. and Verga, M. (2009) Animal welfare: Review of the scientific concept and definition. *Italian Journal* of Animal Science 8 (Suppl. 1), 21–30. http://dx.doi. org/10.4081/iias.2009.s1.21.
- Christiansen, S.B. and Forkman, B. (2007) Assessment of animal welfare in a veterinary context—a call for ethologists. *Applied Animal Behaviour Science* 106, 203–220. http://dx.doi.org/10.1016/j.applanim.2007.01.004.
- Clark, J.D., Rager, D.R., Calpin, J.P. (1997) Animal well-being I. General considerations. *Laboratory Animal Science* 47, 564–570.
- Dawkins, M.S. (1990) From an animal's point of view: Motivation, fitness, and animal welfare. Behavioral and Brain Sciences 13, 1–61. http://dx.doi.org/10.1017/ S0140525X00077104.
- Dawkins, M.S. (1998) Evolution and animal welfare. Quarterly Review of Biology 73, 305–328. http://dx. doi.org/10.1086/420307.
- Dawkins, M.S. (2006) A user's guide to animal welfare science. Trends in Ecology & Evolution 21, 77–82. http://dx.doi.org/10.1016/j.tree.2005.10.017.
- Dawkins, M.S. (2008) The science of animal suffering. *Ethology* 114, 937–945. http://dx.doi.org/10.1111/j.1439-0310.2008.01557.x.
- Dawkins, M. (2015) Animal welfare and the paradox of animal consciousness. *Advances in the Study of Behavior* 47, 5–38. http://dx.doi.org/10.1016/bs.asb.2014.11.001.
- DeGrazia, D. (1998) Well-being of animals. In: Bekoff, M. and Meaney, C.A. (eds.) Encyclopedia of Animal Rights and Animal Welfare. Greenwood Press, Westport, Connecticut, USA, pp. 359–360.
- Dickerson, V.M., Coleman, K.D., Ogawa, M., Saba, C.F., Cornell, K.K., et al. (2015) Outcomes of dogs undergoing limb amputation, owner satisfaction with limb amputation procedures, and owner perceptions regarding postsurgical adaptation: 64 cases (2005– 2012). Journal of the American Veterinary Medical Association 247, 786–792. http://dx.doi.org/10.2460/ iavma.247.7786.
- Diener, E. (1984) Subjective well-being. *Psychological Bulletin* 95, 542–575. http://dx.doi.org/10.1037/0033-2909.95.3.542.
- Diener, E. (2006) Guidelines for national indicators of subjective well-being and ill-being. *Journal of Happiness Studies* 7, 397–404. http://dx.doi.org/10.1007/s10902-006-9000-y.
- Diener, E. and Lucas, R.E. (2000) Subjective emotional well-being. In: Lewis, M. and Haviland-Jones, J.M. (eds.) *Handbook of Emotions*, 2nd edn. The Guilford Press, New York, USA, pp. 325–337.

- Diener, E., Lucas, R.E., Scollon, C.N. (2006) Beyond the hedonic treadmill: Revising the adaptation theory of well-being. *American Psychologist* 61, 305–314. http://dx.doi.org/10.1037/0003-066X.61.4.305.
- Duggan, C.H. and Dijkers, M. (2001) Quality of life after spinal cord injury: A qualitative study. *Rehabilitation Psychology* 46, 3–27.
- Duncan, I.J.H. (2004) A concept of welfare based on feelings. In: Benson, G.J. and Rollin, B.E. (eds.) *The Well-being of Farm Animals*. Blackwell Publishing, Ames, Iowa, USA, pp. 85–101. http://dx.doi. org/10.1002/9780470344859.ch5.
- Duncan, I.J.H. and Dawkins, M.S. (1983) The problem of assessing 'well-being' and 'suffering' in farm animals. In: Smidt, D. (ed.) *Indicators Relevant to Farm Animal Welfare*. Springer, Dordrecht, The Netherlands, pp. 13–24. http://dx.doi.org/10.1007/978-94-009-6738-0_2.
- Duncan, I.J.H. and Fraser, D. (1997) Understanding animal welfare. In: Appleby, M.C. and Hughes, B.O. (eds.) *Animal Welfare*. CAB International, Wallingford, UK, pp. 19–31.
- Fraser, D. and Weary, D.M. (2004) Quality of life for farm animals: Linking science, ethics, and animal welfare. In: Benson, G.J. and Rollin, B.E. (eds.) *The Well-being of Farm Animals*. Blackwell Publishing, Ames, Iowa, USA, pp. 39–60. http://dx.doi.org/10.1002/9780470344859.ch3.
- Fraser, D., Weary, D.M., Pajor, E.A., Milligan, B.N. (1997) A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare* 6, 187–205.
- Galtung, J. (2005) Meeting basic needs: Peace and development. In: Huppert, F.A., Baylis, N., Keverne, B. (eds.) *The Science of Well-being*. Oxford University Press, Oxford, UK, pp. 475–501. http://dx.doi. org/10.1093/acprof:oso/9780198567523.003.0019.
- Gartner, M.C. and Weiss, A. (2013) Scottish wildcat (Felis silvestris grampia) personality and subjective well-being: Implications for captive management. Applied Animal Behaviour Science 147, 261–267. http://dx.doi.org/10.1016/j.applanim.2012.11.002.
- Green, T.C. and Mellor DJ. (2011) Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. New Zealand Veterinary Journal 59, 263–271. http://dx.doi.org/10.1080/00480169.2011. 610283.
- Hetts, S., Estep, D., Marder, A.R. (2005) Psychological well-being in animals. In: McMillan, F.D. (ed.) Mental Health and Well-Being in Animals. Blackwell Publishing, Ames, Iowa, USA, pp. 211–220. http://dx.doi. org/10.1002/9780470384947.ch15.
- Hewson, C.J. (2003a) Can we assess welfare? *Canadian Veterinary Journal* 44, 749–753.
- Hewson, C.J. (2003b) What is animal welfare? Common definitions and their practical consequences. *Canadian Veterinary Journal* 44, 496–499.
- Hewson, C.J., Hiby, E.F., Bradshaw, J.W.S. (2007) Assessing quality of life in companion and kennelled dogs: A critical review. *Animal Welfare* 16(S), 89–95.

- Hubrecht, R. (1995) The welfare of dogs in human care. In: Serpell, J (ed.) The Domestic Dog: Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, UK, pp. 179–198.
- Hurnik, J.F., Webster, A.B., Siegel, P.B. (1995) Dictionary of Farm Animal Behavior. Iowa State University Press, Ames, Iowa, USA.
- Jones, R.B. (2004) Enrichment for chickens. In: Bekoff, M. (ed.) Encyclopedia of Animal Behavior. Greenwood Press, Westport, Connecticut, USA, pp. 1110–1115.
- Kahneman, D. and Riis, J. (2005) Living, and thinking about it: Two perspectives on life. In: Huppert, F.A., Baylis, N., Keverne, B. (eds.) The Science of Well-being. Oxford University Press, Oxford, UK, pp. 285–304. http://dx.doi. org/10.1093/acprof:oso/9780198567523.003.0011.
- Kendrick, K.M. (2007) Quality of life and the evolution of the brain. *Animal Welfare* 16(S), 9–15.
- King, J.E. and Landau, V.I. (2003) Can chimpanzee (Pan troglodytes) happiness be estimated by human raters? Journal of Research in Personality 37, 1–15. http://dx. doi.org/10.1016/S0092-6566(02)00527-5.
- King, L.A. and Napa, C.K. (1998) What makes a life good? *Journal of Personality and Social Psychology* 75, 156. http://dx.doi.org/10.1037/0022-3514.75.1.156.
- Kirkden, R.D. and Pajor, E.A. (2006) Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. *Applied Animal Behaviour Science* 100, 29–47. http://dx.doi.org/10.1016/j.applanim.2006.04.009.
- Kirkwood, J.K. (2007) Introduction Quality of life: The heart of the matter. *Animal Welfare* 16(S), 3–7.
- Lyubomirsky, S., King, L., Diener, E. (2005) The benefits of frequent positive affect: Does happiness lead to success? *Psychological Bulletin* 131, 803–855. http://dx.doi.org/10.1037/0033-2909.131.6.803.
- Mason, G.J. (1991) Stereotypies and suffering. Behavioural Processes 25, 103–115. http://dx.doi. org/10.1016/0376-6357(91)90013-P.
- Mason, G.J. and Mendl, M. (1993) Why is there no simple way of measuring animal welfare? *Animal Welfare* 2, 301–319.
- McMillan, F.D. (2004) Psychological well-being. In: Bekoff, M. (ed.) Encyclopedia of Animal Behavior. Greenwood Press, Westport, Connecticut, USA, pp. 1133–1144.
- Mench, J.A. (1998) Thirty years after Brambell: Whither animal welfare science? *Journal of Applied Animal Welfare Science* 1, 91–102. http://dx.doi.org/10.1207/ s15327604jaws0102_1.
- Mendl, M. (1991) Some problems with the concept of a cut-off point for determining when an animal's welfare is at risk. Applied Animal Behaviour Science 31, 139–146. http://dx.doi.org/10.1016/0168-1591(91)90161-P.
- Merriam-Webster. (2018) Welfare. Available at: https://www.merriam-webster.com/dictionary/welfare (accessed 28 November 2018).
- Morton, D.B. (2000) A systematic approach for establishing humane endpoints. *ILAR Journal* 41, 80–86. http://dx.doi.org/10.1093/ilar.41.2.80.

- Morton, D.B. (2004) Behavior and animal suffering. In: Bekoff, M. (ed.) Encyclopedia of Animal Behavior. Greenwood Press, Westport, Connecticut, USA, pp. 1095–1098.
- Mullan, S. (2015) Assessment of quality of life in veterinary practice: Developing tools for companion animal careers and veterinarians. Veterinary Medicine: Research and Reports 6, 203–210.
- Nicol, C. (2011) Behaviour as an indicator of animal welfare. In: Webster, J. (ed.) Management and Welfare of Farm Animals. Wiley-Blackwell, Chichester, UK, pp. 31–67.
- Nordenfelt, L. (2006) Animal and Human Health and Welfare: A Comparative Analysis. CAB International, Wallingford, UK.
- Novak, M.A. and Suomi, S.J. (1988) Psychological well-being of primates in captivity. *American Psychologist* 43, 765– 773. http://dx.doi.org/10.1037/0003-066X.43.10.765.
- OIE (World Organisation for Animal Health). (2018) Introduction to the Recommendations for Animal Welfare (Article 7.1.1.). *Terrestrial Animal Health Code*. Available at: www.oie.int/standard-setting/terrestrial-code/access-online (accessed 12 November 2018).
- Peterson, C. (2006) A Primer in Positive Psychology. Oxford University Press, New York, USA.
- Robinson, L.M., Waran, N.K., Leach, M.C., Morton, F.B., Paukner, A., et al. (2016) Happiness is positive welfare in brown capuchins (Sapajus apella). Applied Animal Behaviour Science 181, 145–151. http:// dx.doi.org/10.1016/j.applanim.2016.05.029.
- Robinson, L.M., Altschul, D.M., Wallace, E.K., Úbeda, Y., Llorente, M., et al. (2017) Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. Applied Animal Behaviour Science 191, 90–97. http://dx.doi.org/10.1016/j.applanim.2017.02.008.
- Sandem, A.I., Braastad, B.O., Boe, K.E. (2002) Eye white may indicate emotional state on a frustration– contentedness axis in dairy cows. *Applied Animal Behaviour Science* 79, 1–10. http://dx.doi.org/10.1016/ S0168-1591(02)00029-1.
- Sandøe, P. (1999) Quality of life—three competing views. Ethical Theory and Moral Practice 2, 11–23.
- Scott, E.M., Nolan, A.M., Reid, J., Wiseman-Orr, M.L. (2007) Can we really measure animal quality of life? Methodologies for measuring quality of life in people and other animals. *Animal Welfare* 16(S), 17–24.
- Stafford, K. (2006) The Welfare of Dogs. Springer, Dordrecht, The Netherlands. http://dx.doi.org/10.1007/ 1-4020-4362-7.
- Taylor, K.D. and Mills, D.S. (2007) Is quality of life a useful concept for companion animals? *Animal Welfare* 16(S), 55–65.
- Timmins, R.P., Cliff, K.D., Day, C.T., Hart, B.L., Hart, L.A., et al. (2007) Enhancing quality of life for dogs and cats in confined situations. *Animal Welfare* 16(S), 83–87.

- Villalobos, A. (2004) Quality of life scale helps make the final call. Veterinary Practice News September, 38.
- Vitale, A. (2004) Enrichment for New World monkeys. In: Bekoff, M. (ed.) *Encyclopedia of Animal Behavior*. Greenwood Press, Westport, Connecticut, USA, pp. 1120–1122.
- Webb, L.E., Veenhoven, R., Harfeld, J.L., Jensen, M.B. (2019) What is animal happiness? *Annals of the New York Academy of Sciences* 1438, 62–76.
- Webster, A.J. (2001) Farm animal welfare: The five freedoms and the free market. Veterinary Journal 161, 229–237. http://dx.doi.org/10.1053/tvjl.2000.0563.
- Webster, A.J.F., Main, D.C.J., Whay, H.R. (2004) Welfare assessment: Indices from clinical observation. *Animal Welfare* 13, S93–S98.
- Weiss, A., Inoue-Murayama, M., Hong, K.W., Inoue, E., Udono, T., et al. (2009) Assessing chimpanzee personality and subjective well-being in Japan. American Journal of Primatology 71, 283–292. http://dx.doi. org/10.1002/ajp.20649.
- Weiss, A., King, J.E., Perkins, L. (2006) Personality and subjective well-being in orangutans (*Pongo pyg-maeus* and *Pongo abelii*). *Journal of Personality and Social Psychology* 90, 501–511. http://dx.doi. org/10.1037/0022-3514.90.3.501.
- Weiss, A., Adams, M.J., King, J.E. (2011a) Happy orangutans live longer lives. *Biology Letters* 7, 872–874. http://dx.doi.org/10.1098/rsbl.2011.0543.
- Weiss, A., Adams, M.J., Widdig, A., Gerald, M.S. (2011b) Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology* 125, 72–83. http://dx.doi.org/10.1037/a0021187.
- Whay, H.R., Main, D.C.J., Green, L.E., Webster, A.J.F. (2003) Animal-based measures for the assessment of welfare state of dairy cattle, pigs and laying hens: Consensus of expert opinion. *Animal Welfare* 12, 205–217.
- Wiseman-Orr, M.L., Scott, E.M., Reid, J., Nolan, A.M. (2006) Validation of a structured questionnaire as an instrument to measure chronic pain in dogs on the basis of effects on health-related quality of life. *American Journal of Veterinary Research* 67, 1826– 1836. http://dx.doi.org/10.2460/ajvr.67.11.1826.
- Wojciechowska, J.I. and Hewson, C.J. (2005) Quality-oflife assessment in pet dogs. *Journal of the American Veterinary Medical Association* 226, 722–728. http:// dx.doi.org/10.2460/javma.2005.226.722.
- Yeates, J.W. (2011) Is 'a life worth living' a concept worth having? *Animal Welfare* 20, 397–406.
- Yeates, J. (2016) Quality of life and animal behavior. Applied Animal Behaviour Science 181, 19–26. http://dx.doi.org/10.1016/j.applanim.2016.04.018.
- Yeates, J.W. (2017) How good? Ethical criteria for a 'Good Life' for farm animals. *Journal of Agricultural* and Environmental Ethics 30, 23–35. http://dx.doi. org/10.1007/s10806-017-9650-2.

20 F.D. McMillan and J.W. Yeates

3

The Philosophical and Biological Evolution of Feelings in Well-being

IAN J.H. DUNCAN

Department of Animal Biosciences, University of Guelph, Guelph, Ontario, Canada

3.1 Introduction

The foundations for feelings to be considered as the basis for animal well-being or welfare were laid in the nineteenth century. Unfortunately, these foundations were not developed through much of the twentieth century due to the rise of Behaviorism. However, the primacy of feelings for individual welfare has received growing support over the past four decades. This chapter explores how feelings constitute the foundation for mental health in all sentient animals. The role of states of suffering, including pain and discomfort, frustration, fear, maternal separation, and various forms of deprivation in reducing wellbeing are described. States of pleasure are obviously important for animal welfare, but have not been investigated to the same extent as states of suffering. An understanding of feelings will help us to design optimum environments for animals as well as develop best practices of care.

3.2 Early History

A short consideration of the history of how animals have been dealt with by various moral philosophers sets the scene for how they are regarded today. Much of this early history is taken from Preece (2002). Of the early Greek philosophers, Aristotle (384–322 BC) is the one who made specific reference to animals. He believed that the ability to reason is the highest of all abilities and it is this that sets human beings (actually Greeks!) above all other creatures. Aristotle also introduced the teleological argument of 'things being there for a purpose', e.g., 'the purpose of rain is to water the plants'. From these two ideas, a great hierarchical structure was built in which those with more reason

should control those with less, with Gods being superior to men and controlling them, men being superior to women, Greeks being superior to other races, human beings being superior to animals, and so on. According to this structure, human beings had absolute authority over all animals.

This view continued to be held for about 2000 years. In the medieval period, Thomas Aquinas (1224-1274) rediscovered Aristotle's writings and agreed that it was the ability to reason (or rationality) that made human beings distinct from all other animals. However, he gave Aristotle's ideas a Christian twist. He postulated that animals do not have immortal souls. He claimed that human beings had no direct obligations to animals. However, they might have indirect moral obligations, in that people who mistreat animals may (i) pick up cruel habits and then treat other human beings badly, and (ii) perpetrate a property wrong against the owner of the animal. According to Aguinas, animals do not have moral standing; they only have instrumental value.

Jumping to the seventeenth century, René Descartes (1596–1650) is often thought of as the father of modern philosophy. He is usually singled out for special blame for introducing the idea of animals as 'automata' or machines. However, in a more considered review of Descartes' works, Cottingham (1978) points out that even though Descartes states that animals have no thought or language he does not actually say that they have no feelings or sensations. Indeed, Kenny (1970, p.207) translates Descartes as saying, 'Similarly of all the things which dogs, horses and monkeys are made to do, are merely expressions of their fear, their hope, or their joy; and consequently, they can do these things without any thought'. Present-day scholars

continue to argue about what Descartes really meant by this. The fact that he was a vivisectionist, and did not treat animals as if they were sentient, suggests that he thought that 'fear', 'hope', and 'joy' were in some way unconscious emotions. Unconscious emotion' is a difficult concept to understand and is currently being debated (Öhman et al., 2000; Winkielman and Berridge, 2004). Like Aristotle and Aquinas, Descartes also believed that rationality distinguished human beings from other animals and he added that language, which he regarded to be a uniquely human attribute, is the only real test of rationality. However, as suggested by the translated passage above, his translators and interpreters may have gone too far in blaming him for 'animals are machines'. He does seem to allow that animals might have emotions and might be driven by these emotions.

Thomas Hobbes (1588-1679) was an English philosopher living at the same time as Descartes. In 1651 he wrote the famous book Leviathan, which formed the basis for Western political philosophy. Leviathan concerns the structure of society and legitimate government, and is regarded as one of the earliest and most influential examples of social contract theory. Hobbes' contention was that human beings act out of self-interest and that this leads to co-operation and social contracts. Since, in Hobbes' view, animals have no language, they cannot enter into social contracts with other animals or with human beings. They are therefore not worthy of moral consideration. So, whereas Descartes thought that language was important as a sign of rationality, Hobbes thought that it was necessary for the drawing up of social contracts. However, their conclusion was the same: animals do not have language, therefore they do not merit moral consideration.

John Locke (1632–1704) was an English philosopher and considered to be the first of the British Empiricists. Empiricism emphasizes the role of experience, particularly sensory perception, in the formation of ideas. Locke postulated that when people are born, their minds are 'blank slates' or 'tabula rasa'. This was contrary to the previous belief that people were born with innate ideas. Locke also developed Hobbes' ideas on social contract theory. He was one of the earliest and most influential thinkers of the Enlightenment contributing to political philosophy and liberal theory. It is in Locke's writings that we get a first glimpse of a change of view with regard to animals. Locke says that there is evidence that animals (or what he calls 'brutes') have the capacity to remember. He also allows that animals also seem to have some very simple ideas and they can compare one thing to another – but only very imperfectly. To some extent they can compound (put ideas together) but Locke draws the line at abstraction. He clearly states that animals cannot form abstractions. So, Locke concludes that there are huge differences between human beings and other animals, but that animals do have some simple mental capacities. This is a big departure from calling them 'automata'.

The German philosopher Immanuel Kant (1724– 1804) was very important in the development of moral philosophy. He wrote a highly influential little book called Groundwork of the Metaphysic of Morals. Kant believed that morality is a case of following absolute rules. For example, he thought that lying was morally wrong and that we should never lie, regardless of the circumstances. Kant's philosophy was that one should treat a human being as an end in itself and not as a means to an end. He developed the philosophy that human beings have intrinsic (or inherent) value (and not merely instrumental value). The reason they have intrinsic value (once again) is that they have rationality and in particular they can reason about ethics. Animals, on the other hand, cannot reason (particularly about ethics!), and therefore have only instrumental value.

So, these five philosophers, Aristotle, Aquinas, Descartes, Hobbes, and Kant, developed a position that has dominated the traditional Western view of how animals should be treated. The position was based on two claims:

- 1. Human beings have a special attribute that makes them distinct from all other animals. (A factual claim.)
- 2. Having this special attribute makes human beings objects of direct moral concern. (A moral claim.)

The special attribute was rationality, and, in particular, having language and being able to engage in ethical thought. The traditional Christian view incorporated an additional distinction, viz., animals did not have immortal souls. John Locke has been left out of this list because he was the first to realize that the distinction between animals and human beings was not as clear cut as the others suggested.

3.3 The Rise of Utilitarianism

With the emergence of the 'Enlightenment' period in Europe, things started to change. The Scottish

22 I.J.H. Duncan

philosopher, David Hume (1711–1776) wrote, on learning in animals, 'From the tone of voice the dog infers his master's anger, and foresees his own punishment. Make a beating follow upon one sign or motion for some time, and afterwards upon another; and he will successively draw different conclusions, according to his most recent experience' (Hume, 1739, pp.177–178). He thus began to dispute the previous views that animals have no moral standing. Hume was a hardline atheist and so the question of anyone having an immortal soul did not arise.

Jeremy Bentham (1748–1832) was an English social reformer who was very concerned about the conditions that many workers were forced to accept during the Industrial Revolution. He worked closely with James Mill, a like-minded Scottish social reformer. In contrast to Kant, Bentham thought that it was the consequences of actions that were important. So, for example, telling a lie might be morally acceptable if the consequences of doing so were better than not telling a lie. He had little to say about animals, with the exception of a brief mention in one of his books. In it he rejected both of the previous claims about animals - that they cannot reason, and that they have no language - outright, and went on to argue that rationality is not the relevant matter. In a well-known passage, he wrote, 'The question is not, Can they reason? nor, Can they talk? But, Can they suffer?' (Bentham, 1823, p.283).

John Stuart Mill (1806–1873), the son of James Mill, was a close friend of Jeremy Bentham. He developed Bentham's ideas into the philosophy of Utilitarianism or The Greatest Happiness Principle (Mill, 1910). According to this principle, 'Actions are right in proportion as they tend to promote happiness, wrong as they tend to produce the reverse of happiness'. 'Happiness' was defined as pleasure and the absence of pain and 'unhappiness' as pain and the privation of pleasure. Bentham and Mill did not wish their new theory to have the title 'The Greatest Happiness Principle' and they searched around for another name. They came across the word 'utilitarian' in the writings of a Scottish novelist, John Galt, and they asked him if they could use this for the name of their theory, to which Galt agreed.

The person who has vigorously promoted a utilitarian approach to animal welfare is the Australian philosopher Peter Singer (b. 1946) who currently holds the Chair of Bioethics at Princeton University. He published *Animal Liberation* in 1975 with a fourth edition in 2009 and a 40th anniversary

edition in 2015. This was - and remains - a very influential book. Singer (1975) argues that most animal use (including animal agriculture) is deeply objectionable. So, he is arguing about the facts. He says that he is not against using animals or even against killing them, if, and only if, they have a good quality life and a painless death. Interestingly, Singer is also regarded as the father of Animal Rights although he himself is most definitely a utilitarian. The question a utilitarian asks is, 'What course of conduct promotes the greatest amount of happiness for all those who will be affected?' A utilitarian approach has proved to be very useful in dealing with various moral dilemmas in human affairs. However, when animals are involved, it becomes extremely difficult to weigh the happiness of human beings against the suffering of animals. For example, how does one balance the suffering of laboratory rabbits being used for the production of antibodies against the happiness of human beings being protected from some dangerous disease by these same antibodies?

3.4 The Emergence of Animal Rights

The idea of giving animals 'rights' is very recent, having been proposed in the last quarter of the twentieth century by Tom Regan (1938–2017), who was Professor of Philosophy at North Carolina State University. Using much of the evidence produced by Singer in Animal Liberation, Tom Regan developed the philosophy of Animal Rights and in 1983 published *The Case for Animal Rights*. In this book he argues that we are all subject of a life, conscious beings, have individual welfare, want and prefer things, and believe and feel things. Therefore we (and all sentient creatures) have inherent value. Regan builds his argument as follows, 'Individuals who have inherent value have an equal right to be treated with respect... It follows that we must never harm individuals who have inherent value' (Regan, 1983, p.286). According to Regan, killing is the biggest harm we can do to another individual. The term 'harm' is difficult for biologists to understand. A 7-year-old boy being carried kicking and screaming into a clinic to have a flu shot would certainly say he was being harmed. Presumably the parents would say he was not being harmed, but, rather, benefited, by being protected from flu. Exactly the same argument could be made for a cat being taken very reluctantly to the veterinarian to receive some treatment. So, who decides what 'harm' means?

Regan was a respected philosopher. His Case for Animal Rights is very well argued. Perhaps unfortunately, his views have dominated Animal Rights philosophy. A philosophy of animal rights does not need to be as extreme as that proposed by Tom Regan. In fact, when people who call themselves 'animal rightists' are closely questioned, very few of them have adopted all of Regan's philosophy. The majority of them actually believe in some form of 'limited rights' for animals. For example, Tannenbaum (1995), a philosopher who has written a textbook on veterinary ethics, has argued that some form of 'limited rights' might be acceptable. A 'Limited Rights' philosophy could be built up as follows: laboratory animals have a right not to be subjected to painful procedures without an analgesic; farm animals have a right to be free from severe frustration (or be free to express strongly motivated behavior); and companion animals have a right to regular exercise and stimulation. The problem with this approach is that one has to have 'rules' in place to cover every conceivable situation. It is often easier to take a utilitarian stance and ask, 'What happens if...?'. If the answer is that happiness will be increased (or suffering will be diminished) then that is the ethically correct thing to do.

The major weaknesses of Animal Rights would seem to be:

- 1. The concept of 'inherent value' is unclear. For example, where on the phylogenetic scale does inherent value appear? According to Regan (1983), it is only the higher mammals that have inherent value.
- 2. It does not resolve conflicts between individuals.
 3. It does not protect the welfare of all animals. It is a philosophy that dictates how humans interact with animals, viz., 'Do not use them'; it therefore does not protect animals that may be harmed *indirectly* by human activities, such as by habitat loss from urban, industrial, and agricultural development, and environmental pollution and destruction of oceans, lakes, rivers, land, and air.

3.5 Utilitarianism or Animal Rights?

Which philosophy should a person who is interested in improving animal welfare follow, Utilitarianism or Animal Rights? These philosophies are different in a crucial way, viz., they are different *types* of philosophies. Utilitarianism is a *teleological* theory, i.e., a theory that deals with ends or final purposes.

In the case of Utilitarianism, the end being sought is the greatest happiness. Animal Rights is a deontological theory, i.e., a theory that deals with that which is binding. It deals with actions, not ends. Both philosophies use the same evidence that the higher animals are 'subject of a life', are conscious, sentient creatures, experience individual welfare, can suffer, want and prefer things, and believe and feel things. However, this evidence leads them to different positions. A strict utilitarian believes that animals are worthy of moral consideration, therefore we should try to maximize their total happiness. A complete animal rightist believes that animals have inherent value, therefore they should not be used by human beings at all.

3.6 The Science of Animal Welfare

Animal welfare did not begin to be considered scientifically until the last quarter of the twentieth century. This requires some explanation since there is evidence of some acceptance of sentience, at least in mammals, for hundreds of years. 'Sentience' simply means capable of feeling and is the fundamental requirement for an organism to have inherent value. By the time of the Renaissance, there is good evidence from the writings of Leonardo da Vinci, Erasmus, Thomas More, Montaigne, Shakespeare, Francis Bacon, and others, that animal sentience was accepted as part of secular knowledge (Preece, 2002). Many of the great artistic works of this age also portray people treating animals as if they were sentient. However, as previously mentioned, it was not until John Locke (to a minor extent) in the seventeenth century, David Hume in the eighteenth century, and Jeremy Bentham in the nineteenth century that sentience in animals came to be accepted by philosophers. Even then, some eminent philosophers like Immanuel Kant, who lived into the nineteenth century, believed that animals had only instrumental value.

But what of the scientists? It has already been stated that Descartes, living in the eighteenth century, did not treat the live conscious dogs he was dissecting as if they were sentient. In fact, it is not until the middle of the nineteenth century that we find scientists making explicit reference to feelings. William Youatt (1776–1847) was the son of a surgeon who lived in the southwest of England and was educated for the ministry. However, at the age of 34, he gave up his ministry and became assistant to a veterinary surgeon in London. He took classes

I.J.H. Duncan

at the newly founded Veterinary College (later to become the Royal Veterinary College). However, he was not satisfied with the quality of instruction, so he left without a diploma. In those days, formal qualification was not very important, and Youatt soon gained the reputation of being an outstanding veterinarian. He was very prolific and wrote textbooks that are still cited today. Youatt also founded and acted as Editor of The Veterinarian (a professional journal for veterinarians) from 1828 until he died in 1847. However, his humanitarian approach to animals and his understanding of what animal welfare is all about is revealed in a book originally published in 1839 (republished in 2004), entitled The Obligation and Extent of Humanity to Brutes, Principally Considered with Reference to the Domesticated Animals. In this book, Youatt (1839) writes of animals' senses, emotions, consciousness, attention, memory, sagacity, docility, association of ideas, imagination, reason, instinct, social affections, and the moral qualities of friendship and loyalty. He certainly thought that animals have feelings! More than 30 years before Darwin's (1872) The Expression of the Emotions in Man and Animals, Youatt wrote of the intellectual faculties, 'We are endeavoring to shew that the difference [between humans and animals in one of the most essential of all points, is in degree and not in kind' (Youatt, 1839, p.55). He also wrote, 'We are operating on animals that have, probably, as keen feelings of pleasure and of pain as ourselves' (Youatt, 1839, p.234). He condemned as cruel and inhumane many practices that are still being criticized today, including too early training of race horses, steeplechasing (a British sport in which horses are raced over a track with high brushwood fences), transport methods for newly born calves, raising of veal calves, slaughter-house management, taildocking and ear-cropping of dogs, using live bait for fishing, and force-feeding of capons (castrated male chickens) and turkeys to produce foie gras.

The person usually credited with transforming biological concepts completely is Charles Darwin (1809–1882), who published *The Origin of Species* in 1859 (Darwin, 1859). (But remember that Youatt was making similar suggestions more than 30 years before this.) Some scholars believe Darwin had material left over from *The Origin* which he incorporated into *The Descent of Man* (Darwin, 1871) and *The Expression of the Emotions in Man and Animals* (Darwin, 1872). In both of these books he suggests that the emotions had also

evolved, and he gives good descriptions of the expression of these emotions in various species. However, he says nothing about the subjective experience of having emotions. This was left to a prominent biologist and follower of Darwin, George John Romanes (1848-1894), who was explicit about the subjective experience of emotions. In a book entitled Mental Evolution in Animals, he wrote that 'Pleasures and Pains must have been evolved as the subjective accompaniment of processes which are respectively beneficial or injurious to the organism, and so evolved for the purpose or to the end that the organism should seek the one and shun the other' (Romanes, 1884). Later he stated, 'Thus, then we see that the affixing of painful or disagreeable states of consciousness to deleterious changes of the organism, and the reverse states to reverse changes, has been a necessary function of the survival of the fittest.' So, by the 1880s, Romanes was describing emotions almost exactly as would a modern-day welfare scientist (Duncan, 1996).

Why did it take so long for feelings to be accepted as critical for welfare? The reason for the resistance to these enlightened nineteenth-century views lies in the rise of 'Behaviorism', a very important school of psychology, especially in North America. Behaviorists spoke out strongly against paying any attention to 'feelings' or 'consciousness' right through the twentieth century into the 1970s. For example, one of the founding fathers of Behaviorism, William James (1904, p.477), said,

Consciousness ... is the name of a non-entity, and has no right to a place among first principles. Those who still cling to it are clinging to a mere echo, the faint rumor left behind by the disappearing 'soul' upon the air of philosophy... It seems to me that the hour is ripe for it to be openly and universally discarded.

Another founder, J.B. Watson (1928), stated, 'The behaviorist sweeps aside all medieval conceptions. He drops from his scientific vocabulary all subjective terms such as sensation, perception, image, desire and even thinking and emotion.' One of the chief proponents of Behaviorism was B.F. Skinner. He is the person who invented the 'Skinner box' or operant conditioning chamber, much used in the psychology laboratory. He wrote, 'We seem to have a kind of inside information about our behavior — we have feelings about it. And what a diversion they have proved to be!... Feelings have proved to be one of the most fascinating attractions along the

path of dalliance' (Skinner, 1975, p.43). William James, J.B. Watson, and B.F. Skinner were well-respected scientists and there is no doubt that their views had an inhibiting effect on any consideration of feelings through most of the twentieth century.

However, there was the occasional behavioral scientist brave enough to tackle the topic. For example, Buytendijk (1953), a Dutch phenomenologist, carried out an interesting experiment in which he showed that blinded *Octopus* could tell the difference between being touched and reaching out and touching something, whereas *Asterias* (starfish) could not. Buytendijk interpreted this to mean that the octopus with its large neural ganglia had some cognitive representation of the world and its place in it, whereas the starfish, with its nerve net, had no such representation and could only react in a stimulus-response way.

Even the European-founded discipline of Ethology eschewed any consideration of feelings and subjective experiences through the first 70 years of the twentieth century. This pattern was broken when an American ethologist, Donald Griffin, astounded his audience at the 1975 International Ethology Conference by giving a plenary session talk on animal awareness. A year later he published a book entitled *The Question of Animal Awareness* on the same topic (Griffin, 1976) and suddenly there was a burgeoning literature on animal subjective feelings.

The present-day interest in animal welfare can be traced back to Ruth Harrison with publication of her book Animal Machines in which she was very critical of intensive farming methods (Harrison, 1964). She visited various types of farm to see for herself what was happening. She criticized broiler chicken farming on grounds of high density, large group size, and the constant search for a cheap product. She visited packing stations (broiler slaughter plants) and was shocked by transport methods, rough handling, and the lack of humaneness of the slaughter process. She was concerned over the very artificial environment of the battery cage system for laying hens, as well as the lack of space, the low light levels, and the disposal of the spent hens. With regard to veal calves she spoke out against transport methods, the crates the calves were kept in, the high levels of anemia, the darkness, and the fact that the calves got no solid food. She also criticized intensive rabbit production, broiler beef production, and fattening pig production on similar grounds. She concluded that quality was giving way to quantity in animal production and that economic arguments were being used to overthrow humanitarianism and quality of product.

Following the publication of Animal Machines, the public outcry was so intense in the UK that the British Government set up a Committee under the chairmanship of Professor Rogers Brambell to investigate the whole topic. In 1965 this Committee published a report commonly known as The Brambell Report (Command Paper 2836, 1965). This report was very critical of intensive farming methods but made some claims that were not based on any hard evidence. Welfare then began to be investigated scientifically. When scientists first started to investigate animal welfare in the late 1960s and 1970s, it was generally accepted that an animal's welfare would be a reflection of how physiologically stressed it was: an animal that was not stressed would have good welfare and an animal that was highly stressed would have poor welfare (Bareham, 1972; Bryant, 1972; Wood-Gush et al., 1975; Freeman, 1978). In the 1970s, it seemed that assessing welfare was simply a matter of finding a reliable measurement of stress. The argument was convincing. 'Welfare', whatever that might be, was a consequence of certain physiological processes, and the most likely physiological processes to be involved were those connected with stress. Interestingly, in her book Animal Machines, Ruth Harrison laid much more emphasis on animal suffering than on the physiological stress response of animals in intensive agriculture (Harrison, 1964). The Brambell Report also acknowledged that feelings were an important feature of welfare (Command Paper 2836, 1965, p.9). In my view, the Brambell Committee were very farsighted in claiming that,

Welfare is a wide term that embraces both the physical and mental well-being of the animal. Any attempt to evaluate welfare, therefore, must take into account the scientific evidence available concerning the feelings of animals that can be derived from their structure and functions and also from their behavior.

Nevertheless, in spite of these allusions to the feelings of animals in general and the suffering of animals in particular, the widespread view among the scientific community at this time was that welfare was intimately connected with stress. This view changed very rapidly with the publication of Donald Griffin's book *The Question of Animal Awareness* (Griffin, 1976). Suddenly it became

26 I.J.H. Duncan

acceptable for behavioral scientists to consider animals' subjective feelings and incorporate these into models of behavior. As animal welfare science progressed through the 1970s and 1980s, scientists began to search for a suitable definition of 'animal welfare' and different scientists came up with very different definitions. Duncan and Dawkins (1983) reviewed this topic and listed all the definitions that had been given for 'animal welfare' to that time. They concluded that it was impossible to give 'animal welfare' a precise scientific definition. They said that a broad working description would be one that encompassed the notions of: (i) the animal in physical and mental health; (ii) the animal in harmony with its environment; (iii) the animal being able to adapt to the given environment without suffering; and (iv) somehow taking account of the animal's feelings. 'Suffering' was described as a wide range of unpleasant emotional states. This broad working description of 'animal welfare' worked well at first. However, as more and more scientists became involved in welfare research, examples were found in which there was disagreement among the symptoms. For example, cases were identified in which animals: (i) appeared normal but had subclinical disease; (ii) showed stress symptoms when participating in a rewarding activity (e.g., stallions mating) and (iii) were healthy, physiologically normal, but performing stereotyped movements (e.g., polar bears in a zoo environment). In each of these three cases, did the animals have good welfare or not? This led to disagreement and a protracted debate within scientific animal welfare circles over which symptoms should take priority.

Gradually, two schools of thought emerged. The Biological Functioning School argued that animal welfare is principally to do with the satisfaction of the primary needs and much less to do with the satisfaction of the secondary subjective feelings. This implies that welfare is to do with good biological functioning - with the absence of a stress response (or absence of a large stress response), with the animal being able to cope, and with the satisfaction of biological needs (see Broom and Johnson [1993] and Broom [1996] for stress and coping; Hurnik and Lehman [1988] for needs). The Feelings School postulated that animal welfare is all to do with what the animal feels, viz., with the absence of negative emotional states which are commonly known as states of suffering, and with the presence of positive emotional states which are commonly known as states of pleasure (see Dawkins, 1980, 1993; Duncan, 1981, 1993, 2004).

The Feelings School argue that all living organisms have certain needs which have to be satisfied in order that the organism survives, grows, and reproduces. This is as true for a pine tree as it is for a pig. If these needs are not met, the organism will show symptoms of atrophy, stress, ill health, and will perhaps even die. The vertebrates (and some of the higher invertebrates) have evolved 'feelings' or 'subjective affective states' to protect their needs in a flexible way. A lower invertebrate satisfies its needs by means of simple, hard-wired, stimulusresponse behavior. So, a fly on a cow's back can avoid the cow's tail swishing toward it and can do this very efficiently. However, there are no feelings or learning involved and the fly very quickly will land on the cow's back again. A vertebrate, on the other hand, has feelings which help it satisfy its needs in a flexible way. So, a bird avoids a cat moving toward it - but its avoidance is governed by fear. This response is much more flexible. A bird will learn to avoid, not only a cat moving toward it, but a sleeping cat, anything that looks or behaves a little like a cat, locations that cats frequent, and even locations that cats frequent at certain times of day. After much debate, there is now gradual acceptance that welfare is indeed all to do with feelings. Even proponents of the Biological Functioning School are modifying their views (see, for example, Broom, 2014).

The increasing acceptance that animal welfare is all to do with feelings brings with it an apparently insurmountable problem. This is because feelings are subjective:

- Only I can know what my subjective feelings are.
- Only I can know what I experience when I see the color red.
- Only I can know what I experience when I feel hungry.
- Only I can know what I experience when I feel a toothache.

The subjective nature of feelings means that they are not directly accessible to scientific investigation. However, in the animal welfare debate we do not need to know *exactly* how the animal feels – the important factor is whether a feeling is negative or positive, and its intensity. In other words, we do not need to know whether rabbit fear feels exactly like human fear, but simply that rabbit fear is a negative feeling that can vary in intensity and motivate the

appropriate behavior. So, we can never know what a piglet feels when it has its tail docked. Is it like having a finger amputated, or receiving a very bad burn, or experiencing toothache? We can never know. But if we can show that the piglet feels very negatively about the procedure, if the piglet shows much less reaction when it is given an analgesic before the procedure, then we can conclude that tail-docking reduces its welfare.

3.7 Understanding States of Suffering

Many states of suffering have now been investigated indirectly in this way to find out how negatively the animal feels. Pain and discomfort, frustration, fear, maternal separation, and various types of deprivation have all been investigated in animals in some detail. For example, in a series of experiments, hens were thwarted in many different ways while attempting to feed, behave sexually, nest (Fig. 3.1), incubate eggs, and brood chicks, and their behavior was observed and cataloged (Duncan, 1970). When frustration was severe, the symptoms were stereotyped back-and-forward pacing, whereas when it was mild, there was an increase in 'displacement' preening (an unusual type of hurried preening occurring out of context). If two or more hens were frustrated simultaneously, then, in addition to the other responses, the dominant birds showed an increase in aggression toward the subordinates. When this list of behavior patterns was compared to the behavior of hens in battery cages it was found that the symptoms of frustration were not very common. However, there was one notable



Fig. 3.1. Hen pushing open a weighted door to reach a nest box.

exception: most birds in battery cages showed symptoms of severe frustration in the 1-1½ hours before they laid an egg. They did not seem to regard the cage as a suitable nesting site. In later experiments it was shown that hens in the pre-laying phase would work as hard to reach a suitable nesting site as they would to reach food when they had been deprived of food for 28 hours (Follensbee et al., 1992). It has also been shown that the performance of nest-building behavior in hens is more important than the actual construction of a nest (Duncan and Kite, 1989; Hughes et al., 1989). It should be noted that these experiments do not tell us what a hen actually feels when it is denied a nesting site; they do, however, tell us that access to nest site matters a lot to a hen and that its welfare is greatly reduced by not having a nest and being able to perform nest-building behavior.

This technique of 'asking' animals what they feel about the conditions under which they are kept and the procedures to which they are subjected has now been used to investigate different states of suffering in a wide variety of species. For example, it has been shown that when a group of broiler chickens is given a choice of two rations, one of which contains an analgesic drug, lame chickens in the group consume more of the medicated ration and in a quantity sufficient to alleviate their lameness. Non-lame birds do not eat much of the medicated diet presumably because its taste is slightly aversive (Danbury *et al.*, 2000). This indicates that the lameness is caused by pain and that, if given the opportunity, the birds will self-medicate to alleviate the pain.

Fear has also been examined by asking animals what they feel about it. For example, it has been shown that rainbow trout (*Oncorhynchus mykiss*) will quite quickly learn to avoid a frightening stimulus if given a warning signal in a shuttle tank (Yue *et al.*, 2004). This was taken a stage further when it was shown that cichlid fish could learn to operate an underwater push-door, which would allow their motivation to be measured (Galhardo *et al.*, 2011).

In all studies of this type, assessing strength of motivation is crucial. Dawkins (1990) proposed using an approach taken from microeconomics. According to this approach, consumers will buy some commodities even when the price increases or their income decreases; this is described as 'inelastic demand' and these commodities are known as 'necessities'. For other commodities, consumption decreases as price increases; these commodities are said to have 'elastic demand' and are called 'luxuries'. This

I.J.H. Duncan

approach seems to make good sense. However, there are lots of problems associated with it. For example, how do we allocate rewards into discrete amounts (Mason et al., 1998; Kirkden et al., 2003)? In one experiment, dairy heifers were given free access to bedded stalls for 9 hours per day. They had to work for further access to the stalls. It was found that they would work quite hard to gain access to the stalls if each additional period of access was 30-80 minutes; access to stalls showed inelastic demand. However, if each period was limited to 20 minutes or less they were much more reluctant to work, in other words, they showed elastic demand (Jensen et al., 2005). It is also difficult, if not impossible, to use these techniques when the behavior pattern in question shows a distinct diurnal rhythm. For example, nesting motivation in hens shows an extremely strong diurnal rhythm and, when it is triggered, appears to be all-consuming for a period of about 2 hours prior to egg laying (Duncan and Kite, 1989; Hughes et al., 1989). Roosting behavior in chickens also shows a very strong diurnal rhythm with birds being extremely motivated to move to a roost well above ground level at the end of the day (Olsson and Keeling, 2000, 2002). Therefore, when a hen is in 'nesting mode' or 'roosting mode' it is impossible to titrate this motivation against any other. To some extent, the same holds true for dust bathing in chickens, which shows a peak in motivation in the middle of the day – but only every other day (Hogan and van Boxel, 1993) and the effects of external motivating factors are superimposed on this diurnal pattern (Duncan et al., 1998). Fraser and Nicol (2018) discuss the problems associated with preference and motivation testing in some detail.

Investigations into states of suffering including pain and discomfort, frustration, fear, maternal separation, and various types of deprivation have all been investigated in a wide range of species (see for example, Viňuela-Fernández et al., 2018; Boissy et al., 2018; Mason and Burn, 2018; Chapter 23, this volume). There are other states of suffering, experienced by human beings, such as boredom and sadness, which have proved more difficult to investigate in animals. There have been some attempts to define and investigate boredom (Wemelsfelder, 2005; Mason and Burn, 2018), but this state of suffering is notoriously difficult to unravel and explain. With regard to sadness, there have only been occasional anecdotal accounts such as those of Jane Goodall (van Lawick-Goodall, 1968) describing the response of a mother chimpanzee to the death of an offspring; there have been no in-depth investigations into this emotion.

It should also be remembered that there may be other states of suffering experienced by animals and not experienced by human beings. It has already been emphasized that states of suffering (and states of pleasure) are subjective, that is, available only to the organism experiencing them. However, when the sensory systems involved in the animal are very different from those of human beings, then the problem is confounded even further. For example, animals with sensory capacities outside the human range may be exposed to human-produced noises, such as high frequencies from machinery, of which we are unaware but which might be aversive to animals. Mice, dogs, and cats can all hear frequencies much higher than those perceived by human beings and could be disturbed by, for example, fan noises. Marine mammals use underwater vocalizations for communication, with different species using different frequency ranges (Nowacek, 2005), with some using echolocation to find objects in their environment. Human-produced underwater noises such as ships' engines and sonar transmissions could well interfere with these processes and this might lead to suffering. But what would this suffering feel like?

In a famous paper entitled 'What is it like to be a bat?' the philosopher Thomas Nagel has argued that the essential part of consciousness is that there is something that it feels like to be a conscious thing (Nagel, 1974). He then takes the extreme example of a bat, experiencing its world in terms of echolocation, and argues that, of course, human beings can never know what it is like to be a bat. We have a good idea of the suffering involved when a person suddenly loses their sense of sight. But what would the experience be like for a bat who suddenly loses its sense of echolocation? Human pollution of rivers and lakes may result in water with low oxygen content or less than optimal pH value, which could have a very negative effect on fish welfare. We, as humans, have no conception at all of what the suffering might be like from living in an environment of too low or too high a pH. As a final example, if a bird of a species that normally migrates in autumn is kept in a cage, the bird remains highly motivated to fly (as judged by its repeated attempts to escape), and thus may experience suffering (Dawkins, 1990). Without the motivation to migrate, how could we understand what this suffering would feel like?

3.8 What About States of Pleasure?

Compared to the number of investigations into states of suffering in animals, there has been very little research into states of pleasure. This is understandable, since it was obvious in early welfare research that bigger welfare gains could be made by reducing suffering than by increasing pleasure. However, this chapter has argued that many of these gains have now been achieved and that it might be possible to improve welfare even further by encouraging pleasurable states. It has been suggested that negative feelings such as pain, fear, and frustration have evolved to motivate behavior in 'need situations'; that is, where immediate action by the animal is required. Positive feelings such as pleasure and happiness have evolved to motivate behavior in 'opportunity situations' when the benefits of performing the behavior may be far in the future (Fraser and Duncan, 1998). It is taken for granted that some patterns of behavior such as cats purring, dogs tail-wagging, lambs gamboling, and so on, are obvious signs of positive feelings. However, there is little in the way of detailed investigations. The results from a study of dust-bathing behavior in chickens were strongly suggestive that dust bathing is motivated by pleasure, whereas previously it had been thought it was driven by negative feelings associated with dirty feathers (Widowski and Duncan, 2000). A proper understanding of animals' positive emotions is also important because it may not always be possible to eliminate negative feelings completely. So, it may be possible to counter some negative emotions by promoting positive feelings simultaneously - a spoonful of sugar to make the medicine go down. Using this technique of giving desirable treats, Temple Grandin has been able to persuade very flighty antelopes in a zoo to repeatedly enter a chute and accept injections (Grandin et al., 1995).

3.9 Gray Areas

A crucial welfare question is, 'When in ontogenetic development do feelings become functional?'. We cannot simply take birth or hatching as a starting point. A newly born precocial animal such as a guinea pig has fully functional feelings and is able to suffer in many different ways. Presumably, it would also be

capable of suffering *in utero* for some days before birth. On the other hand, a newly born altricial animal such as a kangaroo is embryonic by comparison and not as capable of suffering. Similarly, a newly hatched domestic chick has well-developed feelings and is capable of suffering more than a newly hatched starling (*Sturnus* spp.). Moreover, feelings do not suddenly become switched on: they develop gradually, and different feelings develop at different times and different rates. The question, 'When does it matter to the animal?' has still to be elucidated. This is an area crying out for more research.

Another crucial welfare question is, 'Where on the phylogenetic scale do feelings become important?'. It has already been stated that all the vertebrates have feelings. It is possible that the mammals and birds are more sentient than the reptiles, amphibians, and fish, but there is no hard evidence to back this up. But what about the invertebrates? There is good evidence that the Cephalopods (octopus, squid, etc.) are highly sentient (see, for example, Godfrey-Smith, 2016), and perhaps even more sentient than the cartilaginous fishes (sharks, rays, etc.). It is also generally acknowledged that the Decapods (shrimps, lobsters, crabs, etc.) have some sentience (see, for example, Rowe, 2018). There is continuing debate about sentience in other invertebrate groups. For example, Griffin (1984) has argued that some insects, and in particular honeybees, show behavior that can only be explained in terms of consciousness and sentience. However, it can be argued that sentience is not required to explain honeybee behavior and that a computer could be programmed to behave in this way.

In conclusion, a proper understanding of states of suffering and states of pleasure will help us to design optimum environments for animals as well as develop best practices of care.

3.10 References

Bareham, J.R. (1972) Effects of cages and semi-intensive deep litter pens on the behaviour, adrenal response and production in two strains of laying hens. *British Veterinary Journal* 128, 153–163. http://dx.doi.org/10.1016/S0007-1935(17)37088-4.

Bentham, J. (1823) An Introduction to the Principles of Morals and Legislation. Clarendon Press, Oxford, UK.

Boissy, A., Dwyer, C.M., Jones, R.B. (2018) Fear and other negative emotions. In: Appleby, M.C., Olsson, I.A.S., Galindo, F. (eds.) *Animal Welfare*, 3rd edn. CAB International, Wallingford, UK, pp. 92–113. http://dx.doi.org/10.1079/9781786390202.0092.

I.J.H. Duncan

- Broom, D. (1996) Animal welfare defined in terms of attempt to cope with the environment. Acta Agriculuræ Scandinavica, Section A, Animal Science Supplementum 27, 22–28.
- Broom, D. (2014) Sentience and Animal Welfare. CAB International, Wallingford, UK. http://dx.doi.org/10.1079/9781780644035.0000.
- Broom, D. and Johnson, K. (1993) Stress and Animal Welfare. Chapman and Hall, London, UK. http://dx.doi.org/10.1007/978-94-024-0980-2.
- Bryant, M.J. (1972) The social environment: Behaviour and stress in housed livestock. *Veterinary Record* 90, 351–359. http://dx.doi.org/10.1136/vr.90.13.351.
- Buytendijk, F.J.J. (1953) Toucher et être touché. *Archives Néerlandaises de Zoologie* 10, 34–44.
- Command Paper 2836 (1965) Report of the Technical Committee to Enquire into the Welfare of Animals kept under Intensive Livestock Husbandry Conditions. Her Majesty's Stationery Office, London.
- Cottingham, J. (1978) 'A brute to the brutes?' Descartes' treatment of animals. *Philosophy* 53, 551–559. http://dx.doi.org/10.1017/S0031819100026371.
- Danbury, T.C., Weeks, C.A., Chambers, J.P., Waterman-Pearson, A.E., Kestin, S.C. (2000) Self-selection of the analgesic drug carprofen by lame broiler chickens. *Veterinary Record* 146, 307–311. http://dx.doi. org/10.1136/vr.146.11.307.
- Darwin, C. (1859) *The Origin of Species by Natural Selection*. John Murray, London, UK.
- Darwin, C. (1871) The Descent of Man, and Selection in Relation to Sex. John Murray, London, UK. http:// dx.doi.org/10.5962/bhl.title.121292.
- Darwin, C. (1872) The Expression of the Emotions in Man and Animals. John Murray, London, UK. http:// dx.doi.org/10.1037/10001-000
- Dawkins, M.S. (1980) Animal Suffering: The Science of Animal Welfare. Chapman and Hall, London, UK. http://dx.doi.org/10.1007/978-94-009-5905-7.
- Dawkins, M.S. (1990) From an animal's point of view: Motivation, fitness, and animal welfare. *Behavioral and Brain Sciences* 13, 1–9 and 54–61. http://dx.doi.org/10.1017/S0140525X00077104.
- Dawkins, M.S. (1993) Through Our Eyes Only? The Search for Animal Consciousness. W.H. Freeman, Oxford, UK.
- Duncan, I.J.H. (1970) Frustration in the fowl. In: Freeman, B.M. and Gordon, R.F. (eds.) Aspects of Poultry Behaviour. British Poultry Science Ltd., Edinburgh, UK, pp. 15–31.
- Duncan, I.J.H. (1981) Animal rights Animal welfare: A scientist's assessment. *Poultry Science* 60, 489–499. http://dx.doi.org/10.3382/ps.0600489.
- Duncan, I.J.H. (1993) Welfare is to do with what animals feel. *Journal of Agricultural and Environmental Ethics* 6 (Suppl. 2), 8–14.
- Duncan, I.J.H. (1996) Animal welfare defined in terms of feelings. Acta Agriculturæ Scandinavica, Section A, Animal Science Supplement 27, 29–35.

- Duncan, I.J.H. (2004) A concept of welfare based on feelings. In: Benson, G.J. and Rollin, B.E. (eds.) The Well-Being of Farm Animals: Challenges and Solutions. Blackwell Publishing, Ames, Iowa, USA, pp. 85–101. http://dx.doi.org/10.1002/9780470344859.ch5.
- Duncan, I.J.H. and Dawkins, M.S. (1983) The problem with assessing 'well-being' and 'suffering' in farm animals. In: Smidt, D. (ed.) *Indicators Relevant to Farm Animal Welfare*. Martinus Nijhoff, The Hague, The Netherlands, pp. 13–24. http://dx.doi.org/10.1007/978-94-009-6738-0_2.
- Duncan, I.J.H. and Kite, V.G. (1989) Nest site selection and nest-building behaviour in domestic fowl. *Animal Behaviour* 37, 215–231. http://dx.doi.org/10.1016/ 0003-3472(89)90112-7.
- Duncan, I.J.H., Widowski, T.M., Malleau, A.E., Lindberg, A.C., Petherick, J.C. (1998) External factors and causation of dustbathing in domestic hens. *Behavioural Processes* 43, 219–228. http://dx.doi.org/10.1016/ S0376-6357(98)00017-5.
- Follensbee, M.E., Duncan, I.J.H., Widowski, T.M. (1992) Quantifying nesting motivation of domestic hens. *Journal of Animal Science* 70 (Suppl. 1), 164.
- Fraser, D. and Duncan, I.J.H. (1998) 'Pleasures', 'pains' and animal welfare; toward a natural history of affect. *Animal Welfare* 7, 383–396.
- Fraser, D. and Nicol, C.J. (2018) Preference and motivation research. In: Appleby, M.C., Olsson, I.A.S., Galindo, F. (eds.) *Animal Welfare*, 3rd edn. CAB International, Wallingford, UK, pp. 213–231. http://dx.doi.org/10.1079/9781786390202.0213.
- Freeman, B.F. (1978) Stress in caged layers. In: Sørensen, L.Y. (ed.) First Danish Seminar on Poultry Welfare in Egglaying Cages. Danish National Committee for Poultry and Eggs, Copenhagen, Denmark, pp. 55–65.
- Galhardo, L., Almeida, O., Oliveira, R.F. (2011) Measuring motivation in a cichlid fish: An adaptation of the push-door paradigm. *Applied Animal Behaviour Science* 130, 60–70. http://dx.doi.org/10.1016/j.applanim.2010.12.008.
- Godfrey-Smith, P. (2016) Other Minds: The Octopus, the Sea, and the Deep Origins of Consciousness. Farrar, Strauss and Giroux, New York, USA.
- Grandin, T., Rooney, M.B., Phillips, M., Cambre, R.C., Irlbeck, N.A., et al. (1995) Conditioning of Nyala (*Tragelaphus angasi*) to blood sampling in a crate with positive reinforcement. Zoo Biology 14, 261–273. http://dx.doi.org/10.1002/zoo.1430140307.
- Griffin, D.R. (1976) *The Question of Animal Awareness*. Rockefeller University Press, New York, USA.
- Griffin, D.R. (1984) *Animal Thinking*. Harvard University Press, Cambridge, Massachusetts, USA.
- Harrison, R. (1964) *Animal Machines*. Vincent Stuart, London, UK.
- Hogan, J.A. and van Boxel, F. (1993) Causal factors controlling dustbathing in Burmese red junglefowl, some results and a model. *Animal Behaviour* 46, 627–635. http://dx.doi.org/10.1006/anbe.1993.1239.

- Hughes, B.O., Duncan, I.J.H., Brown, M.F. (1989) The performance of nest building by domestic hens: Is it more important than the construction of a nest? *Animal Behaviour* 37, 210–214. http://dx.doi. org/10.1016/0003-3472(89)90111-5.
- Hume, D. (1739; new edition edited by L.A. Selby Bigge, 1888) A Treatise of Human Nature. Clarendon Press, Oxford, UK.
- Hurnik, J.F. and Lehman, H. (1988) Ethics and farm animal welfare. *Journal of Agricultural Ethics* 1, 305–318. http://dx.doi.org/10.1007/BF01826794.
- James, W. (1904) Does 'consciousness' exist? Journal of Philosophy, Psychology and Scientific Methods 1, 477–491. http://dx.doi.org/10.2307/2011942.
- Jensen, M.B., Pedersen, L.J., Munksgaard, L. (2005) The effect of reward duration on demand functions for rest in dairy heifers and lying requirements as measured by demand functions. Applied Animal Behaviour Science 90, 207–217. http://dx.doi.org/10.1016/j. applanim.2004.08.006.
- Kenny, A. (1970) Descartes' Philosophical Letters. Clarendon Press, Oxford, UK.
- Kirkden, R.D., Edwards, J.S.S., Broom, D.M. (2003) A theoretical comparison of the consumer surplus and the elasticities of demand as measures of motivational strength. *Animal Behaviour* 65, 157–178. http://dx.doi.org/10.1006/anbe.2002.2035.
- Mason, G.J. and Burn, C.C. (2018) Frustration and boredom in impoverished environments. In: Appleby, M.C., Olsson, I.A.S., Galindo, F. (eds.) *Animal Welfare*, 3rd edn. CAB International, Wallingford, UK, pp. 114–138. http://dx.doi.org/10.1079/9781786390202.0114.
- Mason, G., McFarland, D., Garner, J. (1998) A demanding task: Using economic techniques to assess animal priorities. *Animal Behaviour* 55, 1071–1075. http://dx.doi.org/10.1006/anbe.1997.0692.
- Mill, J.S. (1910) *Utilitarianism*. J.M. Dent, London, UK. Nagel, T. (1974) What is it like to be a bat? *The Philosophical Review* 83, 435–450. http://dx.doi.org/10.2307/2183914.
- Nowacek, D.P. (2005) Acoustic ecology of foraging bottlenose dolphins (*Tursiops truncates*), habitat-specific use of three sound types. *Marine Mammal Science* 21, 587–602. http://dx.doi.org/10.1111/j.1748-7692.2005.tb01253.x
- Őhman, A., Flykt, A., Lundqvist, D. (2000) Unconscious emotion: Evolutionary perspectives, psychophysiological data and neuropsychological mechanisms. In: Ekman, P. and Davidson, R.J. (eds.) *Cognitive Neuroscience of Emotion*. Oxford University Press, Oxford, UK, pp. 296–327.
- Olsson, I.A.S. and Keeling, L.J. (2000) Night-time roosting in laying hens and the effect of thwarting access to perches. Applied Animal Behaviour Science 68, 243–256. http://dx.doi.org/10.1016/S0168-1591(00)00097-6.
- Olsson, I.A.S. and Keeling, L.J. (2002) The push-door for measuring motivation in hens: Laying hens are motivated to perch at night. *Animal Welfare* 11, 11–19.

- Preece. R. (2002) Awe for the Tiger, Love for the Lamb: A Chronicle of Sensibility to Animals. UBC Press, Vancouver. Canada.
- Regan, T. (1983) *The Case for Animal Rights*. University of California Press, Berkeley, California, USA.
- Romanes, G.J. (1884; reprinted 1969) *Mental Evolution in Animals*. AMS Press, New York, USA.
- Rowe, A. (2018) Should scientific research involving decapod crustaceans require ethical review? Journal of Agricultural and Environmental Ethics 31, 625–634. http://dx.doi.org/10.1007/s10806-018-9750-7.
- Singer, P. (1975) *Animal Liberation*. Random House, New York, USA.
- Skinner, B.F. (1975) The steep and thorny way to a science of behavior. American Psychologist 30, 42–49. http://dx.doi.org/10.1037/0003-066X.30.1.42.
- Tannenbaum, J. (1995) Veterinary Ethics. Mosby, St. Louis, Missouri, USA.
- Van Lawick-Goodall, J. (1968) The behaviour of freeliving chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs 1, 161–309. http:// dx.doi.org/10.1016/S0066-1856(68)80003-2.
- Viňuela-Fernández, I., Weary, D.M., Flecknell, P.A. (2018) Pain. In: Appleby, M.C., Olsson, I.A.S., Galindo, F. (eds.) *Animal Welfare*, 3rd edn. CAB International, Wallingford, UK, pp. 76–91.
- Watson, J.B. (1928) *Behaviorism*. Routledge and Kegan Paul, London, UK.
- Wemelsfelder, F. (2005) Animal boredom: Understanding the tedium of confined lives. In: McMillan, F.D. (ed.) Mental Health and Well-Being in Animals. Blackwell Publishing, Oxford, UK, pp. 79–93.
- Widowski, T.M. and Duncan, I.J.H. (2000) Working for a dustbath: Are hens increasing pleasure rather than reducing suffering? *Applied Animal Behaviour Science* 68, 39–53. http://dx.doi.org/10.1016/S0168-1591 (00)00088-5.
- Winkielman, P. and Berridge, K.C. (2004) Unconscious emotion. *Current Directions in Psychological Science* 13, 120–123. http://dx.doi.org/10.1111/j.0963-7214.2004.00288.x.
- Wood-Gush, D.G.M., Duncan, I.J.H., Fraser, D. (1975) Social stress and welfare problems in agricultural animals. In: Hafez, E.S.E. (ed.) *The Behaviour of Domestic Animals*, 3rd edn. Williams and Wilkins, Baltimore, Maryland, USA, pp. 182–200.
- Youatt, W. (1839) The Obligation and Extent of Humanity to Brutes, Principally Considered with Reference to the Domesticated Animals. Republished in 2004. Edited, introduced and annotated by Preece, R. Edwin Mellen Press, Lewiston, New York, USA.
- Yue, S., Moccia, R.D., Duncan, I.J.H. (2004) Investigating fear in domestic rainbow trout, *Oncorhynchus* mykiss, using an avoidance learning task. *Applied Animal Behaviour Science* 87, 343–354. http://dx.doi. org/10.1016/j.applanim.2004.01.004.

32 I.J.H. Duncan

4

The Relationship Between Mental and Physical Health

MELISSA BAIN AND C.A. TONY BUFFINGTON

Department of Medicine and Epidemiology, UC Davis School of Veterinary Medicine, Davis, California, USA

4.1 Introduction

Animals interact with their environments on a time constant of milliseconds. When animals act on their environment, their environment responds (Fig. 4.1). Animals perceive this response through variable combinations of their senses, which transmit the received information chemically, electrically, and hormonally to various parts of the brain. The brain then compares the received information with predictions it makes based upon its history (genetic, epigenetic, and environmental), the context of the interaction, and its expectation (predicted response versus received response) and decides on the next action (Pezzulo *et al.*, 2018).

Animals must be able to perceive environmental events as either threats or opportunities to survive long enough to transmit their DNA to the next generation. In a world containing more threats than opportunities, animals have developed a number of physiological and behavioral responses to environmental threats; which pattern of responses gets deployed seems to depend upon the ratio of the animals' perception of control to its perception of threat (pC/pT) in its environment. When this ratio becomes less than one, the brain activates the central threat response system (CTRS), which directs variable combinations of its downstream effector systems to mount an appropriate response to the threat. Acute activation of the CTRS can restore the animal's homeostasis, albeit sometimes requiring a change in activities of the threat response systems ('allostasis'; McEwen and Wingfield, 2003) Chronic activation of the system, however, can negatively affect both health and welfare ('allostatic overload'; McEwen, 2017a).

4.2 Mental and Physical Health

4.2.1 Definitions

We first define health to address the relationship between mental and physical health. In 1948, in the wake of WWII, the World Health Organization stated as the first principle of its constitution that, 'Health is a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity' (World Health Organization, 1948). Although the definition was applied to humans, and has been critiqued by others (Witt *et al.*, 2017), it seems to be a reasonable starting place for a definition of mental and physical heath for mammals in general.

Broom (2006, p.75) observed that views on the concept of health differ among food animal producers, ethologists, and some veterinarians. He observed that, '...for most people, health refers to the state of the body and brain in relation to the effects of pathogens, parasites, tissue damage or physiological disorder', that is, physical pathology. Studies of confined animals however – in zoos, production facilities, and people's homes – have found that the quality of the environment also can affect animals' mental and physical health.

Defining the concept of 'mental health' is particularly tricky, since mental processes appear to be an emergent property of brains that cannot (yet) be measured directly, but rather might be inferred from the behavior of animals, or potentially from evaluation of pertinent biomarkers (see Section 4.4). Just as organ functions are emergent properties of their cell biology, we perceive mental processes to be generated from and

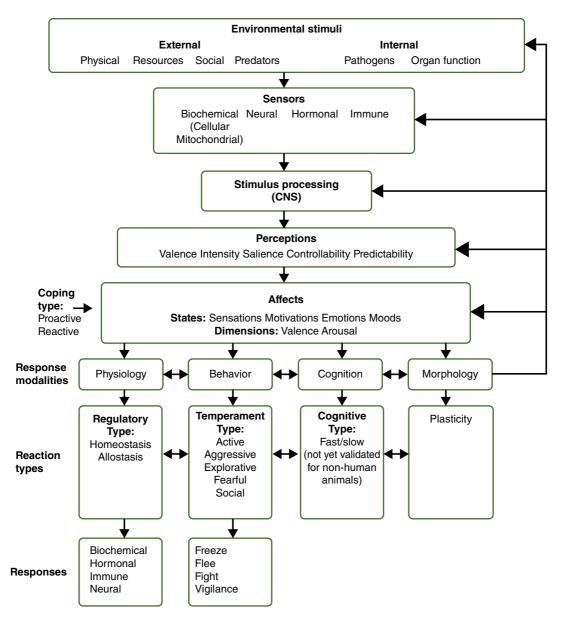


Fig. 4.1. A simplified representation of environmental stimuli processing by animals. External and internal stimuli activate variable combinations of sensors, which transduce the stimuli into signals interpretable by the central nervous system (CNS). The CNS creates prediction perceptions based on input, which are then compared with subsequent input to determine responses and their associated affects. Responses vary based on the nature of the stimuli and the animal's reaction types. (Adapted and redrawn from Colditz and Hine [2016], used with permission.)

dependent upon neural activity (Anderson, 1998), but nonetheless separate from it (Voneida, 1998). From this perspective, mental health implies brain health, so health results from variable contributions of genetic, epigenetic, and environmental

interactions on animals. The challenge for writers of chapters that span these domains is daunting; to paraphrase Kozak and Cuthbert (2016, p.292), 'Behavioral science studies what the brain does; genetics, cell and molecular biology, endocrinology

neuroscience, immunology and physiology study how the brain does it'.

Behaviors often associated with poor mental health include defensive aggression, withdrawal, hiding, and sickness behaviors, whereas those often associated with good mental health include play, exploration, and the like; the specifics of which may depend on the animal's species and environmental context. Although behaviors may appear maladaptive when they develop secondary to a physical condition, one must be careful to avoid thinking of all behaviors associated with poor health or welfare as inappropriate, maladaptive, or malfunctional. For example, piloerection and lack of grooming are adaptive sickness behaviors that contribute to greater well-being by increasing insulating ability and water conservation, and decreasing heat loss and energy expenditure. And the increase in metabolic energy expenditure during a febrile episode can be made up later, after the inappetence due to lack of desire to hunt or forage for food that occurs during this episode has subsided, which may have served to protect the animal from predation (Hart, 2010, 2011).

The word 'stress' means different things to different people (Del Giudice et al., 2018). In the context of mental and physical health, we define stress to mean effects of the (internal and external) environment on the organism. The eminent neuroendocrinologist and stress scientist Bruce McEwen (2017b) describes three categories of CTRS responses: good, tolerable, and toxic. Good CTRS responses, defined as brief and mild-to-moderate in magnitude, occur when an individual's pC/pT permits it to perceive opportunities, take risks, rise to challenges, and feel rewarded by (often) positive outcomes. These responses are part of normal development and help develop threat coping skills when they occur in the safe, predictable environments with stable and supportive relationships. Examples of events resulting in positive responses in young companion animals include non-threatening visits to the veterinarian and exposure to novel situations and foods. These responses will be discussed further in the discussion on resilience (see Section 4.3).

Tolerable CTRS responses occur with exposure to experiences that present greater threats, such as boredom or environmental instability (as may be seen, for example, by pet animals in a disruptive or chaotic household), serious illness or injury, or exposure to a natural disaster. As with positive responses, when these events occur in an otherwise

safe environment, recovery to normal is likely. Thus, the essential characteristic that makes this level of threat intensity tolerable is the extent to which protective surroundings permit adaptive coping and a sense of control.

In the most threatening environments, where the animal's perception of threat exceeds its perception of control, a toxic CTRS response can result (McEwen, 2017a). Toxic CTRS responses, especially when frequent or sustained, are the most dangerous to the animal's long-term health and welfare. Examples of early life threats that can result in toxic CTRS responses include severe nutritional deprivation (Bouret *et al.*, 2015), separation (Lippmann *et al.*, 2007), or life-threatening maternal or personal threats. When sustained, it is this level of perception of threat that is most damaging to mental and physical health (National Scientific Council on the Developing Child, 2005/2014).

And what of well-being? The National Institute of Food and Agriculture states that 'animal well-being is a complex topic' (Anonymous, 2016). In addition to optimizing their list of, '...environmental conditions, such as temperature, humidity, duration of daylight, bedding, size and shape of living quarters, or the number of other animals sharing an environment', we add the ability to engage in species-typical behaviors and to maintain a positive pC/pT.

Understanding the relationships between mental and physical health also requires consideration across levels of analysis. For animals, these include the interactions of the macro and micro environments with the individual's genetic, epigenetic, molecular, cellular, circuit, physiological, and behavioral domains. These relationships are depicted in Fig. 4.1.

4.2.2 Genetic influences

Genes obviously play a role in animals' mental and physical health. The publication of many mammalian genomes during the past two decades has led to the hope that genetic causes for many chronic diseases would be identified, permitting more personalized disease treatment and prevention strategies. Unfortunately, most genome-wide-association studies in humans have failed to find large genetic effects (Rappaport, 2018). Genetic relationships between health and disease are complex and appear to result from relatively small effects contributed by many genes.

Although we cannot yet directly treat gene-related health problems, they need to be understood. For example, diseases such as syringomyelia in Cavalier King Charles spaniels may present as a primary behavior problem of 'compulsive circling'. Other genetic influences, such as the propensity for hip dysplasia, may directly affect animals' quality of life. Painful conditions, and potentially the effects that exercise restriction exert, also can negatively affect an animal's welfare. Moreover, some breeds are predisposed to display specific abnormal behaviors, such as the propensity for doberman pinschers to display the repetitive behavior of self-sucking. There is evidence for a genetic linkage to these behaviors, whether due primarily to behavioral predispositions or to a malformation of the brain (Dodman *et al.*, 2010; Ogata *et al.*, 2013).

In addition to genetic influences on the physical health of animals, genes also can directly affect behavior. For example, animals bred to particular conformational standards, such as corkscrew tails in English bulldogs or polledness in Hereford cattle, may have difficulties communicating with a conspecific. If their signaling is misinterpreted by other animals, it could result in displays of aggression, some of which could directly affect their welfare, or the welfare of others in their groups.

In addition to the individuals' genetics (G), their mental and physical health is influenced by the environmental (E) influences they are exposed to during life (the 'exposome'; Wild, 2005) plus their gene-environment (G-E) interactions. Rappaport (2016) recently used published data from Western European monozygotic twins to estimate the proportion of disease risk attributable to G (plus shared E) for 28 chronic diseases by calculating 'population attributable fractions' (PAFs). He reported that genetic PAFs ranged from 3.4% for leukemia to 48.6% for asthma, with a median value of 18.5% and interquartile range of 9.9% to 24.2%. Cancers had the lowest PAFs (median = 8.3%), whereas neurological (median = 26.1%) and lung (median = 33.6%) diseases had the highest PAFs. The effects of G and shared E exposures on development of the chronic diseases studied tended to be modest, with 75% of the phenotypes having PAFs less than 25%. Only two G-related PAFs were greater than 40%: thyroid autoimmunity (42%) and asthma (49%).

McEwen (2017a) has also recently reviewed evidence showing that different alleles of commonly occurring genes within the CTRS influence how individuals will respond to environmental experiences. Moreover, while these alleles may exacerbate the negative effects of threatening environments on

mental health outcomes and thus be labeled 'bad genes', 'reactive' or 'context-sensitive' may be better descriptors because in positive, nurturing environments these same alleles may lead to successful outcomes, particularly during development (Boyce, 2016).

4.2.3 Early life and epigenetic influences

A momentous recent advance in our understanding of the origins of mental and physical health occurred with the documentation of the developmental origins of health and disease (DOHaD; Hanson and Gluckman, 2015). Although the effects of early life events on health and disease had long been surmised, recent developments can be traced to David Barker's 1990 hypothesis of the fetal and infant origins of adult disease (Barker, 1990). Since then, examples of the effects of early life events on health, disease, and productivity have been reported in cats (Buffington, 2009), livestock (Reynolds *et al.*, 2010; Gotoh, 2015) rodents (Anacker *et al.*, 2014), and humans beings (Anda *et al.*, 2006).

Evidence from clinical, epidemiological, and experimental observations has shown how evolutionarily conserved developmental processes can interact with environmental cues, often transmitted from the mother via the placenta to the offspring, to attempt to match the physiology of the fetus to its postnatal environment. The sequence of events that has emerged from this research proposes that when a pregnant female is exposed to a sufficiently harsh and salient threat, the neuroendocrine products resulting from activation of her CTRS can cross the placenta and affect the course of fetal development (Meaney *et al.*, 2007; Cottrell *et al.*, 2014).

The biological purpose of transmitting environmental cues to the fetus may be to guide the development of the fetal CTRS and associated behaviors to increase the probability of survival (Matthews, 2002; Gluckman and Hanson, 2006a). As Gluckman and Hanson (2005) described, the fetus may use cues from its intra-uterine environment to make predictive adaptive response 'decisions'. In a practical sense, if a threatening or nutrient-limiting environment is perceived, the developmental trajectory of the fetus may change in response to the available information to enhance reproductive fitness in the predicted environment. Sensitizing the CTRS may be part of a more general 'survival phenotype' that includes smaller (or larger) size at birth (Parlee and MacDougald, 2014). Although the phenotype does not appear to affect reproductive capacity, it has been associated with a variety of adverse health outcomes.

Studies of the enduring effects of stressful developmental experiences on health have now been published in a wide variety of mammalian species, including rodents (Molet et al., 2014), carnivores (Buffington, 2011), food production animals (Reynolds et al., 2010; Merlot et al., 2013), and nonhuman (Meyer and Hamel, 2014) as well as human (Griffiths and Hunter, 2014) primates. Such problems can arise when the actual adult environment does not match the predicted one; studies have found that cardiovascular disease, type 2 diabetes, metabolic syndrome, respiratory, gastrointestinal, urinary tract, dental, and mood disorders all can result from a mismatch between the predicted and actual environment the animal inhabits (Gluckman and Hanson, 2006b; Godfrey, 2006). Cognitive function too is affected by both genetic (Matzel et al., 2006) and developmental (Chwang et al., 2006) influences.

Recent research suggests that one mechanism underlying the sensitization of the CTRS involves a process called epigenetic modulation of gene expression (Hunter and McEwen, 2013). Whereas genetics is the study of the genes one has, epigenetics is the study of the genes one expresses. Our interest in epigenetics developed from a serendipitous finding in cats with chronic lower urinary tract signs (called feline interstitial cystitis, FIC). During a study of the effects of a corticotrophin releasing factor antagonist on hypothalamic-pituitary-adrenal (HPA) axis function, we observed that cats with FIC we were studying had normal adrenocorticotrophic hormone release, but limited adrenocortical release of cortisol (Westropp et al., 2003). This study led to histological examination of these cats' adrenal glands. The glands appeared normal histologically, with no evidence of hemorrhage, inflammation, infection, fibrosis, or necrosis. Morphometric evaluation, however, identified reduced size of the fasciculata and reticularis zones of the adrenal cortex. Inappropriately low plasma cortisol concentrations also have been observed in human beings with chronic pelvic pain (Raison and Miller, 2003; Buffington, 2004). The most parsimonious explanation found to date for these findings in the absence of a genetic disorder is a developmental event that results in perception of threat in a pregnant animal that was sufficiently intense that it 'sensitized' the CTRS of the offspring (Griffiths and Hunter, 2014; Gatchel and Neblett, 2018).

Epigenetic modulation of gene expression was presciently described as the 'epicenter of modern medicine' 10 years ago (Feinberg, 2008). This general biological process results in such commonplace outcomes as sex- and organ-specific patterns of gene expression that lead to the final phenotype of the organism by silencing genes not appropriate to the particular tissue environment (Fig. 4.2). While the detailed molecular mechanisms of epigenetics are beyond the scope of this review, fuller explanations are available on the Internet (Farina, 2019; Wikipedia, 2019).

The effects of environmental threats to the mother on fetal development seem to depend both on the timing and magnitude of exposure to products of the maternal CTRS response in relation to the activity of the developmental 'programs' that determine the maturation of the various body systems during gestation and early postnatal development (Gluckman and Hanson, 2005). For example, the small adrenal cortices found in some cats with FIC suggested that the event occurred during adrenocortical maturation. If the developing fetus had been exposed before initiation of adrenocortical maturation, the effect may not have been observed, whereas if it had occurred after adrenocortical maturation, adrenal size and subsequent adrenocortical responses to the CTRS might have been increased (Matthews, 2002).

What influences the outcome of a fetus is not always directly related to what 'should' affect it. As an example, the negative effects of restricting a ewe's caloric intake during pregnancy on a fetus or offspring is frequently understood (Ford *et al.*, 2007). However, it has been demonstrated that *excess* energy intake also can have a negative influence on the offspring (Dong *et al.*, 2008). The overfeeding is also in relation to the balance of other nutrients, so it does not occur in a vacuum.

The effects of the behavior of the dam on her offspring have been demonstrated in dogs raised to be service dogs for the vision-impaired (Bray et al., 2017). By observing the behavior of the dams during their offspring's first 3 weeks of life, testing the individuals via cognitive and temperament tests, and following up with the success, or lack thereof, of the offspring, dogs raised by dams with high maternal behavior scores had a higher chance of displaying anxiety-related behaviors and were more likely to be released from the program. The thought behind these results is that, while understood that too much stress is deleterious, too little

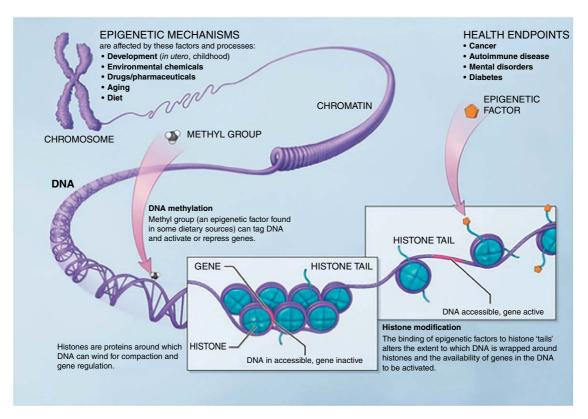


Fig. 4.2. Epigenetic mechanisms are affected by several factors and processes during development, including environmental threats, chemicals, drugs and pharmaceuticals, aging, and diet. DNA methylation and histone modification are two of a variety of identified epigenetic mechanisms. DNA methylation occurs when methyl groups bind to promoter regions of DNA to activate or repress gene expression. Histones are proteins around which DNA can wind for compaction and control of gene expression. Histone modification occurs when the binding of epigenetic factors to histone 'tails' alters the extent to which DNA is wrapped around histones and the availability of genes in the DNA to be activated. All of these factors and processes can have an effect on health and disease risk (National Institutes of Health, 2019).

stress, as evidenced by higher maternal care, can deny the offspring the opportunity to learn how to effectively deal with stress.

Two recent reviews have expanded our understanding of early life experiences in dogs. In 2017, McMillan (2017) reviewed seven published studies and one anecdotal report of behavioral and psychological outcomes of dogs exposed to commercial breeding establishments as neonates. These studies revealed an increased incidence of behavioral and emotional problems that caused distress during adulthood compared with dogs from other sources, especially noncommercial breeders. The most consistent finding was an increase in aggression toward the dog's owners and family members, unfamiliar people, and other dogs. Increased fear

toward unfamiliar people, children, other dogs, nonsocial stimuli, and when taken on walks also was identified, as well as undesirable behaviors related to separation and/or attention seeking, and a heightened sensitivity to touch. All published studies suggested that exposure to major stressors during puppy development from the prenatal stage through adolescence was associated with the development of many behavioral (mental health) problems. Another review (Dietz *et al.*, 2018) found similar results, concluding that,

Early life experiences, such as maternal care, attachment and socialization, have long lasting and serious consequences for the behavioral and physiological development of an individual. The complex interplay between these factors is likely to have consequences

for the future dog-owner bond and the vulnerability to develop behavioral disorders.

Opposite results have also been revealed. Longer daily duration of maternal care during the first 3 weeks of life was associated with more exploratory behavior and less signs of stress (Guardini *et al.*, 2016). In another study, pups that were separated from their dam at approximately 1 month of age, compared to those separated at 2 months of age, were more likely to display problem behaviors related to anxiety, such as noise reactivity and fearfulness on walks (Pierantoni *et al.*, 2011).

Sensitization is not restricted to early life, of course (Tsankova *et al.*, 2006), but is more likely to occur during the time of growth and maturation of the neural, endocrine, and immune systems (Godfrey *et al.*, 2010). Sometimes the 'susceptible individual' is revealed only by another adverse experience later in life, possibly by additional rounds of epigenetic modulation of gene expression (Daskalakis *et al.*, 2013; Koss and Gunnar, 2018). Subsequent rounds of changes in gene expression may be quite stable and resistant to current medical interventions. Thus, confining 'sensitive' individuals in 'provocative' environments can have particularly strong implications for their mental and physical health (Buffington *et al.*, 2014).

The effects of adverse events, particularly during the vulnerable period of early life, on the long-term mental and physical health of animals demonstrate the importance of identification of risk factors and provision of effective education of owners of companion animals by primary care veterinarians about appropriate environments for confined animals across the lifespan. From this perspective, initial vaccination appointments become anything but 'routine', and may in fact be the most important appointments of the pet animal's life. This is because such visits present opportunities to teach husbandry appropriate for the animal based on the environment it is confined to at a time when owners are likely to be most motivated and responsive to recommendations.

Shonkoff (2010) described three foundational domains to promote long-term health and welfare that can be adapted to preventive veterinary medical care. These include:

1. A stable and responsive environment which provides consistent, nurturing, and protective interactions that enhance learning and support development of adaptive capacities that promote a well-regulated CTRS.

- 2. A safe and supportive physical, chemical, and built environment that is free from toxins and other threats, allows active exploration without significant risk of harm, and offers support for families raising the animal.
- 3. Satisfactory nutrition for the animal's age, including feeding management practices that maintain an appropriate body condition, beginning with the future mother prior to conception if possible. (See also Chapter 10.)

Consideration of DOHaD also has important therapeutic implications. For example, drugs to modulate gene expression are under active investigation in oncology (Bai *et al.*, 2018) and psychiatry (Mahgoub and Monteggia, 2013; Robinson, 2018) that may become available in veterinary medicine. Given that these drugs also may modulate expression of other genes in potentially unpredictable ways, the availability of a naturally occurring animal model of diseases likely influenced by these mechanisms offers the opportunity to 'field-test' these compounds before they are introduced for use in human beings (Buffington, 2009).

Environments also are known to epigenetically modulate gene expression through 'endogenous pharmacology' (Sale *et al.*, 2014; Eisinger and Zhao, 2018; Tai *et al.*, 2018), which may explain the value of behavior-based approaches to treatment in humans (Kohrt *et al.*, 2015), and effective environmental enrichment in animals (Francis *et al.*, 2002).

In summary, the changing view of medicine from one of an isolated organ-originating disease in otherwise healthy adults to one of an underlying DOHaD perspective has important implications. First, it provides a more parsimonious explanation for many findings that previously were quite difficult to account for, including the unfortunate lack of beneficial effect of therapies directed at the peripheral organ of interest by a particular medical subspecialty. It also helps explain the presence of multiple comorbid disorders in many patients with chronic disorders but not in patients with other individual organ diseases, the unpredictable order of appearance of the comorbidities, and the altered functioning of the CTRS. More importantly, it opens new approaches to therapy that may escape consideration from the individual medical specialty perspective. The available data only suggest this perspective, however, and permit generation of testable hypotheses. One might imagine a number of additional complementary or alternative 'systemic'

hypotheses related to variable combinations of genetic, epigenetic, and environmental influences; these remain to be explored.

4.2.4 Environmental influences

The impact of environment on clinical signs was dramatically demonstrated during research into the use of cats with FIC as a model for a chronic pelvic pain syndrome in humans called interstitial cystitis (Buffington, 2004). Two important initial observations were: (i) many of the cats had a variety of comorbid disorders, which had often preceded the onset of the lower urinary tract signs; and (ii) all of the signs essentially resolved within 6 months of housing in the environmentally enriched vivarium.

After observing the rather remarkable recovery of the cats donated to the investigator's research colony, Dr. Judi Stella discovered that a variety of 'sickness behaviors' occurred in some of the cats, both those with FIC and healthy controls, after exposure to 'unusual external events' (Stella et al., 2011). Sickness behaviors are variable combinations of nonspecific clinical and behavioral signs that include diarrhea, vomiting, fever, lethargy, somnolence, and decreased general activity, body-care activities (grooming), social interactions, and food and water intake (Dantzer et al., 2008). Sickness behaviors are thought to reflect a change in motivation of the organism to one that promotes recovery by inhibiting metabolically expensive activities (e.g., foraging, reproducing) and favoring those that contribute to recovery (e.g., reduced activity, hiding). These behaviors are well-documented physiologic and behavioral responses to injury and infection found in all animal species studied (Hart, 1985, 1988).

Sickness behaviors also can occur in response to aversive environmental events (Marques-Deak *et al.*, 2005; Reed and Raison, 2016), through CTRS-mediated activation of inflammatory pathways in peripheral blood mononuclear cells (Bierhaus *et al.*, 2003; Bierhaus, 2006). Bierhaus *et al.* (2003) found that subjecting human volunteers to a laboratory stress test resulted in rapid increases in circulating concentrations of catecholamines, cortisol, and the transcription factor nuclear factor kappa beta (NF-κB). In follow-up studies in mice, they found that the increase in NF-κB response could be reduced in the presence of the α1-adrenergic inhibitor prazosin. Finally, they demonstrated in cultured cells that only norepinephrine induced NF-κB and

NF- κ B-dependent gene expression, which was reduced by both α 1- and β -adrenergic inhibitors.

Stimulation of NF-κB-dependent gene expression by perceived threat thus results in increases in circulating concentrations of pro-inflammatory cytokines just as infection and injury do. Miller and Raison (2016) recently speculated that the behavioral responses, such as avoidance and alarm, that are likely to have provided early mammals with an evolutionary advantage in their interactions with pathogens and predators may have become adapted to perceived psychosocial threats as well. They proposed that early evolutionary pressures from interactions with pathogens, predators, and conspecifics resulted in an inflammatory bias that included an integrated suite of immunological and behavioral responses that conserved energy for fighting infection and healing wounds while maintaining vigilance against attack. They believe that this inflammatory bias was held in check during much of evolution by exposure to minimally pathogenic, tolerogenic organisms in ancient environments that engendered immunological responses characterized by the induction of regulatory T and B cells, immunoregulatory macrophages, and production of anti-inflammatory cytokines (Raison and Miller, 2013).

In cats with FIC, for example, Stella et al. (2011) recorded sickness behaviors referable to the gastrointestinal and urinary tracts, the skin, and behavior problems for 77 weeks. 'Unusual external events', e.g., changes in caretakers, vivarium routine, and lack of interaction with the investigator were identified during 11 of the 77 weeks. No instances were identified during the remaining 66 weeks, which were considered control weeks. They found that exposure to these events (especially of older cats), but not disease status, significantly increased total number of sickness behaviors when results were controlled for other factors. Older cats in both groups were at a slightly greater relative risk for upper gastrointestinal tract signs (1.2-fold, P < 0.001) and avoidance behavior (1.7-fold, P = 0.001). Exposure to unusual environmental events also significantly increased the relative risk for decreased food intake (9.3-fold, P < 0.001), for no eliminations in 24 hours (6.4-fold, P < 0.001), and for defecation (9.8-fold, P < 0.001) and urination (1.6-fold, P = 0.005) outside the litter box. Thus, some of the most commonly observed abnormalities in client-owned cats, including upper gastrointestinal signs, house-soiling, and inappetence, were observed after exposure to unusual environmental events in both healthy cats and cats with FIC.

In addition to inflammation, environmental threats can also induce oxidative stress through activation of the CTRS. Recent studies have provided evidence that mitochondria, subcellular organelles that engage both in ATP production and intracellular signaling, can be both targets of the CTRS as well as mediators of threat pathophysiology (Picard and McEwen, 2018a,b). Mitochondria can respond to a variety of the products of the CTRS, including norepinephrine (Zhang *et al.*, 2017), glucocorticoids, estrogen, angiotensin, and cannabinoids (Picard and McEwen, 2018a). In response, mitochondrial energy production is reduced, production of reactive oxygen species and cytokines increases, and gene expression in the nucleus is affected through epigenetic modulation.

A recent study provided an example of the effects of CTRS-induced autonomic dysregulation of mitochondrial function in the rat urothelium (Kullmann et al., 2018). In this study, adult female Wistar Kyoto rats were exposed to 10 days of water avoidance stress, after which bladders were harvested for Western blot and single cell imaging in culture. Mitochondria in urothelial cells from stressed rats were ~30% more depolarized compared to those from control rats. In addition, expression of the fusion protein mitofusion-2 was upregulated, suggesting mitochondrial structural changes consistent with altered cellular metabolism, and intracellular calcium concentrations were increased, consistent with impaired cellular function. Stimulating the cultured urothelial cells with α -adrenergic receptor agonists increased reactive oxidative species production, suggesting a direct catecholamine action on the cells; adrenergic receptor antagonists prevented most of stress-induced changes.

4.3 Resilience

Resilience, the animal's ability to resist the deleterious effects of exposure to chronic threats, is a particularly impactful factor for mental health (Russo et al., 2012; Colditz and Hine, 2016). In fact, based on research in humans (where the concept has been most commonly studied), resilience is the rule rather than the exception. More than two-thirds of the general population experiences a significant traumatic event at some time in their lives, and as many as 20% of United States residents may experience one in any given year (Galea et al., 2005). Despite this high frequency of exposure, the prevalence of pathology resulting from the experience in the general population has been estimated to be

only 5–10%, depending on the type, intensity, and duration of the exposure (Norris *et al.*, 2002; see also Chapter 14).

The mechanisms underlying resilience remain incompletely known, but likely involve variable combinations of passive (genetic) and active (environmental) CTRS-associated differences that confer increased resistance to the pathological effects of exposure to chronic threat (Russo et al., 2012). Studies in humans and rodents have found some differences in genes underlying CTRS responsiveness, although the associations are relatively weak. In contrast, it has long been known (Levine, 1962) that neonatal rats exposed to intermittent foot shocks subsequently respond more effectively when confronted with novel situations compared to their nonstressed counterparts, a phenomenon known as 'stress inoculation'. A body of research developed since this seminal study has found that exposure to moderate degrees of threat during early life, adolescence, and adulthood can reduce vulnerability to threat and broaden the range of tolerable threat for animals (Bock et al., 2014; Guardini et al., 2016; McEwen, 2017a; see also Chapter 14).

Epigenetic modulation of gene expression related to early life experiences also appears to play a role in this 'inoculation'. For example, recent studies (Roth, 2013; Köhler et al., 2018) have reported that epigenetic changes in dopamine function in the hippocampus might modulate the outcome of adverse early life exposure. In Köhler et al.'s study, mouse pups were separated from their mothers for 3 hours from either 14-16 days of age (short-term) or from 1-21 days (long-term), after which they subjected the mice to a forced swim test (threat). They found that short- and long-term separation of the pups from their mothers resulted in changes in dopaminergic molecular pathways, some of which were epigenetically regulated and which either increased (long-term) or decreased (long-term) depressive-like behaviors later in life. Future studies will likely reveal even greater complexity as more circuits and mechanisms are uncovered.

Neural effects of early intermittent separation also include increases in cortical volume and synaptic function, decreased glutamatergic tone in the nucleus accumbens, and normalization of neuronal excitability in resilient animals. Strategies like environmental enrichment can confer resilience by normalizing HPA-axis function (Russo *et al.*, 2012). Resilience also can affect immune function, and vice versa (Dantzer *et al.*, 2018). Interested readers are referred to the cited references for more detail.

4.4 Evaluating Mental and Physical Health

The state of activation of the CTRS can be evaluated by assessing physiological (Table 4.1) and behavioral (Table 4.2) parameters. Animals differ in their responses to threat, and not all animals display all possible signs of threat. Moreover, both increased (e.g., defensive aggression) and decreased (e.g., freezing) activity can be associated with activation of the CTRS. Thus, a thorough assessment of all parameters is most likely to provide the best estimator of CTRS activity in any given animal in any particular context.

4.5 Biomarkers

Some of the chemical mediators of the CTRS have been used as 'allostatic load indices' or diagnostic biomarkers of toxic stress responses (Seeman *et al.*, 1997; Hellhammer *et al.*, 2012, 2018). Molecular biomarkers are substances whose concentrations or amounts correlate with some pathological process (Ghezzi *et al.*, 2018). They are used as diagnostic or

Table 4.1. Physiological parameters that may indicate the state of the central threat response system in animals.

Parameter	Normal	Threatened
Temperature Heart rate Blood pressure Respiratory rate Pupil diameter	No change	May be increased
'Sweaty' paws Excessive shedding Flushing Apprehensive lip licking	Absent	May be present

prognostic indicators and to monitor the progression of pathological processes. Some common examples of biomarkers used to monitor chronic threat are presented in Table 4.3 (Edes and Crews, 2017), although many more genetic, epigenetic, neuroendocrine, metabolic, cardiovascular, immune, pulmonary, and excretory molecules have been investigated among different pathological processes and species.

To date no single biomarker or allostatic load index has been found to unambiguously identify the presence of chronic threats, for a variety of reasons. As one example, different threats – physical (e.g., cold, heat), physiological (e.g., injury, infection, inflammation), and social/emotional (e.g., competition for food, mates, or other precious resources) – result in variable outputs of the CTRS (Pacak and Palkovits, 2001). And for any given threat, responses also vary with context (Proudfoot *et al.*, 2012) and among different individuals (Koolhaas, 2008).

In addition to variation across threat, context, and individuals, the relationship of the biomarker to the process of interest also can vary. For example, the biomarker may be related to the etiology of the disorder or the body's response to it, and may or may not have pathophysiological implications beyond the process that generated it (e.g., inflammation, oxidation). Moreover, the response may not be linearly related to the pathophysiological process. Common examples of this are cortisol (Raison and Miller, 2003), serotonin (Andrews *et al.*, 2015), and brain-derived neurotrophic factor (BDNF; Logan and McClung, 2016), whose concentrations appear to depend upon variable combinations of the disorder, the stage of progression, and the tissue sampled.

Chemical biomarkers also have been used to investigate the effects of environmental enrichment on mental health (Sale *et al.*, 2014; Eisinger and

Table 4.2. Behavioral parameters that may indicate the state of the central threat response system in animals.

Parameter	Normal	Threatened
Behavioral	Affiliative behaviors – purring, rubbing, etc.	Attempts to flee
	Appetitive lip licking	Apprehensive lip licking
	Interest in eating and drinking	Decreased or absent eating or drinking
	Normal eliminations	Decreased or absent eliminations for longer than 48 hours
	Approach behaviors	Defensive aggression (hissing, growling, spitting, tail twitching, ear flicking, scratching, biting)
	Relaxed postures	Trembling
	Slow eye blinks	Freezing, hiding, or other fearful postures Averting gaze or other displacement behaviors
Sickness behaviors	Absent	Present

Zhao, 2018). Some examples are presented in Table 4.4. Reported effects associated with changes in these biomarkers include enhanced brain plasticity, which leads to faster brain development and repair, improved aging, and brain health (Sale *et al.*, 2014). The same caveats suggested for allostatic load indicators also apply to these chemicals.

4.6 Improving Mental and Physical Health in Animals

Animals need environments that are compatible with their physical and behavioral needs to enjoy mental and physical health. We define environmental enrichment (EE) as provision of resources that effectively improve the animals mental and physical

health. Provision of effective EE is built on the foundation of the Five Freedoms of Animal Welfare (Anonymous, 1993), which include freedom from: (i) hunger and thirst; (ii) discomfort; (iii) pain, injury, and disease; and (iv) fear and distress; and freedom to (v) express normal, species-typical behaviors. These have now been extended (Mellor and Beausoleil, 2015) and updated (Mellor, 2016). Not only must we think about the effects of the physical environment on an animal's behavior, but there is evidence of the effects of human behavior, and even chemosignals on dog behavior (D'Aniello *et al.*, 2018; Jamieson *et al.*, 2018).

For confined animals (at least) these environmental needs include the availability of knowledgeable caretakers, safe resting, eating, and toileting places,

Table 4.3. Examples of biomarkers used to investigate pathophysiological responses to chronic threat.

System	Biomarker	Indicator of
Neuroendocrine	Glucocorticoids	HPA activity
	Epinephrine, norepinephrine	SNS, SAM activity
Metabolic	Glucose	Rapid energy release
	Insulin	Insulin resistance
	Reactive oxygen species	Mitochondrial function
Cardiovascular	Heart rate	Cardiovascular activity
	Heart rate variability	SNS/PSNS balance
	Blood pressure	Cardiovascular activity/peripheral resistance
Immune	C-reactive factor	Inflammation (nonspecific)
	Erythrocyte sedimentation rate	Inflammation (nonspecific)
	Interleukin 6 (IL-6)	Inflammation (cytokine)
	Tumor necrosis factor-α	Inflammatory (cytokine)

HPA, hypothalamic-pituitary-adrenal; SNS, sympathetic nervous system; SAM, sympathetic-adrenal-medullary; PSNS, parasympathetic nervous system.

Table 4.4. Examples of biomarkers used to investigate physiological responses to environmental enrichment (Sale *et al.*, 2014; Eisinger and Zhao, 2018).

System	Biomarker	Change with EE
Outstands for the st	Insulin-like growth factor 1	Increase
Growth factor	Brain-derived neurotrophic factor	Increase (depending on source)
Transcription factor	Cyclic AMP response element-binding protein	Increase
Process	Histone acetylation	Increase
	DNA methylation	Decrease
Synaptic receptors	N-methyl-p-aspartate	Increase
Neural adhesion	Neural cell adhesion molecule	Increase
Neurotransmitter	Serotonin	Increase
Protein	β-amyloid	Decrease
Hormone	Adiponectin	Increase
Myokine	Cathepsin B	Increase
Chemokine	Fractalkine	Increase
Mitochondria	Reactive oxygen species	Decrease

EE, environmental enrichment.

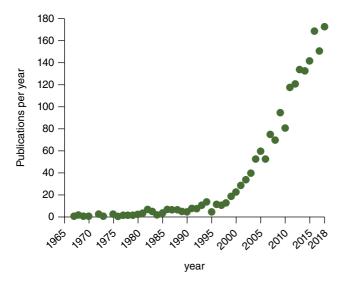


Figure 4.3. National Library of Medicine (NLM) publications of 'environmental enrichment' on PubMed (Sperr, 2016). A total of 1,930 papers on the topic were published from 1967 through 2018 (National Library of Medicine, 2019).

choice of food and water, control of interactions with others, and enough novelty to provide mental stimulation (Veasey, 2017). Environmental enrichment is a relatively new concept, but is based on the ancient art of animal husbandry. As shown in Fig. 4.3, a total of 1,930 papers on EE were published from 1967 through 2018, the majority after 2000. Effective EE to address the needs of an animal has been found to decrease sickness behaviors in confined domestic cats (Stella *et al.*, 2011), to improve mental and physical health in a variety of species, and to normalize behavioral and physiological parameters associated with the CTRS (Sale *et al.*, 2014; Mármol *et al.*, 2015, 2017; Eisinger and Zhao, 2018; Montes *et al.*, 2018; Sadek *et al.*, 2018).

4.7 Concluding Remarks

It is an apropos time to evaluate interrelationships between mental and physical health in animals, especially as these relationships are being re-evaluated in the human literature, and to see the research that is being done in nonhuman animals. Environmental events have a strong effect on animals in ways that we are still trying to understand. Moreover, recent research has found both negative (threatening) and positive (enriching) environmental influences on a variety of processes affecting mental and physical health, including inflammation and mitochondrial (dys)function.

A rapidly expanding body of literature has now given us a much greater understanding of the

interactions between the environment, emotional states, and mental and physical health. The most evident direct and immediate application of this knowledge is in the field of veterinary medicine, where veterinarians can provide the best medical care only by including mental health in their patient evaluations and treatments. As one example, research has shown how the most important factor in the development and recurrence of chronic lower urinary tract signs in domestic cats appears to be a mental factor (i.e., persistent activation of the CTRS in response to perception of environmental threat), and that an environmental rather than a physical health approach has been found to be the most effective way to treat this condition (Carney et al., 2014). We also now know that animals, like people, may eat to 'self-medicate' in anxiogenic environments (McMillan, 2013), which can lead to obesity.

Knowing this, and the fact that virtually every aspect of health and disease is influenced by mental factors, suggests that veterinarians may unknowingly encounter many other conditions influenced by the mental health of the patient (Buffington, 2018). Moreover, the latest scientific studies show that while negative emotions such as anxiety, fear, anger, and loneliness can have extensive adverse effects on animal health, positive environments, which provide appropriate amounts of safety, predictability, novelty, and social interaction, can have impressively beneficial effects on both the mental and physical health of the animals in our care.

4.8 References

- Anacker, C., O'Donnell, K.J., Meaney, M.J. (2014) Early life adversity and the epigenetic programming of hypothalamic-pituitary-adrenal function. *Dialogues in Clinical Neuroscience* 16, 321–333. http://hdl.handle. net/11212/2397.
- Anda, R.F., Felitti, V.J., Bremner, J.D., Walker, J.D., Whitfield, C., et al. (2006) The enduring effects of abuse and related adverse experiences in childhood A convergence of evidence from neurobiology and epidemiology. European Archives of Psychiatry and Clinical Neuroscience 256, 174–186. https://doi.org/10.1007/s00406-005-0624-4.
- Anderson, N.B. (1998) Levels of analysis in health science: A framework for integrating sociobehavioral and biomedical research. *Annals of the New York Academy of Sciences* 840, 563–576. https://doi.org/10.1111/j.1749-6632.1998.tb09595.x.
- Andrews, P.W., Bharwani, A., Lee, K.R., Fox, M., Thomson Jr, J.A. (2015) Is serotonin an upper or a downer? The evolution of the serotonergic system and its role in depression and the antidepressant response. *Neuroscience and Biobehavioral Reviews* 51, 164–188. https://doi.org/10.1016/j.neubiorev.2015.01.018.
- Anonymous. (1993) Second report on priorities for research and development in farm animal welfare. Farm Animal Welfare Council (FAWC), Department of Environment, Food and Rural Affairs, London, UK.
- Anonymous. (2016) Washington, DC: National Institute of Food and Agriculture. Animal well-being. Available at: https://nifa.usda.gov/program/animal-well-being (accessed 15 January 2019).
- Bai, Z.T., Bai, B., Zhu,J., Di, C.X., Li, X., et al. (2018) Epigenetic actions of environmental factors and promising drugs for cancer therapy. Oncology Letters 15, 2049–2056. https://doi.org/10.3892/ol.2017.7597.
- Barker, D.J. (1990) The fetal and infant origins of adult disease. *British Medical Journal* 301, 1111. https://doi. org/10.1136/bmj.301.6761.1111.
- Bierhaus, A. (2006) Linking stress to inflammation. Anesthesiology Clinics of North America 24, 325–340. https://doi.org/10.1016/j.atc.2006.01.001.
- Bierhaus, A., Wolf, J., Andrassy, M., Rohleder, N., Humpert, P. M., et al. (2003) A mechanism converting psychosocial stress into mononuclear cell activation. Proceedings of the National Academy of Sciences of the United States of America 100, 1920–1925. https://doi.org/10.1073/pnas.0438019100.
- Bock, J., Rether, K., Gröger, N., Xie, L., Braun, K. (2014) Perinatal programming of emotional brain circuits: An integrative view from systems to molecules. *Frontiers* in Neuroscience 8, 1–16. https://doi.org/10.3389/ fnins.2014.00011.
- Bouret, S., Levin, B.E., Ozanne, S.E. (2015) Geneenvironment interactions controlling energy and glucose homeostasis and the developmental origins of

- obesity. *Physiological Reviews* 95, 47–82. https://doi.org/10.1152/physrev.00007.2014.
- Boyce, W.T. (2016) Differential susceptibility of the developing brain to contextual adversity and stress. *Neuropsychopharmacology* 41, 142–162. https://doi.org/10.1038/npp.2015.294.
- Bray, E.E., Sammel, M.D., Cheney, D.L., Serpell, J.A., Seyfarth, R.M. (2017) Effects of maternal investment, temperament, and cognition on guide dog success. Proceedings of the National Academy of Sciences of the United States of America 114, 9128–9133. https:// doi.org/10.1073
- Broom, D.M. (2006) Behaviour and welfare in relation to pathology. *Applied Animal Behaviour Science* 97, 73–83.https://doi.org/10.1016/j.applanim.2005.11.019.
- Buffington, C.A.T. (2004) Comorbidity of interstitial cystitis with other unexplained clinical conditions. *Journal of Urology* 172, 1242–1248. https://doi.org/10.1097/01.ju.0000137953.49304.6c.
- Buffington, C.A. (2009) Developmental influences on medically unexplained symptoms. *Psychotherapy and Psychosomatics* 78, 139–144. https://doi.org/10.1159/000206866.
- Buffington, C.A. (2011) Idiopathic cystitis in domestic cats-beyond the lower urinary tract. *Journal of Veterinary Internal Medicine* 25, 784–796. https://doi.org/10.1111/j.1939-1676.2011.0732.x.
- Buffington, C.A.T. (2018) Pandora Syndrome in cats: Diagnosis and treatment. *Today's Veterinary Practice* 8, 31–41.
- Buffington, C.A T., Westropp, J.L., Chew, D.J. (2014) From FUS to Pandora Syndrome: Where are we, how did we get here, and where to now? *Journal of Feline Medicine and Surgery* 16, 385–394.
- Carney, H.C., Sadek, T.P., Curtis, T.M., Halls, V., Heath, S., et al. (2014) AAFP and ISFM guidelines for diagnosing and solving house-soiling behavior in cats. *Journal of Feline Medicine and Surgery* 16, 579–598. https://doi.org/10.1177/1098612X14539092.
- Chwang, W.B., O'Riordan, K.J., Levenson, J.M., Sweatt, J.D. (2006) ERK/MAPK regulates hippocampal histone phosphorylation following contextual fear conditioning. *Learning & Memory* 13, 322–328. www.learnmem.org/ cgi/doi/10.1101/lm.152906.
- Colditz, I.G. and Hine, B.C. (2016) Resilience in farm animals: Biology, management, breeding and implications for animal welfare. *Animal Production Science* 56, 1961–1983. https://doi.org/10.1071/AN15297.
- Cottrell, E.C., Seckl, J.R., Holmes, M.C., Wyrwoll, C.S. (2014) Foetal and placental 11 beta-HSD2: A hub for developmental programming. *Acta Physiologica* 210, 288–295. https://doi.org/10.1111/apha.12187.
- D'Aniello, B., Semin, G.R., Alterisio, A., Aria, M., Scandurra, A. (2018) Interspecies transmission of emotional information via chemosignals: From humans to dogs (*Canis lupus familiaris*). *Animal Cognition* 21, 67–78. https://doi.org/10.1007/s10071-017-1139-x.

- Dantzer, R., O'Connor, J.C., Freund, G.G., Johnson, R.W., Kelley, K.W. (2008) From inflammation to sickness and depression: When the immune system subjugates the brain. *Nature Reviews Neuroscience* 9, 46–56. https://doi.org/10.1038/nrn2297.
- Dantzer, R., Cohen, S., Russo, S., Dinan, T. (2018) Resilience and immunity. *Brain, Behavior, and Immunity* 74, 28–42. https://doi.org/10.1016/j.bbi.2018.08.010.
- Daskalakis, N.P., Bagot, R.C., Parker, K.J., Vinkers, C.H., de Kloet, E.R. (2013) The three-hit concept of vulnerability and resilience: Toward understanding adaptation to early-life adversity outcome. *Psychoneuroendocrinology* 38, 1858–1873. https://doi.org/10.1016/j.psyneuen.2013.06.008.
- Del Giudice, M., Buck, C.L., Chaby, L.E., Gormally, B.M., Taff, C.C., et al. (2018) What is stress? A systems perspective. Integrative and Comparative Biology 58, 1019–1032. https://doi.org/10.1093/icb/icv114.
- Dietz, L., Arnold, A.-M.K., Goerlich-Jansson, V C., Vinke, C.M. (2018) The importance of early life experiences for the development of behavioural disorders in domestic dogs. *Behaviour* 155, 83–114. https://doi. org/10.1163/1568539X-00003486.
- Dodman, N.H., Karlsson, E.K., Moon-Fanelli, A., Galdzicka, M., Perloski, M., et al. (2010) A canine chromosome 7 locus confers compulsive disorder susceptibility. Molecular Psychiatry 15, 8. https://doi. org/10.1038/mp.2009.111.
- Dong, F., Ford, S.P., Nijland, M.J., Nathanielsz, P.W., Ren, J. (2008) Influence of maternal undernutrition and overfeeding on cardiac ciliary neurotrophic factor receptor and ventricular size in fetal sheep. *The Journal of Nutritional Biochemistry* 19, 409–414. https://doi.org/10.1016/j.jnutbio.2007.06.003.
- Edes, A.N. and Crews, D. (2017) Allostatic load and biological anthropology. American Journal of Physical Anthropology 162, 44–70. https://doi.org/10.1002/ajpa.23146.
- Eisinger, B.E. and Zhao, X. (2018) Identifying molecular mediators of environmentally enhanced neurogenesis. *Cell and Tissue Research* 371, 7–21. https://doi.org/10.1007/s00441-017-2718-5.
- Farina, D. (2019) Professor Dave explains regulation of gene expression: Operons, epigenetics, and transcription factors. Available at: https://www.youtube.com/ watch?v=J9jhg90A7Lw (accessed 31 January 2019).
- Feinberg, A.P. (2008) Epigenetics at the epicenter of modern medicine. *Journal of the American Medical Association* 299, 1345–1350. https://doi.org/10.1001/jama.299.11.1345.
- Ford, S., Hess, B., Schwope, M., Nijland, M., Gilbert, J., et al. (2007) Maternal undernutrition during early to mid-gestation in the ewe results in altered growth, adiposity, and glucose tolerance in male offspring. *Journal of Animal Science* 85, 1285–1294. https://doi. org/10.2527/jas.2005-624.

- Francis, D.D., Diorio, J., Plotsky, P.M., Meaney, M.J. (2002) Environmental enrichment reverses the effects of maternal separation on stress reactivity. *Journal of Neuroscience* 22, 7840–7843. https://doi.org/10.1523/ JNEUROSCI.22-18-07840.2002.
- Galea, S., Nandi, A., Vlahov, D. (2005) The epidemiology of post-traumatic stress disorder after disasters. *Epidemiologic Reviews* 27, 78–91. https://doi.org/10.1093/epirev/mxi003.
- Gatchel, R.J. and Neblett, R. (2018) Central sensitization: A brief overview. *Journal of Applied Biobehavioral Research* 23, 1–5. https://doi.org/10.1111/jabr.12138.
- Ghezzi, P., Davies, K., Delaney, A., Floridi, L. (2018) Theory of signs and statistical approach to big data in assessing the relevance of clinical biomarkers of inflammation and oxidative stress. Proceedings of the National Academy of Sciences of the United States of America 115, 2473–2477. https://doi.org/10.1073/ pnas.1719807115.
- Gluckman, P.D. and Hanson, M.A. (2005) The Fetal Matrix: Evolution, Development and Disease. Cambridge University Press, Cambridge, UK.
- Gluckman, P.D. and Hanson, M.A. (2006a) The conceptual basis for the developmental origins of health and disease. In: Gluckman, P.D. and Hanson, M.A. (eds.) Developmental Origins of Health and Disease. Cambridge University Press, Cambridge, UK, pp. 1–5.
- Gluckman, P.D. and Hanson, M.A. (2006b) *Mismatch:* Why Our World No Longer Fits Our Bodies. Oxford University Press, Oxford, UK.
- Godfrey, K. (2006) The 'developmental origins' hypothesis: Epidemiology. In: Gluckman, P.D. and Hanson, M.A. (eds.) *Developmental Origins of Health and Disease*. Cambridge University Press, Cambridge, UK, 6–32.
- Godfrey, K.M., Gluckman, P.D., and Hanson, M.A. (2010) Developmental origins of metabolic disease: Life course and intergenerational perspectives. *Trends in Endocrinology and Metabolism* 21, 199–205. https://doi.org/10.1016/j.tem.2009.12.008.
- Gotoh, T. (2015) Potential of the application of epigenetics in animal production. *Animal Production Science* 55, 145–158. https://doi.org/10.1071/AN14467.
- Griffiths, B.B. and Hunter, R.G. (2014) Neuroepigenetics of stress. *Neuroscience* 275, 420–435. https://doi. org/10.1016/j.neuroscience.2014.06.041.
- Guardini, G., Mariti, C., Bowen, J., Fatjó, J., Ruzzante, S., et al. (2016) Influence of morning maternal care on the behavioural responses of 8-week-old Beagle puppies to new environmental and social stimuli. Applied Animal Behaviour Science 181, 137–144. https://doi.org/10.1016/j.applanim.2016.05.006.
- Hanson, M.A. and Gluckman, P.D. (2015) Developmental origins of health and disease – Global public health implications. Best Practice & Research Clinical Obstetrics & Gynaecology 29, 24–31. https://doi. org/10.1016/j.bpobgyn.2014.06.007.

- Hart, B.L. (1985) Animal behavior and the fever response: Theoretical considerations. *Journal of the American Veterinary Medical Association* 187, 998–1001.
- Hart, B.L. (1988) Biological basis of the behavior of sick animals. Neuroscience and Biobehavioral Reviews 12, 123-137. https://doi.org/10.1016/S0149-7634(88)80004-6.
- Hart, B. (2010) Beyond fever: Comparative perspectives on sickness behavior. In: Breed, M.D. and Moore, J. (eds.) Encyclopedia of Animal Behavior. Academic Press, Oxford, UK, pp. 205–210.
- Hart, B.L. (2011) Behavioural defences in animals against pathogens and parasites: Parallels with the pillars of medicine in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366, 3406–3417. https://doi.org/10.1098/rstb.2011.0092.
- Hellhammer, D., Hero, T., Gerhards, F., Hellhammer, J. (2012) Neuropattern: A new translational tool to detect and treat stress pathology I. Strategical consideration. Stress 15, 479–487. https://doi.org/10.3109/10253890. 2011.644604.
- Hellhammer, D., Meinlschmidt, G., Pruessner, J.C. (2018) Conceptual endophenoypes: A strategy to advance the impact of psychoneuroendocrinology in precision medicine. *Psychoneuroendocrinology* 89, 147–160. https://doi.org/10.1016/j.psyneuen.2017.12.009.
- Hunter, R.G. and McEwen, B.S. (2013) Stress and anxiety across the lifespan: Structural plasticity and epigenetic regulation. *Epigenomics* 5, 177–194. https://doi.org/10.2217/epi.13.8.
- Jamieson, L., Baxter, G., Murray, P. (2018) You are not my handler! Impact of changing handlers on dogs' behaviours and detection performance. *Animals* 8, 1–11. https://doi.org/10.3390/ani8100176.
- Köhler, J.C., Gröger, N., Lesse, A., Ciurana, S.G., Rether, K., et al. (2018) Early-life adversity induces epigenetically regulated changes in hippocampal dopaminergic molecular pathways. *Molecular Neurobiology*, 1–10. https://doi.org/10.1007/s12035-018-1199-1.
- Kohrt, B.A., Jordans, M.J., Koirala, S., Worthman, C.M. (2015) Designing mental health interventions informed by child development and human biology theory: A social ecology intervention for child soldiers in Nepal. *American Journal of Human Biology* 27, 27–40. https://doi.org/10.1002/ajhb.22651.
- Koolhaas, J.M. (2008) Coping style and immunity in animals: Making sense of individual variation. *Brain Behavior and Immunity* 22, 662–667. https://doi. org/10.1016/j.bbi.2007.11.006.
- Koss, K.J. and Gunnar, M.R. (2018) Annual research review: Early adversity, the hypothalamic–pituitary–adrenocortical axis, and child psychopathology. *Journal of Child Psychology and Psychiatry* 59, 327–346. https://doi. org/10.1111/jcpp.12784.
- Kozak, M.J. and Cuthbert, B.N. (2016) The NIMH research domain criteria initiative: Background, issues, and pragmatics. *Psychophysiology* 53, 286–297. https:// doi.org/10.1111/psyp.12518.

- Kullmann, F.A., McDonnell, B.M., Wolf-Johnston, A.S., Kanai, A.J., Shiva, S., et al. (2018) Stress-induced autonomic dysregulation of mitochondrial function in the rat urothelium. *Neurourology and Urodynamics*. https://doi.org/10.1002/nau.23876.
- Levine, S. (1962) Plasma-free corticosteroid response to electric shock in rats stimulated in infancy. *Science* 135, 795–796. https://doi.org/10.1126/science.135.3506.795-a.
- Lippmann, M., Bress, A., Nemeroff, C.B., Plotsky, P.M., Monteggia, L.M. (2007) Long-term behavioural and molecular alterations associated with maternal separation in rats. *European Journal of Neuroscience* 25, 3091–3098. https://doi. org/10.1111/j.1460-9568.2007.05522.x.
- Logan, R.W. and McClung, C.A. (2016) Animal models of bipolar mania: The past, present and future. *Neuroscience* 321, 163–188. https://doi.org/10.1016/j. neuroscience.2015.08.041.
- Mahgoub, M. and Monteggia, L.M. (2013) Epigenetics and psychiatry. *Neurotherapeutics* 10, 734–741. https://doi.org/10.1007/s13311-013-0213-6.
- Mármol, F., Rodríguez, C.A., Sánchez, J., Chamizo, V.D. (2015) Anti-oxidative effects produced by environmental enrichment in the hippocampus and cerebral cortex of male and female rats. *Brain Research* 1613, 120–129. https://doi.org/10.1016/j.brainres.2015.04.007.
- Mármol, F., Sánchez, J., Torres, M., Chamizo, V. (2017) Environmental enrichment in the absence of wheel running produces beneficial behavioural and antioxidative effects in rats. *Behavioural Processes* 144, 66–71. https://doi.org/10.1016/j.beproc.2017.09.009.
- Marques-Deak, A., Cizza, G., Sternberg, E. (2005) Brain-immune interactions and disease susceptibility. *Molecular Psychiatry* 10, 239–250. https://doi.org/10.1038/sj.mp.4001643.
- Matthews, S.G. (2002) Early programming of the hypothalamo-pituitary-adrenal axis. *Trends in Endocrinology & Metabolism* 13, 373–380. https://doi.org/10.1016/S1043-2760(02)00690-2.
- Matzel, L.D., Townsend, D.A., Grossman, H., Han, Y.R., Hale, G., et al. (2006) Exploration in outbred mice covaries with general learning abilities irrespective of stress reactivity, emotionality, and physical attributes. Neurobiology of Learning and Memory 86, 228–240. https://doi.org/10.1016/j.nlm.2006.03.004.
- McEwen, B.S. (2017a) Neurobiological and systemic effects of chronic stress. Chronic Stress 1, 1–11. https://doi. org/10.1177/2470547017692328.
- McEwen, B.S. (2017b) When is stress good for you? Available at: https://aeon.co/essays/how-stress-works-in-the-human-body-to-make-or-break-us (accessed 26 January 2019).
- McEwen, B.S. and Wingfield, J.C. (2003) The concept of allostasis in biology and biomedicine. *Hormones* and *Behavior* 43, 2–15. https://doi.org/10.1016/ S0018-506X(02)00024-7.

- McMillan, F.D. (2013) Stress-induced and emotional eating in animals: A review of the experimental evidence and implications for companion animal obesity. Journal of Veterinary Behavior: Clinical Applications and Research 8, 376–385. https://doi.org/10.1016/j.jveb.2012.11.001.
- McMillan, F.D. (2017) Behavioral and psychological outcomes for dogs sold as puppies through pet stores and/or born in commercial breeding establishments: Current knowledge and putative causes. *Journal of Veterinary Behavior* 19, 14–26. https://doi.org/10.1016/j.jveb.2017.01.001.
- Meaney, M.J., Szyf, M., Seckl, J.R. (2007) Epigenetic mechanisms of perinatal programming of hypothalamic-pituitary-adrenal function and health. *Trends* in *Molecular Medicine* 13, 269–277. https://doi. org/10.1016/j.molmed.2007.05.003.
- Mellor, D.J. (2016) Updating animal welfare thinking: Moving beyond the 'Five Freedoms' towards 'a Life Worth Living'. Animals 6, 1–20. https://doi.org/10.3390/ ani6030021.
- Mellor, D. and Beausoleil, N. (2015) Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare* 24, 241–253. https://doi.org/10.7120/09627286.24.3.241.
- Merlot, E., Quesnel, H., Prunier, A. (2013) Prenatal stress, immunity and neonatal health in farm animal species. *Animal* 7, 2016–2025. https://doi.org/10.1017/ S175173111300147X.
- Meyer, J.S. and Hamel, A.F. (2014) Models of stress in nonhuman primates and their relevance for human psychopathology and endocrine dysfunction. *ILAR Journal* 55, 347–360. https://doi.org/10.1093/ilar/ilu023.
- Miller, A.H. and Raison, C.L. (2016) The role of inflammation in depression: From evolutionary imperative to modern treatment target. *Nature Reviews Immunology* 16, 22–34. https://doi.org/10.1038/nri.2015.5.
- Molet, J., Maras, P.M., Avishai-Eliner, S., Baram, T.Z. (2014) Naturalistic rodent models of chronic early-life stress. *Developmental Psychobiology* 56, 1675–1688. https://doi.org/10.1002/dev.21230.
- Montes, S., Yee-Rios, Y., Páez-Martínez, N. (2018) Environmental enrichment restores oxidative balance in animals chronically exposed to toluene: Comparison with melatonin. *Brain Research Bulletin* 144, 58–67. https://doi.org/10.1016/j.brainresbull.2018.11.007.
- National Institutes of Health. (2019) A scientific illustration of how epigenetic mechanisms can affect health. Available at: https://commonfund.nih.gov/epigenomics/figure (accessed 31 January 2019).
- National Library of Medicine. (2019) Best matches for 'Environmental Enrichment'. Available at: https://www.ncbi.nlm.nih.gov/pubmed/?term=%22environmental+Enrichment%22 (accessed 27 March 2019).
- National Scientific Council on the Developing Child. (2014) Excessive stress disrupts the architecture of the developing brain: Working Paper 3. Updated edition.

- Available at: https://developingchild.harvard.edu/resources/wp3 (accessed 26 January 2019).
- Norris, F.H., Friedman, M.J., Watson, P.J., Byrne, C.M., Diaz, E., et al. (2002) 60,000 disaster victims speak: Part I. An empirical review of the empirical literature, 1981–2001. Psychiatry: Interpersonal and Biological Processes 65, 207–239. https://doi.org/10.1521/ psyc.65.3.207.20173.
- Ogata, N., Gillis, T.E., Liu, X., Cunningham, S.M., Lowen, S.B., et al. (2013) Brain structural abnormalities in doberman Pinschers with canine compulsive disorder. Progress in Neuro-Psychopharmacology and Biological Psychiatry 45, 1–6. https://doi.org/10.1016/j. pnpbp.2013.04.002.
- Pacak, K. and Palkovits, M. (2001) Stressor specificity of central neuroendocrine responses: Implications for stress-related disorders. *Endocrine Reviews* 22, 502–548. https://doi.org/10.1210/edrv.22.4.0436.
- Parlee, S.D. and MacDougald, O.A. (2014) Maternal nutrition and risk of obesity in offspring: The Trojan horse of developmental plasticity. *Biochimica et Biophysica Acta (BBA) Molecular Basis of Disease* 1842, 495–506. https://doi.org/10.1016/j.bbadis.2013.07.007.
- Pezzulo, G., Rigoli, F., Friston, K.J. (2018) Hierarchical active inference: A theory of motivated control. *Trends in Cognitive Sciences* 22, 294–306. https://doi.org/10.1016/j.tics.2018.01.009.
- Picard, M. and McEwen, B.S. (2018a) Psychological stress and mitochondria: A conceptual framework. *Psychosomatic Medicine* 80, 126–140. https://doi. org/10.1097/PSY.000000000000544.
- Picard, M. and McEwen, B.S. (2018b) Psychological stress and mitochondria: A systematic review. *Psychosomatic Medicine* 80, 141–153. https://doi.org/10.1097/PSY.000000000000545.
- Pierantoni, L., Albertini, M., Pirrone, F. (2011) Prevalence of owner-reported behaviours in dogs separated from the litter at two different ages. *Veterinary Record* 169, 468. http://dx.doi.org/10.1136/vr.d4967.
- Proudfoot, K.L., Weary, D.M., von Keyserlingk, M.A. (2012) Linking the social environment to illness in farm animals. Applied Animal Behaviour Science 138, 203– 215. https://doi.org/10.1016/j.applanim.2012.02.008.
- Raison, C.L. and Miller, A.H. (2003) When not enough is too much: The role of insufficient glucocorticoid signaling in the pathophysiology of stress-related disorders. *The American Journal of Psychiatry* 160, 1554–1565. https:// doi.org/10.1176/appi.ajp.160.9.1554.
- Raison, C.L. and Miller, A. (2013) The evolutionary significance of depression in Pathogen Host Defense (PATHOS-D). *Molecular Psychiatry* 18, 15–37. https://doi.org/10.1038/mp.2012.2.
- Rappaport, S.M. (2016) Genetic factors are not the major causes of chronic diseases. *PLoS ONE* 11, 1–9. https://doi.org/10.1371/journal.pone.0154387.
- Rappaport, S.M. (2018) Redefining environmental exposure for disease etiology. NPJ Systems Biology

- Applications, 4, 6. https://doi.org/10.1038/s41540-018-0065-0.
- Reed, R.G. and Raison, C.L. (2016) Stress and the immune system. In: Esser, C. (ed.) Environmental Influences on the Immune System. Springer, Vienna, Austria, pp. 97–126.
- Reynolds, L.P., Borowicz, P.P., Caton, J.S., Vonnahme, K.A., Luther, J.S., et al. (2010) Developmental programming: The concept, large animal models, and the key role of uteroplacental vascular development. *Journal of Animal Science* 88, E61–72. https://doi. org/10.2527/jas.2009-2359.
- Robinson, E. (2018) Psychopharmacology: From serendipitous discoveries to rationale design, but what next? Brain and Neuroscience Advances 2, 1–11. https://doi.org/10.1177/2398212818812629.
- Roth, T.L. (2013) Epigenetic mechanisms in the development of behavior: Advances, challenges, and future promises of a new field. *Development and Psychopathology* 25, 1279–1291. https://doi.org/10.1017/S0954579413000618.
- Russo, S.J., Murrough, J.W., Han, M.H., Charney, D.S., Nestler, E.J. (2012) Neurobiology of resilience. *Nature Neuroscience* 15, 1475–1484. https://doi.org/10.1038/nn.3234.
- Sadek, T., Hamper, B., Horwitz, D., Rodan, I., Rowe, E., et al. (2018) Feline feeding programs: Addressing behavioural needs to improve feline health and wellbeing. Journal of Feline Medicine and Surgery, 20, 1049–1055. https://doi.org/10.1177/1098612X18791877.
- Sale, A., Berardi, N., Maffei, L. (2014) Environment and brain plasticity: Towards an endogenous pharmacotherapy. *Physiological Reviews* 94, 189–234. https:// doi.org/10.1152/physrev.00036.2012.
- Seeman, T.E., Singer, B.H., Rowe, J.W., Horwitz, R.I., McEwen, B.S. (1997) Price of adaptation—allostatic load and its health consequences: MacArthur studies of successful aging. *Archives of Internal Medicine* 157, 2259–2268. https://doi.org/doi:10.1001/archi nte.1997.00440400111013.
- Shonkoff, J.P. (2010) Building a new biodevelopmental framework to guide the future of early childhood policy. *Child Development* 81, 357–367. https://doi.org/10.1111/j.1467-8624.2009.01399.x.
- Sperr, E. 2016. PubMed by Year. Available at: http://esperr. github.io/pubmed-by-year (accessed 27 March 2019).
- Stella, J.L., Lord, L.K., Buffington, C.A. (2011) Sickness behaviors in response to unusual external events in

- healthy cats and cats with feline interstitial cystitis. *Journal of the American Veterinary Medical Association* 238, 67–73. https://doi.org/10.2460/javma.238.1.67.
- Tai, L.W., Yeung, S.C., Cheung, C.W. (2018) Enriched environment and effects on neuropathic pain: Experimental findings and mechanisms. *Pain Practice*, 1068–1082. https://doi.org/10.1111/papr.12706.
- Tsankova, N.M., Berton, O., Renthal, W., Kumar, A., Neve, R.L., et al. (2006) Sustained hippocampal chromatin regulation in a mouse model of depression and antidepressant action. Nature Neuroscience 9, 519–525. https://doi.org/10.1038/nn1659.
- Veasey, J.S. (2017) In pursuit of peak animal welfare: The need to prioritize the meaningful over the measurable. Zoo Biology 36, 1–13. https://doi.org/10.1002/ zoo.21390.
- Voneida, T.J. (1998) Sperry's concept of mind as an emergent property of brain function and its implications for the future of humankind. *Neuropsychologia* 36, 1077–1082. https://doi.org/10.1016/S0028-3932(98)00061-X.
- Westropp, J.L., Welk, K.A., Buffington, C.A. (2003) Small adrenal glands in cats with feline interstitial cystitis. *The Journal of Urology* 170, 2494–2497. https://doi.org/10.1097/01.ju.0000095566.63870.66.
- Wikipedia. (2019) Epigenetics. Available at: http://en. wikipedia.org/wiki/Epigenetics (accessed 6 February 2019).
- Wild, C.P. (2005) Complementing the genome with an 'exposome': The outstanding challenge of environmental exposure measurement in molecular epidemiology. *American Association for Cancer Research* 14, 1847– 1850. https://doi.org/10.1158/1055-9965.EPI-05-0456.
- Witt, C.M., Chiaramonte, D., Berman, S., Chesney, M.A., Kaplan, G.A., et al. (2017) Defining health in a comprehensive context: A new definition of integrative health. American Journal of Preventive Medicine 53, 134–137. https://doi.org/10.1016/j.amepre.2016.11.029.
- World Health Organization. (1948) Constitution of WHO: Principles. Available at: https://www.who.int/about/mission/en (accessed 15 January 2019).
- Zhang, J., Xiao, H., Shen, J., Wang, N., Zhang, Y. (2017)
 Different roles of β-arrestin and the PKA pathway in mitochondrial ROS production induced by acute β-adrenergic receptor stimulation in neonatal mouse cardiomyocytes. *Biochemical and Biophysical Research Communications*, 489, 393–398. https://doi.org/10.1016/j.bbrc.2017.05.140.

Moving Beyond a Problem-based Focus on Poor Animal Welfare Toward Creating Opportunities to Have Positive Welfare Experiences

DAVID J. MELLOR AND NGAIO J. BEAUSOLEIL

Animal Welfare Science and Bioethics Centre, School of Veterinary Science; Massey University, New Zealand

5.1 Introduction

The primary purposes of this chapter are to consider current scientific knowledge supporting the existence of positive affective states in animals, and to describe some useful strategies for enhancing positive experiences and the long-term well-being of animals. However, current thinking needs to be placed in the context of how previously dominant conceptual frameworks have contributed to the developmental trajectory of relevant animal welfare science theory and applications. Accordingly, the following areas are considered here: problem-based thinking and investigation; limitations of the Five Freedoms paradigm; biological significance of negative affective experiences; surviving or thriving as animal welfare objectives; Five Domains model for assessment of animal welfare; positive animal welfare experiences and their promotion; and finally, reconfigured animal welfare aims that promote positive experiences.

5.2 Problem-based Thinking and Investigation

5.2.1 Early problem-based investigation of biological functioning

Early in the twentieth century many nutritional, environmental, disease, and other animal-related problems were poorly understood (Webster, 1994; Fraser, 2008; Mellor *et al.*, 2009). This seriously hampered the capacity to manage animals effectively, so

that farmers in particular struggled to keep their livestock alive and healthily productive. It was recognized that improving scientific knowledge of the underlying biological processes could lead to solutions. Accordingly, there followed at least seven decades of problem-based research into body mechanisms and their manipulation, especially in farm livestock. This commonly involved a now wellrecognized iterative approach to these investigations: identify the problem; clarify the underlying mechanism; and manipulate the mechanism to solve the problem (Mellor et al., 2009). The outcome was the development of numerous strategies for more effectively meeting animals' basic survival needs related mainly to the adequacy of their nutrition, shelter/shade and protection against disease (Mellor et al., 2009; Fraser et al., 2013). Application of this scientific knowledge mitigated many problems that otherwise would have had major negative functional and production impacts on animals (Mellor et al., 2009). Such problem-based research, extending well beyond farm animals, continues to this day, but during the past 20-30 years this has increasingly included consideration of animal welfare impacts. This was partly because formulation of the Five Freedoms paradigm, which incorporated consideration of nutrition, environment, health, behavioral expression, and some mental experiences (Anonymous, 1993; Webster, 1994, 2005), provided an accessible way of understanding animal welfare (Mellor 2016a,b). Additionally, many of the earlier health- and production-based remedies were then understood to have had previously unrecognized animal welfare benefits (Broom, 1986; Webster, 1994, 2005; Fraser, 2008; Mellor *et al.*, 2009; Fraser *et al.*, 2013).

5.2.2 A problem-based perspective on the Five Freedoms paradigm

After its formulation in 1993/1994 the Five Freedoms paradigm had a profound impact on animal welfare thinking and management (Anonymous, 1993; Webster, 2005; Mellor, 2016a,b). Each freedom represented a specific welfare aim and was aligned with a stated Provision that indicated the practical means of achieving the aim (Webster, 1994, 2005; Mellor, 2016a,b). Together the freedoms and provisions focused attention on avoiding or minimizing negative affective experiences (thirst, hunger, discomfort, pain, fear, and distress) and functional states (malnutrition, injury, disease, and behavioral restriction) that were understood to reflect the presence of potentially serious welfare problems (Anonymous, 1993; Webster, 1994, 2005). Thus, a major aim of the paradigm was to motivate the discovery and application of practical remedies for these welfare problems. The general focus was therefore on *problems* and the aim was to be *free* of them, which represented an overall orientation toward animal welfare that was conceptually consistent and usefully informative (Mellor, 2016a). Note, however, that four of the freedoms were described in much more specific terms than this: namely, freedom from: (i) thirst, hunger, and malnutrition; (ii) discomfort and exposure; (iii) pain, injury, and disease; and (iv) fear and distress (Anonymous, 1993; Webster, 1994, 2005). The fifth freedom was expressed more generally and focused on restricted opportunities to engage in normal behaviors (Anonymous, 1993; Webster, 1994).

5.3 Limitations of the Five Freedoms Paradigm

It is important to reiterate that the Five Freedoms paradigm beneficially influenced animal welfare thinking and management for most of the first 20 years after it was formulated (Mellor, 2016a,b). It was understood initially that use of the word 'freedom' as part of each welfare aim was not intended to mean that animals should to be kept 'completely free' from the stipulated negative affective experiences or states; rather, it was understood that animals

should be kept 'as free as possible' from them (Anonymous, 1993; Webster, 1994). However, the meaning and usage of the term 'freedom' changed over time, being strongly influenced, for example, by individuals or groups who had only a cursory knowledge of animal welfare science or who favored animal rights thinking (Mellor, 2016a). Thus, in some sectors the aim of being 'free' of negative affects and states was taken to imply that completely eliminating them was both desirable and possible (Mellor, 2016a). This misconception was reinforced because the particular affects and states referred to in the freedoms were described simply as negative or unpleasant. They were therefore considered to be 'bad', and, importantly, no corrective clarification was offered regarding their critical biological roles or significance (Mellor, 2016a).

5.4 Biological Significance of Negative Affective Experiences

Research during the past 15–20 years has expanded the list of negative affects that most mammals are now considered likely to experience (Denton *et al.*, 2009; Mellor *et al.*, 2009; Mellor, 2012a; Mellor and Beausoleil, 2015; McMillan, 2016). Two main types have been distinguished: those that are *survival-related* and others that are *situation-related* (Mellor and Beausoleil, 2015; Mellor, 2016a, 2017). They have broadly different sensory origins, biological roles, and impacts on animal welfare.

5.4.1 Survival-related or survival-critical negative affects

Originally referred to as homeostasis-related motivational affects (Mellor, 2015a), then survival-related negative affects (Mellor and Beausoleil, 2015), and finally survival-critical negative affects (Mellor, 2017), they are now considered to include the qualitatively different experiences of breathlessness, thirst, hunger, pain, nausea, dizziness, debility, weakness, and sickness (Fraser and Duncan, 1998; Gregory, 2004; Panksepp, 2005; Denton et al., 2009; Mellor et al., 2009; Mellor, 2012a; Beausoleil and Mellor, 2015; Mellor and Beausoleil, 2015, 2017). Generated mainly by sensory inputs that register imbalances or disruptions in the internal physical/functional state of the animal, these negative affects are essential components of genetically embedded mechanisms which elicit behaviors that are designed to secure the survival of the animals (Fraser and Duncan, 1998; Panksepp, 2005; Denton et al., 2009). The unmistakable negativity of these affects creates a sense of urgency to engage in behaviors that are specific to each affect (Fraser and Duncan 1998; Denton et al., 2009); for example, breathlessness elicits increased respiratory activity, thirst provokes water seeking and drinking, hunger food acquisition, and pain escape or avoidance responses to injury (Gregory, 2004; Denton et al., 2009; Verbeek et al., 2012; Beausoleil and Mellor, 2015; Mellor and Beausoleil, 2015). Moreover, the greater the intensity of the negative affect, the greater is the sense of urgency to engage in the aligned behavior, and vice versa, so that once the behavior achieves the required corrective physical/functional outcome the intensity of the negative affect declines (Fraser and Duncan 1998; Denton et al., 2009).

It is apparent that animals are genetically preprogrammed to experience these affects in order to motivate them to engage in affect-specific behaviors that are essential for their survival. Accordingly, a key welfare aim in managed animals is to keep the intensity of these negative affects at tolerably low levels that nevertheless still motivate the essential life-sustaining behaviors (Mellor, 2015a; Mellor and Beausoleil, 2015). As will be outlined in Section 5.7.3, this has other benefits, especially with regard to impacts on animals' motivation to engage in rewarding behaviors.

5.4.2 Situation-related negative affects

These negative affects arise from brain processing of sensory inputs that originate from outside the body. Such outward-focused sensory inputs contribute to the animal's cognitive perceptions of its external circumstances, i.e., its *situation* (Denton *et al.*, 2009; Mellor, 2016a). Specifically, these affects are considered to include frustration, anger, helplessness, loneliness, boredom, depression, anxiety, fear, panic and nervous vigilance (Wemelsfelder, 1997, 2005; King and Rowan, 2005; Panksepp, 2005; Mason and Rushen, 2006; Boissy *et al.*, 2007; Beausoleil *et al.*, 2008; Boissy and Lee, 2014; Mellor, 2015c, 2016a). Animals may experience various combinations of these affects when in impoverished and/or threatening situations.

Examples of impoverished circumstances include indoor or outdoor enclosures distinguished by their invariant or barren features and very limited space, situations which severely restrict opportunities to engage in environment-focused exploration and/or interactive social behaviors; also nutrient-dense feeds are provided as small meals that are consumed rapidly (Mason and Rushen, 2006; Boissy *et al.*, 2007; Mellor, 2015a,b,c; Mellor and Beausoleil, 2015). The development of such affects in severely restricted circumstances has been attributed to the thwarting of genetically pre-programmed or learned motivations to engage in behaviors that animals find rewarding, and/or failure to gain the anticipated rewards (Kirkden and Pajor, 2006; Mason and Rushen, 2006; Spinka and Wemelsfelder, 2011). Rewarding behaviors are considered in more detail in Section 5.5.3.

Situations that are cognitively perceived as threatening include possible or actual attack by predators (including humans), victimization by conspecifics in confined spaces, separation from others that provide protection, overstimulation, or challenging novelty, and hazardous environmental events such as fire, flood, or extreme winds (Mellor, 2015b,c). The negative affects experienced in these situations likely include anxiety, fear, panic, and/or nervous vigilance (Panksepp 2005; Boissy *et al.*, 2007; Beausoleil *et al.*, 2008; Mellor, 2015c).

As decisions about the way animals are managed are responsible for many of these situations, introducing more congenial circumstances is an obvious path to devising remedies. The overall objective is to keep social animals together with congenial others in spacious, appropriately variable, and safe environments, as opposed to keeping them closely confined and isolated in barren and/or threatening environments. This is a well-established foundational principle underlying many environmental enrichment strategies (Young, 2003; Mason and Rushen, 2006; Edgar *et al.*, 2013; Fraser *et al.*, 2013; Mellor and Beausoleil, 2015; Mellor *et al.*, 2015).

5.5 Surviving or Thriving as Animal Management Objectives

Ethically responsible husbandry practices aim at achieving more than merely keeping animals alive; their aim is, or should be, for animals to thrive (Kagan *et al.*, 2015).

5.5.1 Survival – the minimalist approach

Survival-focused husbandry is directed at meeting animals' basic needs for water/food, shade/shelter, and disease/injury control, which are undoubtedly important, but such a restricted focus cannot deliver

overall welfare experiences that are positive (Webster, 1994, 2011; Fraser, 2008; Yeates and Main, 2008; Mellor et al., 2009; Edgar et al., 2013; Mellor, 2016a). This is because the negativity of the aligned survival-related affects is critical for motivating essential life-sustaining behaviors and therefore can at best be neutralized temporarily, not eliminated (Denton et al., 2009; Mellor, 2012a, 2015a; Mellor and Beausoleil, 2015). In other words, even in animals whose nutrition, environment, and health are well managed, the valence of the associated affects ranges from negative to neutral, so that with regard to these affects the overall experience remains negative (Mellor, 2017). Of course, when such management is poor the animals' overall affective experience can be more intensely negative.

5.5.2 Improving upon mere survival

In this regard, the situation-related negative affects stand in marked contrast to the survival-critical affects. This is because introducing environmental improvements aimed at providing opportunities for animals to engage in rewarding behaviors can replace some negative affects with positive ones, leading to a better overall experiential balance for the situation-related affects (Mellor and Beausoleil, 2015; Mellor, 2015a,b, 2016a,b, 2017). Note that this has been understood for some years based largely on investigations into resource inputs, behavioral outputs, and assessments of animals' preferences, aversions, and priorities (Young, 2003; Dawkins, 2006; Mason and Rushen, 2006; Kirkden and Pajor, 2006; Yeates and Main, 2008; Fraser and Nicol, 2011; Edgar et al., 2013; Fraser et al., 2013); note also, it is only recently in this context that increasing reference has been made to the specific positive affects the animals may experience (Mellor and Beausoleil, 2015; Mellor et al., 2015; Mellor, 2015a,b, 2016a,b, 2017). A combination of both orientations may guide initiatives that contribute to animals thriving.

5.5.3 Rewarding behaviors that may contribute to animals thriving

Rewarding behaviors are those that reflect 'positive affective engagement', key constituents of which are the anticipation, current experience, and/or memory of all positive affects linked to each behavior (Mellor, 2015a). These behaviors are more commonly observed when social animals are kept with

congenial others in spacious, stimulus-rich, and safe environments (Mason and Rushen, 2006; Fraser, 2008; Yeates and Main, 2008; Mellor and Beausoleil, 2015; Mellor, 2016b). They include environment-focused activities of exploration and food acquisition (foraging or hunting), and the animal-to-animal interactive activities of bonding and bond affirmation, maternal, paternal, or group care of young, play behavior, and sexual activity (Mellor, 2016a,b). In general terms, the associated positive affects are considered likely to include various forms of comfort, pleasure, interest, confidence, and a sense of being in control (Yeates and Main, 2008; Fraser, 2008; Mellor et al., 2015; Mellor, 2015c). More specifically, they may include feelings of being energized, engaged, affectionately sociable, rewarded maternally, paternally or as a group, nurtured, secure or protected, excitedly joyful, and/or sexually gratified (McMillan, 2005, 2007; Panksepp, 2005; Mellor and Beausoleil, 2015; Mellor, 2015a,b,c).

Understanding this should increase the drive to provide animals with environments that offer such opportunities, especially as this is likely to achieve longer term and more varied beneficial welfare outcomes which would contribute to animals thriving. Of course, as with negative affects, the duration, intensity, and frequency of animals' experiences of positive affects are likely to vary (Mellor, 2015c).

5.6 Five Domains Model for Animal Welfare Assessment

5.6.1 General background trends in animal welfare understanding

It is apparent that during most of the past 30 years animal welfare science has largely focused on negative states, their recognition and management (Broom, 1986; Webster, 1994, 2011; Gregory, 2004; Mellor et al., 2009; Appleby et al., 2011; Grandin, 2015; Mellor, 2016a). Initially, poor welfare states were identified using predominantly physical, physiological, and clinical indices, characterized as the 'biological functioning' orientation, which reflected the then commonly used problem-solving, mechanismfocused approach (see Section 5.2). Subsequently, increasing reference was made to inferred negative subjective experiences or affects that animals may have, an approach characterized as the 'affective state' orientation (Fraser et al., 1997; Green and Mellor, 2011; Mellor, 2016a, 2017).

Until about 10 years ago these two orientations appeared to be competing frameworks that gave rise to apparently conflicting conclusions about animal welfare (Fraser et al., 1997), for example, lowstress animals exhibiting high productivity but having poor affective experiences. Now, however, they are widely accepted to be dynamically interactive elements within the body operating as a whole integrated entity (Green and Mellor, 2011; Hemsworth et al., 2015; Mellor, 2016a, 2017). Thus, it is currently understood that the welfare state of an animal refers largely to the affects it may experience, and that these reflect the operation of biological mechanisms linked to physical/functional states within the body and to other mechanisms underlying the brain processing that gives rise to animals' cognitive perception of their external circumstances (Mellor, 2016a). Finally, during the past 10-15 years attention has increasingly been given to positive welfare states, their recognition and promotion (McMillan, 2005, 2007; Panksepp, 2005; Fraser, 2008; Yeates and Main, 2008; Mellor 2015a,b,c; Mellor and Beausoleil, 2015; Clegg et al., 2017).

5.6.2 Formulation and evolution of the model

When formulated in 1994 (Mellor and Reid, 1994), the Five Domains model was the most comprehensive and systematic means then available to prospectively and retrospectively identify and grade the negative welfare impacts caused by research, teaching, and testing (RTT) procedures conducted on sentient animals (Orlans, 2000; Elzanowski, 2006; Williams *et al.*, 2006). In 1997, use of the model became a mandatory part of the New Zealand institutional animal ethics committee approval system for proposed RTT manipulations (Williams *et al.*, 2006), and its mandatory use by all animal-based science investigators in New Zealand continues to this day.

The original explicit focus of the model was animal welfare compromise. The five domains are: (i) nutrition; (ii) environment; (iii) health; (iv) behavior; and (v) mental state. The first three domains mainly focus on *internal* imbalances or disturbances, whereas the focus of the fourth domain is on *external* restrictive confinement or restraint or otherwise unusual space availability, and/or negative impacts of the presence or absence of other animals (Mellor and Reid, 1994; Mellor, 2004a). Once objective evidence is collated by reference to the first four domains, the subjective, emotional, or affective experiences inferred to be associated with those

disturbances or restrictions are assigned to the fifth mental domain, and it is these experiences that form the endpoint of the welfare assessment.

After its formulation in 1994 the model was regularly refined and extended to take account of fresh developments in animal welfare science thinking at each stage. Nevertheless, the original model anticipated some later developments in thinking. For example, its structure already reflected the dynamically integrated biological functioning/ affective state interactivity that underlies an animal's overall welfare state expressed in terms of what the animal itself experiences (Green and Mellor, 2011; Hemsworth *et al.*, 2015; Mellor, 2016a, 2017). At that time the focus was entirely on welfare compromise so that the named experiences were negative. The original list was limited to thirst, hunger, pain, anxiety, fear, and distress (Mellor and Reid, 1994).

Subsequently, this list was progressively expanded in order to specify what additional affects may be included under the generic term 'distress'. This specificity was designed to direct attention to previously unrecognized negative impacts (Mellor *et al.*, 2009; Mellor, 2012b; Mellor and Webster, 2014). As outlined above, the current list totals 19, which have been characterized as *survival-critical negative affects* and *situation-related negative affects* (see Sections 5.4.1 and 5.4.2). Clear descriptions of the key features of each of these negative affects have now also been published (Ledger and Mellor, 2018).

Finally, the most extensive revision of the model to date involved including in each of the first four domains internal and external circumstances that give rise to positive affective experiences evaluated in the fifth domain (Mellor and Beausoleil, 2015). Moreover, the distinction between survival-related affects (negative) and situation-related affects (both negative and positive) was first made an explicit part of the model during this revision.

5.6.3 Validating inferences about affect referred to in the model

The discipline of affective neuroscience focuses on the brain processes that underlie aversive and rewarding experiences and their manifestation as specific affects (Panksepp, 2005; Rolls, 2007). Thus, there is now objective neuroscience evidence for cautiously inferring that specific internal states and/or expressed behaviors are suggestive of animals experiencing particular negative or positive affects (see below). Importantly, this evidence successfully

challenges accusations of anthropomorphism (Panksepp, 2005). Nevertheless, as the focus of model-based welfare assessment is on specific affects, or groups of affects, and their sources, it is important to consider how well supported the inferences are regarding the presence of each affect (Beausoleil and Mellor, 2017). Confidence in such inferences depends on how well-described the underlying affective neuroscience is, the specificity of any physical/functional indices, and/or the distinctiveness of indicative behaviors, all of which must be evaluated in the context of the animal's physical, biotic, and social environment (Beausoleil and Mellor, 2017; Mellor, 2017). For further consideration of the assessment of affect (negative and positive) see Chapter 23, this volume.

Survival-critical negative affects

Identification of, and distinguishing between, breathlessness, thirst, hunger, pain, and sickness are well supported by the underlying neuroscience knowledge, physical/functional/clinical indices, and behaviors (Gregory, 1998, 2004; Denton et al., 2009; Mendl et al., 2010; Viňuela-Fernández et al., 2011; Beausoleil and Mellor, 2015; Mellor, 2015a). However, distinguishing between nausea, dizziness, debility, weakness, and sickness is not as easy unless the specific circumstances of the animal and/or specific functional indices provide sufficient justification to identify a particular affect (Gregory, 1998, 2004). If this is not possible, affects might be considered in groups, for example, nausea and dizziness or debility, weakness, and sickness, thereby allowing for less specific, but still informative consideration.

Situation-related negative affects

There are sound neuroscience bases for using indicative behaviors to cautiously distinguish among anxiety, fear, panic, depression, frustration, and anger when evaluated in relation to the animals' particular circumstances (Panksepp, 1998, 2005, 2006; Gregory, 2004; Panksepp and Zellner, 2004; King and Rowan, 2005; Rolls, 2007; Jones and Boissy, 2011; Panksepp *et al.*, 2011; McMillan, 2016). However, behavioral indices may not enable helplessness, loneliness, and/or boredom to be distinguished as easily (Wemelsfelder, 1997, 2005; Mason and Rushen, 2006; McMillan, 2016), so identifying these affects should be done with greater caution. This caveat is not intended to cast doubt on the

existence of these affects; rather, it is to note that identifying or distinguishing between them behaviorally may be difficult.

Situation-related positive affects

Affective neuroscience observations support interpretation of particular behaviors as indicating experiences of 'positive affective engagement' (Mellor, 2015a). More specifically, the neuroscience of rewardseeking and the generation of positive affects supports the interpretation that animals will likely have pleasurable experiences when exhibiting the following behaviors (Mellor, 2015b): positively motivated, energized environmental exploration, and food acquisition activities, i.e., which are not motivated by significant negative survival-critical affects (Figs 5.1 and 5.2); bonding and bond affirmation (Fig. 5.3); maternal, paternal, or group care of young (Fig. 5.4); play behavior (Fig. 5.5); and sexual activity (Panksepp, 1993, 2005; Berridge, 1996; Nelson and Panksepp, 1998; Ikemoto and Panksepp, 1999; Numan and Insel, 2003; Burgdorf and Panksepp, 2006; Lim and Young, 2006; Boissy et al., 2007). These largely neuroscience-supported inferences from animals' behavior generally accord with, and are thereby strengthened by, prior interpretation of predominantly behavior-based investigations of animals' preferences, aversions, and priorities conducted independently (Wemelsfelder, 1997; Dawkins, 2006; Kirkden and Pajor, 2006; Mason and Rushen, 2006; Fraser and Nicol, 2011).

5.6.4 Wide applications of the model

From 1997 in New Zealand, the mandatory use of the model to assess the negative welfare impacts of RTT procedures has been applied to a wide range of sentient animals being investigated for very diverse purposes. They include horses, cattle, deer, goats, sheep, pigs, domestic poultry, game birds, other birds including endemic, native, and introduced species, dogs, cats, guinea pigs, mice, rats, rabbits, ferrets, stoats, weasels, wallabies, possums, cetaceans, reptiles, amphibians, and fishes. The purposes include fundamental and applied biomedical, veterinary, agricultural, ecological, welfare, and other approved investigations. Beyond the specific RTT regulatory context, the model has also been prospectively and/ or retrospectively used to assess negative and positive welfare impacts of proposed new or modified approaches to housing, managing, and/or interacting with farm (Mellor et al., 2009; Hemsworth et al., 2015), working (Littlewood and Mellor, 2016), sport (McGreevy et al., 2018), zoo (Mellor et al., 2009, 2015; Portas, 2013; Sherwen et al., 2018), 'pest' (Sharp and Saunders, 2008, 2011; Beausoleil et al., 2012; Beausoleil and Mellor, 2012, 2015; Littin et al., 2014; Baker et al., 2016), research (Mellor, 2004b,

2012b), and other animals (Mellor *et al.*, 2009), including whales (Butterworth, 2017; Clegg and Delfour, 2018).

This diversity of animals and applications highlights the necessity of having access to scientifically informed experts who collectively can provide detailed input on species-specific biology, behav-



Fig. 5.1. Depiction of potentially positive experiences of unrestricted open-field grazing, where pleasurable tastes influence which plants among several are chosen to be eaten, and being part of a herd engenders experiences of safety. (Image used under license from Shutterstock.com.)



Fig. 5.2. Natural occurrence of *both* energized, highly focused, and exhilarating hunting (cheetah) and panic, fear, and alert vigilance (the hunted game buck). (Image used under license from Shutterstock.com.)



Fig. 5.3. Examples of the pleasures of *both* exercise with bonded others and the vitality of physical fitness in social animals. (Image used under license from Shutterstock.com.)



Fig. 5.4. The comfort and warm emotional cohesiveness of bonded nurturing. (Image used under license from Shutterstock.com.)

ior, ecology, physiology, pathophysiology, health, and management (Mellor *et al.*, 2012), as well as affect-related, neuroscience-supported behavioral expertise and experience with the operation of the Five Domains model (Beausoleil and Mellor, 2015; Mellor and Beausoleil, 2015; Mellor, 2017). Utilizing widely experienced panels or consultative networks is helpful with such evaluations (Sharp and Saunders, 2011; Edgar *et al.*, 2013; Buckland *et al.*, 2014; Littin *et al.*, 2014; Mellor

et al., 2015; Beausoleil et al., 2016; Butterworth, 2017; McGreevy et al., 2018).

5.6.5 An aide-memoire for sources of different affects identified using the model

Up-to-date details of the operation of the model and the science upon which it is based are readily available elsewhere (Mellor and Beausoleil, 2015; Mellor, 2016a, 2017; Ledger and Mellor, 2018). Nevertheless, it is helpful to emphasize some key points. The model is not intended to be a definition of animal welfare, nor is it an accurate representation of body structure and function. Rather, it is a focusing device designed to facilitate assessment of animal welfare in a systematic, structured, thorough, and coherent manner. Thus, the purpose of each domain is to draw attention to areas that are relevant to welfare assessments, taking into consideration the understanding outlined above. As the body functions as a dynamically integrated whole entity, the specific body functions or states, external circumstances, and related affective experiences identified via the model inevitably interact. Accordingly, there may be overlap between factors considered within different domains; for example, anxiety and fear associated with a particular cause may be identified in Domains 2 and 4. However, it is necessary to consider the particular origin of each affect only



Fig. 5.5. Dogs exhibiting the joyful excitement and fun of playing. (Image used under license from Shutterstock.com.)

once; if it is identifiable in more than one domain, it may be arbitrarily assigned to one of them. This avoids concerns about duplication; it also avoids fruitless arguments about domain specificity.

Table 5.1 provides examples of some potentially negative and positive internal states or external circumstances, assigned to Domains 1 to 4, as well as their aligned negative and positive affects, assigned to Domain 5. The details provided are not definitive or exhaustive because the particular experiential implications of many affects are beyond direct human experience. Examples include unique sensory modalities such as echolocation, ultrasonic communication, highly adapted chemical and vibrational sensitivity, as well as the exaggerated or low acuity of the common modalities of sight, hearing, and smell in different taxa (see Mellor, 2018), and the affective experience of flight in birds. Moreover, essential information about some affects and their generation is very limited or nonexistent in less well studied animals, such as in many zoo or free-living wildlife species (Mellor et al., 2015; Sherwen et al., 2018). Accordingly, each example should be assessed by reference to what is known about the animals' species-specific behavior, biology, and ecology considered in relation to its particular physical, biotic, and social environment (Mellor, 2017). Table 5.1 is therefore a guiding aide-memoire; the examples in it should be considered carefully and, only after sufficient justification, be retained, deleted, or amended, and/or others added as deemed appropriate for each species (Littlewood and Mellor, 2016; Beausoleil et al., 2016; Butterworth, 2017).

Finally, note that the 'unavoidable/imposed conditions' listed for Domain 2 identify areas of increased risk that related welfare problems may arise. However, the mere existence of such conditions does not mean that the anticipated welfare problems will arise. Such a conclusion must be supported by directly observed animal-based physical, physiological, clinical, and/or behavioral evidence. Only then can inferences be made regarding aligned affects. This emphasizes the general point: that objective animal-based evidence (Domains 1–4) must form the foundations of any inferences about welfare-relevant affects (Domain 5) (Mellor, 2017).

5.7 Positive Welfare Experiences and their Promotion

5.7.1 'Positive affective engagement' and 'agency'

A new defining point of reference has been proposed for states of enhanced animal welfare, that is, states reflective of positive welfare experiences (Mellor 2015a). Its focus is on the extent to which animals may experience positive affective engagement (Mellor 2015a; Mellor and Beausoleil, 2015) as distinct from an absence of suffering, which has been the primary reference point for negative welfare experiences (Mellor *et al.*, 2009).

Table 5.1. The Five Domains model. The examples provided for Domains 1 to 3, labeled 'Nutrition', 'Environment', and 'Health', are intended to direct attention toward mainly *internal survival-critical factors*, and those provided for Domain 4, labelled 'Behavior', focus attention largely on *external situation-related factors*. For each of Domains 1 to 4, examples of negative and positive factors are provided and are aligned with inferred negative or positive affective experiences, assigned to Domain 5, labelled 'Mental state/affects'. The overall affective experience in the mental domain equates to the welfare status of the animals. Note that an animal exercises 'agency' (Domain 4 – Behavior) when it engages in voluntary, self-generated, and goal-directed behaviors (Wemelsfelder, 1997; Spinka and Wemelsfelder, 2011).

Negative conditions		Positive conditions	
	Domain 1 (Nutrition) and Do	main 5 (Mental state/affects)
Nutritional imbalances:	Associated negative affects:	Nutritional opportunities to:	Associated positive affects:
Restricted water intake	Thirst	Drink enough water	Wetting/quenching pleasures of drinking
Restricted food intake	Hunger (general)	Eat enough food	Pleasures of food tastes/ smells/textures (i)
Poor food quality	Hunger (salt)	Eat a balanced diet	Pleasure of salt taste
Restricted food variety	Malnutrition malaise	Eat a variety of foods (i)	Masticatory pleasures
Voluntary overeating	Feeling bloated or overfull	Eat correct quantities of food	Postprandial satiety
Force-feeding	Gastrointestinal pain	·	Gastrointestinal comfort
Do	main 2 (Environment) and	Domain 5 (Mental state/affec	ts)
Unavoidable/imposed conditions:	Associated negative affects:	Available conditions:	Associated positive affects:
Thermal extremes	Forms of discomfort:	Thermally tolerable	Forms of comfort:
Unsuitable substrate	Thermal: chilling, overheating	Suitable substrate	Thermal
Close confinement	Physical: joint pain, skin irritation	Space for freer movement (i)	Physical
Atmospheric pollutants:	Physical: stiffness, muscle tension	Fresh air	
ammonia, CO _{2,} , dust, smoke	Respiratory: e.g., breathlessness		Respiratory
Aversive odors		Pleasant/tolerable odors	
Loud/otherwise	Olfactory	Noise exposure	Olfactory
unpleasant noise		acceptable	
Light: inappropriate	Auditory: impairment, pain	Light intensity tolerable	Auditory
intensity	Visual: glare/darkness eye strain		Visual
Environmental monotony:		Normal environmental	
ambient, physical, lighting	Malaise from unnatural constancy	variability	Variety-related comfort (i)
Unpredictable events		Predictability	
	Anxiety, fear, alert vigilance		Calm, at ease (i)
	Domain 3 (Health) and Dor	nain 5 (Mental state/affects)	
Negative Conditions		Positive Conditions	
Presence of:	Associated negative affects	Little or no:	Associated positive affects
Disease: acute, chronic	Breathlessness	Disease	Comfort of good health
Injury: acute, chronic;	Pain: many types	Injury	and functional capacity
husbandry mutilations	Debility, weakness	Functional impairment	
Functional impairment due to	·		
limb amputation, or lung, heart, vascular, kidney,	Nausea Dizziness		
neural, or other problems			
Poisons		Poisoning	
Obesity/leanness		-	
Poor physical fitness,	B	Body condition appropriate	NO. 11. 65. (11)
muscle de-conditioning	Physical exhaustion	Good fitness level	Vitality of fitness (iii) Continued

Negative conditions		Positive conditions	
Domain 4 (Behavior) and Domain 5 (Mental state/affects)			
Exercise of 'agency' impeded by:	Associated negative affects	'Agency' exercised via:	Associated positive affects
Invariant, barren environment	Anger	Varied, novel environment	Interested
(ambient, physical, biotic)	Frustration	Congenial sensory inputs	Calmness
Inescapable sensory impositions	Boredom	Available engaging choices	Pleasantly occupied (i)
Choices markedly restricted	Helplessness	Free movement	In control
Constraints on environment-focused activity	Depression	Exploration	Energized (ii)
	Loneliness	Foraging/hunting (ii)	Focused (ii)
Constraints on animal-to-	Insecurity	Bonding/reaffirming bonds	Affectionate sociability
animal interactive activity	Isolation	Rearing young	Rewards of rearing young (iv)
	Sexual frustration	Playing	Excitation/playfulness (v)
		Sexual activity	Sexually gratified
Limits on threat avoidance, escape, or	Anxiety, fearfulness, panic (ii), anger	Using refuges, retreat, or defensive attack	Secure, protected, confident (iv) Likes novelty
defensive activity Limitations on sleep/rest	Neophobia Exhaustion	Sleep/rest sufficient	Energized refreshed
Limitations on sleep/lest	LAHAUSHUH	Oleep/rest suilicient	Lifergized refreshed

(i), Fig. 5.1; (ii), Fig. 5.2; (iii), Fig. 5.3; (iv), Fig. 5.4; (v), Fig. 5.5.

Positive affective engagement represents the experience animals may have when they actively respond to motivations to undertake behaviors they find rewarding, and it potentially incorporates all of the associated affects that are positive (Mellor, 2015a,b). These include the genetically pre-programmed, or learned, affectively positive motivations to engage in such behaviors and also the experience of positive affects related to anticipation, goal achievement, and memory of success (Fraser and Duncan 1998; Panksepp, 2005; Biossy *et al.*, 2007). This understanding constitutes strong justification for framing a reference standard that acknowledges the importance to animals of having opportunities to express those behaviors (Mellor, 2015a,c).

Accordingly, positive affective engagement aligns with the rewards an animal may experience when exercising 'agency'; that is, when it engages in voluntary, self-generated, and goal-directed behaviors (Wemelsfelder, 1997) associated with a general sense of being in control (Spinka and Wemelsfelder, 2011). More specifically, agency denotes the intrinsic propensities (genetic or learned) of an animal to actively engage cognitively and behaviorally with its physical, biotic, and social environment, beyond the degree demanded by its momentary needs, in order to gather knowledge and enhance its skills for future use in responding effectively to varied and

novel challenges (Wemelsfelder, 1997; Spinka and Wemelsfelder, 2011). Thus, positive affective engagement includes the rewarding content of an animal's experiences while exercising agency. Note, however, that positive experiences may also arise in ways not directly related to the exercise of agency (Mellor and Beausoleil, 2015); for example, pleasant tastes of food provided indoors, as opposed to the same food selected while grazing outdoors.

5.7.2 Promoting opportunities for rewarding behaviors involving agency

Promotion of such opportunities is clearly facilitated by referring to extensive lists of potential positive affects and their generation; for example, those included in the Five Domains model (Table 5.1; Mellor and Beausoleil, 2015). In addition, there is a list of questions that can aid this process (Anonymous, 2009; Mellor, 2015c, 2016a). Overall, what opportunities are available for the animals' comfort, pleasure, interest, confidence, and sense of being in control? More specifically, what provisions ensure that consuming the food provided will be an enjoyable experience? How are expressions of normal behavior encouraged and harmless wants met? What environmental choices are available that will encourage exploratory and food acquisition activities that are

rewarding? And what provisions enable social species to engage in bonding and bond affirming activities and, as appropriate, other affiliative interactions such as maternal, paternal, and group care of young, play behavior, and sexual activity?

These questions are clearly directed at environmental enrichment initiatives (see Section 5.5.3). For example, improving the levels of environmental complexity and variety may replace boredom, depressive inactivity, or frustration with the enlivening rewards of energized goal-directed exploratory and feeding behaviors. In addition, ensuring that animals have the company of others of their own kind or an appropriate alternative species (including human beings) and taking measures to encourage affiliative interactions and minimize the separation of bonded animals, would tend to replace feelings of loneliness, isolation, helplessness, separation distress, and abandonment with feelings of affectionate sociability and of being secure and protected. And minimizing visual, auditory, olfactory, environmental, handling, and other cues that generate a sense of threat may likewise replace anxiety, fear, and nervous vigilance with feelings of security and calmness that may in turn augment the pleasure of harmonious interactions with other animals and human beings (Mellor, 2012b, 2016a, 2017; Mellor and Beausoleil, 2015). Recognizing that such a wide range of positive affects is potentially available should stimulate fresh thought about what enrichment strategies might be possible and practicable.

5.7.3 Importance of minimizing survivalcritical negative affects

There are potential interactions between the survival-critical negative affects, captured by Domains 1 to 3 of the model, and the motivation of animals to engage in rewarding behavior, largely captured by Domain 4 (Mellor and Beausoleil, 2015; Littlewood and Mellor, 2016). When the intensity of such negative affects is significant (Domain 5), animals usually do not, or are not able to, engage in rewarding behaviors even when opportunities to do so are available (Mellor, 2016a, 2017) (Fig. 5.6). Four specific examples illustrate this point (Mellor and Beausoleil, 2015). (i) Acute or chronic cardiorespiratory or respiratory impairment leading to breathlessness may restrict animals to low levels of physical activity, thereby hindering their capacity to, for example, hunt, forage extensively, play, or respond actively to circumstances requiring escape or defensive attack (Beausoleil and Mellor, 2015). (ii) Significant acute or chronic pain, whether caused by traumatic injury or pathological processes, may induce immobility, restrict movement, or otherwise impair behavioral responsiveness to potentially pleasurable opportunities (McMillan, 2003). (iii) Sickness, weakness, nausea, dizziness, and other debilitating affects may motivate animals to remain inactive and isolated from others, and may make them disinclined to engage in activities that might be pleasurable (McMillan, 2003). (iv) Amputation, traumatic deformation, or paralysis of a limb that severely hinders mobility and generates a sense of helplessness would demotivate animals from fully utilizing resources requiring agility (McMillan, 2003), for example, in tree-dwelling or climbing animals, and could also engender demotivating anxiety or fear due to severely impaired escape capacities (Gregory, 2004). Of course, in less severe cases, such as in cats or dogs with one limb amputated, the animals may retain the ability to engage in a wide range of behaviors, including enjoyable ones. Clearly, welfare management must aim to minimize survivalcritical negative affects toward tolerably low levels so that animals are not demotivated from utilizing available opportunities to behave in ways they find rewarding (Mellor, 2016a, 2017).

5.8 Provisions and Welfare Aims that Promote Positive Experiences

A Five Provisions/Welfare Aims framework has been formulated as a coherent alternative to the Five Freedoms paradigm (Mellor, 2016b). Using generalized language, it incorporates current scientific knowledge that now informs our understanding and management of animal welfare (Table 5.2). It also retains the memorable simplicity of the Five Freedoms and clearly has links to that paradigm, but it avoids the acknowledged complications that arise by using the term 'freedom'. Moreover, the names of the five provisions (in bold italics) make clear reference to the five domains of the model, and the first four provisions have the same names as the four European Welfare Quality (WQ®) principles.

Importantly, the first four Animal Welfare Aims refer to both minimizing negative experiences or situations and promoting positive ones, and the fifth one is entirely directed toward promoting positive experiences that have beneficial impacts on animal welfare (Table 5.2). Using this general framework in

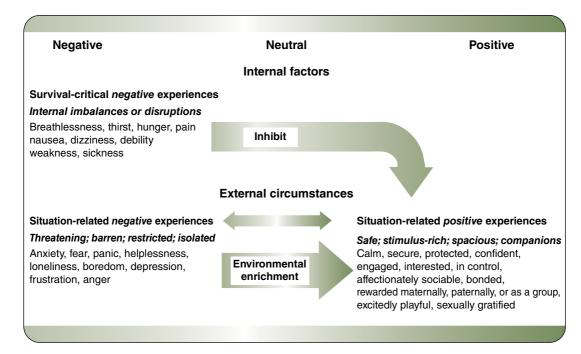


Fig. 5.6. Depiction of different subjective experiences, or affects, over the full valence range from negative to neutral to positive and relationships between the different types of experience. Internal factors, which include naturally occurring or induced functional imbalances or disruptions (captured mainly by Domains 1 to 3), give rise to survival-critical experiences (e.g., breathlessness, thirst, hunger, pain, nausea, sickness) that motivate animals to engage in behaviors aimed at securing life-sustaining resources (e.g., oxygen, water, food) or minimizing life-threatening harms (e.g., injury, food poisoning, infection). The valence of these experiences is negative, and their intensity ranges from exceptionally negative to neutral. External factors, which influence animals' perception of the levels of threat or safety, degrees of under-stimulation, or pleasurable stimulation from low to high, restrictions on or ease of movement, and social isolation or opportunities for companionable interaction with other animals (captured mainly by Domain 4), give rise to situation-related experiences over the full valence range from strongly negative to strongly positive. Environmental enrichment initiatives can replace situation-related negative experiences with positive experiences. Interactions between the different types of experience are apparent when the intensity of negative survival-critical experiences is sufficiently severe to demotivate or inhibit animals from utilizing available opportunities to engage in behaviors that would generate positive situation-related experiences. (Reproduced from Mellor [2017] with permission from the journal *Animals*.)

Table 5.2. Five Provisions and their aligned Animal Welfare Aims (Mellor, 2016b).

Provisions	Animal Welfare Aims
Good nutrition: Provide ready access to fresh water and a diet to maintain full health and vigor	Minimize thirst and hunger and enable eating to be a pleasurable experience
Good environment: Provide shade/shelter or suitable housing, good air quality, and comfortable resting areas	Minimize discomfort and exposure and promote thermal, physical, and other comforts
 Good health: Prevent or rapidly diagnose and treat disease and injury, and foster good muscle tone, posture, and cardiorespiratory function 	Minimize breathlessness, nausea, pain, and other aversive experiences and promote the pleasures of robustness, vigor, strength, and well-coordinated physical activity
 Appropriate behavior: Provide sufficient space, proper facilities, congenial company, and appropriately varied conditions 	Minimize threats and unpleasant restrictions on behavior and promote engagement in rewarding activities
Positive mental experiences: Provide safe, congenial, and species-appropriate opportunities to have pleasurable experiences	Promote various forms of comfort, pleasure, interest, confidence, and a sense of control

conjunction with the Five Domains model (Table 5.1) can guide wide ranging but highly focused, implementation of animal welfare initiatives.

5.9 Managing Welfare Using the Provisions Guided by the Welfare Aims

Finally, a question remains: given that affective experiences of welfare significance are subjective and therefore cannot be measured directly, how can animal welfare be managed practically?

The answer: by deploying fully updated provisions that improve nutritional and health inputs, husbandry actions, and physical facilities (Table 5.2). The provisions also have three key affect-related Welfare Aims: *first*, to minimize all known internal disturbances and/or imbalances to keep the related survival-critical negative affects at tolerably low levels; *second*, to improve opportunities for animals to engage in rewarding behaviors linked to positive situation-related affects that can replace some negative ones; *third*, to minimize the remaining known situation-related negative affects where their replacement remains difficult (Mellor, 2016b, 2017).

Knowledge of affects and their sensory origins therefore expands the focus of the provisions so they are more effective in achieving the updated Animal Welfare Aims (Mellor, 2016a,b). Thus, it is not necessary to measure affective experiences directly in order to manage them practically in ways that promote positive welfare states and improve overall animal welfare (Mellor, 2017).

5.10 References

- Anonymous. (1993) Second Report on Priorities for Research and Development in Farm Animal Welfare. Department of Environment, Food and Rural Affairs, Farm Animal Welfare Council, London, UK.
- Anonymous. (2009) Farm Animal Welfare in Great Britain:
 Past, Present and Future. Farm Animal Welfare Council,
 London, UK, pp. 243–254.
- Appleby, M.C., Mench, J.A., Olsson, J.A.S., Hughes, B.O. (eds.) (2011) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK. http://dx.doi.org/10.1079/ 9781845936594.0000.
- Baker, S.E., Sharp, T.M., Macdonald, D.W. (2016) Assessing animal welfare impacts in the management of European rabbits (*Oryctolagus cuniculus*), European moles (*Talpa europaea*) and carrion crows (*Corvus corone*). *PLoS ONE* 11, e0146298. http://dx. doi.org/10.1371/journal.pone.0146298.
- Beausoleil, N.J. and Mellor, D.J. (2012) Complementary roles for systematic analytical evaluation and qualitative

- whole animal profiling in welfare assessment for Three Rs applications. *ALTEX Proceedings* 1 (WC8), 455–460.
- Beausoleil, N.J. and Mellor, D.J. (2015) Advantages and limitations of the 'Five Domains' model for assessing animal welfare impacts associated with vertebrate pest control. *New Zealand Veterinary Journal* 63, 37–43. http://dx.doi.org/10.1080/00480169.2014.956832.
- Beausoleil, N.J. and Mellor, D.J. (2017) Validating sheep animal welfare indicators. In: Greyling, J. (ed.) Achieving Sustainable Production for Sheep. Burleigh Dodds Science Publishing Limited, Cambridge, UK, pp. 327–348
- Beausoleil, N.J., Blache, D., Stafford, K.J., Mellor, D.J., Noble, A.D.L. (2008) Exploring the basis of divergent selection for 'temperament' in domestic sheep. *Applied Animal Behaviour Science* 109, 261–274. http://dx.doi.org/10.1016/j.applanim.2007.03.013.
- Beausoleil, N.J., Fisher, P., Mellor, D.J., Warburton, B. (2012) Ranking the negative impacts of wildlife control methods may help to advance the Three Rs. *ALTEX Proceedings* 1 (WC8), 481–485.
- Beausoleil, N.J., Fisher, P., Littin, K.E., Warburton, B., Mellor, D.J., et al. (2016) A systematic approach to evaluating and ranking the relative animal welfare impacts of wildlife control methods: Poisons used for lethal control of brushtail possums (*Trichosurus* Vulpecula) in New Zealand. Wildlife Research 43, 553–565. http://dx.doi.org/10.1071/WR16041.
- Berridge, K.C. (1996) Food reward: Brain substrates of wanting and liking. *Neuroscience and Biobehavioral Reviews* 20, 1–25. http://dx.doi.org/10.1016/0149-7634(95)00033-B.
- Boissy, A. and Lee, C. (2014) How assessing relationships between emotions and cognition can improve farm animal welfare. *Scientific and Technical Review, Office International des Epizooties* 33, 103–110.
- Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., et al. (2007) Assessment of positive emotions in animals to improve their welfare. *Physiology* and Behavior 92, 375–397. http://dx.doi.org/10.1016/j. physbeh.2007.02.003.
- Broom, D.M. (1986) Indicators of poor welfare. *British Veterinary Journal* 142, 524–526.
- Buckland, E.L., Corr, S.A., Abeyesinghe, S.M., Wathes, C.M. (2014) Prioritisation of companion dog welfare issues using expert consensus. *Animal Welfare* 23, 39–46.
- Burgdorf, J. and Panksepp, J. (2006) The neurobiology of positive emotions. *Neuroscience and Biobehavioral Reviews* 30, 173–187. http://dx.doi.org/10.1016/j. neubiorev.2005.06.001.
- Butterworth, A. (2017) Report of the Workshop to Support the IWC's Consideration of Non-Hunting Related Aspects of Cetacean Welfare (IWC/66/WKM&WI Report 01). International Whaling Commission, Cambridge, UK. Available at: https://www.researchgate.net/publication/315492266_Report_of_the_

- Workshop_to_Support_the_IWC's_Consideration_ of_Non-Hunting_Related_Aspects_of_Cetacean_ Welfare (accessed 17 November 2018).
- Clegg, I.L.K. and Delfour, F. (2018) Can we assess marine mammal welfare in captivity and in the wild? Considering the example of bottlenose dolphins. *Aquatic Mammals* 44, 181–200. http://dx.doi.org/10.1578/AM.44.2.2018.181.
- Clegg, I.L.K., Van Elk, C.E., Defour, F. (2017) Applying welfare science to bottlenose dolphins (*Tursiops trun*catus). Animal Welfare 26, 165–176.
- Dawkins, M.S. (2006) Through the eyes of animals: What behaviour tells us. *Applied Animal Behaviour Science* 100, 4–10. http://dx.doi.org/10.1016/j.applanim. 2006.04.010.
- Denton, D.A., McKinley, M.J., Farrell, M., Egan, G.F. (2009) The role of primordial emotions in the evolutionary origin of consciousness. *Consciousness and Cognition* 18, 500–514. http://dx.doi.org/10.1016/j.concog.2008.06.009.
- Edgar, J.L., Mullan, S.M., Pritchard, J.C., McFarlane, U.J.C., Main, D.C.J. (2013) Towards a 'good life' for farm animals: Development of a resource tier framework to achieve positive welfare for laying hens. *Animals* 3: 584–605. https://doi.org/10.3390/ani3030584.
- Elzanowski, A. (2006) Establishing the Three Rs principle: A plea for an international severity standard. *ALTEX* 23. Special Issue. 135–140.
- Fraser, D. (2008) Understanding Animal Welfare: The Science in Its Cultural Context. Wiley-Blackwell, Oxford, UK. http://dx.doi.org/10.1186/1751-0147-50-S1-S1.
- Fraser, D. and Duncan, I.J.H. (1998) 'Pleasures', 'pains' and animal welfare: Towards a natural history of affect. Animal Welfare 7, 383–396.
- Fraser, D. and Nicol, C.J. (2011) Preference and motivation research. In: Appleby, M.C., Mench, J.A., Olsson, J.A.S. and Hughes, B.O. (eds.) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK, pp. 183–199. http://dx.doi.org/10.1079/9781845936594.0183.
- Fraser, D., Weary, D.M., Pajor, E.A., Milligan, B.N. (1997) A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare* 6, 187–205.
- Fraser, D., Duncan, I.J.H., Edwards, S.A., Grandin, T., Gregory, N.G., et al. (2013) General principles for the welfare of animals in production systems: The underlying science and its application. The Veterinary Journal 198, 19–27. http://dx.doi.org/10.1016/j.tvjl.2013.06.028.
- Grandin, T. (ed.) (2015) Improving Animal Welfare: A Practical Approach, 2nd edn. CAB International, Boston, Massachusetts, USA. http://dx.doi.org/10.1079/ 9781780644677.0000.
- Green, T.C. and Mellor, D.J. (2011) Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. New Zealand Veterinary Journal 59, 316–324. http://dx.doi.org/10.1080/00480169.2011 .610283.

- Gregory, N.G. (1998) Physiological mechanisms causing sickness behaviour and suffering in diseased animals. Animal Welfare 7, 293–305.
- Gregory, N.G. (2004) Physiology and Behaviour of Animal Suffering. Blackwell Science, Oxford, UK. http://dx.doi.org/10.1002/9780470752494.
- Hemsworth, P.H., Mellor, D.J., Cronin, G., Tilbrook, A. (2015) Scientific assessment of animal welfare. *New Zealand Veterinary Journal* 63, 24–30. http://dx.doi.org/10.1080/00480169.2014.966167.
- Ikemoto, S. and Panksepp, J. (1999) The role of nucleus accumbens dopamine in motivated behavior: A unifying interpretation with special reference to rewardseeking. *Brain Research Reviews* 31, 6–41. http://dx. doi.org/10.1016/S0165-0173(99)00023-5.
- Jones, B. and Boissy, A. (2011) Fear and other negative emotions. In: Appleby, M.C., Mench, J.A., Olsson, J.A.S. and Hughes, B.O. (eds.) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK, pp. 78–97. http://dx.doi.org/10.1079/9781845936594.0078.
- Kagan, R., Carter, S., Allard, S. (2015) A universal animal welfare framework for zoos. *Journal of Applied Animal Welfare Science* 18, S1–S10. http://dx.doi.org/10.1080/10888705.2015.1075830.
- King, L. and Rowan, A.N. (2005) The mental health of laboratory animals. In: McMillan, F.D. (ed.) Mental Health and Well-being in Animals. Blackwell Publishing, Oxford, UK, pp. 259–276. http://dx.doi.org/10.1002/ 9780470384947.ch19.
- Kirkden, R.D. and Pajor, E.A. (2006) Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. Applied Animal Behaviour Science 100: 29–47. http://dx.doi.org/10.1016/j. applanim.2006.04.009.
- Ledger, R.A. and Mellor, D.J. (2018) Forensic use of the Five Domains Model for assessing suffering in cases of animal cruelty. *Animals* 8, 101. doi:10.3390/ ani8070101 http://dx.doi.org/10.3390/ani8070101.
- Lim, M.M. and Young, L.J. (2006) Neuropeptidergic regulation of affiliative behavior and social bonding in animals. Hormones and Behavior 50, 506–517. http://dx.doi.org/10.1016/j.yhbeh.2006.06.028.
- Littin, K., Fisher, P., Beausoleil, N.J., Sharp, T. (2014) Welfare aspects of vertebrate pest control and culling: Ranking control techniques for humaneness. Scientific and Technical Review, Office International des Epizooties 33, 281–289.
- Littlewood, K.E. and Mellor, D.J. (2016) Changes in the welfare of an injured working farm dog assessed using the Five Domains Model. *Animals* 6, 58. https:// doi.org/10.3390/ani6090058.
- Mason, G. and Rushen, J. (eds.) (2006) Stereotypic Animal Behaviour: Fundamentals and Implications for Animal Welfare, 2nd edn. CAB International, Wallingford, UK. http://dx.doi.org/10.1079/ 9780851990040.0000.
- McGreevy, P., Berger, J., de Brauwere, N., Doherty, N.O., Harrison, A., et al. (2018) Using the five domains

- model to assess the adverse impacts of husbandry, veterinary, and equitation interventions on horse welfare. *Animals* 8, 41. https://doi.org/10.3390/ani8030041
- McMillan, F.D. (2003) Maximizing quality of life in ill animals. Journal of the American Animal Hospital Association 39, 227–235. http://dx.doi.org/10.5326/0390227.
- McMillan, F.D. (2005) The concept of quality of life in animals. In: McMillan, F.D. (ed.) Mental Health and Wellbeing in Animals. Blackwell Publishing, Oxford, UK, pp. 183–200. http://dx.doi.org/10.1002/9780470384947. ch13.
- McMillan, F.D. (2007) Predicting quality of life outcomes as a guide for decision-making: The challenge of hitting a moving target. *Animal Welfare* 16, 135–142.
- McMillan, F.D. (2016) The psychobiology of social pain: Evidence for a neurocognitive overlap with physical pain and welfare implications for social animals with special attention to the domestic dog (*Canis familiaris*). *Physiology and Behavior* 167, 154–171. http://dx.doi.org/10.1016/j.physbeh.2016.09.013.
- Mellor, D.J. (2004a) Comprehensive assessment of harms caused by experimental, teaching and testing procedures on live animals. *Alternatives to Laboratory Animals* 32(Suppl. S1), 453–457.
- Mellor, D.J. (2004b) Taming and training of pregnant sheep and goats and of newborn lambs, kids and calves before experiment. Alternatives to Laboratory Animals 32(Suppl. S1), 143–146.
- Mellor, D.J. (2012a) Animal emotions, behaviour and the promotion of positive welfare states. New Zealand Veterinary Journal 60, 1–8. http://dx.doi.org/10.1080/ 00480169.2011.619047.
- Mellor, D.J. (2012b) Affective states and the assessment of laboratory-induced animal welfare impacts. *ALTEX Proceedings* 1(WC8), 445–449.
- Mellor, D.J. (2015a) Enhancing animal welfare by creating opportunities for 'positive affective engagement'. New Zealand Veterinary Journal 63, 3–8. http://dx.doi.org/10.1080/00480169.2014.926799.
- Mellor, D.J. (2015b) Positive welfare states and promoting environment-focused and animal-to-animal interactive behaviours. New Zealand Veterinary Journal 63, 9–16. http://dx.doi.org/10.1080/00480169.2014.92 6800.
- Mellor, D.J. (2015c) Positive animal welfare states and reference standards for welfare assessment. *New Zealand Veterinary Journal* 63, 17–23. http://dx.doi.org/10.1080/00480169.2014.926802.
- Mellor, D.J. (2016a) Updating animal welfare thinking: Moving beyond the 'Five Freedoms' to 'A Life Worth Living'. Animals 6, 21. https://doi.org/10.3390/ ani6030021.
- Mellor, D.J. (2016b) Moving beyond the 'Five Freedoms' by updating the 'Five Provisions' and introducing aligned 'Animal Welfare Aims'. *Animals* 6, 59. doi:10.3390/ ani6100059.

- Mellor, D.J. (2017) Operational details of the Five Domains Model and its key applications to the assessment and management of animal welfare. *Animals* 7, 60. doi:10.3390/ani7080060.
- Mellor, D.J. (2018) Tail docking of canine puppies: Reassessment of the tail's role in communication, the acute pain caused by docking and interpretation of behavioural responses. *Animals* 8, 82. www.mdpi. com/2076-2615/8/6/82.
- Mellor, D.J. and Beausoleil, N.J. (2015) Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare* 24, 241–253.
- Mellor, D.J. and Beausoleil, N.J. (2017) Equine welfare during exercise: An evaluation of breathing, breathlessness and bridles. *Animals* 7, 41. doi:10.3390/ani7060041.
- Mellor, D.J. and Reid, C.S.W. (1994) Concepts of animal well-being and predicting the impact of procedures on experimental animals. In: Australian and New Zealand Council for the Care of Animals in Research and Teaching. Improving the Well-being of Animals in the Research Environment. Glen Osmond, South Australia, pp. 3–18.
- Mellor, D.J. and Webster, J.R. (2014) Development of animal welfare understanding drives change in animal welfare standards. Scientific and Technical Review, Office International des Epizooties 33, 121–130.
- Mellor, D.J., Patterson-Kane, E., Stafford, K.J. (2009) *The Sciences of Animal Welfare*. Wiley-Blackwell, Oxford, UK.
- Mellor, D.J., Hemsworth, P.H., Barnett, J.L., Young, I.R. (2012) Species-specific approaches are needed for effective implementation of the Three Rs in farm animal research. ALTEX Proceedings 1(WC8), 469–476.
- Mellor, D.J., Hunt, S., Gusset, M. (eds.) (2015) Caring for Wildlife: The World Zoo and Aquarium Animal Welfare Strategy. World Association of Zoos and Aquariums Executive Office, Gland, Switzerland.
- Mendl, M., Burman, O.H.P., Paul, E.S. (2010) An integrative and functional framework to the study of animal emotion and mood. *Proceedings of the Royal Society B, Biological Science* 277, 2895–2904. http://dx.doi.org/10.1098/rspb.2010.0303.
- Nelson, E. and Panksepp, J. (1998) Brain substrates of infant–mother attachment: Contributions of opioids, oxytocin, and norepinepherine. *Neuroscience and Biobehavioral Reviews* 22, 437–452. http://dx.doi. org/10.1016/S0149-7634(97)00052-3.
- Numan, M. and Insel, T.R. (2003) *The Neurobiology of Parental Behavior*. Springer, New York, USA.
- Orlans, F.B. (2000) Public policies on assessing and reporting degrees of animal harm: International perspectives. In: Balls, M., van Zeller, A.-M. and Halder, M.E. (eds.) *Progress in Reduction, Refinement and Replacement of Animal Experimentation*. Elsevier Science, Amsterdam, The Netherlands, pp. 1075–1082.

- Panksepp, J. (1993) Rough-and-tumble play: A fundamental brain process. In: MacDonald, K.B. (ed.) *Parents and Children Playing*. SUNY Press, Albany, New York, USA, pp. 147–184.
- Panksepp, J. (1998) Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, London, UK.
- Panksepp, J. (2005) Affective consciousness: Core emotional feelings in animals and humans. Consciousness and Cognition 14, 30–80. http://dx.doi.org/10.1016/j.concog.2004.10.004.
- Panksepp, J. (2006) Emotional endophenotypes in evolutionary psychiatry. *Progress in Neuropsychopharmacology and Biological Psychiatry* 30, 774–784. http://dx.doi.org/10.1016/j.pnpbp.2006.01.004.
- Panksepp, J. and Zellner, M.R. (2004) Towards a neurologically based unified theory of aggression. *Revue Internationale de Psychologie Sociale* 17, 37–61.
- Panksepp, J., Fuchs, T., Iacobussi, P. (2011) The basic neuroscience of emotional experience in mammals: The case of subcortical FEAR circuitry and implications for clinical anxiety. *Applied Animal Behaviour Science* 129, 1–17. http://dx.doi.org/10.1016/j.applanim.2010.09.014.
- Portas, T. (2013) Achieving positive animal welfare outcomes in zoos and aquariums. In Proceedings of the 2013 RSPCA Australia Scientific Seminar, When Coping Is Not Enough: Promoting Positive Welfare States in Animals, Canberra, Australia, pp. 46–50. Available at: https://www.rspca.org.au/sites/default/files/website/The-facts/Science/Scientific-Seminar/2013/SciSem_2013_Proceedings.pdf (accessed 30 November 2018).
- Rolls, E.T. (2007) *Emotion Explained*. Oxford University Press, Oxford, UK.
- Sharp, T. and Saunders, G. (2008) A Model for Assessing the Relative Humaneness of Pest Animal Control Methods. Australian Government Department of Agriculture, Fisheries and Forestry, Canberra, Australia.
- Sharp, T. and Saunders, G.A (2011) Model for Assessing the Relative Humaneness of Pest Animal Control Methods, 2nd edn. Australian Department of Agriculture and Water Resources, Canberra, Australia.
- Sherwen, S.L., Hemsworth, L.M., Beausoleil, N.J., Embury, A., Mellor, D.J. (2018) An animal welfare

- risk assessment process for zoos. *Animals* 8, 130. https://doi.org/10.3390/ani8080130
- Spinka, M. and Wemelsfelder, F. (2011) Environmental challenge and animal agency. In: Appleby, M.C., Mench, J.A., Olsson, I.A.S. and Hughes, B.O. (eds.) Animal Welfare, 2nd edn. CAB International, Wallingford, UK, pp. 27–43. http://dx.doi.org/10.1079/9781845936594.0027.
- Verbeek, E., Waas, J.R., Oliver, M.H., McLeay, L.M., Ferguson, D.M., et al. (2012) Motivation to obtain a food reward of pregnant ewes in negative energy balance: Behavioural, metabolic and endocrine considerations. Hormones and Behavior 62, 162–172. http:// dx.doi.org/10.1016/j.yhbeh.2012.08.007.
- Viňuela-Fernández, I., Weary, D.M., Flecknell, P. (2011) Pain. In: Appleby, M.C., Mench, J.A., Olsson, I.A.S. and Hughes, B.O. (eds.) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK, pp. 64–77.
- Webster, J. (1994) Assessment of animal welfare: The five freedoms. In: Animal Welfare: A Cool Eye Towards Eden. Blackwell Science, Oxford, UK, pp. 10–14.
- Webster, J. (2005) Animal Welfare: Limping Towards Eden. Wiley-Blackwell, Chichester, UK. http://dx.doi. org/10.1002/9780470751107.
- Webster, J. (2011) Management and Welfare of Farm Animals. UFAW Farm Handbook. Wiley-Blackwell, Chichester, UK.
- Wemelsfelder, F (1997) The scientific validity of subjective concepts in models of animal welfare. *Applied Animal Behaviour Science* 53: 75–88. http://dx.doi.org/10.1016/S0168-1591(96)01152-5.
- Wemelsfelder, F. (2005) Animal boredom: Understanding the tedium of confined lives. In: McMillan, F.D. (ed.) Mental Health and Well-being in Animals. Blackwell Publishing, Oxford, UK, pp. 79–91.
- Williams, V.M, Mellor, D.J., Marbrook, J. (2006) Revision of a scale for assessing the severity of live animal manipulations. ALTEX 23 (Special Issue), 163–169.
- Yeates, J.W. and Main, D.C.J. (2008) Assessment of positive welfare: A review. *The Veterinary Journal* 175, 293–300. http://dx.doi.org/10.1016/j.tvjl.2007.05.009.
- Young, R.J. (2003) Does environmental enrichment work? In: Environmental Enrichment for Captive Animals. Blackwell Science, Oxford, UK, pp. 31–44. http://dx.doi.org/10.1002/9780470751046.ch3.

6

The Mental Health and Well-being Benefits of Personal Control in Animals

FRANKLIN D. McMILLAN

Best Friends Animal Society, Kanab, Utah, USA

The value of perceived control in the lives of humans and nonhuman animals (hereafter animal) has been the subject of investigation for over a half century. What began as a concept of control in life overall (Rotter, 1966) has been subsequently characterized to also include control over specific domains of one's life and even a specific aversive event. All of these conceptualizations of control have demonstrated links to animal mental health and well-being.

It has long been known that stressors come in a vast array of forms, and while the various factors that make stressors more or less impactful on the individual are not fully understood, the concept of control has emerged as a crucial factor (Steptoe and Poole, 2016). Stressors differ in the degree to which they can be controlled, and the relation between control over an aversive event and the amount of stress or pain the event produces has formed the basis for control becoming a dominant idea in psychological theory and research (Wallston, 2004; Thompson, 2005). Common sense would suggest that the greater the extent that individuals believe that they can prevent, terminate, or lessen the severity of aversive events, the less reason they would have to worry about or fear them (Rodin, 1986). In humans, control is now a major concept in a number of theories of emotional well-being and happiness (Thompson and Kyle, 2000), and Larsen (1989) has written that the ability to yield control for the short term and endure life's inevitable occasions of discontrol without substantial distress could reasonably be seen as a defining criterion of mental health.

Research has found control to be crucial for a wide range of animal species, including apes, rodents, birds, and fish, indicating that the organism's desire to influence the impact of aversive and appetitive interactions with the world appears to be central to animal life (Franks and Higgins, 2012). However, one of the defining features distinguishing captive and wild environments is the reduced amount of control captive animals have over what happens to them and the conditions that affect them (Franks and Higgins, 2012; Bassett and Buchanan-Smith, 2007; Jones and McGreevy, 2007) (Fig. 6.1). Noting this, Markowitz and Eckert (2005) have questioned how we can expect animals in our charge to be mentally healthy if they perceive that nothing that they do matters.

This chapter will focus on the importance of the perception of control in animals, drawing on the human literature to inform and supplement our understanding where communication barriers impair our ability to obtain relevant information from the animals.

6.1 Defining and Characterizing Control¹

In the presence of an aversive stimulus,² control may be defined as the perception that one has the ability to produce a response that can influence the aversiveness of an event in a way that maximizes desired outcomes and/or minimizes undesired ones (Thompson, 1981, 2005; Peterson, 1999). Such a response allows the individual to, at will, terminate the event, make it less probable or less intense, or change its duration or timing (Thompson, 1981; Foa et al., 1992) (see Fig. 6.2).

Choice has frequently been considered an important feature of control. For example, Leotti *et al.* (2010) argue that choice is the means by which organisms exert control over the environment. They maintain that although much of the cognitive

processing for behavior involving choice occurs below the state of explicit awareness, all voluntary behavior involves choice, nonetheless. Accordingly, to choose is to express a preference, and that preference is for options that are conducive to achieving favored rewards (Leotti *et al.*, 2010). People report that the acquisition of choice leads to an increased sense of personal control (Rotter, 1966).

Research has further refined the concept of control to whether *actual* control is required to be present or if the individual only has to think that it is. Data indicate in both animals and humans that the beneficial psychological and physiological effects of



Fig. 6.1. Captive animals very often have little or no control over their lives. (Image used under license from Shutterstock.com.)

control are experienced even in the absence of true control over aversive events, as well as if the individual has the opportunity to exert control but never actually exercises that option (Perlmuter and Monty, 1977). It is the mere *perception* of control, independent of whether it is exercised, that appears to be important (Bollini *et al.*, 2004).

6.2 Locus of Control

Rotter (1966) presented evidence that people differ in the extent to which they believe that valued outcomes are determined by forces within or outside their own control. He termed this construct the *locus of control* (LOC), where the locus referred to whether the person perceives that rewards follow from, or are contingent upon, his own behavior or attributes – an *internal* locus of control – as opposed to the belief that rewards are controlled by forces outside of himself and tend to occur independently of his own actions – an *external* locus of control (Rotter, 1966).

Rotter (1966) further noted that one's sense of control applies to both individual aversive experiences and life overall. This has created confusion in the literature, as 'perceived control' is often used without clarification as to whether the writer is referring to a specific event, life in general, or a particular domain of life (Thompson, 2005; Steptoe and Poole, 2016). Yet because the scope of control can differ, one could have a high degree of internal LOC in life yet have no perceived control over a specific situation,

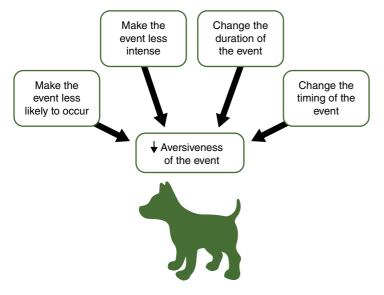


Fig. 6.2. Different ways the perception of control is believed to decrease the aversiveness of unpleasant stimuli and events.

and, conversely, have a high degree of perceived control over a specific situation but a low external LOC for life overall. In Rotter's (1966) original conceptualization LOC referred nonspecifically to either control over specific events or control in life events overall; however, the latter is now the generally accepted interpretation of LOC.

The extent to which the construct of the LOC exists in animals is an unanswered question. Little direct evidence exists, and tests designed for determining LOC in children are not useful for animals as they ask the children whether they attribute causes of imaginary events to internal or external forces. Importantly, however, LOC is conceived as a generalized expectancy construct, meaning that it represents individuals' expectations about receiving desired reinforcements (Rotter, 1966; Wallston, 2004). This in turn raises the consideration of another psychological attribute for which expectancy is a central element: optimism (Scheier and Carver 1992; Peacock and Wong 1996; Gruber-Baldini et al., 2009). Optimism consists of the expectation that good things, rather than bad things, will happen and is considered an aspect of personality (Bollini et al., 2004; Gruber-Baldini et al., 2009). While retaining certain conceptual differences, optimism and LOC have been found to be moderately related and overlapping concepts (Peacock and Wong, 1996). The primary difference is that LOC is the belief that one has control over desirable outcomes, whereas optimism is the expectation of positive outcomes regardless of whether or not they are a result of one's own actions (Peacock and Wong, 1996). The trait of optimism/pessimism has been tentatively identified in animals over the past decade in the studies of cognitive and judgment bias (Rygula et al., 2015). Still often placed in quotation marks to avoid accusations of anthropomorphism, optimism and pessimism in animals describe a system of expectations analogous to the corresponding cognitive mechanisms in humans.

The optimism connection offers a plausible link between animals and LOC, but an additional connection derives from Rotter's (1966, pp. 19–20) original proposal that the scale which measures internal versus external LOC 'appears to measure a psychological equivalent of ... the sense of powerlessness'. As we will see, powerlessness – or the perception of uncontrollability – has been extensively studied in animals.

However, because LOC as characterized in humans has not been definitively identified in animals, the use of this term in this chapter will be exclusive to humans. Thus, for animals as well as humans, the two types of control – that which is specific to a particular stimulus or event and that which applies to life in general – will be referred to as, respectively, *event-specific control* and *general control* (both terms will refer to perceived rather than actual control). General control may be considered in humans to be analogous to LOC.

6.3 The Desirability of Control

Human psychology research has found that the preference for control varies widely among individuals; some individuals appear to have a high desire for control while others prefer to wield less and even no control (Verme, 2009; Steptoe and Poole, 2016). In experimental studies it is not uncommon for some people, when given a choice between controllable and uncontrollable aversive events, to opt for the uncontrollable (Rodin, 1986). More recently, Buchanan-Smith and Badihi (2012) have identified in marmosets comparable individual preferences for making choices.

Notwithstanding the interindividual variance in the desire for control, research indicates that control is generally desired (Catania and Sagvolden, 1980; Overmier et al., 1980; Suzuki, 1999) and likely a psychological necessity in humans and animals (Leotti et al., 2010). In a series of experiments with rodents, Kavanau (1964, 1967) reported that captive rodents exercise control virtually any chance they get, apparently finding it rewarding to exert a high degree of control over their environment. If a light is turned on by the experimenter the animal will turn it off, but if the experimenter turns the light off, the animal, even though nocturnal, will turn it back on. If the experimenter turns on a motorized running wheel, the animal immediately and invariably turns the motor off. However, if the animal is running on such a wheel and the experimenter turns the motor off, the animal immediately turns the motor back on. If mice were awakened from sleep and emerged from their nest boxes, they would soon go back inside on their own. If, however, the experimenters picked the mice up and placed them in the nest box, they would immediately come back out, even if they were placed repeatedly back in the box. In all,

rodents repeatedly turn on and off (or otherwise modify) any suitable variable placed under their control, whether it is intracranial stimulation, a motor-driven activity wheel, lights or sound, or whether it is merely the ability to visit a nest, run a wheel, jump on and off a platform, patrol an enclosure, traverse mazes, or gnaw wood into fine fibers. (Kavanau, 1964, p. 490)

Earlier it was mentioned that one of the basic ways an organism can exert control is through choice. The desire for choice has been studied in several species. When deciding between two options, pigeons (Catania and Sagvolden, 1980) and macaques (Suzuki, 1999) preferred the option that led to a second choice over one that did not, even though both options ultimately led to the same outcome and making a second choice required greater energy expenditure. Rats expressed a preference for a pathway that led to a choice between additional pathways rather than a pathway leading directly to the reward, despite the fact that all pathways eventually led to the same reward (Voss and Homzie, 1970).

The desire for control also appears to at least partially explain the phenomenon of contra-freeloading, in which animals choose to work for an outcome even when the outcome is freely available (Franks and Higgins, 2012). As just one of many examples, Carder and Berkowitz (1970) reported that rats able to acquire free food from a dish would instead push the food dish aside in order to access a pressable lever that would cause a pellet of the same food to fall out for them to eat.

Collectively, these findings imply that the actual nature of the stimulus might not matter as long as the animal can exert some form of control over it and that exercising control can be rewarding in and of itself (Leotti *et al.*, 2010). That the existence of the desire for control is found in many animal species as well as very young human infants led Leotti *et al.* (2010) to propose that this desire is innate and likely a psychological and biological imperative for survival.

6.4 The Relationship of Control to Mental Health and Well-being

In humans, an extensive theoretical and empirical literature has documented consistent positive correlations between personal control and each of the principal well-being constructs, including general well-being (Larson, 1989; Peterson, 1999), subjective well-being (Spector *et al.*, 2001), emotional well-being (Thompson, 2005; Thompson and Kyle, 2000), and happiness (Larson, 1989; Peterson, 1999; Verme, 2009). Another well-being construct, life

satisfaction, is very strongly associated with freedom of choice combined with one's LOC (Verme, 2009). Most broadly, a general sense of control over one's life appears to be a requirement for positive mental health (Larson, 1989).

Optimism, mentioned earlier in regard to its overlapping relationship to LOC, has been found in humans to be correlated with happiness (Verme, 2009). Similarly, optimism has been shown to have numerous beneficial effects on psychological wellbeing, including improved coping with stress and adversity (Scheier and Carver, 1992).

General effects of perceived control on well-being, happiness, and life satisfaction have been well researched in humans. However, due to limitations in animals of self-reporting and accurate assessment of long-term affective well-being states, evidence of a connection between control and well-being in nonhuman species has relied on the demonstration of indirect links between these two concepts, specifically, correlations between control and separate elements, which, taken together, comprise mental health and well-being. For instance, studies may focus on how control impacts the contributors and indicators of well-being, such as reduced stress, but not necessarily identify a direct impact on wellbeing itself. The evidence for this has emerged from two general areas: the positive effects of possessing control (see Section 6.5), and the negative effects of being denied control (discussed with the concept of learned helplessness, see Section 6.7).

6.5 Effects of Control in Animals

Determining the effects of a cognitive process in animals requires an experimental design that equates all variables between two animals except the cognitive process itself, which allows the conclusion that the observed differences between the animals may be attributed to that specific cognitive process. The classic experimental method for this purpose has been the yoked design, in which a pair of animals are exposed to the same aversive stimulus (e.g., electric shocks or loud noise). One animal, but not the other (yoked), is able to make a behavioral response which terminates the stimulus. The yoked animal thereby receives the same amount of the aversive stimulus as the first animal allows – or disallows - for itself, and any differences in outcomes (physiological or pathological) are presumed to result from the (non)availability of control (Steptoe and Poole, 2016).

Animals with perceived control over aversive events benefit from a diverse array of robust effects, such as a reduced intensity of physiological stress responses (autonomic reactivity and corticosteroid levels) (Joffe et al., 1973; Rodin, 1986), improved coping with a stressful situation (Seligman, 1975), an increase in calm activity (Buchanan-Smith and Badihi, 2012), and a greater ability to relax and function effectively even in potentially dangerous situations (Joffe et al., 1973). The perception of control allays the emotions of fear and anxiety (Solomon and Wynne, 1953; Sambrook and Buchanan-Smith, 1997) and may delay the onset of distress (Russell and Burch, 1959; Wolfensohn et al., 2018). Control appears to exert at least part of its effects through an active fear-inhibitory process such that when an animal processes that it has control over the aversive stimulus neural mechanisms are activated that reduce the generalization of fear, and the fear diminishes (Foa et al., 1992).

Cognitive functioning is also influenced by perceived control. When rats were given control over food or electric shock they subsequently exhibited enhanced learning in a shock avoidance task (Goodkin, 1976). When rats were able to control environmental lighting they performed significantly better over time in a discrimination task compared with rats without such control (Alliger and Moller, 2011).

6.5.1 How does control exert its beneficial effects?

The neuropsychological processes explaining how the perception of control exerts its beneficial effects are still far from understood (Thompson, 2005). Miller (1979) hypothesized that individuals who believe that they have control know that an aversive situation can be allayed at any time and thus can always be kept within the limits of what the individual can endure. The individual thereby feels comforted by the knowledge that he or she is protected against experiences becoming unbearable, allowing the individual to be relaxed and fully functional even in potentially threatening situations. From a different perspective, the benefits of control may derive from the ability to alter the various affective experiences of life. A prominent theoretical model of well-being in humans (Bradburn, 1969; Lyubomirsky et al., 2005) and animals (Broom, 2007; Green and Mellor, 2011; Yeates, 2011) is that well-being results from, or is otherwise associated with, a predominantly positive balance of pleasant feelings

over unpleasant. In this view, control would exert its mental benefits by being a major factor in the animal's (or person's) ability to tip this balance in the desired direction. Overall, despite the gaps in knowledge of specific mechanisms it is clear that the perception of control in humans and animals provides broad and profound benefits for mental health and well-being.

6.6 Predictability

The question of why control should reduce the stress related to an aversive event has been approached differently by researchers who propose that the *predictability* of the event plays an integral role (Mineka and Hendersen, 1985; Foa *et al.*, 1992). An event is unpredictable when its probability of occurrence is the same regardless of the events preceding it (Foa *et al.*, 1992). An overlapping and complex interrelationship between control and predictability has been well-recognized, and several authors have questioned whether the two concepts are distinct and separable (Dess-Beech *et al.*, 1983; Mineka and Hendersen, 1985; Foa *et al.*, 1992).

The interrelationship of controllability and predictability can be summarized succinctly. When an animal is given the control to terminate a noxious event then the end of the aversiveness necessarily becomes predictable. However, predictable events may or may not be controllable (Mineka and Hendersen, 1985). In many studies, events that were uncontrollable also tended to be unpredictable, and those that were controllable were also predictable, making it difficult to discern which of the two factors was responsible for the observed effects (Foa et al., 1992; Bassett and Buchanan-Smith, 2007). Even so, some researchers have argued that the two are separable variables with distinguishable effects (Miller, 1979; Overmier et al., 1980) and in experiments that have separated controllability and predictability, controllability has been found to have effects over and above the predictability it provides (Thompson, 1981).

The effects of predictability (in some cases in combination with or indistinguishable from the effects of control) beneficial to well-being include general findings such as predictable aversive events (electric shock) are less physically and psychologically deleterious than unpredictable events (Dess-Beech et al., 1983; Bassett and Buchanan-Smith, 2007). Predictability effectively reduces stress (Seligman, 1968; Rodin, 1986) and unpredictability can be a

cause of stress to animals (Taylor and Mills, 2007) as well as making aversive stimuli more stressful (Seligman, 1968; Sapolsky, 1994). For example, animals have more pronounced stress responses when aversive handling is unpredictable than when the same handling is conducted in a predictable way (Anonymous, 2001). Even in the absence of any stressor, the loss of predictability itself elicited a physiologic stress response (Sapolsky, 1994) in laboratory cats (Carlstead *et al.*, 1993b) and dogs (Dess-Beech *et al.*, 1983).

Fear and fear-related disorders are influenced by the degree of predictability. For example, unpredictable shock produces greater generalized fear and arousal than predictable shock, and danger unpredictability can directly produce increased generalized fear regardless of the degree of control (Foa et al., 1992). Studies using animal models of posttraumatic stress disorder (PTSD) have shown that the greater the degree of uncontrollability and unpredictability associated with a given stressor, the more likely the organism will be to develop symptoms of PTSD (Foa et al., 1992).

In contrast to the voluminous evidence of beneficial effects of predictability, some studies have indicated that predictable, but not unpredictable, events can *exacerbate* stress. Based on behavioral and physiological measures, stressors in some cases have been shown to be more aversive for animals if they are predictable (Dess-Beech *et al.*, 1983; Mineka and Hendersen, 1985; Bassett and Buchanan-Smith, 2007).

The question as to how predictability exerts its beneficial effects parallels the same question for controllability. For some theorists, the benefits of one can be ascribed to the other. For example, Averill (1973) has argued that the positive outcomes of having control can be attributed to the predictability inherent in control, while others reduce the effects of predictability to the effects of added control that comes by allowing the organism to 'prepare' for the forthcoming stressful event and thereby modify its impact (Mineka and Hendersen, 1985). This might occur, for instance, when animals receiving predictable shocks would change their posture in order to minimize the experienced intensity of the shocks (Bassett and Buchanan-Smith, 2007). Another explanation for the benefits of predictability is that knowledge of when a stressful event is going to occur also informs the animal when the event is not going to occur, i.e., safe periods (Thompson, 1981; Bassett and Buchanan-Smith, 2007). This 'Safety Signal' hypothesis posits that the feedback about safe periods alleviates the chronic state of fear elicited by the uncertainty of when danger might occur. The animal able to predict the event can therefore relax and not feel the need to be on constant alert for the threat (Tsuda *et al.*, 1983; Mineka and Hendersen, 1985). Sapolsky (1994, p. 258) illustrated this using a personal anecdote:

I've never appreciated the importance of predictability as much as after living through the 1989 San Francisco earthquake. Now I think, 'Those lucky people elsewhere, they know what time of year you don't have to worry much about tornadoes or hurricanes. But an earthquake, now that could be any second, maybe even while I'm sitting bumper-to-bumper beneath this highway overpass'.

Just as evidence argues for the desirability of control, substantial evidence also supports the desirable nature of predictability. Pigeons and rats showed a consistent preference for conditions allowing them to use signals to predict the presence or absence of food, compared with conditions where they were unable to predict food (Bassett and Buchanan-Smith, 2007). More compellingly, the preference for predictable over unpredictable electric shock is so pronounced that rats chose signaled rather than unsignaled shock even when the predictable shock was four to nine times longer and two to three times stronger than the unpredictable shock(Bassett and Buchanan-Smith, 2007).

6.7 Effects of No Control: Learned Helplessness

The above discussion of the effects of control in animals focused on the benefits observed when an animal perceives that it has control over aversiveness. Most research on the concepts of control (and predictability) has taken the opposite approach; that is, determining the harmful effects of *not* having control (or predictability). This work largely falls under the banner of *learned helplessness* (LH) and encompasses the most detrimental consequences for the mental health and well-being of animals and humans.

In 1967, Overmier and Seligman (1967) introduced the term learned helplessness to explain the constellation of effects they observed in dogs exposed to an uncontrollable and inescapable aversive stimulus (electric shock). Approximately 24 hours after

the shock exposure treatment 50% of the dogs, as compared to 12.5% of the unshocked control dogs, showed greatly impaired learning of a new shock avoidance task and would come to passively endure the shocks. The researchers suggested that the dogs realized that nothing they did mattered – the shocks occurred independently of any behavioral response. This, the researchers proposed, indicated that the dogs learned to be helpless. Subsequent studies found that repeated exposure to inescapable aversive stimuli led to a relatively consistent combination of cognitive, emotional, and motivational deficits that do not occur if the stressor is controllable (Maier and Watkins, 2005; McGreevy and McLean, 2009).

It quickly became established that animals and humans who experience uncontrollability in one situation become passive in that situation, but at the same time it became increasingly evident that the deficits associated with LH generalized, extending to situations beyond the specific aversive event to others that are normally amenable to control (Peterson, 1999) (see Fig. 6.3). It is now widely accepted that LH is characterized by: (i) the triad of emotional, cognitive, and motivational impairments; and (ii) evidence of generalization to new situations, i.e., the signs occur in circumstances different from the one in which uncontrollability was first encountered (Peterson, 1999; Maier and Watkins, 2005). Indeed, Peterson (1999, p. 295) has stated that, 'It is impossible to argue that learned helplessness is present without the demonstration of passivity in new situations.' The generalization



Fig. 6.3. Environments that deny the animal any meaningful control are detrimental to mental health and well-being. (Image used under license from Shutterstock.com.)

of LH effects in animals has been shown to be quite broad, making coping difficult with an array of tasks and challenges, even the most routine such as competing for food or avoiding social aggression (Joffe *et al.*, 1973; Seligman, 1975). Notably, this pronounced tendency for LH effects to generalize provides additional evidence for the existence of a sense of general control discussed in Section 6.2. In addition, the range of species in which LH has been identified has steadily expanded over the past 50 years (Franks and Higgins, 2012). The neurobiology of LH is complex, not fully understood, and has been reviewed elsewhere (Maier and Watkins, 2005).

To date the occurrence of LH in animals outside of the laboratory setting has been primarily speculation. Dogs in the kennel environment frequently show signs of apathy and loss of interest in surroundings, which increase with the duration of stay in the kennel (Wells et al., 2002), and several authors have suggested that this apathy may represent a form of LH (Wells et al., 2002; Taylor and Mills, 2007). Some equine researchers (Hall et al., 2008; McGreevy and McLean, 2009) have suggested the likelihood that some behavioral responses exhibited by the domestic horse, such as reduced motivation, anhedonia, lethargy, and cognitive deficits, are examples of LH. In fact, LH appears to be the objective of traditional 'breaking' of horses (Hall et al., 2008) and elephants (Bradshaw, 2009; Kontogeorgopoulos, 2009) – a training method that frequently involves extreme forms of restraint with ties and hobbles to prevent the animal from defying or escaping from the aversive punishment that is implemented. The animal is considered to be ready to be ridden or worked once it has ceased to resist, or 'given up'. LH has been suggested recently to be a consequence of lack of control in captive cetaceans (Atkinson and Dierauf, 2018; see also Chapter 22).

6.8 Implications and Practical Applications

6.8.1 Enhancing control in animals

Enhancing control is now well accepted in humans as a means to promote overall well-being and research continues on the best methods for increasing perceived control among those who are in low-control circumstances (Thompson and Kyle, 2000; Steptoe and Poole, 2016). Of course, the latter describes the lives of many if not most captive animals. There is

now a wide consensus that positive welfare can be promoted by providing captive animals with a degree of control (Yeates and Main, 2008; Sambrook and Buchanan-Smith, 1997). However, in the endeavor to positively affect animal well-being it is important to keep in mind that because of uncertainties such as control (and predictability) appearing to be beneficial in most circumstances but detrimental in others and, too, there being substantial individual variability in the desire for control, a potential exists for misapplication of current knowledge. Accordingly, care must be exercised in any efforts to increase control in individual and groups of animals.

Event-specific versus general control

In the approach to enhancing control in animals, it will be recalled that there are two types of control: event-specific control and general control. The first type has been the focus of the vast majority of research of control in animals, during which the animal is exposed to a very specific aversive stimulus such as electric shock. Enhancement of this specific type of control would involve providing resources needed for alleviation of the animal's distress about the specific aversive stimulus or event becoming too

much to bear (practical examples here include such things as a hiding place to escape 'bully' animal housemates and interactive toys to alleviate boredom). A noted study by Carlstead et al. (1993a) found that when the living environment of captive leopard cats was enriched with a complex of branches and hiding places, urinary cortisol concentrations and stereotypic pacing decreased. In addition, concealment locations that camouflage were more often used for lying down when urinary cortisol was elevated. These results suggested that for confined felids the provision of hiding places facilitates coping with aversive stimulation (see Fig. 6.4). The second type of control – general control (LOC in humans) – would, when enhanced, help alleviate general fears and worries not limited to a specific problem. Based on evidence in humans, this type of control appears to have the greatest impact on overall well-being and happiness.

Recognizing that control may be event-specific or general, it seems reasonable to develop enhancement methods for each type. But fortunately for therapeutic contexts, these two types are not separate and distinct. Evidence in animals (Peterson, 1999) and humans (Thompson and Kyle, 2000) suggests that enhancing perceived control in areas







Fig. 6.4. A secure hiding place – (a) in a closet, on an upper shelf; (b) under a bed; (c) near a burrow opening – provides a sense of control over numerous sources of fear. (Images used under license from Shutterstock.com.)

unconnected to a specific area of concern (e.g., one's physical health) can also help foster an *overall* sense of control. In fact, any activities that affirm a causal relationship between one's own action and a desired outcome may increase overall perceived control (Thompson and Kyle, 2000). Therefore, at our current level of understanding it may be unnecessary to make a distinction as to which type of control we are enhancing; efforts to enhance event-specific or general control are both likely to enhance the perception of general control.

Individualizing the enhancement of control

The recognition in humans of the interindividual variability in the desire for control (Verme, 2009; Steptoe and Poole, 2016) has led some investigators to posit that control may be helpful only if it matches recipients' desires and capabilities for exercising control (Thompson and Kyle, 2000). Because this individuality of desire has also been observed in animals (Buchanan-Smith and Badihi, 2012), similar notions may be applicable to nonhuman species. However, the means to determine animals' individual preferences for control outside the laboratory setting are lacking.

Individuality also appears to factor into the finding in humans that when it comes to control, more is not always better. For example, for some people the exercise of personal control can be taxing when choices are too numerous, too complex, or too difficult to act on (Peterson, 1999). Although some evidence in animals has shown that more options lead to greater benefits (e.g., Starr and Mineka [1977] found that rats learning 27 correct avoidance responses showed a greater reduction of fear of an aversive stimulus than those learning only three or nine responses), the human data would indicate that blanket recommendations such as 'captive animals should be provided with as many opportunities to control their environment as possible' (Buchanan-Smith and Badihi, 2012, p. 166) may be imprudent. Furthermore, there is a concern regarding the possibility of providing the circumstances for so much control and predictability that the environment becomes detrimental to animal well-being. For example, Wolfensohn et al. (2018) noted that the ideal environment is not one that is totally predictable and controllable, and that there is evidence that a certain degree of unpredictability is necessary to avoid the negative aspects of boredom. Another consideration involves the potential for too much control being a contributing element for the development of clinical behavior problems in companion animals. For example, Horwitz and Neilson (2007, p. 37) wrote that one risk factor for human-directed aggression in dogs is 'allowing the dog to determine the outcome in day-to-day interactions with humans in the home' – clearly an issue of the animal exercising control.

6.8.2 Methods for enhancing specific and general control

Enhancing control in early life

Some researchers in the human field believe that the contribution of LOC to happiness means that efforts to improve the sense of control in children may improve the likelihood of happiness during the later years of life (Verme, 2009). Evidence for such effects in animals is inferential, based on how the enhancement of control in very early life is associated with beneficial emotional well-being outcomes in adulthood. For example, Joffe et al. (1973) found that rats reared in environments where they could control access to food, water, and visual stimulation were subsequently less emotional and showed more exploratory behavior as compared to rats receiving the same food, water, and lighting conditions but without control over their occurrence. Similarly, two studies in rhesus monkeys demonstrated that an early life consisting of experiences of controllable events resulted in later reduced reactivity to stressful events (Suomi, 1991) and less fear in the presence of a toy robot, increased eagerness to enter and explore a novel and somewhat frightening playroom situation, and improved adaptability to stressful separations from peers (Mineka et al., 1986). Conflicting findings, where less control in early life led to better outcomes, seemed evident in a study with puppy owners who were given advice by a veterinary behaviorist that included removal of much if not all of the young dog's control. Instructions to the puppies' owners stated that the owner, not the puppy, should initiate all dog-human interactions, should not reward persistent attention-seeking behaviors, and should make all decisions regarding when to play with, pet, or feed the dog (Gazzano et al., 2008). When compared to dogs whose owners did not receive these instructions, the dogs whose owners received this advice went on to later exhibit fewer undesirable behaviors, including house soiling, mouthing of people, and aggressive behaviors.

Immunizing against adverse effects of uncontrollability

In a process showing similar effects as the early life exposure to controllability, but not restricted to the animal's developmental period, experience with controllable events imparts a protective effect – 'immunization' – against later detrimental effects of uncontrollability (Peterson, 1999). It appears that during this process the animal learns that events can be controlled, which provides positive expectations upon encountering subsequent uncontrollable events. As a result, the likelihood of LH is lessened (Peterson, 1999). Importantly, a major finding in these experiments was that the protective effects generalize, extending to situations and settings different from the ones used in the immunization procedure (Williams and Maier, 1977).

Practical applications

Recommendations for providing animals with control have been proposed. However, knowledge limitations have thus far prevented these recommendations from containing the specificity and detail necessary for reliable effectiveness. In contrast to the situation in humans (Rotter, 1966), there is currently no method to measure perceived control in animals. This leaves the biggest questions lacking answers, such as how do we know which animals need enhanced control, and what kind(s) and how much control? As a result, many recommendations for enhancing control for animals have consisted solely of the minimally helpful recommendations to 'provide control' or 'offer choices'.

The complex relationship between controllability and predictability further complicates the task of developing explicit applications for animal care. Addressing this interrelationship, Bassett and Buchanan-Smith (2007) proposed that in situations where providing control is impractical, making the events as predictable as possible may serve as a viable alternative and minimize the stress associated with a lack of control. As described earlier, predictability may be effective as a 'safety signal', indicating when aversive events would not occur and during which time the animal need not be in a constant state of anticipation of the events. Yet once again, deficiencies in our understanding could mislead us in applying the knowledge correctly. For example, animals with separation anxiety learn the signals predicting the aversive event (the owner leaving the home) very clearly, and a major objective of treatment is to *eliminate* those signals and make the undesired event – the owner leaving – *less* predictable (Landsberg *et al.*, 2013). Although the discussion below focuses on control, much research suggests that many of the same points and recommendations could apply to enhancing predictability.

Recommendations appearing in the animal welfare and behavior literature are compiled in Table 6.1. A number of methods of control enhancement are included, which range from altering the environment to managing the way humans interact with the animals, such as training methods used. In short, methods involve anything that can promote the animals' learning that their actions can improve their chances for desirable things to happen, in particular for those things that matter most, i.e., alleviating aversive experiences (McGreevy and McLean, 2009). It should be kept in mind, too, that because the effects of control can involve stimuli that are appetitive as well as aversive² (Peterson, 1999), both types should be included when considering the options for enhancing the degree of control for the captive animals.

6.8.3 Therapeutic considerations

In addition to the preventive effects of enhanced control being a safeguard and improving mental health and well-being, a more recent line of research has demonstrated that if an individual has already suffered harm as a result of insufficient control over major aversiveness (as found in LH) then enhanced control may be effective in ameliorating the detrimental effects. In humans, attempts to reverse the deleterious effects of uncontrollability by reinstilling a sense of control have resulted in positive effects on psychological as well as physical well-being (Mineka and Hendersen, 1985; Peterson, 1999). In animals, therapeutic success for LH effects has been observed when individuals who have been exposed to uncontrollable stimulation are given experience with 'easy' tasks in order to re-establish a sense of control (Mineka and Hendersen, 1985). Treatments involving more active interventions, such as physically forcing an animal with LH to experience the contingency between behavior and outcome (e.g., moving the animal's legs in walkingtype motions in the direction of the reward), have been shown by some studies to help undo LH deficits (Peterson, 1999). Pharmacologic treatments

Table 6.1. Methods for enhancing control and predictability in the animal welfare and behavior literature.

Species	Setting	Methods	Reference
Dogs, cats	Kennels, shelters	 Increasing the complexity of the kennel may provide some control by having choices about where to sit, stand, or lie. For example, provide animals with both indoor and outdoor access Provide the ability to escape or hide from aversion, including hiding places 	Taylor and Mills, 2007
Horses	Unspecified	 When kept in groups and provided adequate space, allow horses to choose if and how they engage in social interactions Allow some control over other environmental features such as lighting, feeding, flooring, and an out-in-the-open or inside environment (and design housing systems accordingly) 	Hall <i>et al.</i> , 2008
Unspecified	Unspecified	 Provide the ability to gain control over aversive stimuli Take extra care when training animals using aversive stimuli because of animals' imperative to achieve control over such stimuli 	McGreevy and McLean, 2009
Unspecified captive animals	Unspecified	 Increase the environmental complexity, which increases the animals' available choices as well as helping animals to cope better with novel or stressful situations Provide animals with choice through the use of retreat areas, pen dividers, or natural vegetation that create opportunities for concealment from other animals or from people 	Jones and McGreevy, 2007
Dogs	Shelter	 Provide an elevated place to retreat and the ability to move out of sight Provide food-dispensing devices controllable by the dogs 	Moesta et al., 2015
Dogs	Home	Allow dogs to have control on walks	McGreevy, 2010
Cats	Shelter	 Offer heated and unheated beds and shelves near windows, which allows the cats a choice of temperatures and a choice of a location in the sun or the shade Provide scratch pads, climbing poles, and ropes to allow a choice of height and play area 	Loveridge et al., 1995
Various species	Zoos	 Providing different types of enrichment that could be interacted with as the animal chooses Provide switches which animals could learn to manipulate to alter lighting, temperature, and humidity Allow the animal to move between microclimates within an exhibit Allow the animal to get water on demand by manipulating a drinker Use instrumental learning to give animals control over their environments. For example, animals could learn to use tools that would allow them to communicate their needs, as demonstrated in a dog and chimpanzees who learned to request specific objects, activities, interactions by pressing keys on a keyboard is it possible to increase the space between these columns to avoid this clash. 	Siegford, 2013
Various species	Laboratories, zoos	 In laboratories, teach the animals a reliable signal to indicate the onset of an aversive event, e.g., cage cleaning, or restraint for injection or blood draws (and thus the absence of such a signal indicates that the situation is safe) Implement training that uses positive reinforcement techniques to provide captive animals with a degree of control and predictability Give animals control over environmental music 	Bassett and Buchanan-Smith, 2007
Companion animals	Home, veterinary hospital	 Offer meaningful opportunities to make choices (e.g., going outside or staying inside, which food to eat today, which toy to play with, etc.) Give animal 'say-so' in its life by allowing requests to be made (e.g., the pet signaling to the owner when the pet would like to go outside or on a walk, when the pet would like the owner to play, etc.) Assure that the pet has a meaningful ability to lessen the intensity of unpleasant feelings or to improve an unpleasant situation, such as boredom, loneliness, frustration, fear, or pain (e.g., by having a secure place to escape or hide, seeking out stimulation or better conditions, or actively easing any discomforts) 	McMillan, 2003

have also been shown to be effective in reversing adverse behavioral and neurobiological changes associated with helplessness in animals (Vollmayr and Henn, 2003).

As promising as the research has been for treatment of the emotional damage of LH in animals, it is important to note that these findings are much too preliminary to be applied to clinical cases. Crucial limitations to implementing these techniques include our incomplete understanding and ability to definitively identify LH in animals as well as our ability to predict which animals would respond positively to which techniques. Notably, the fact that such treatments can involve the infliction of stress indicates that they pose substantial risk of causing harm if misapplied.

6.9 Mental Health Implications

The mental health impact of controllability, particularly when its absence leads to LH, cannot be overstated. Indeed, the fact that LH has been used in animals to model aspects of severe psychological disorders of humans such as depression (Vollmayr and Henn, 2003; Maier and Watkins, 2005) and PTSD (King *et al.*, 2001) attests to the highly injurious potential of insufficient control for the mental health and well-being of animals.

While we do not yet have a clear understanding of why and how a sense of control exerts its effects on psychological well-being, numerous studies in animals show that it is primarily beneficial and is generally desired. Evidence in humans indicates that good mental health results, at least partially, from the feelings of comfort that the perception of control provides as it promises to protect against serious adversity becoming intolerable. In the most general sense, the perception of control offers *peace of mind*. The individual person or animal who perceives that he or she has a meaningful degree of control is more able to enjoy their life and be less burdened by major anxieties, fears, and worries of impending danger.

But good mental health appears to be promoted not only by the protection against adversity. Studies show that animals desire control for the sake of control, that is, control is rewarding in itself, and that control is desired for appetitive as well as aversive stimuli. Together, these findings indicate that the benefits to mental health and well-being extend well beyond minimizing undesirable experiences in life.

Notes

- ¹ In this chapter control will refer to behavioral control, acknowledging that other types of control, e.g., cognitive control (which utilizes cognitive reappraisal, calming self-talk, selective attention, imagery, and distraction [Thompson, 1981]), have been identified in humans.
- ² The effects of control have been found to involve stimuli and events that are appetitive as well as aversive (Peterson, 1999); however, the emphasis in this chapter will be control in the face of aversiveness. It is worth noting, however, that the portion of the definition of control referring to maximizing desired outcomes and/or minimizing undesired ones is applicable to control in the face of either aversiveness or appetitiveness.

6.10 References

- Alliger, A.A. and Moller, P. (2011) The effects of environmental control on cognition in rats (*Rattus norvegicus*). *Journal of Applied Animal Welfare Science* 14, 271–285. http://dx.doi.org/10.1080/10888705.2011.60 0153.
- Anonymous. (2001) Scientists' assessment of the impact of housing and management on animal welfare. Journal of Applied Animal Welfare Science 4, 3–52. http://dx.doi.org/10.1207/S15327604JAWS0401_2.
- Atkinson, S.K.C. and Dierauf, L.A. (2018) Stress and marine mammals. In: Gulland, F.M.D., Dierauf, L.A., Whitman, K.L. (eds.) CRC Handbook of Marine Mammal Medicine. CRC Press, Boca Raton, Florida, USA, pp. 141–156.
- Averill, J.R. (1973) Personal control over aversive stimuli and its relationship to stress. *Psychological Bulletin* 80, 286–303. http://dx.doi.org/10.1037/h0034845.
- Bassett, L. and Buchanan-Smith, H.M. (2007) Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science* 102, 223–245. http://dx.doi.org/10.1016/j.applanim.2006.05.029.
- Bollini, A.M., Walker, E.F., Hamann, S., Kestler, L. (2004) The influence of perceived control and locus of control on the cortisol and subjective responses to stress. *Biological Psychology* 67, 245–260. http://dx.doi.org/10.1016/j.biopsycho.2003.11.002.
- Bradburn, N.M. (1969) *The Structure of Psychological Well-Being*. Aldine Publishing Company, Chicago, Illinois, USA.
- Bradshaw, G.A. (2009) *Elephants On the Edge*. Yale University Press, New Haven, Connecticut, USA.
- Broom, D.M. (2007) Quality of life means welfare: How is it related to other concepts and assessed? *Animal Welfare* 16(S), 45–53.
- Buchanan-Smith H.M., Badihi I. (2012) The psychology of control: Effects of control over supplementary light on welfare of marmosets. *Applied Animal Behaviour Science* 137, 166–174. http://dx.doi.org/10.1016/j.applanim.2011.07.002.

- Carder, B. and Berkowitz, K. (1970) Rats' preference for earned in comparison with free food. *Science* 167, 1273– 1274. http://dx.doi.org/10.1126/science.167.3922.1273.
- Carlstead, K.J., Brown, J., Seidensticker, J. (1993a) Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biology* 12, 321–331. http://dx.doi.org/10.1002/ zoo.1430120403.
- Carlstead, K., Brown, J.L., Strawn, W. (1993b) Behavioral and physiological correlates of stress in laboratory cats. *Applied Animal Behaviour Science* 38, 143–158. http://dx.doi.org/10.1016/0168-1591(93)90062-T.
- Catania, A.C. and Sagvolden, T. (1980) Preference for free choice over forced choice in pigeons. *Journal of* the Experimental Analysis of Behavior 34, 77–86. http://dx.doi.org/10.1901/jeab.1980.34-77.
- Dess-Beech, N., Linwich, D., Patterson, J., Overmier, J. (1983) Immediate and proactive effects of controllability and predictability on plasma cortisol response to shocks in dogs. *Behavioural Neuroscience* 97, 1005–1016.
- Foa, E.B., Zinbarg, R., Rothbaum, B.O. (1992) Uncontrollability and unpredictability in post-traumatic stress disorder: An animal model. *Psychological Bulletin* 112, 218–238. http://dx.doi.org/10.1037/0033-2909.112.2.218.
- Franks, B. and Higgins, E.T. (2012) Effectiveness in humans and other animals: A common basis for well-being and welfare. In: Olson, J.M. and Zanna, M.P. (eds.) Advances in Experimental Social Psychology, Vol. 46. Academic Press, Burlington, Massachusetts, USA, pp. 285–346. http://dx.doi.org/10.1016/B978-0-12-394281-4.00006-4.
- Gazzano, A., Mariti, C., Alvares, S., Cozzi, A., Tognetti, R., et al. (2008) The prevention of indesirable behaviors in dogs: Effectiveness of veterinary behaviorists' advice given to puppy owners. Journal of Veterinary Behavior: Clinical Applications and Research 3, 125–133.http://dx.doi.org/10.1016/j.jveb.2008.04.004.
- Goodkin, F. (1976) Rats learn the relationship between responding and environmental events: An expansion of the learned helplessness hypothesis. *Learning and Motivation* 7, 382–393. http://dx.doi.org/10.1016/0023-9690(76)90044-8.
- Green, T.C. and Mellor, D.J. (2011) Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. *New Zealand Veterinary Journal* 59, 263–271. http://dx.doi.org/10.1080/00480169. 2011.610283.
- Gruber-Baldini, A.L., Ye, J., Anderson, K.E., Shulman, L.M. (2009) Effects of optimism/pessimism and locus of control on disability and quality of life in Parkinson's disease. *Parkinsonism & Related Disorders* 15, 665–669. http://dx.doi.org/10.1016/j.parkreldis.2009.03.005.
- Hall, C., Goodwin, D., Heleski, C., Randle, H., Waran, N. (2008) Is there evidence of learned helplessness in horses? *Journal of Applied Animal Welfare Science* 11, 249–266. http://dx.doi.org/10.1080/10888700802101130.

- Horwitz, D.F. and Neilson, J.C. (2007) Blackwell's Five-Minute Veterinary Consult Clinical Companion – Canine and Feline Behavior. Blackwell Publishing, Ames, Iowa, USA.
- Joffe, J.M., Rawson, R.A., Mulick, J.A. (1973) Control of their environment reduces emotionality in rats. *Science* 180, 1383–1384. http://dx.doi.org/10.1126/ science.180.4093.1383.
- Jones, S. and McGreevy, P. (2007) How much space does an elephant need? The impact of confinement on animal welfare. *Journal of Veterinary Behavior:* Clinical Applications and Research 2, 185–187. http:// dx.doi.org/10.1016/j.jveb.2007.06.001.
- Kavanau, J. (1964) Behavior, confinement, and compulsory regime in laboratory studies. Science 143, 490. http://dx.doi.org/10.1126/science.143.3605.490.
- Kavanau, J.L. (1967) Behavior of captive white-footed mice. Science 155, 1623–1639. http://dx.doi.org/10.1126/ science.155.3770.1623.
- King, J.A., Abend, S., Edwards, E. (2001) Genetic predisposition and the development of posttraumatic stress disorder in an animal model. *Biological Psychiatry* 50, 231–237. http://dx.doi.org/10.1016/ S0006-3223(01)01071-X.
- Kontogeorgopoulos, N. (2009) The role of tourism in elephant welfare in northern Thailand. *Journal of Tourism* 10, 1–19.
- Landsberg, G., Hunthausen, W., Ackerman, L. (2013) Behavior Problems of the Dog and Cat, 3rd edn. Saunders, Edinburgh, UK.
- Larson, R. (1989) Is feeling 'in control' related to happiness in daily life? *Psychological Reports* 64, 775–784. http://dx.doi.org/10.2466/pr0.1989.64.3.775.
- Leotti, L.A., Iyengar, S.S., Ochsner, K.N. (2010) Born to choose: The origins and value of the need for control. *Trends in Cognitive Sciences* 14, 457–463. http:// dx.doi.org/10.1016/j.tics.2010.08.001.
- Loveridge, G.G., Horrocks, L.J., Hawthorne, A.J. (1995) Environmentally enriched housing for cats when housed singly. *Animal Welfare* 4, 135–141.
- Lyubomirsky, S., King, L., Diener, E. (2005) The benefits of frequent positive affect: Does happiness lead to success? *Psychological Bulletin* 131, 803–855. http://dx.doi.org/10.1037/0033-2909.131.6.803.
- Maier, S.F. and Watkins, L.R. (2005) Stressor controllability and learned helplessness: The roles of the dorsal raphe nucleus, serotonin, and corticotropin-releasing factor. *Neuroscience and Biobehavioral Reviews* 29, 829–841. http://dx.doi.org/10.1016/j.neubiorev.2005.03.021.
- Markowitz, H. and Eckert, K. (2005) Giving power to animals. In: McMillan, F.D. (ed.) *Mental Health and Well-Being in Animals*. Blackwell Publishing, Ames, Iowa, USA, pp. 201–209. http://dx.doi.org/10.1002/9780470384947.ch14.
- McGreevy, P. (2010) A Modern Dog's Life. The Experiment, New York, USA.

- McGreevy, P.D., McLean, A.N. (2009) Punishment in horse-training and the concept of ethical equitation. *Journal of Veterinary Behavior: Clinical Applications* and Research 4, 193–197. http://dx.doi.org/10.1016/j. jveb.2008.08.001.
- McMillan, F.D. (2003) Maximizing quality of life in ill animals. Journal of the American Animal Hospital Association 39, 227–235. http://dx.doi.org/10.5326/0390227.
- Miller, S.M. (1979) Controllability and human stress: Method, evidence and theory. *Behaviour Research and Therapy* 17, 287–304. http://dx.doi.org/10.1016/0005-7967(79)90001-9.
- Mineka, S. and Hendersen, R.W. (1985) Controllability and predictability in acquired motivation. *Annual Review of Psychology* 36, 495–529. http://dx.doi. org/10.1146/annurev.ps.36.020185.002431.
- Mineka, S., Gunnar, M., Champoux, M. (1986) Control and early socioemotional development: Infant rhesus monkeys reared in controllable versus uncontrollable environments. *Child Development* Oct 1, 1241–1256. http://dx.doi.org/10.2307/1130447.
- Moesta, A., McCune, S., Deacon, L., Kruger, K.A. (2015) Canine enrichment. In: Weiss, E., Mohan-Gibbons, H., Zawistowski, S. (eds.) *Animal Behavior for Shelter Veterinarians and Staff*. Wiley Blackwell, Ames, Iowa, USA, pp. 160–171. http://dx.doi.org/10.1002/9781119421313.ch8.
- Overmier, J.B. and Seligman, M.E.P. (1967) Effects of inescapable shock upon subsequent escape and avoidance learning. *Journal of Comparative and Physiological Psychology* 63, 28–33. http://dx.doi.org/10.1037/h0024166.
- Overmier, J.B., Patterson, J., Wielkiewicz, R.M. (1980). Environmental contingencies as sources of stress in animals. In: Levine, S., Ursin, H. (eds.) *Coping and Health*. Springer, Boston, Massachusetts, USA, pp. 1–38. http://dx.doi.org/10.1007/978-1-4684-1042-6_1.
- Peacock, E.J. and Wong, P.T.P. (1996) Anticipatory stress: The relation of locus of control, optimism, and control appraisals to coping. *Journal of Research in Personality* 30, 204–222. http://dx.doi.org/10.1006/jrpe.1996.0014.
- Perlmuter, L.C. and Monty, R.A. (1977) The importance of perceived control: Fact or fantasy? *American Scientist* 65, 759–765.
- Peterson, C. (1999) Personal control and well-being. In: Kahneman, D., Diener, E., Schwarz, N. (eds.) Well-being: The Foundations of Hedonic Psychology. Russell Sage Foundation, New York, USA, pp. 288–301.
- Rodin, J. (1986) Aging and health: Effects of the sense of control. *Science* 233, 1271–1276. http://dx.doi.org/10.1126/science.3749877.
- Rotter, J.B. (1966) Generalized expectancies for internal versus external control of reinforcements. *Psychological Monographs* 80, 1–28. http://dx.doi.org/10.1037/h0092976.

- Russell, W.M.S. and Burch, R.L. (1959) *The Principles of Humane Experimental Technique*. Methuen, London, UK.
- Rygula, R., Golebiowska, J., Kregiel, J., Kubik, J., Popik, P. (2015). Effects of optimism on motivation in rats. Frontiers in Behavioral Neuroscience 9, 32. http:// dx.doi.org/10.3389/fnbeh.2015.00032.
- Sambrook, T.D. and Buchanan-Smith, H.M. (1997) Control and complexity in novel object enrichment. Animal Welfare 6, 207–216.
- Sapolsky, R.M. (1994) Why Zebras Don't Get Ulcers. W.H. Freeman and Company, New York, USA.
- Scheier, M.F. and Carver, C.S. (1992) Effects of optimism on psychological and physical well-being: Theoretical overview and empirical update. *Cognitive Therapy and Research* 16, 201–228. http://dx.doi.org/10.1007/BF01173489.
- Seligman, M.E.P. (1968) Chronic fear produced by unpredictable shock. *Journal of Comparative and Physiological Psychology* 66, 402–411. http://dx.doi. org/10.1037/h0026355.
- Seligman, M.E. (1975) *Helplessness: On Depression, Development, and Death.* W.H. Freeman and Company, San Francisco, USA.
- Siegford, J.M. (2013) Multidisciplinary approaches and assessment techniques to better understand and enhance zoo nonhuman animal welfare. *Journal of Applied Animal Welfare Science* 16, 300–318. http://dx.doi.org/10.1080/10888705.2013.827914.
- Solomon, R.L. and Wynne, L.C. (1953) Traumatic avoidance learning: Acquisition in normal dogs. *Psychological Monographs* 67, 1–19. http://dx.doi.org/ 10.1037/h0093649.
- Spector, P.E., Cooper, C.L., Sanchez, J.I., O'Driscoll, M., Sparks, K., et al. (2001) Do national levels of individualism and internal locus of control relate to wellbeing: an ecological level international study. *Journal* of Organizational Behavior 22, 815–832. http:// dx.doi.org/10.1002/job.118.
- Starr, M.D. and Mineka, S. (1977) Determinants of fear over the course of avoidance learning. *Learning and Motivation* 8, 332–350. http://dx.doi.org/10.1016/0023-9690(77)90056-X.
- Steptoe, A. and Poole, L. (2016). Control and stress. In: Fink, G. (ed.) Stress: Concepts, Cognition, Emotion, and Behavior. Academic Press, Burlington, Massachusetts, USA, pp. 73–80.
- Suomi, S.J. (1991) Early stress and adult emotional reactivity in rhesus monkeys. Ciba Foundation Symposium 156, 171–183.
- Suzuki, S. (1999) Selection of forced- and free-choice by monkeys (Macaca fascicularis). Perceptual and Motor Skills 88, 242–250. http://dx.doi.org/10.2466/ pms.1999.88.1.242.
- Taylor, K.D. and Mills, D.S. (2007) The effect of the kennel environment on canine welfare: A critical review of experimental studies. *Animal Welfare* 16, 435–447.

- Thompson, S.C. (1981) Will it hurt less if I can control it? A complex answer to a simple question. *Psychological Bulletin* 90, 89–101. http://dx.doi.org/10.1037/0033-2909.90.1.89.
- Thompson, S.C. (2005) The role of personal control in adaptive functioning. In: Snyder, C.R. and Lopez, S.J. (eds.) *Handbook of Positive Psychology*. Oxford University Press, Oxford, UK, pp. 202–213.
- Thompson, S.C. and Kyle, D.J. (2000). The role of perceived control in coping with the losses associated with chronic illness. In: Harvey, J.H. and Miller, E.D. (eds.) Loss and Trauma: General and Close Relationship Perspectives. Bruner/Mazel, Philadelphia, Pennsylvania, USA, pp. 131–145.
- Tsuda, A., Tanaka, M., Hirai, H., Pare, W. P. (1983) Effects of coping behavior on gastric lesions in rats as a function of predictability of shock. *Japanese Psychological Research* 25, 9–15. http://dx.doi.org/10.4992/psycholres 1954.25.9.
- Verme, P. (2009) Happiness, freedom and control. *Journal of Economic Behavior & Organization* 71, 146–161. http://dx.doi.org/10.1016/j.jebo.2009.04.008.
- Vollmayr, B. and Henn, F.A. (2003). Stress models of depression. Clinical Neuroscience Research 3, 245–251. http://dx.doi.org/10.1016/S1566-2772(03)00086-0.

- Voss, S.C. and Homzie, M.J. (1970). Choice as a value. Psychological Reports 26, 912–914. http://dx.doi. org/10.2466/pr0.1970.26.3.912.
- Wallston, K. (2004) Control and health. In: Anderson, N.S. (ed.) Encyclopedia of Health & Behavior. Vol 1. Sage Publications, Thousand Oaks, California, USA, pp. 217–220. http://dx.doi.org/10.4135/9781412952576.n67.
- Wells, D.L., Graham, L., Hepper, P.G. (2002) The influence of length of time in a rescue shelter on the behaviour of kennelled dogs. *Animal Welfare* 11, 317–325.
- Williams, J.L. and Maier, S.F. (1977). Transituational immunization and therapy of learned helplessness in the rat. *Journal of Experimental Psychology: Animal Behavior Processes* 3, 240–252.
- Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., et al. (2018) Assessment of welfare in zoo animals: Towards optimum quality of life. Animals 8, 110. http://dx.doi.org/10.3390/ ani8070110.
- Yeates, J.W. (2011) Is 'a life worth living' a concept worth having? *Animal Welfare* 20, 397-406.
- Yeates, J.W., Main, D.C.J. (2008) Assessment of positive welfare: A review. Veterinary Journal 175, 293–300. http://dx.doi.org/10.1016/j.tvjl.2007.05.009.

7

Quality of Life of Animals in Veterinary Medical Practice

JAMES W. YEATES

Cats Protection, Haywards Heath, UK

7.1 Introduction

Over the past two decades, the veterinary field has seen expanding awareness and discussions of animals' quality of life (QOL). The concept (or perhaps concepts) has been applied to human medical patients, veterinary patients, and public social policymaking. Over this time, discussions on veterinary patient QOL have become increasingly mainstream within the veterinary literature. Anecdotally, this seems to have been reflected in more explicit considerations of QOL within consulting conversations, although doubtless some veterinary surgeons have long been considering, assessing, and improving their patients' QOL without necessarily using the term. The construct of QOL has been developed primarily by conceptual analysis, extrapolation from human medical literature, and by learnings from researchers trying to develop assessment methods and tools (McMillan, 2000, 2003; Wojciechowska and Hewson, 2005; Scott et al., 2007; Yeates and Main, 2009; Giuffrida and Kerrigan, 2014; Belshaw et al., 2015; Mullan, 2015).

This chapter examines the complex concept of quality of life. An emphasis is placed on the practical application of QOL for animals. We suggest how veterinary surgeons, and animal owners, might better assess and improve animals' QOL. Arguably, QOL is – or should be – the single most important factor involved in the most consequential decisions made in veterinary medical and nursing practice and policy. It can guide decisions regarding clinical diagnosis, therapeutic options, and elective euthanasia, as well as help us to evaluate societal management practices and to test novel therapies.

7.2 Qualities of Quality of Life

The World Health Organization defines QOL in humans as 'The individuals' perception of their position

in life in the context of the culture and value systems in which they live and in relation to their goals, expectations, standards and concerns' (World Health Organization, 1996). At first glance this definition appears to be problematic for use in animals, but it is actually more useful than it may initially seem. What it does is relate QOL to the individual's perception, motivations, and predictions, and to what matters for that individual. These ideas, as we shall see, are very applicable to animals.

More specifically for animals, QOL has been described as 'a subset of welfare' (Wojciechowska and Hewson, 2005; Broom, 2007; Taylor and Mills, 2007). Others have suggested treating it as equivalent (or at least related) to other concepts such as 'wellbeing, welfare, happiness, life satisfaction, and contentment' (see Chapter 2, this volume). However, there is limited consensus on what QOL is in animals (e.g., for dogs, see Belshaw et al., 2015). Indeed, many reports of QOL tools do not adequately describe the concepts of QOL involved (Giuffrida and Kerrigan, 2014; Belshaw et al., 2015). That said, it is reasonable to suggest that we do not need a strict 'scientific' definition (Yeates, 2013) so long as the term meets certain criteria to assure that all who use the term QOL are actually referring to the same thing.

In the absence of a consensus definition useful for nonhuman animals (see below), we might consider several characteristics that QOL has as a concept. In broad terms, we might think of QOL as what gives animals' lives – from the animal's perspective – value. Operationally, we can describe it as what animals would (most likely) want for themselves.

7.2.1 Evaluative

QOL is, as the name suggests, the quality that life has for that animal. In this sense, the technical term is well connected to the philosophical use of 'quality' to refer to a property of something (e.g., the 'quality of mercy'). More specifically, we are not concerned with just any property of an animal's life (e.g., whether a life is rational, verbal, or even useful to others). We are concerned with the characteristic, or characteristics, that make life good for that animal.

This view that QOL is inherently evaluative has three key implications. The most evident is that 'evaluative' implies some idea of value. There are varying views on what is valuable for animals, including health, resources, security, control, social interactions, and human–animal relationships. Some might be said to have direct, intrinsic value; others are considered indirect for what they cause or represent.

A second, related implication is that QOL is not merely a factual description – it has ethical importance. As such, it is somehow directly relevant to what we should try to achieve or avoid. (How it is relevant is discussed below.) Of course, it is not the only relevant factor, but all else being equal it can provide a guide to our moral interactions with animals.

A third implication of QOL being evaluative is that it requires evaluators - or, at least, valuers - who use data to generate some assessment. Because our focus here is animal QOL, it is important to note that this does not necessarily imply that the individual forms such evaluations through some conscious and explicit cognitive process, i.e., animals do not need to comprehend the concept of QOL for their lives to have quality. Animals evaluate specific aspects or factors affecting their lives while we might serve as proxies to evaluate their lives on their behalf (we shall consider below how these different evaluative processes might be used together to base our proxy evaluations on animals' first-person evaluations). So, this aspect of QOL does not require the ability to provide verbal self-reports of one's QOL - the preferred method for evaluating QOL in conscious adult humans – it does restrict QOL to animals for whom aspects of their lives can have 'value' based on these positive and negative evaluations. This in turn would suggest that QOL is limited to sentient animals. Rocks and trees do not have a QOL, but tree squirrels, rock doves, rockfish, tree frogs, and rock pythons do.

7.2.2 Broad

The value of a life can range from severely negative to extremely positive: QOL can be good, poor, or indifferent. QOL goes beyond those facets linked directly to survival and maintenance (e.g., eating, drinking, toileting, and grooming) to also consider less immediate matters (e.g., play, exploration, and social engagement). It includes both aspects of 'coping' and, even more positively, 'flourishing'. It covers animals' prudential motivations to *avoid* (e.g., suffering) and to *achieve* (e.g., satisfaction). It covers what animals should be free *from*, and what they should have opportunities *for* (Table 7.1).

QOL also has breadth as a holistic concept. It relates to or is constructed from many different domains or facets that are potentially valuable (Wojciechowska and Hewson, 2005; Mullan and Main, 2007; Taylor and Mills, 2007; Hielm-Björkman *et al.*, 2009). Considering QOL is therefore helpful to ensure that an array of aspects is considered holistically, in proportion to their importance for each animal. It is also well worth bearing in mind that the different facets interact in complex ways, so that the value of one facet may depend on others, for example, the interplay between stressors and previous exposure or learning.

QOL is also broad insofar as it covers an extended period of time. An animal might have good or bad

Table 7.1. What animals should be free from and what they should have opportunities for.

Animals should be free from ^a	Animals should have opportunities forb
Hunger and thirst	Selection of dietary inputs (by provision of a diet that is preferentially selected)
Discomfort	Control of environment (by allowing the achievement of motivations)
Pain, injury, and disease	Pleasure, development, and vitality (by maintaining and improving beneficial inputs)
Restrictions on expressing (most) normal behavior	To express normal behavior (by providing sufficient space, a proper range of facilities, and the company of the animal's own kind)
Fear and distress	Interest and confidence (by providing conditions and treatment which lead to enjoyment)

^aFAWC (2010); ^bsee Chapter 5, this volume.

welfare at any given point, but QOL is essentially considered over a longer interval. Indeed, we might characterize it as animal welfare over time (see Chapter 2, this volume). This extended temporal nature makes it important to consider duration and chronicity alongside intensity.

7.2.3 Individualistic

It is generally considered that QOL relates to what is valuable for the individual animal (McMillan, 2003). The individual's perspective and perception has been described in the literature in animals for both welfare (Green and Mellor, 2011) and QOL (Wiseman-Orr et al., 2006). This individualism links to the consideration of positive states, insofar as these might vary more between individuals. In general, we see widespread uniformity in the dislike of injury or disease, whereas, in contrast, sources of enjoyment exhibit a wide variation among animals. This individualism also reflects the complex interactions between personalities, preferences, previous experiences, development, and learning, which results in two animals faring quite differently in the same circumstances and responding differently to analogous stimuli.

7.2.4 Mental

There is one (and perhaps only one) aspect of animals' lives that (i) definitely and intrinsically has value; (ii) covers a wide range, multiple facets, and extends over time; and (iii) is completely personal to the individual: the individual's mental states (including their etiologies and symptoms). Intrinsically, the affective experience of pain is worth avoiding, and conscious desires are worth seeking. As noted earlier, while these mental states are subjective experiences, they may also be viewed as subjective evaluations. In other words, the value of an animal's life relates to that animal's subjective experiences.

These subjective experiences appear to play a predominant, if not exclusive, role in how animals evaluate aspects of their lives. Two subjective processes seem inherently evaluative: affective and motivational (see Berridge, 1996; Berridge and Robinson, 1998). Affect is the subjective experience of reward or its opposite: in everyday terms, 'liking' and 'disliking', such as pleasure and pain, and enjoyment and suffering. Many authors have suggested QOL represents the balance of pleasant and unpleasant feelings (see Chapter 2, this volume). Motivation is the

subjective preference for a particular outcome: in everyday terms, 'wanting' to achieve or avoid given stimuli or outcomes. Pleasure and reward imply positive evaluations; displeasure and aversion imply negative evaluations. To rephrase Nagel's (1974) classic question of 'What is it like to be a bat?', QOL can be viewed as 'How enjoyable it is to be a bat?'.

7.3 QOL and Other Concepts: What QOL is Not (Only)

Recognizing that many factors may affect QOL, it is also useful to consider those factors which QOL does not directly consider.

7.3.1 Quality versus quantity

We commonly differentiate between quality and quantity of life. In one sense, QOL is absolutely not about death, birth, or longevity (although these might be co-affected by the same factors). QOL is independent of any idea of sanctity of life. Rather, QOL is a matter of what each animal 'gets out of' its life from that animal's point of view. So, in fact, QOL provides a way of assessing whether a specific quantity of an animal's life is, or is expected to be, good (see Fig. 7.1). Life is valuable where the QOL is good, and worth avoiding where the QOL is poor. So improving QOL is always good. Increasing quantity of life is only good if the expected QOL is good.

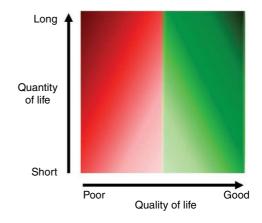


Fig. 7.1. Interrelationship of quality and quantity of life in the overall value of a life. Red indicates lower value and green indicates higher value; darkness of colors indicates best to worst, with dark = best, and light = worst.

7.3.2 Pain

Pain is an important facet of QOL (Brown *et al.*, 2009; Belshaw and Yeates, 2018), but clearly QOL is much more than pain. QOL is about the overall – net – value of life. Pain constitutes just one form of suffering; there are many others, such as fear, anxiety, boredom, frustration, loneliness, and the like. Plus, as considered above, good QOL is not simply the absence of negatives: it also involves positive aspects of life such as pleasure, enjoyment, engagement, achievement, and flourishing.

7.3.3 Health

Health is important for animals' QOL (Wiseman-Orr et al., 2006; Reid et al., 2013), but QOL encompasses more than health (Smith et al., 1999). It is not its physical state, nor is it restricted to an animal's biological 'function'. It also is not its 'normality' – another commonly used factor in health and welfare assessments. In contributing to an animal's QOL, some health problems may be less important than some other aspects of life. Most importantly, an animal's QOL depends on how it is affected by, and responds to, any pathologies or physiological disturbances. Two animals (or humans) may have the same degree of disease or pathology, yet experience much different impacts on their QOL.

However, even allowing for individual variation in responses to health disorders, unless health – including mental health - is at least adequate, an animal is unlikely to have a high quality of life. Severely poor health can be an important determinant – as well as indicator - of poor QOL. However, because of the prominent involvement of QOL in veterinary medicine there is a real risk of ignoring (or at least deemphasizing) QOL factors that are not health related. We should recognize that 'health related' and 'nonhealth related' are interrelated characteristics and it is impossible to disentangle the QOL effects of a disease from all the other impacts on a patient's QOL, including emotional factors, environment, genetics, etc. In the absence of clear demarcations between what facets of QOL are health related or not, we risk overlooking relevant aspects of QOL that would be included in a more holistic consideration of QOL.

7.3.4 Relationships and instrumental value

The value that QOL denotes is independent of any instrumental value of animals' lives to humans (e.g.,

as a source of eggs, progeny, meat, as an experimental subject, or even as a companion). An animal's QOL is the value of its life for that animal, not for the owner. An owner might consider an animal valuable for its usefulness and performance, and an owner might value their relationship with the animal in terms of affection, affinity, and companionship. But although these factors may be linked to other factors or signs that affect OOL, they are not themselves directly relevant. For example, a beloved or valued animal might actually have a lower QOL than another animal that is less loved, but better cared for, by its owner. Measures of human-animal relationships (HAR) are decidedly not a proxy for QOL, and Serpell (2019) has recently detailed the difficulties that these relationships create in obtaining an accurate assessment of a pet's QOL.

7.4 What Affects QOL

7.4.1 Inputs and indicators

QOL can be affected by many different aspects of animals' lives. In a way, the lack of clarity over exactly what constitutes QOL (e.g., objective and subjective aspects) has meant that previous work is often unclear whether what is being assessed is a constituent of QOL, a factor of QOL, or an indicator of QOL.

Nevertheless, we can identify a wide range of aspects that might affect, or be affected by, QOL. Proximately, we can consider inputs over a given period, such as diet, environment, social companionship, and care. Ultimately, these in turn depend on owners'/stockpersons' compassion, expertise, and resources. Animals' health can be both causes of OOL (e.g., disease may diminish OOL) and indicators of QOL (e.g., feline interstitial cystitis resulting from stress [Stella et al., 2011]). Indeed, so can most factors insofar as variations in intakes (e.g., appetence) or interactions (e.g., explorations) may be symptomatic of QOL changes. As we said above, facets need to be considered holistically, and with regard to how valuable those inputs are, as indicated by how each animal responds.

We might base our QOL assessments on animals' evaluations without necessarily reflecting their actual views naively. For example, one approach is to think of QOL in terms of what animals prudentially *should* be motivated to avoid or achieve, i.e., what would they want if they were perfectly rational and informed. This does not mean that

QOL is the satisfaction of whatever motivations animals express. Animals (including humans) are not perfectly rational and happen to have many desires that conflict, for example, a dog's expressed motivation to eat chocolate might conflict with an (implicit) motivation to avoid the suffering from theobromide poisoning (cf. Yeates, 2018). However, if the dog were informed on the dangers of consuming chocolate, this motivational conflict would be, for that dog, more easily resolved. This approach is crucial in avoiding flawed QOL assessments for animals (and humans, for that matter) in deprived living conditions, who, because they know no better life, view their own QOL as satisfactory (the 'it's-all-he-knows' situation). This is the 'Happy Slave Problem' (Phillips, 2006), and the implications for deprived animals is that it is possible that because these animals have an incomplete knowledge of what is possible, the animal may not be aware of a gap between his current experience and the possibilities of a life he would find more desirable. Using a measuring stick for QOL that emphasizes desires, we might imagine asking the animal if he has everything he wants - and the answer is yes. But if the animal based its response on a fully informed view, the answer would be no.

7.4.2 Evaluating multiple inputs

When making an overall evaluation of an animal's QOL, we typically desire to reach a single assessment based on a broad range of all facets of an animal's life, extended over a period of time. Sometimes, one facet may be so bad or good that we do not need to consider others. Severe suffering may preclude the possibility of significant enjoyment, effectively making other aspects of the animal's life irrelevant to whether the life is worth living. An animal with an extended aggressive bone tumor can be expected to have a poor QOL whether or not his bedding is comfortable. (This does not mean that his bedding should not be made more comfortable - we might still want greater precision of assessment to mitigate some of his suffering.) The situation where the negativity of one facet 'overshadows' all other aspects of QOL, however, appears to be the exception rather than the rule.

The most common situation asks us to combine or aggregate all facets into a single score. Human patients may perform this aggregation for themselves. However, nonhuman animals cannot assess and report their QOL, and we cannot observe it objectively. We must therefore infer QOL from observations about all of an animal's positive and negative experiences over the specified period of time. This aggregation adds a difficulty of combining seemingly incommensurable data into one overall evaluation (including the problem of QOL predictions, which is discussed in Section 7.6). One drawback of combining all facets into a single score is the potential for 'hiding' inter-observer variation in how individual facets are evaluated while risking worsened reliability. In addition, numerical scores may be arbitrary if the scale is not linked to a fixed comparison point (Craven *et al.*, 2004).

Because different factors have different levels of importance to different individual animals, a QOL evaluation that gives the same weight of every facet to every animal may not result in an accurate QOL assessment. For example, if one dog seems fine being left home alone all day and another dog exhibits great distress when alone, then a score for 'level of human companionship' that was weighted equally between the two dogs would show the same effect on the total QOL score, when in fact the overall QOL would be impacted much differently between the dogs. One approach to overcome this problem is to assign 'weights' to different QOL facets based on presumed importance of that facet to that individual animal, and then aggregate these weighted facet scores into an overall evaluation (McMillan, 2003; Morton, 2007; Budke et al., 2008). As logical as this approach appears, the precise method for determining weights clearly involves much subjectivity, and, hence, error. These weighting approaches have been questioned in the human field (Trauer and Mackinnon, 2001).

7.5 Using QOL

Before applying the concept of QOL to animals, some general issues are important to consider.

7.5.1 Using proxy assessments

Insofar as QOL can be considered as the subjective assessment of how one's own life is faring, this requires us to tap into each individual animal's own evaluations. As previously mentioned, the assessment of communicative human patients is usually based on asking individuals to evaluate their own QOL. The individual has access to their own subjective states, can make relative assessments across

positive and negative states, decides trade-offs, and can aggregate assessments across multiple domains.

Might animals meaningfully assess their own QOL? We currently lack convincing evidence that they can, at least explicitly. This would require not only that the animals communicate their QOL assessments, but also that we can clearly comprehend what they are communicating. Fortunately, however, the use of QOL with animals (and, for that matter, pre-verbal human infants and other noncommunicative humans) does not require that animals explicitly assess and communicate their own QOL. It need not be the individuals themselves who make the overall QOL assessment even if the concept is based on their subjective evaluations of QOL facets. Animals' inabilities to articulate a QOL means that we serve as proxy assessors for them with the goal of producing an objective evaluation based on their subjective states.

Ultimately, we rely on observable data from which to infer QOL. We cannot 'see into' animals' minds, and need to use what we can 'see' such as their circumstances, pathophysiology, and behavior, analyzed using analogical methods. This is, of course, true for humans too – but those data might include their verbal self-reports (which we assume are more reliable representations of their actual mental states). We might usefully consider factors that are observable and representative of the animals' own subjective perceptions, such as their expressed preferences and decisions, and their apparent degree of satisfaction with those choices.

7.5.2 Measuring quality of life

As an inherently evaluative concept, we do not have a 'natural' unit of measurement for QOL. So, while many facets can be measured quantitatively, overall QOL cannot be counted, measured, or calculated using methods like those we employ for phenomena such as blood pressure or body temperature. This is one of the reasons why it is difficult to establish any cut off point between 'acceptable' and 'unacceptable' QOL.

We might give up on quantification and judge animals' overall QOL qualitatively. We use every-day words such as 'good/poor', or 'high/low'. We use explicitly ethical words such as 'acceptable' and 'unacceptable'. We might explicitly consider whether an animal's continued life is of sufficient net quality overall to be 'worth living' (FAWC, 2010; Yeates, 2011).

Alternatively, we could try to use numerical representations of our relative assessments. For example, one approach to calibrating the numbers might be to evaluate QOL relative to quantity of life. The dividing line between a 'life worth living' and 'life worth avoiding' could provide a zero point, as the representation of a QOL that has the same value as nonexistence. We could explicitly evaluate periods of time in terms of their relative value, for example, whether it would be worthwhile for the animal to make a trade-off between two periods. For example, if 1 month of pain would be considered comparable to 1 year of a different suffering, then we could argue the value of the former is, pro rata, 12 times worse than the latter. Together, these could give us a ratio scale for QOL.

7.5.3 Minimizing bias and error

As human proxies, there will be biases in our assessments (Serpell, 2019), and in our effort to be 'objective' we should strive to recognize and overcome any such biases. Systematic approaches can help identify and eliminate invalid assessment methods that might, for example, prioritize or ignore certain facets of QOL that are important for humans but not necessarily for nonhumans. It is important here to note that humans' self-assessments of QOL which would seem to be tautologically unassailable in terms of accuracy - have been shown to be subject to biases and changing contextual factors. Poor intraobserver reliability occurs as an individual's situation changes, suggesting that assessments are at least partly contextual. For example, human patients may shift their self-assessed responses over time (Breetvelt and Van Dam, 1991; Sprangers, 1996; Sprangers and Schwartz, 1999), as they age, or if they assess injuries as less bad than they previously seemed. This may be due to recalibration (to different benchmark or thresholds) or reprioritization (of the various factors in their life). The crucial point is that if these errors can occur when humans assess themselves, then they may be expected to present similar problems in owners' assessment of animals (McMillan, 2007).

7.5.4 Tool validation

Practicing veterinarians seeking to select the best assessment tool(s) for use in their patients will understand the preferability of choosing tools that have been validated. The immediate problem, however, is that there are few such tools (yet) available (current QOL assessments tools is discussed in Section 7.6.2). The lack of a 'gold standard' (Sharkey, 2013) as an independent and objective point for comparison makes it challenging to definitively validate newly developed QOL assessment tools. Consequently, many of the published tools are only partially validated (Belshaw et al., 2015). Also important for the practitioner to keep in mind is that there are important reasons for using QOL assessment tools that do not require robust validation. For example, Yeates et al. (2011) proposed that a valuable use of QOL assessments is to promote discussions and facilitate decisions between veterinarians and pet owners, which requires a comprehensive overview of all aspects of the animal's life rather than precise scores. This was not intended to be validated by conventional measures, since the concepts were grounded in each owner's (and practitioner's) own conceptualizations and context.

7.5.5 Recognizing assessment limitations

When using tools, we should understand the underlying psychometrics and evaluative aspects – never using a score from an algorithm we cannot access and understand. One of our most important risks is mistakenly thinking a particular tool is generating an assessment of overall QOL when it actually only covers a significantly restricted range of facets, such as health or pain. We should certainly ensure that the impacts of pain and poor health are considered in QOL assessments, but also remember that QOL assessments are not limited to facets that are affected by health. At the same time, we should also recognize that our assessments are based on our viewpoints and values. They are never definitive evaluations of animals' QOL. Never should we believe we have 'determined' an animal's QOL with precise accuracy, especially when others' opinions disagree. However, even with such limitations it is still important to assess QOL as well as we can.

7.6 Applications of QOL Thinking

Broadly speaking, QOL can be used in four ways: screening, assessing, predicting, and decision-making. Of course, we might employ multiple uses at the same time (e.g., using current assessments to stimulate screening discussions or inform predictions). Indeed, we probably should use multiple

applications; for example, euthanasia discussions can be useful to move from screening to assessments, to predictions, to decisions.

One important basic question is who should do the evaluating. Veterinary surgeons and nurses may have a wide range of knowledge and experience, and seem more 'objective'. Owners may have biases from misplaced anthropomorphism or their emotional investment, but also have direct empathetic knowledge of their animals over an extended period in their everyday environment. Where possible, evaluations should be the product of all relevant views, with each party helping others to explore, identify, interpret, and evaluate different facets and form an overall collective evaluation. Indeed, each should be reliant on the others. For example, veterinarians often are reliant on owners' assessments in the home environment, while owners are reliant on veterinarians to predict disease progression. Veterinarians can help owners to explore each of the below applications, guiding them through screening to a decision.

7.6.1 Screening

QOL screening can help look for a wide variety of potential issues, among which health is a primary but not the only factor. Screening is particularly useful for identifying treatment side-effects or new conditions over time. The benefits of using QOL for screening is that it can help us consider a wide range of facets rather than simple screening for narrow predetermined concerns. Screening is most important when outcomes are uncertain, for example, in novel treatments or assessments for new health problems. It is important not to use screening tools for overall assessments, unless we are confident they are comprehensive and we are clear how we are formulating our overall assessments.

7.6.2 Assessment

Assessment of QOL can target overall QOL or only particular facets of QOL. There are now a number of tools available for assessing overall QOL and are compiled in Table 7.2 (also see Hewson *et al.*, 2007 and Belshaw *et al.*, 2015 for reviews in dogs). We might make these assessments as a comparison (e.g., to an earlier time of life or to another treatment group) or against some particular predefined criteria. Many QOL assessment tools ask people to rate animals' QOL subjectively (e.g., Mellanby *et al.*,

Table 7.2. Assessment tools and general discussions about overall quality of life.

Animal	Reference
Cats	Rochlitz, 2007
Cats	Tatlock et al., 2017a
Cats	Tatlock et al., 2017b
Dogs	Hewson et al., 2004
Dogs	Wojciechowska and Hewson, 2005
Dogs	Wojciechowska et al., 2005a,b
Dogs	Morton, 2007
Dogs	Mullan and Main, 2007
Dogs	Yeates et al., 2008
Dogs	Schneider et al., 2010
Dogs	Lavan, 2013
Kenneled dogs	Kiddie and Collins, 2014
Kenneled dogs	Kiddie and Collins, 2015
Dogs living in rescue shelters	Valsecchi et al., 2007
Companion animals	Schneider, 2005
Companion animals	Yeates and Main, 2009
Companion animals	Belshaw, 2018
Farm animals	Botreau et al., 2007

2002; Craven *et al.*, 2004; Brown *et al.*, 2007). Others ask assessors about multiple facets, with or without some overall mathematical assessment.

As mentioned earlier, 'health-related' and 'nonhealth-related' factors in QOL are inextricably linked. Nonetheless, multiple assessment tools for health-related QOL (HR-QOL) have been developed, and they have been shown to have important uses. Philosophically, they may provide a 'bridge' from thinking about specific biological functions or clinical measures, begging to expand our concerns more widely. Practically, QOL assessment using these tools can focus more extensively on a specific population (e.g., those with a specific medical disorder), potentially identifying factors that might be overlooked with assessment tools for overall QOL. Many assessment tools designed for assessing specific health problems in animals have been published in recent years and are compiled in Table 7.3.

Additionally, as horizon scanning, some future ideas might use 'big data' and/or personalized data from individual animals. A recent step in that direction is the NewMetrica QOL tool (Reid *et al.*, 2018), which analyses owner data via an online algorithm, to generate assessments of each dog's energy, happiness, comfort, and calmness. The future might combine such algorithmic analysis with data from new technology (e.g., wireless GPS collars) to

minimize owner biases. One risk of such new methods might be that the algorithmic analysis displaces expertise, possibly bypassing owner and veterinarian insights. Another risk is that such methods, especially where commercially based, may not be properly validated, or those validations (and the underlying algorithms) made public.

7.6.3 Predictions

QOL assessments are not restricted to the present; decisions in animal care necessarily involve predictions of *future* QOL. In such cases we are trying to predict the possible outcomes for each care option – whether between different foods, exercise regimes, adoptive homes, or medical treatment – in terms of the animal's subjective experiences. Predictions we make regarding QOL (i.e., in response to some therapeutic intervention) should come with the understanding that we are trying to estimate probabilities and we should recognize our degrees of confidence in any prediction. Most importantly, we should predetermine some factors that would prompt us to revise our prediction, particularly when later assessments suggest that previous predictions were fallacious.

Knowing that assessments of an animal's current QOL are challenging, we can expect predictions of QOL to be even more difficult since we are actually trying to assess future QOL (McMillan, 2007). However, we still need to make decisions based on looking ahead. In effect, we need to decide how to maintain or improve QOL in circumstances of uncertainty. This may mean we should make 'balance of probability' decisions (although 'probability' is perhaps the wrong word - 'balance of confidence' might be better). We might take a precautionary approach, giving animals 'the benefit of the doubt', at least in terms of their capacity and likelihood to suffer, to minimize the risks of causing them harm. Our decisions should always retain some humility, insofar as we might cross-check them with others' suggestions, and build in conditions and caveats (e.g., prompts for reassessment and reprediction of QOL). In particular, we should build in subsequent QOL reviews to compare later assessments with prior predictions and re-predict as needed.

7.6.4 Treatment decisions

If QOL is what animals should want for themselves and we should aim for their QOL, it is self-evident

Table 7.3. Assessment tools for specific health disorders in the veterinary literature (includes validated and unvalidated).

Health disorder	Species	Reference
Cardiac disease	Dogs	Freeman et al., 2005
Cardiac disease	Cats	Freeman et al., 2012
Epilepsy	Dogs	Lord and Podell, 1999
Idiopathic epilepsy	Dogs	Chang and Anderson, 2005
Spinal cord injury	Dogs	Budke <i>et al.</i> , 2008; Levine <i>et al.</i> , 2008
Palliative chemotherapy for lymphoma	Dogs	Mellanby et al., 2002
Cancer-related pain	Dogs	Yazbek and Fantoni, 2005
Hematological cancer	Dogs	Wiseman-Orr et al., 2008
Cancer	Dogs and cats	Lynch et al., 2011
Neoplastic hemoperitoneum	Dogs	Crawford et al., 2012
Cancer treated with chemotherapy	Small animals	Iliopoulou et al., 2013
Cancer	Dogs and cats	Giuffrida and Kerrigan, 2014
Receiving chemotherapy	Dogs and cats	Vøls et al., 2017
Cancer	Dogs	Giuffrida et al., 2018
Idiopathic Fanconi syndrome	Dogs	Yearley et al., 2004
Chronic renal failure	Dogs	Jacob et al., 2004
Chronic kidney disease	Cats	Bijsmans et al., 2016
Atopic dermatitis	Dogs	Favrot et al., 2009
Atopic dermatitis	Dogs	Ahlstrom et al., 2010
Atopic dermatitis	Dogs	Linek and Favrot, 2010
Skin diseases	Dogs	Noli et al., 2011a,b
Atopic and allergic skin disease	Dogs	Cosgrove et al., 2015
Skin disease	Cats	Noli et al., 2016
Pain from chronic degenerative joint disease	Dogs	Wiseman-Orr et al., 2004, 2006
Osteoarthritis	Cats	Klinck et al., 2010
Degenerative joint disease	Cats	Benito et al., 2012
Diabetes mellitus	Dogs	Graham et al., 2002
Diabetes mellitus	Cats	Niessen et al., 2010
Diabetes mellitus	Dogs	Niessen et al., 2012
Obesity	Dogs	German et al., 2012
Overweight and obesity	Dogs	Yam et al., 2016
Feline infectious peritonitis	Cats	Ritz et al., 2007
Congenital portosystemic shunt	Dogs	Greenhalgh et al., 2014
Progressive disease, unspecified	Companion animals	Villalobos, 2004
Geriatric health disorders, unspecified	Geriatric zoo animals	Föllmi et al., 2007
Health disorders, unspecified	Farmed pigs	Wiseman-Orr et al., 2011a,b
Health disorders, unspecified	Dogs	Reid et al., 2013
Health disorders, unspecified	Cats	Freeman et al., 2016
Health disorders, unspecified	Cats	Noble et al., 2019

that we should want for animals what animals should want for themselves. QOL should be the single most important factor involved in the most consequential decisions made in veterinary medical practice – guiding decisions regarding diagnosis, therapeutic options, and electing euthanasia. These decisions should be based on predictions of what we think the animal's QOL will (or for comparing options, would) be. In making these decisions, we should decide what is best – overall – for each individual patient (i.e., treat the patient, not the disease).

We should avoid biases about what is good for longevity, or the owner, or the breed, or the human-animal relation – in particular, we should avoid deciding to let animals have a poor QOL because of benefits to humans. We should also consider how trade-offs between positive and negative aspects of an animal's life might result in a net benefit to the animal, for example, vaccinations and exposure of fearful animals to their object of fear might involve a degree of unpleasantness but lead to better later coping or responses.

7.6.5 Policy

Human OOL assessment has, at least nominally, been used to inform public policymaking. We might, as a veterinary profession, consider QOL when evaluating wider ideas, such as breeding strategies, management regimes, and legislation. For example, we might assess the (predicted) QOL for each and all individuals in a given population. We could then apply different ethical frameworks to direct decisions at a policy level. One approach might be to bring together considerations of QOL and quantity of life. Human medical resource-allocation considers quality adjusted life years to assign a value to treatments based on their extension of life (when QOL is good) and/or improvements to QOL (discounting euthanasia). This might be used for animals, recognizing that we could score QOL negatively (i.e., worse than death) and permit euthanasia. An alternative approach might be to set an overarching policy that, as a minimum, no animal should have a life worth avoiding. Ethically, these approaches might reflect either utilitarian (either hedonic, after Bentham, 1781, or preferenceutilitarianism, after Singer, 1993) or Rawls's (1971) Maximin principle (cf. Yeates, 2010).

7.6.6 Communication

As mentioned earlier, one constructive use of QOL is to facilitate important discussions with pet owners. At least some owners appear to want more support on QOL assessment (e.g., Christiansen et al., 2016). Some might be switched off by ideas of 'welfare' or clinical parameters. OOL provides a platform in which specialists and owners can both communicate. Owners' thinking – like veterinarians' – may be helped by explicit considerations of nonphysiological motivations (e.g., to make euthanasia decisions before their animals stop eating) and more critical anthropomorphism and empathy. Our considerations of OOL might also alter how we think about patients and clients ourselves. Rather than taking paternalistic approaches, or uncritically ceding to owners the absolute right to make decisions about their property, we can more readily come to an agreement that all of our decisions are directed at the same goal: improving the animal's QOL. This can help ensure that our conversations with owners are supportive and affirm their confidence that their thinking is also focused on their animals. To this end, Yeates et al. (2011) found that discussions of QOL helped facilitate discussions and led to

more relevant decisions to improve pets' care. Adapting this tool, the People's Dispensary for Sick Animals (PDSA) 'PetWise MOTs' (a QOL assessment based on the Five Welfare Needs – Environment, Diet, Behavior, Companionship, and Health) led to a higher frequency of positive green scores, compared to amber and red scores, at a repeat MOT consultation (Roberts, 2018).

7.7 References

- Ahlstrom, L.A., Mason K.V., Mills, P.C. (2010) Barazone decreases skin lesions and pruritus and increases quality of life in dogs with atopic dermatitis: A randomized, blinded, placebo-controlled trial. *Journal of Veterinary Pharmacology and Therapeutics* 33, 573–582. http://dx.doi.org/10.1111/j.1365-2885.2010.01181.x.
- Belshaw, Z. (2018) Quality of life assessment in companion animals: What, why, who, when and how. *Companion Animal* 23, 264–268. http://dx.doi.org/10.12968/coan.2018.23.5.264.
- Belshaw, Z. and Yeates, J. (2018) Assessment of quality of life and chronic pain in dogs. *The Veterinary Journal* 239, 59–64. http://dx.doi.org/10.1016/j.tvjl.2018.07.010.
- Belshaw, Z., Asher, L.A., Harvey, N.D., Dean, R.S. (2015) Quality of life assessment in dogs: An evidence based rapid review. *The Veterinary Journal* 206, 203–212. http://dx.doi.org/10.1016/j.tvjl.2015.07.016.
- Benito, J., Gruen, M.E., Thomson, A., Simpson, W., Lascelles, B.D.X. (2012) Owner-assessed indices of quality of life in cats and the relationship to the presence of degenerative joint disease. *Journal of Feline Medicine and Surgery* 14, 863–870. http://dx.doi.org/ 10.1177/1098612X12453904.
- Bentham, J. (1781/2000) An Introduction to the Principles of Morals and Legislation. Batoche Books, Ontario, Canada. Available at http://socserv.mcmaster.ca/econ/ugcm/3ll3/bentham/morals.pdf (accessed 8 February 2019).
- Berridge, K.C. (1996) Food reward: Brain substrates of wanting and liking. *Neuroscience and Biobehavioral Reviews* 20, 1–25. http://dx.doi.org/10.1016/0149-7634(95)00033-B.
- Berridge, K.C. and Robinson, T.E. (1998) What is the role of dopamine in reward: Hedonic impact, reward learning, or incentive salience? *Brain Research Reviews* 28, 309–369. http://dx.doi.org/10.1016/S0165-0173(98)00019-8.
- Bijsmans, E.S., Jepson, R.E., Syme, H.M., Elliott, J., Niessen, S.J.M. (2016) Psychometric validation of a general health quality of life tool for cats used to compare healthy cats and cats with chronic kidney disease. *Journal of Veterinary Internal Medicine* 30, 183–191. http://dx.doi.org/10.1111/jvim.13656.
- Botreau, R., Veissier, I., Capdeville, J., Bracke, M., Butterworth, A., et al. (2007) Multicriteria assessment of the quality of farm animals' life. Animal Welfare 16(S), 166.

- Breetvelt, I.S. and Van Dam, F.S.A.M. (1991) Underreporting by cancer patients: The case of responseshift. *Social Science and Medicine* 32, 981–987. http://dx.doi.org/10.1016/0277-9536(91)90156-7.
- Broom, D. (2007) Quality of life means welfare: How is it related to other concepts and assessed? *Animal Welfare* 16(S): 45–53.
- Brown, D.C., Boston, R.C., Coyne, J.C., Farrar, J.T. (2007)
 Development and psychometric testing of an instrument designed to measure chronic pain in dogs with osteoarthritis. *American Journal of Veterinary Research* 68, 631–637. http://dx.doi.org/10.2460/ajvr.68.6.631
- Brown, D.C., Boston, R., Coyne, J.C., Farrar, J.T. (2009) A novel approach to the use of animals in studies of pain: Validation of the canine brief pain inventory in canine bone cancer. *Pain Medicine* 10, 133–142. http://dx.doi.org/10.1111/j.1526-4637.2008.00513.x.
- Budke, C.M., Levine, J.M., Kerwin, S.C., Levine, G.J., Hettlich, B.F., et al. (2008) Evaluation of a questionnaire for obtaining owner-perceived, weighted quality of life assessments for dogs with spinal cord injuries. Journal of the American Veterinary Medical Association 233, 925–930. http://dx.doi.org/10.2460/ javma.233.6.925.
- Chang, Y.P. and Anderson, T.J. (2005) The impact of idiopathic epilepsy and its management on the dog's quality of life and the owner's lifestyle. In: *Proceedings of the 17th Annual Symposium of European Society of Veterinary Neurology*, Glasgow, Scotland.
- Christiansen, Z.B., Kristensen, A.T., Lassen, J., Sandoe, P. (2016) Veterinarians' role in clients' decision-making regarding seriously ill companion animal patients. Acta Veterinaria Scandinavica 58, 30.
- Cosgrove, S.B., Cleaver, D.M., King, V.L., Gilmer, A.R., Daniels, A.E., et al. (2015) Long-term compassionate use of oclacitinib in dogs with atopic and allergic skin disease: Safety, efficacy and quality of life. Veterinary Dermatology 26, 171–179; e35. http://dx.doi.org/10.1111/vde.12194.
- Craven, M., Simpson, J.W., Ridyard, A.E., Chandler, M.L. (2004) Canine inflammatory bowel disease: retrospective analysis of diagnosis and outcome in 80 cases (1995–2002). *Journal of Small Animal Practice* 45, 336–342. http://dx.doi.org/10.1111/j.1748-5827.2004.tb00245.x.
- Crawford, A.H., Tivers, M.S., Adamantos, S.E. (2012) Owner assessment of dogs' quality of life following treatment of neoplastic haemoperitoneum. *Veterinary Record* 170, 566. http://dx.doi.org/10.1136/vr.100595
- Favrot, C., Linek, M., Mueller, R., Zini, E. (2009) Development of a questionnaire to assess the impact of atopic dermatitis on health-related quality of life of affected dogs and their owners. *Veterinary Dermatology* 21, 64–70.
- FAWC. (2010) Annual Review 2009–2010. Farm Animal Welfare Council, London, UK.
- Föllmi, J., Steiger, A., Walzer, C., Robert, N., Geissbuhler, U., et al. (2007) A scoring system to evaluate physical

- condition and quality of life in geriatric zoo animals. *Animal Welfare* 16, 309–318.
- Freeman, L.M., Rush, J.E., Farabaugh, A.E., Must, A. (2005) Development and evaluation of a questionnaire for assessing health-related quality of life in dogs with cardiac disease. *Journal of the American Veterinary Medical Association* 226, 1864–1868. http://dx.doi.org/10.2460/javma.2005.226.1864.
- Freeman, L.M., Rush, J.E., Oyama, M.A., MacDonald, K.A., Cunningham, S.M., et al. (2012) Development and evaluation of a questionnaire for assessment of health-related quality of life in cats with cardiac disease. Journal of the American Veterinary Medical Association 240, 1188–1193. http://dx.doi.org/10.2460/ javma.240.10.1188.
- Freeman, L.M., Rodenberg, C., Narayanan, A., Olding, J., Gooding, M.A., et al. (2016) Development and initial validation of the Cat HEalth and Wellbeing (CHEW) Questionnaire: A generic health-related quality of life instrument for cats. Journal of Feline Medicine and Surgery 18, 689–701. http://dx.doi.org/10.1177/10986 12X16657386.
- German, A.J., Holden, S.L., Wiseman-Orr, M.L., Reid, J., Nolan, A.M., et al. (2012) Quality of life is reduced in obese dogs but improves after successful weight loss. The Veterinary Journal 192, 428–434. http://dx. doi.org/10.1016/j.tvjl.2011.09.015.
- Giuffrida, M.A. and Kerrigan, S.M. (2014) Quality of life measurement in prospective studies of cancer treatments in dogs and cats. *Journal of Veterinary Internal Medicine* 28, 1824–1829. http://dx.doi.org/10.1111/ jvim.12460.
- Giuffrida, M.A., Brown, D.C., Ellenberg, S.S., Farrar, J.T. (2018) Development and psychometric testing of the Canine Owner-Reported Quality of Life questionnaire, an instrument designed to measure quality of life in dogs with cancer. *Journal of the American Veterinary Medical Association* 252, 1073–1083. http://dx.doi.org/10.2460/javma.252.9.1073.
- Graham, P.A., Maskell, I.E., Rawlings, J.M., Nash, A.S., Parkwell, P.J. (2002) Influence of a high fibre diet on glycaemic control and quality of life in dogs with diabetes mellitus. *Journal of Small Animal Practice* 43, 67–73. http://dx.doi.org/10.1111/j.1748-5827.2002. tb00031.x.
- Green, T.C. and Mellor, D.J. (2011) Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. New Zealand Veterinary Journal 59, 263–271. http://dx.doi.org/10.1080/00480 169.2011.610283.
- Greenhalgh, S.N., Reeve, J.A., Johnstone, T., Goodfellow, M.R., Dunning, M.D., et al. (2014) Long-term survival and quality of life in dogs with clinical signs associated with a congenital portosystemic shunt after surgical or medical treatment. Journal of the American Veterinary Medical Association 245, 527–533. http://dx.doi.org/10.2460/javma.245.5.527.

- Hewson, C.J., Wojciechowska, J.I., Guy, N.C., Timmons, V., Patronek, G.J., et al. (2004) 'But is she suffering?' A novel instrument to assess pet dogs' quality of life. Animal Welfare 13(Suppl), S243–S244.
- Hewson, C.J., Hiby, E.F., Bradshaw, J.W.S. (2007) Assessing quality of life in companion and kennelled dogs: A critical review. *Animal Welfare* 16(S): 89–95.
- Hielm-Björkman, A K., Rita, H., Tulamo, R.M. (2009) Psychometric testing of the Helsinki chronic pain index by completion of a questionnaire in Finnish by owners of dogs with chronic signs of pain caused by osteoarthritis. *American Journal of Veterinary Research* 70, 727–734. http://dx.doi.org/10.2460/ ajvr.70.6.727.
- Iliopoulou, M.A., Kitchell, B.E., Yuzbasiyan-Gurkan, V. (2013) Development of a survey instrument to assess health-related quality of life in small animal cancer patients treated with chemotherapy. *Journal of the American Veterinary Medical Association* 242, 1679–1687. http://dx.doi.org/10.2460/javma.242.12.1679.
- Jacob, F., Osborne, C., Polzin, D., Neaton, J., Kirk, C., et al. (2004) Effect of dietary modification on healthrelated quality of life (HRQL) in dogs with spontaneous chronic renal failure (CRF). In: Proceedings of the ACVIM Forum. Minneapolis, Minnesota, USA.
- Kiddie, J.L. and Collins, L.M. (2014) Development and validation of a quality of life assessment tool for use in kennelled dogs (*Canis familiaris*). *Applied Animal Behaviour Science* 158, 57–68. http://dx.doi. org/10.1016/j.applanim.2014.05.008.
- Kiddie, J. and Collins, L. (2015) Identifying environmental and management factors that may be associated with the quality of life of kennelled dogs (*Canis familiaris*). *Applied Animal Behaviour Science* 167, 43–55. http:// dx.doi.org/10.1016/j.applanim.2015.03.007.
- Klinck, M., Frank, D., Rialland, P., Guillot, M., Moreau, M., et al. (2010) Psychometric validation of pain and quality of life questionnaires in osteoarthritic cats. In: Proceedings of the Association of Veterinary Society of Behavior. Atlanta, Georgia, USA.
- Lavan, R.P. (2013) Development and validation of a survey for quality of life assessment by owners of healthy dogs. *The Veterinary Journal* 197, 578–582. http://dx.doi.org/10.1016/j.tvjl.2013.03.021.
- Levine, J.M., Budke, C.M., Levine, G.J., Kerwin, SC., Hettlich, BF., et al. (2008) Owner-perceived, weighted quality-of-life assessments on dogs with spinal cord injuries. Journal of the American Veterinary Medical Association 233, 931–935. http://dx.doi.org/10.2460/ javma.233.6.931
- Linek, M. and Favrot, C. (2010) Impact of canine atopic dermatitis on the health-related quality of life of affected dogs and quality of life of their owners. Veterinary Dermatology 21, 456–462. http://dx.doi.org/10.1111/j.1365-3164.2010.00899.x
- Lord, L.K. and Podell, M. (1999) Owner perception of the care of long-term phenobarbital-treated epileptic

- dogs. *Journal of Small Animal Practice* 40, 11–15. http://dx.doi.org/10.1111/j.1748-5827.1999.tb03246.x
- Lynch, S., Savary-Bataille, K., Leeuw, B., Argyle, D.J. (2011) Development of a questionnaire assessing health-related quality-of-life in dogs and cats with cancer. *Veterinary and Comparative Oncology* 9, 172–182. http://dx.doi.org/10.1111/j.1476-5829.2010.00244.x.
- McMillan, F.D. (2000) Quality of life in animals. *Journal of the American Veterinary Medical Association* 216, 1904–1910. http://dx.doi.org/10.2460/jayma.2000.216.1904.
- McMillan, F.D. (2003) Maximising quality of life in ill animals. Journal of the American Animal Hospital Association 39, 227–235. http://dx.doi.org/10.5326/0390227.
- McMillan, F.D. (2007) Predicting quality of life outcomes as a guide for decision-making: The challenge of hitting a moving target. *Animal Welfare* 16(S), 135–142.
- Mellanby, R.J., Herrtage, M.E., Dobson, J.M. (2002) Owners' assessments of their dog's quality of life during palliative chemotherapy for lymphoma. *Journal of Small Animal Practice* 43, 100–103. http://dx.doi.org/10.1111/j.1748-5827.2002.tb00037.x.
- Morton, D.B. (2007) A hypothetical strategy for the objective evaluation of animal well-being and quality of life using a dog model. *Animal Welfare* 16(S), 75–81.
- Mullan, S. (2015) Assessment of quality of life in veterinary practice: Developing tools for companion animal carers and veterinarians. Veterinary Medicine: Research and Reports 6, 203–210.
- Mullan, S. and Main, D. (2007) Preliminary evaluation of a quality-of-life screening programme for pet dogs. *Journal of Small Animal Practice* 48, 314–322. http://dx.doi.org/10.1111/j.1748-5827.2007.00322.x.
- Nagel, T. (1974) What is it like to be a bat? *Philosophical Review* 83, 435–456. http://dx.doi.org/10.2307/2183914.
- Niessen, S.J.M., Powney, J., Guitian, J., Niessen, A.P.M., Pion, P.D., et al. (2010) Evaluation of a quality-of-life tool for cats with diabetes mellitus. Journal of Veterinary Internal Medicine 24, 1098–1105. http:// dx.doi.org/10.1111/j.1939-1676.2010.0579.x.
- Niessen, S.J.M., Powney, S., Guitian, J., Niessen, A.P.M., Pion, P.D., et al. (2012) Evaluation of a quality-of-life tool for dogs with diabetes mellitus. Journal of Veterinary Internal Medicine 26, 953–961. http://dx.doi.org/10.1111/j.1939-1676.2012.00947.x.
- Noble, C.E., Wiseman-Orr, L.M., Scott, M.E., Nolan, A.M., Reid, J. (2019) Development, initial validation and reliability testing of a web-based, generic feline health-related quality-of-life instrument. *Journal of Feline Medicine and Surgery* 21(2), 84–94.
- Noli, C., Minafò, G., Galzerano, M. (2011a) Quality of life of dogs with skin diseases and their owners. Part 1: Development and validation of a questionnaire. Veterinary Dermatology 22, 335–343. http://dx.doi. org/10.1111/j.1365-3164.2010.00954.x.
- Noli, C., Colombo, S., Cornegliani, L., Ghibaudo, G., Persico, P., et al. (2011b). Quality of life of dogs with skin disease and of their owners. Part 2: Administration of a

- questionnaire in various skin diseases and correlation to efficacy of therapy. *Veterinary Dermatology* 22, 344–351. http://dx.doi.org/10.1111/j.1365-3164.2011.00956.x.
- Noli, C., Borio, S., Varina, A., Schievano, C. (2016) Development and validation of a questionnaire to evaluate the Quality of Life of cats with skin disease and their owners, and its use in 185 cats with skin disease. Veterinary Dermatology 27, 247–257. http:// dx.doi.org/10.1111/vde.12341.
- Phillips, D. (2006) Quality of Life: Concept, Policy and Practice. Routledge, London, UK. http://dx.doi.org/ 10.4324/9780203356630.
- Rawls, J. (1971) *A Theory of Justice*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, LISA
- Reid, J., Wiseman-Orr, M.L., Scott, E.M., Nolan, A.M. (2013) Development, validation and reliability of a webbased questionnaire to measure health-related quality of life in dogs. *Journal of Small Animal Practice* 54, 227–233. http://dx.doi.org/10.1111/jsap.12059.
- Reid, J., Nolan, A., Scott, M. (2018) When is the right time? Veterinary Record 182, 85–86. http://dx.doi. org/10.1136/vr.k274.
- Ritz, S., Egberink, H., Hartmann, K. (2007) Effect of feline interferon-omega on the survival time and quality of life of cats with feline infectious peritonitis. *Journal of Veterinary Internal Medicine* 21, 1193–1197. http:// dx.doi.org/10.1111/j.1939-1676.2007.tb01937.x.
- Roberts. C. (2018) Quality of life assessment in pet cats and dogs using the five welfare needs. In: *Proceedings of the British Small Animal Veterinary Association (BSAVA) Congress*. BSAVA, Birmingham, UK.
- Rochlitz, I. (2007) An approach to the assessment of quality of life in domestic cats. *Animal Welfare* 16(S), 176.
- Schneider, T.R. (2005) Methods for assessing companion animal quality of life. In: *Proceedings of the North American Veterinary Conference*. Orlando, Florida, USA.
- Schneider, T.R., Lyons, J.B., Tetrick, M.A., Accortt, E.E. (2010) Multidimensional quality of life and humananimal bond measures for companion dogs. *Journal* of Veterinary Behavior 5, 287–301. http://dx.doi. org/10.1016/j.jveb.2010.06.002.
- Scott, E.M., Nolan, A.M., Reid, J., Wiseman-Orr, M.L. (2007) Can we really measure animal quality of life? Methodologies for measuring quality of life in people and other animals. *Animal Welfare* 16(S), 17–24.
- Serpell, J.A. (2019) How happy is your pet? The problem of subjectivity in the assessment of companion animal welfare. *Animal Welfare* 28, 57–66.
- Sharkey, M. (2013) The challenges of assessing osteoarthritis and postoperative pain in dogs. *The AAPS Journal* 15, 598–607. http://dx.doi.org/10.1208/s12248-013-9467-5.
- Singer, P. (1993) *Practical Ethics*, 2nd edn. Cambridge University Press, Cambridge, UK.
- Smith, K.W., Avis, N.E., Assmann, S.F. (1999) Distinguishing between quality of life and health

- status in quality of life research: A meta-analysis. *Quality of Life Research* 8, 447–459. http://dx.doi.org/10.1023/A:1008928518577.
- Sprangers, M.A. (1996) Response-shift bias: A challenge to the assessment of patients' quality of life in cancer clinical trials. Cancer Treatment Reviews 22, 55–62. http://dx.doi.org/10.1016/S0305-7372(96)90064-X.
- Sprangers, M.A.G. and Schwartz, C.E. (1999) Integrating response shift into health-related quality of life research: A theoretical model. Social Science & Medicine 48, 1507–1515. http://dx.doi.org/10.1016/ S0277-9536(99)00045-3.
- Stella, J.L., Lord, L.K., Buffington, C.A. (2011) Sickness behaviors in response to unusual external events in healthy cats and cats with feline interstitial cystitis. *Journal of the American Veterinary Medical Association* 238, 67–73. https://doi.org/10.2460/javma.238.1.67.
- Tatlock, S., Gober, M., Williamson, N., Arbuckle, R. (2017a) Development and preliminary psychometric evaluation of an owner-completed measure of feline quality of life. *The Veterinary Journal* 228, 22–32. http://dx.doi.org/10.1016/j.tvjl.2017.10.005.
- Tatlock, S., Williamson, N., Arbuckle, R., Gober, M. (2017b) Development and psychometric evaluation of an owner-completed measure of feline health and quality of life. Value in Health 20, A761. http://dx.doi. org/10.1016/j.jval.2017.08.2154.
- Taylor, K.D. and Mills, D.S. (2007) Is quality of life a useful concept for companion animals? *Animal Welfare* 16, 55–65.
- Trauer, T. and Mackinnon, A. (2001) Why are we weighting? The role of importance ratings in quality of life measurement. Quality of Life Research 10, 579–585. http://dx.doi.org/10.1023/A:1013159414364.
- Valsecchi, P., Prato Previde, E., Accorsi, P. (2007) Quality of life assessment in dogs living in rescue shelters. *Animal Welfare* 16(1 Suppl), 178.
- Villalobos, A. (2004) Quality of life scale helps make the final call. *Veterinary Practice News* Sept, 38.
- Vøls, K.K., Heden, M.A., Kristensen, A.T., Sandøe, P. (2017) Quality of life assessment in dogs and cats receiving chemotherapy – a review of current methods. *Veterinary and Comparative Oncology* 15, 684–691. http://dx.doi.org/10.1111/vco.12242.
- Wiseman-Orr, M.L., Nolan, A.M., Reid, J., Scott, E.M. (2004) Development of a questionnaire to measure the effects of chronic pain on health-related quality of life in dogs. *American Journal of Veterinary Research* 65, 1077–1084. http://dx.doi.org/10.2460/ajvr.2004.65.1077.
- Wiseman-Orr, M.L., Scott, E.M., Reid, J., Nolan, A.M. (2006) Validation of a structured questionnaire as an instrument to measure chronic pain in dogs on the basis of effects on health-related quality of life. *American Journal of Veterinary Research* 67, 1826–1836. http:// dx.doi.org/10.2460/ajvr.67.11.1826.
- Wiseman-Orr, M.L., Reid, J., Scott, E.M., Nolan, A.M., Massie, A. (2008) Measurement of health-related

- quality of life (HRQL) in dogs with haematological cancer: a pilot study. Poster session, *UFAW Animal Welfare Conference*, Birmingham, UK.
- Wiseman-Orr, M.L., Scott, E.M., Nolan, A.M. (2011a)
 Development and testing of a novel instrument to
 measure health-related quality of life (HRQL) of farmed
 pigs and promote welfare enhancement (Part 1).

 Animal Welfare 20, 535–549.
- Wiseman-Orr, M.L., Scott, E.M., Nolan, A.M. (2011b)
 Development and testing of a novel instrument
 to measure health-related quality of life (HRQL) of
 farmed pigs and promote welfare enhancement
 (Part 2). Animal Welfare 20, 549–558.
- Wojciechowska, J.I. and Hewson, C.J. (2005) Quality-oflife assessment in pet dogs. *Journal of the American Veterinary Medical Association* 226, 722–728. http:// dx.doi.org/10.2460/javma.2005.226.722.
- Wojciechowska, J.I., Hewson, C.J., Stryhn, H., Guy, N.C., Patronek, G.J., et al. (2005a) Development of a discriminative questionnaire to assess nonphysical aspects of quality of life of dogs. American Journal of Veterinary Research 66, 1453–1460. http://dx.doi. org/10.2460/ajvr.2005.66.1453.
- Wojciechowska, J.I., Hewson, C.J., Stryhn, H., Guy, N.C., Patronek, G.J., et al. (2005b) Evaluation of a questionnaire regarding nonphysical aspects of quality of life in sick and healthy dogs. American Journal of Veterinary Research 66, 1461–1467. http://dx.doi. org/10.2460/ajvr.2005.66.1461.
- World Health Organization. (1996) WHOQOL-BREF: Introduction, administration, scoring and generic version of the assessment. Available at: www.who.int/mental_health/media/en/76.pdf (accessed 22 February 2018)
- Yam, P.S., Butowski, C.F., Chitty, J.L., Naughton, G., Wiseman-Orr, M.L., et al. (2016) Impact of canine overweight and obesity on health-related quality of life. Preventive Veterinary Medicine 127, 64–69. http://dx.doi.org/10.1016/j.prevetmed.2016.03.013.

- Yazbek, K.V.B. and Fantoni, D.T. (2005) Validity of a health-related quality-of-life scale for dogs with signs of pain secondary to cancer. *Journal of the American Veterinary Medical Association* 226, 1354–1358. http://dx.doi.org/10.2460/javma.2005.226.1354.
- Yearley, J.H., Hancock, D.D., Mealey, K.L. (2004) Survival time, lifespan, and quality of life in dogs with idiopathic Fanconi syndrome. *Journal of the American Veterinary Medical Association* 225, 377–383. http:// dx.doi.org/10.2460/javma.2004.225.377.
- Yeates, J. (2010) 'Reasonable suffering': The application of stem cell technologies to non-human animals. In: Capps, B.J. and Cambell, A.V. (eds.) Bioethics and the Global Politics of Stem Cell Science: Medical Applications in a Pluralistic World. Imperial College Press, Singapore, pp. 241–287.
- Yeates, J.W. (2011). Is 'a life worth living' a concept worth having? *Animal Welfare* 20, 397–406.
- Yeates, J.W. (2013) Animal Welfare in Veterinary Practice. UFAW/Wiley, Oxford, UK. http://dx.doi. org/10.1002/9781118782958.
- Yeates, J.W. (2018) Why keep a dog and bark yourself? Making choices for non-human animals. *Journal of Applied Philosophy* 35, 168–185. http://dx.doi.org/10.1111/japp.12155.
- Yeates, J. and Main, D. (2009) Assessment of companion animal quality of life in veterinary practice and research. *Journal of Small Animal Practice* 50, 274–281. http:// dx.doi.org/10.1111/j.1748-5827.2009.00755.x.
- Yeates, J.W., Stone, M., Mullen, S.M., Main, D.C.M. (2008) Owner-rated assessment of quality of life in dogs: Development of a qualitative tool. Poster session, UFAW Animal Welfare Conference, Birmingham, UK.
- Yeates, J.W., Mullan, S., Stone, M., Main, D.C. (2011)
 Promoting discussions and decisions about dogs'
 quality-of-life. *Journal of Small Animal Practice* 52,
 459–463. http://dx.doi.org/10.1111/j.1748-5827.2011.
 01094.x.

8

The Mental Health and Well-being Benefits of Social Contact and Social Support in Animals

FRANKLIN D. McMILLAN

Best Friends Animal Society, Kanab, Utah, USA

8.1 Benefits of Social Support in Humans and Nonhuman Animals

8.1.1 General fitness benefits

A large literature now exists to affirm that social animals¹ – human and nonhuman – have a fundamental biological need to form emotional connections with others and that they experience distress when socially isolated or separated from other valued individuals (Panksepp, 1998; Hostinar and Gunnar, 2015; McMillan, 2016). The evolutionary value of sociality – for parental care, food and other resource acquisition, mate selection, and predator defenses – has been extensively reviewed (Alexander, 1974). This chapter addresses the positive effects of social affiliation that extend beyond these fitness benefits.

Current evidence convincingly demonstrates that social mammals (including humans, as well as some nonmammalian species) share a distinct attribute, referred to as social support, whereby individuals in the company of affiliative conspecifics experience improved physical and psychological well-being (Kikusui et al., 2006; Rault, 2012). There is currently no universally agreed upon definition of social support (Uchino, 2006). Some definitions limit the benefits to times of stress; for example, social support has been defined as 'a social network's provision of psychological and material resources intended to benefit an individual's ability to cope with stress' (Hostinar and Gunnar, 2015). However, as we will see, the benefits of social contact and social support occur prominently - but not exclusively - during times of stress (Taylor et al., 2005) and, accordingly, social support in this chapter will use the definition inclusive of all benefits derived from social interactions both within and outside of stressful contexts. The subset of social support that functions during and shortly after stressful conditions is termed *social buffering* (or *stress buffering*), and refers to the phenomenon in which individuals experience less overall stress and/or recover more rapidly from stress when in the presence of compatible conspecifics than when not (Kikusui *et al.*, 2006; Hennessy *et al.*, 2009).

8.1.2 Health benefits

Physical health

One of the most robust empirical findings regarding social support in humans and nonhuman animals (hereafter 'animals') is its association with physical health and mortality (Hawkley et al., 2012). In humans, hundreds of empirical investigations have demonstrated ties between social support and reduced health risks of all kinds and involving all major body systems (e.g., cardiovascular, endocrine, and immune), affecting both the initial likelihood of disease as well as the course of recovery among those who are already ill (Uchino et al., 1996; Taylor et al., 2005). In animal species, a small sampling of adverse effects of social isolation on physical health include exacerbation of coronary artery atherosclerosis among female long-tailed macaques, promotion of the development of obesity and type 2 diabetes in mice, exacerbation of infarct size and edema and decreased post-stroke survival rate following experimentally induced stroke in mice, neuroinflammation and cell death following experimental cerebral ischemia, and detrimental neurological changes (reviewed by Cacioppo et al., 2011, 2014a). In addition, when compared with people who report having meaningful social bonds with others, people who perceive themselves as socially isolated or lacking strong connections with others have a significantly shorter lifespan (Cacioppo and Patrick, 2008; Cacioppo and Hawkley, 2009), and social animals who form strong relationships and are integrated most strongly into group living are most likely to survive, reproduce, and raise offspring to reproductive age (MacDonald and Leary, 2005).

Mental health

In addition to the benefits to physical health, empirical investigations spanning the past century support the notion that social ties and social support in humans are positively correlated with improved mental health and psychological well-being (Achat et al., 1998; Ethgen et al., 2004; Thoits, 2011; Rault, 2012; Hostinar and Gunnar, 2015). Social connections predict decreased negative affect (Siedlecki et al., 2014) and can lessen the risk of anxiety and depression (Kikusui et al., 2006; Neumann, 2009; Thoits, 2011; Siedlecki et al., 2014) as well as promote the positive aspects of mental health (Feeney and Collins, 2015). In studies looking at the relationship between social relationships and the more general well-being concepts, social support was determined to be associated with improved quality of life (Bennett et al., 2001), subjective well-being (Feeney and Collins, 2015), and life satisfaction (Siedlecki et al., 2014).

Stress is the most readily recognized factor connecting social inclusiveness and enhanced mental health and well-being. Evidence in humans indicates that social support buffers the harmful mental health impacts of stress exposure (Thoits, 2011; Smith and Wang, 2014) and that during stressful events receiving caring support from social partners increases feelings of calmness and security, decreases depression and anger, and increases positive mood (Feeney and Collins, 2015).

Research has elucidated the stress buffering effect of social support. Stress responses comprise an adaptive mechanism that enables biological organisms to respond to changes in the environment, with the hypothalamic–pituitary–adrenocortical (HPA) axis being widely regarded as the body's primary stress-responsive neuroendocrine system (Hennessy *et al.*, 2009; Rault, 2012). A broad array of aversive and/or arousing situations elicit

increased HPA activity, which in the short-term promotes successful coping (greater resilience) with stressors (Hennessy *et al.*, 2009). However, repeated or prolonged HPA activation is associated with mental disturbances, emotional dysfunction, and psychopathological conditions such as depression (Taylor *et al.*, 2005; Ditzen and Heinrichs, 2014).

Knowledge of the connection of social factors and stress dates back to the 1950s. In a literature review, Bovard (1959, p.269) concluded that, 'Taken together, these studies at the human and animal levels suggest presence of another animal of the same species has protective effect under stress'. Seeman and McEwen (1996) reviewed the animal and human studies between the 1960s and mid-1990s for evidence of social environment influencing neuroendocrine reactivity, including effects on activity of the HPA axis, sympathetic nervous system (SNS), and cardiovascular system. The key finding of the reviewed studies was that positive social relationships can attenuate patterns of neuroendocrine responses to stressors: both HPA and SNS activity are dampened during and briefly following stressful experiences (reviewed by Seeman and McEwen, 1996). Subsequent research has produced ample evidence to confirm these findings in humans and animals (reviewed by Kikusui et al., 2006; Hennessy et al., 2009; Rault 2012; Hostinar et al., 2014; Hostinar and Gunnar 2015; Sullivan and Perry 2015).

Evidence demonstrating that social support dampens physiologic stress responses converges well with a line of research examining how animals behave when exposed to stress. A large body of work now exists to show that in general, a stressed social animal (human and nonhuman) is highly attracted to conspecifics and that seeking social proximity or social contact and acquiring such contact can lead to a reduction in their stress hormone levels and distress vocalizations (Rault, 2012; Hostinar et al., 2014; Smith and Wang, 2014). As just one example, Coe et al. (1982) found that when monkeys were exposed in pairs to the fearinducing stimulus of a snake they exhibited a strong preference for staying in close proximity with each other. These findings have led to the suggestion that social buffering may be a crucial component of the motivation underlying formation and maintenance of social relationships, since stress alleviation would be expected to be reinforcing (Hennessy et al., 2009; Hostinar et al., 2014).

8.2 Social Support and Social Buffering in Animals

8.2.1 How social support benefits mental health and well-being

Categorizing the effects of social support

The analysis of social support benefits is hampered by the existence of multiple methods of subdividing and categorizing the important constructs. In addition, all methods of categorization yield overlaps and indistinct lines between the different divisions (see Fig. 8.1). The two major methods of subdividing the positive social support effects are stress-related versus nonstress-related and isolation-related stress versus nonisolation-related stress.

STRESS-RELATED VERSUS NONSTRESS-RELATED **EFFECTS** The social support literature has focused on stress buffering effects of social support (resulting in the aforementioned occurrence of some definitions of social support confining the effects to a stress context). However, numerous studies have indicated that social support can protect and promote well-being both when individuals are and are not experiencing stress (Thoits, 2011; Feeney and Collins, 2015). That social support is beneficial in the absence of adversity led to new thinking, one influential approach being that of Cohen and Wills (1985), who proposed that social support refers to two theoretical mechanisms. The main effects

hypothesis states that social support exerts positive effects on well-being irrespective of stressors (Fig. 8.1). In this way, there is a direct relationship between well-being and social support: the more social support an individual has, the better the well-being, regardless of the individual's level of stress. Here, the relation between quality of life and social support is linear (Helgeson, 2003; Ditzen and Heinrichs, 2014). In contrast, the social buffering hypothesis views social support as operational and beneficial only during episodes of stress and adversity, reducing the impact of stressors on the individual's well-being (Fig. 8.1). Under these effects the individual's level of stress or adversity determines the relation of social support to well-being: in the absence of stress, well-being is independent of social support, whereas in instances of adversity, well-being is enhanced by the stress-buffering effects of social support (Helgeson, 2003; Rault, 2012). There is evidence to support the existence, as well as the coexistence, of both mechanisms (Cohen and Wills, 1985; Ditzen and Heinrichs, 2014).

The existence of the social buffering effects is well documented empirically in both animals (Rault, 2012) and humans (Kikusui *et al.*, 2006); however, in animals the main effects hypothesis has received virtually no attention by researchers until quite recently. Wittig *et al.* (2016) tested the main effects and social buffering hypotheses by measuring urinary glucocorticoid levels in wild chimpanzees with or without their bond partners in three situations:

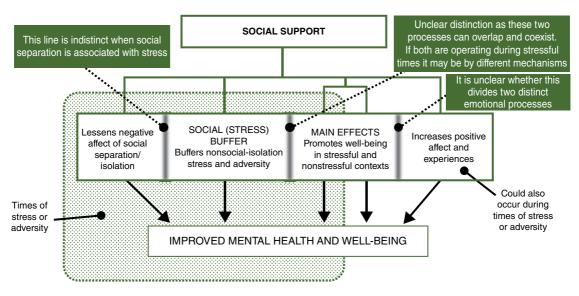


Fig. 8.1. Proposed pathways linking social support with positive effects on mental health and well-being.

a natural stressor, everyday affiliation, and resting. Results showed HPA axis dampening during daily engagement with bond partners both within and outside of stressful contexts, thereby supporting the existence of a main effects mechanism. This is consistent with substantial research demonstrating that when social animals are permitted to interact with conspecifics they had decreased plasma glucocorticoid levels (reviewed by Kikusui *et al.*, 2006; DeVries *et al.*, 2007). These findings suggest that the well-being of nonhuman animals may benefit from social support during all aspects of life, not simply during times of stress.

ISOLATION-RELATED AND NONISOLATION-RELATED STRESS If we consider the stress-related benefits of social support, there are two types of stress that are relevant: that associated with and that not associated with social isolation. Because social isolation is itself a stressor (see next section) some confusion exists when social buffering operates in situations of isolation. The presence of social companions generally has, by its very nature, an alleviating effect on such isolation stress. The question, then, is whether social interaction in this context constitutes a 'true' buffering effect on neuroendocrine stress systems, or simply eliminates the stressor itself by reestablishing social interaction. As generally conceived, social buffering refers to the capacity of an animal to cope with a broader array of stressful challenges - isolation-related as well as nonisolation-related - when accompanied by conspecifics (Rault, 2012). As Rault (2012) has noted, the presence of partners has more to contribute to an animal's well-being than simply nullifying social separation distress.

With the addition of a third factor – the elaboration of pleasant feelings (discussed in the 'Promotion of positive affect' section, p. 104) – we can now configure the above subdivisions of social support into three major components that comprise the connection between social factors and well-being: (i) alleviation of negative affect (including stress) of social separation or isolation; (ii) buffering of nonsocialisolation stress and adversity; and (iii) promotion of positive affect (see Fig. 8.1).

Alleviation of negative affect (including stress) of social separation or isolation

Given the crucial importance of social connectedness in group-living species, there is a clear adaptive benefit to having a strong aversive response upon social separation as a potent motivator of social connection or reconnection (Eisenberger, 2012; Cacioppo et al., 2014a), just as there is a benefit to having negative affect signaling and motivating corrective behavior for other conditions threatening survival, such as thirst, hunger, and tissue damage (MacDonald and Leary, 2005; Cacioppo et al., 2006, DeWall et al., 2010). Panksepp (2011) contends that research in humans and animals now strongly supports the notion that emotional pain arising from the disruption of social relationships – whether it be through the loss of contact with or death of a social partner - is a basic emotional response of mammalian brains. Social separation and/or isolation has been shown to rank among the most reliable and potent stimuli for producing a stress response in a diverse array of social mammals (reviewed by Cacioppo et al., 2011, 2014b, 2015a; Hawkley et al., 2012; Rault 2012), and is widely used as an experimental model for inducing stress (Cacioppo et al., 2014b) (Fig. 8.2).

The adverse affective experience associated with social separation (referred to as social pain) is actually composed of a number of different emotions (reviewed by McMillan, 2016), each demonstrated to have powerful adverse effects on mental health and well-being across phylogeny. In humans and animals, loneliness and social isolation distress result when, respectively, an individual's actual level of social relationships - in terms of quality and/or quantity - fails to match their desired level of relations and from objectively being alone (Weiss, 1973; Cacioppo et al., 2014b, 2015a,b; Capitanio et al., 2014). In this way, an individual person or animal could experience loneliness when separated from desired partners, even if in the company of other conspecifics (Capitanio et al., 2014). Accumulating research suggests that fear is a component of the negative affect of social pain (reviewed by McMillan, 2016). Being socially separated presents a survival risk (e.g., from predation, health disorders), and current evidence indicates that the brain of social animals evolved mechanisms to put individuals into a short-term, self-preservation mode when they find themselves without companionship or mutual protection/assistance (Cacioppo et al., 2015b). Indeed, the brain's social and fear circuitry share the amygdala as a core structure, so social relationships and fear modulation appear to be closely related (Panksepp, 2001). Overlapping the research noted earlier that in stressful situations animals seek the





Fig. 8.2. In Switzerland a law enacted in 2008 states that animals classified as 'social species' – such as guinea pigs and parrots – will be considered victims of abuse if they don't live or interact regularly with others of their species (Howard, 2008). (Images used under license from Shutterstock.com.)

company of others, fear increases rats' preference for conspecific contact and appears to be allayed when conspecific animals are together, suggesting that fear reduction may contribute to the forces of social attraction between individuals (Kikusui *et al.*, 2006).

Specific adverse mental health effects include social separation in adulthood producing behavioral indicators of depression or anxiety in a number of species (Grippo et al., 2007). Currently, chronic social isolation serves as an animal model for studying elicitation, course trajectory, and treatment responses of affective disorders in several species (reviewed by Capitanio et al., 2014; Cacioppo et al., 2015b). For example, in prairie voles the absence of social contact can cause dysregulation of HPA axis activity and produce behaviors that mimic symptomatology of depression and anxiety disorders in humans (Smith and Wang, 2014). Taken together, current evidence indicates that social separation and isolation are risk factors for impaired mental health and the development of psychopathologies (Neumann, 2009) (see Fig. 8.3).

Social pain is elicited whenever the level of social interaction is inadequate to meet an individual's needs, which can include separation from a *specific* social partner, from *any* social partner, or complete isolation. The ways social pain is alleviated vary correspondingly, in accord with the nature of the social deprivation eliciting emotional distress. In addition, specific modulating factors (presented in 'Factors modulating the efficacy of social buffering' section) influence how social companionship alleviates social

pain and benefits mental health and well-being. Interestingly, some research suggests that alleviating the distress of social pain requires only a reasonable facsimile of the missing social element. For example, da Costa *et al.* (2004) demonstrated that simply providing a picture of a conspecific's face to an isolated adult sheep caused major reduction in the animals' behavior, autonomic, and endocrine stress responses.

Buffering of nonsocial-isolation stress and adversity

Evidence accumulating over the past 50 years demonstrates the buffering effect of social support for stress and adversity unrelated to social deprivation. Positive effects have been documented in two major groups of animals: the young (infants and juveniles) and adults. Stress buffering in these two groups may or may not involve the same neurobiological mechanisms.

INFANT AND JUVENILE ANIMALS The most extensively investigated form of social buffering is that exerted by the mammalian mother on her infant's stress responses (Hennessy *et al.*, 2009). Rat pups (Hostinar *et al.*, 2014) and goat kids (Liddell, 1949) exposed to a stressor exhibit less physiological and behavioral signs of stress when the mother is present compared to when she is not. Stress buffering in the young has been demonstrated in nonhuman primates in several studies (reviewed by Kikusui *et al.*, 2006). For example, when squirrel



Fig. 8.3. Social animals denied companionship experience social pain and decreased physical health. (Image used under license from Shutterstock.com.)

monkey infants were separated from their mother they showed a lower HPA axis response if they remained in the company of their social group, indicating that the conspecific companions acted as a buffer to maternal separation stress. Similarly, when infants are exposed to the stress of separation from their social companions, the presence of the mother blunts the elevation of cortisol levels that occur in the mother's absence.

While social buffering of the HPA axis in early life has been studied most extensively in mammals (Hennessy *et al.*, 2009), recent work has begun to include avian species. Edgar *et al.* (2015) compared stress responses of chicks in the presence and absence of their mother and found that mother hens are able to buffer their chicks' stress response to an aversive stimulus such as a puff of air.

ADULT ANIMALS Research methodology for studying social buffering in adult animals have varied widely in terms of species (e.g., numerous mammalian orders), type of stressor (e.g., electric shock, white noise, exposure to a novel environment, social defeat by a dominant conspecific, exposure to a live snake, and human encounter), and timing of the support relative to stressor exposure (e.g., before, during, or after) (Rault, 2012). The following represents a relatively small sampling of the research in this field.

Livestock animals - Sheep exposed to a stressful fear eliciting stimulus (sudden opening of umbrella) showed fewer behavioral signs of reactivity (attempts to escape and fast movements) if in a group than if socially isolated (González et al., 2013). Lower stress levels (measured by behavior and cortisol levels) occurred in bulls during pre-slaughter handling if maintained in physical or visual contact with their familiar social group (Mounier et al., 2006). Fear-inducing stimuli elicit fewer behavioral signs of disturbance in heifers when near companion peers (Boissy and Le Neindre, 1990). In horses, the stress of stabling for the first time - as indicated by behaviors such as neighing, pawing, nibbling, snorting, and stereotypies – was significantly less in horses with companions than those without (Ditzen and Heinrichs, 2014). When horses were transported by trailer, those traveling with a companion showed significantly reduced physiological responses than those traveling alone (Kay and Hall, 2009).

Rodents – In prairie voles, immobilization-induced increases in stress-related behaviors and corticosterone levels occurred in females recovering from the stressor alone, but not if recovering with their male partner (Smith and Wang, 2014). Davitz and Mason (1955) reported that rats showed a lesser degree of immobilization when shocked in the presence of a companion than when shocked alone. Training rats with electric shock as punishment

was less effective when the subject rat was accompanied by conspecifics than when trained alone (Rasmussen, 1939). Rats exposed to a fear stimulus or a novel environment showed fewer indicators of fear, such as fearful withdrawal behavior and a lower corticosterone response, if with a partner rat than when alone (Davitz and Mason, 1955; Taylor, 1981; Kikusui et al., 2006) (Fig. 8.4). Similarly, following forced exposure to a novel environment, group-housed mice showed a significantly lower increase in corticosterone levels than did solitaryhoused mice (Bartolomucci et al., 2003). Isolated rats, as compared to socially housed rats, show significantly greater corticosterone responses to restraint stress (Hermes et al., 2006). Immobilization and cold stress elicits greater reactivity of the HPA axis in isolated rats than in rats housed in groups (Dronjak et al., 2004). Rats tested alone in a chronic approach-avoidance conflict situation showed significantly greater gastric ulceration than rats tested with companions present (Conger et al., 1958). Ruis et al. (1999) found that if rats are isolated after social defeat by a dominant rat they will show long-lasting, anxiety-like behavioral and physiological changes, but if placed with familiar rats these adverse effects are greatly reduced.

Dogs – Dogs with storm phobia were exposed to a simulated thunderstorm and evaluated for behavioral signs of fear (pacing, whining, hiding) and cortisol level (Dreschel and Granger, 2005). Dogs with other canine companions in the household, compared to



Fig. 8.4. Rats with companions present show less fear to a threatening stimulus than rats without companions (Davitz and Mason, 1955). (Image used under license from Shutterstock.com.)

dogs without, showed less pronounced reactivity during and more rapid HPA axis recovery after the stressor.

Primates – In numerous nonhuman primate species, social relationships act as a potent buffer against stress (reviewed by Hostinar et al., 2014). For example, when a conditioned stimulus using electric shock was induced in squirrel monkeys, later reexposure to the training cue elicited an increase in fear responses and cortisol levels in monkeys without a social partner present but not in monkeys with companions present (Stanton et al., 1985). Squirrel monkey mothers who were separated from their infants showed an increase in cortisol if they lived alone, but not if they lived in a group (Mendoza et al., 1978). When wild male Barbary macaques were exposed to naturalistic stressors (low temperatures or group aggression), the monkeys with stronger social ties had lower fecal cortisol levels than monkeys with weaker bonds (Young et al., 2014). Finally, it is worth noting that some of the most compelling evidence regarding social buffering in human primates has come from studies involving severe - or traumatic - stress and adversity in humans (for animals, see also Chapter 14, this volume). In a metaanalysis of 77 published papers investigating risk factors for posttraumatic stress disorder (PTSD) in trauma-exposed adult humans, Brewin et al. (2000) found that the single most important posttraumatic risk factor was lack of social support. In another meta-analysis Ozer et al. (2003) examined 66 studies on predictors of PTSD and determined that social support provides significant protection against the development of PTSD. Helgeson (2003, p.26) wrote that 'The person who faces high stress with support resources is almost as well off as the person who is not experiencing the stressor'.

NEUROENDOCRINE MECHANISMS UNDERLYING SOCIAL BUFFERING Substantial empirical support now exists for the notion that social buffering has reliable and beneficial effects on mental (and physical) health and well-being, and that the cause—effect mechanisms or pathways are mediated at least in part by a dampening of sympathetic and HPA responses to stress (Taylor *et al.*, 2005). However, our understanding of the underlying neurobiology and relevant components that produce these HPA activity-regulating effects remains vastly incomplete (Hostinar *et al.*, 2014; Smith and Wang, 2014). Research has now increasingly been directed at determining the nature of these mechanisms, which

is crucial to developing the best methods of using the social buffering effect to promote an individual's ability to cope with adversity. Some answers are beginning to emerge.

Developments to date have placed neuropeptides and opioids at the forefront of likely mediators linking social buffering and well-being. Of these, oxytocin has amassed the most supporting evidence.

Oxytocin - Oxytocin (OT) has been strongly conserved throughout evolution and has similar functions across vertebrates to promote affiliative social interactions and the formation of social bonds (Hennessy et al., 2009; Hostinar et al., 2014). In both humans and animals OT is released in response to a variety of stressors (Taylor et al., 2005) and data support an inhibitory effect on sympathetic and HPA responses to stress (Taylor et al., 2005; Neumann, 2009). Exogenous OT administered during social isolation can eliminate the negative emotional effects of isolation (Smith and Wang, 2014). In rodents, OT has anxiolytic effects (Neumann, 2009; Smith and Wang, 2014) and central administration of OT inhibits the activity of the HPA axis and reduces anxietylike behavior to acute psychological stressors in several mammalian species (Smith and Wang, 2014; Hostinar and Gunnar, 2015). When experimental stress in mice (Norman et al., 2010) and hamsters (Hostinar et al., 2014) elicits increased cortisol and depression-like behavior in isolated but not grouphoused animals, treatment with OT attenuates these effects in the isolated animals. Conversely, injections of an OT receptor antagonist increases HPA activity (Hennessy et al., 2009) and negates the social buffering effect of social contact on HPA responses to stressors (Smith and Wang, 2014) and prevents the group housing benefits on depression- and anxietylike behaviors in rodents (Smith and Wang, 2014).

In addition, affiliative physical contact with a conspecific promotes OT release (Kikusui *et al.*, 2006; Hennessy *et al.*, 2009). Animals prefer to spend time with conspecifics in whose presence they experienced high brain OT levels in the past (Taylor *et al.*, 2005), a finding in accord with the studies mentioned earlier showing that animals and humans experiencing stress are highly attracted to conspecifics. Overall, current data strongly support a role for OT that is both necessary and, in at least some cases, sufficient, for mediating social buffering effects (Smith and Wang, 2014).

Opioids and other neurohormones – Endogenous opioids have also been implicated as a biological mediator for the beneficial effects of social buffering

(Kikusui et al., 2006). Evidence suggests that endogenous opioids are, like OT, secreted in response to stress and to positive social contact and as well associated with down-regulation of sympathetic and HPA responses to stress (Taylor et al., 2005). Other potential neurohormonal mediators for stress buffering effects include norepinephrine, serotonin, and prolactin (Taylor et al., 2005). All evidence considered, it is generally accepted that social buffering effects are likely supported by multiple and potentially overlapping neurobiological pathways (Hostinar et al., 2014; Smith and Wang, 2014; Sullivan and Perry, 2015).

FACTORS MODULATING THE EFFICACY OF SOCIAL BUFFERING As research on social buffering progressed it soon became evident that there was a substantial variability and degree of inconsistency among individual responses to social companionship. It seemed clear that the presence of conspecifics interacts with other factors to produce a buffering effect (Ditzen and Heinrichs, 2014; Hostinar *et al.*, 2014).

It is first important to note that social contact in humans and animals is not always positive; social interactions and relationships can be a source of conflict, stress, and tension – with the potential to increase, rather than decrease, HPA reactivity in stressful situations (Zajonc, 1965; Seeman and McEwen, 1996; Helgeson, 2003). Accordingly, in considering modulating influences on social buffering it is taken as a given that the benefits derived from social support are enabled by compatible partners and impeded by incompatible and antagonistic partners, the latter being inherent sources of stress (Proudfoot and Habing, 2015). This is the basis for the general agreement among farm animal researchers that frequent regrouping of herbivores should be minimized as it often results in an increase in aggressive and agonistic behavior as the animals reestablish their social relationships (Proudfoot and Habing, 2015). This may then render social support less effective, resulting in animals more rather than less fearful and reactive when encountering stressful procedures (Rault, 2012). Specific factors identified as having modulating influence on social buffering effects include familiarity, number, and emotional state of the social partner as well as social experiences during early life.

The familiarity of the social partner has been demonstrated in numerous studies to be important in social suffering effects in animals. A familiar conspecific appears to be the most effective buffering

influence (reviewed by Kikusui et al., 2006; Rault, 2012); however, there is substantial variability among studies which is likely due to context and other factors. The variations include: (i) a familiar conspecific is an effective buffer but an unfamiliar one is not (Hennessy et al., 2009; reviewed by Rault, 2012); (ii) familiar and unfamiliar conspecifics both buffer, but familiar is more effective (Kiyokawa et al., 2014; reviewed by Kikusui et al., 2006); (iii) familiarity makes no difference (Boissy and Le Neindre, 1997); and (iv) a familiar conspecific is a less effective buffer than an unfamiliar companion (reviewed by Kikusui et al., 2006; Hostinar et al., 2014).

The efficacy of social buffering is also influenced by the number of social partners. As with familiarity, research has revealed variability in which buffering patterns are most effective: in some species and situations a single partner provides the best buffering but in other circumstances multiple companions are necessary for stress buffering to occur (reviewed by Kikusui et al., 2006). Some studies in humans have shown that as the size of a social group increases a rise in negative affect and social conflict may cause the benefits of social support to decline, indicating that with regard to social support, more is not always better (Segerstrom, 2008). Likewise, increasing numbers in animals may result in overcrowding, leading to increased stress from antagonistic behavior as well as greater pathogen exposure between animals (Proudfoot and Habing, 2015).

Factors may also combine in their effects. One study in cattle (Takeda *et al.*, 2003) demonstrated an effect of both group size and familiarity: results indicated that a calming effect on emotional stress was greatest when conspecifics were familiar rather than unfamiliar and in groups of five rather than groups of two.

The emotional state of the social partner also appears to influence the social buffering effect (reviewed by Kikusui et al., 2006; Rault, 2012). For example, Davitz and Mason (1955) showed that emotional responses in fear-conditioned rats were lower when the rat was accompanied by an unafraid rat than when the partner showed fearful behavior. More recently, Rørvang and Christensen (2018) found that when suddenly exposed to a novel stimulus, horses with a nonfearful companion exhibited decreased physiological and behavioral signs of fear as compared to horses with a fearful companion.

Social experiences during early life in humans and animals are associated with variations in the quality and nature of social relationships throughout life. Such specific factors as being reared by the mother as opposed to a surrogate, the quality of parental care, and early positive social interactions with conspecifics (socialization) all appear to influence the individual's ability to benefit from social buffering at later points in life (reviewed by Hennessy et al., 2009; Sullivan and Perry, 2015).

Promotion of positive affect

Up to this point all of the ways by which social support promotes mental health and well-being have involved an alleviation of unpleasant experiences, i.e., negating the emotional distress of social deprivation and buffering non-isolation-related stress. The other major benefit comes through the promotion of positive aspects of well-being (Boissy *et al.*, 2007; Feeney and Collins, 2015).

Current evidence supports the hypothesis that the social brain has evolved in such a way that engaging in adaptive social interactions activates the reward systems of the brain and generates positive affect (Boissy *et al.*, 2007; Cacioppo and Cacioppo, 2012). For example, brain scan studies of humans have shown that individuals who report being socially bonded with a partner exhibit activation of the subcortical brain areas that are associated with euphoria, reward, and motivation (Ortigue *et al.*, 2010). In animals, social activity such as male–female and mother–offspring interactions stimulate brain neuronal systems assumed to be part of the reward system (reviewed by Neumann, 2009).

In addition to their role in negative social emotional experiences, oxytocin, dopamine, and endorphins appear to play a major role in the central reward circuitry through regulation of pleasurable affect, including the sense of security and comfort, in social relationships (Cozolino, 2006). In humans, evidence points to the possibility of a link between an oxytocin-opiate system and soothing, calming, and feelings of social connectedness and safeness (Gilbert et al., 2008). In a study involving lactating female rats, Febo et al. (2005) used functional magnetic resonance imaging to demonstrate that mother-pup interactions during suckling resulted in an activation of the dopamine reward system in the mother. In addition, the researchers reported that the mother rat will prefer to spend time with pups over receiving cocaine, suggesting that the reward

value of social interaction with nursing offspring can outweigh that of cocaine (Febo *et al.*, 2005). In all, the provision of social support appears to help to sustain a positive affective balance (Feeney and Collins, 2015), leading Galindo *et al.* (2018) to suggest that social companionship may be the most effective way of enriching the lives of social species in captivity.

8.2.2 The special case of dogs

To summarize the argument thus far, the connection between social factors and well-being appears to consist of three somewhat overlapping components: (i) the negative affect (emotional distress) of social deprivation; (ii) buffering nonisolation-related stress; and (iii) the promotion of positive affect. The research on social support has overwhelmingly focused on interactions and relationships among conspecifics. The domestic dog stands out as the species where this conspecific selectivity underwent dramatic changes to include - robustly - interspecific social interactions and relationships. There is considerable evidence that the domestication of the dog involved the formation and amplification of all three components in social interactions directed toward a different species – humans. Domestication of the dog (in concert with evolutionary changes in humans) appears to have enabled humans to assume the role of alleviator of negative affect of isolation, stress buffer, and elicitor of positive affect for dogs² (Hennessy et al., 2009; reviewed by McMillan, 2016).

In a recent review of literature reports published from 2000 to 2014, Pop *et al.* (2014) found that when dogs interacted with humans in various settings (specifically, animal shelters, laboratory, or clinical settings such as animal assisted therapy), despite a few contradictory findings the reviewed studies showed positive human–dog interaction was most often associated with a significant decrease in stress in dogs as measured by cortisol levels, blood pressure, and behavior. In addition, dogs receiving human contact also displayed significant increases in the levels of oxytocin, dopamine, and β-endorphin.

Specific studies have shown that dogs in the novel environment will seek proximity and solicit interaction from a human, suggesting stress reduction to be a motivational element for these pro-social behaviors (Tuber *et al.*, 1996). Most dogs seek contact with humans and, when given the choice between interacting with another dog or a human, they often prefer social interaction and proximity



Fig. 8.5. Dogs with plentiful canine companionship will often still desire human companionship. (Image used under license from Shutterstock.com.)

with people (Tuber et al., 1996) (Fig. 8.5). Dogs also express more excitement toward gaining access to a human as compared to access to another dog (McGowan et al., 2014), and show a lower stress response to a novel situation in the presence of a human compared to the presence of another dog (Tuber et al., 1996) (Fig. 8.6). Many dogs show a specific affinity toward petting and will seek out this close contact from both familiar and unfamiliar people (Feuerbacher and Wynne, 2015).

Taken together, these studies suggest that isolation relief, stress buffering, and elevated positive affect may all be an important contributors to the domestic dog's propensity to form attachments with humans. Accordingly, these factors – each promoters of mental health and well-being in the dog – may have been (unwittingly) selected for during domestication and selective breeding practices.

Lastly, it is important to keep in mind that the benefits described above are contingent upon positive, or at least neutral, influences of the previously discussed modulators, in particular, early socialization with humans.

8.3 Concluding Remarks

The evidence accumulated over the past 80 years is clear: for social animals – human and nonhuman alike – health and well-being are promoted by positive social interactions and relationships and adversely affected when individuals are deprived of adequate social inclusion. The three major components of the connection between social factors and well-being are: (i) the harmful effect of social pain experienced in response to social deprivation;

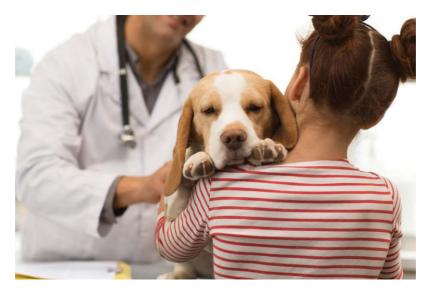


Fig. 8.6. Dogs in stressful circumstances comforted by the physical proximity and touch of humans have benefited emotionally (McMillan, 2016). (Image used under license from Shutterstock.com.)

(ii) the beneficial effect of positive social interactions in buffering general stress; and (iii) the beneficial effect of positive affect experienced in response to affiliative social interaction. While all three components appear to contribute to the attractive forces between social animals, the stress buffering aspect has received the most attention. But the importance of stress buffering may extend well beyond the influence on health. In reviewing the literature Hennessy et al. (2009) reasoned that because stress alleviation would likely be rewarding, social buffering appears to serve, at least in part, to promote social cohesion in specific arrangements. On this basis they construct a compelling argument that because partners with which an individual has a strong affiliative relationship (e.g., infants to mothers) seem particularly effective as social buffers, an important reason why certain conspecifics become preferred companions is precisely because they are the best at buffering one's stress responses. Moreover, they assert, it is reasonable to suggest that social buffering evolved to impel changes in those social preferences in order to facilitate developmental transitions in social interactions most beneficial at different life stages (i.e., first toward the mother, then toward conspecifics, then toward mates, then toward offspring) (Hennessy et al., 2009). In all of these functions, the quality of social relationships is strongly tied to health (mental and physical) and well-being. With our current knowledge, it is not surprising that after

combining the findings of multiple studies involving chimpanzees, gorillas, orangutans, rhesus macaques, and humans, Robinson *et al.* (2017) concluded that sociability is one of the pillars of primate happiness.

Notes

- ¹ 'Animal' in this chapter refers to nonhuman animals unless otherwise specified. In addition, the term 'social animal' is used in this chapter primarily in reference to mammals, as this has been where most research on the neurophysiology of sociality has been conducted. It is also important to note that among asocial mammals, such as skunks, bears, Arctic foxes, aardvarks, and moose, among many others, social processes between mother and infant show no apparent differences from those of social mammals.
- ² This is not to suggest that no other species is able to receive social support and social buffering from humans, but that dogs have attracted the most research and as a result of changes during domestication appear to experience greater benefits from interactions with humans than do other species (reviewed by McMillan, 2016).

8.4 References

Achat, H., Kawachi, I., Levine, S., Berkey, C., Coakley, E, et al. (1998) Social networks, stress and health-related quality of life. *Quality of Life Research* 7, 735–750. http://dx.doi.org/10.1023/A:1008837002431.

- Alexander, R.D. (1974) The evolution of social behavior. Annual Review of Ecology and Systematics 5, 325–383. http://dx.doi.org/10.1146/annurev.es.05.110174.001545.
- Bartolomucci, A., Palanza, P., Sacerdote, P., Ceresini, G., Chirieleison, A., et al. (2003) Individual housing induces altered immuno-endocrine responses to psychological stress in male mice. Psychoneuroendocrinology 28, 540–558. http://dx.doi.org/10.1016/S0306-4530(02)00039-2.
- Bennett, S.J., Perkins, S.M., Lane, K.A., Deer, M., Brater, D.C., et al. (2001) Social support and health-related quality of life in chronic heart failure patients. Quality of Life Research 10, 671–682. http://dx.doi.org/10.1023/A:1013815825500.
- Boissy, A. and Le Neindre, P. (1990) Social influences on the reactivity of heifers: Implications for learning abilities in operant conditioning. *Applied Animal Behaviour Science* 25, 149–165. http://dx.doi.org/10.1016/0168-1591(90)90077-Q.
- Boissy, A. and Le Neindre, P. (1997) Behavioral, cardiac and cortisol responses to brief peer separation and reunion in cattle. *Physiology & Behavior* 61, 693–699. http://dx.doi.org/10.1016/S0031-9384(96)00521-5.
- Boissy, A., Arnould, C., Chaillou, E., Désiré, L., Duvaux-Ponter, C., et al. (2007). Emotions and cognition: a new approach to animal welfare. *Animal Welfare* 16, 37–43.
- Bovard, E.W. (1959) The effects of social stimuli on response to stress. *Psychological Review* 66, 267–277. http://dx.doi.org/10.1037/h0045556.
- Brewin, C.R., Andrews, B., Valentine, J.D. (2000) Metaanalysis of risk factors for posttraumatic stress disorder in trauma-exposed adults. *Journal of Consulting* and Clinical Psychology 68, 748–766. http://dx.doi. org/10.1037/0022-006X.68.5.748.
- Cacioppo, S. and Cacioppo, J.T. (2012) Decoding the invisible forces of social connections. Frontiers in Integrative Neuroscience 6, 354–360. http://dx.doi. org/10.3389/fnint.2012.00051.
- Cacioppo, J.T. and Hawkley, L.C. (2009) Perceived social isolation and cognition. *Trends in Cognitive Science* 13, 447–454. http://dx.doi.org/10.1016/j.tics.2009.06.005.
- Cacioppo, J.T. and Patrick, W. (2008) Loneliness: Human Nature and the Need for Social Connection. W.W. Norton & Company, New York, USA.
- Cacioppo, J.T., Hawkley, L.C., Ernst, J.M., Burleson, M., Berntson, G.G., et al. (2006) Loneliness within a nomological net: An evolutionary perspective. *Journal of Research in Personality* 40, 1054–1085. http://dx.doi.org/10.1016/j.jrp.2005.11.007.
- Cacioppo, J.T., Hawkley, L.C., Norman, G.J., Berntson, G.G. (2011) Social isolation. *Annals of the New York Academy of Sciences* 1231, 17–22. http://dx.doi.org/10.1111/j.1749-6632.2011.06028.x.
- Cacioppo, J.T., Cacioppo, S., Boomsma, D.I. (2014a) Evolutionary mechanisms for loneliness. *Cognition* &

- Emotion 28, 3–21. http://dx.doi.org/10.1080/02699931 .2013.837379.
- Cacioppo, S., Capitanio, J.P., Cacioppo, J.T. (2014b)
 Toward a neurology of loneliness. *Psychological Bulletin* 140, 1464–1504. http://dx.doi.org/10.1037/a0037618
- Cacioppo, J.T., Cacioppo, S., Capitanio, J.P., Cole, S.W. (2015a) The neuroendocrinology of social isolation. Annual Review of Psychology 66, 733–767. http:// dx.doi.org/10.1146/annurev-psych-010814-015240.
- Cacioppo, J.T., Cacioppo, S., Cole, S.W., Capitanio, J.P., Goossens, L., et al. (2015b) Loneliness across phylogeny and a call for comparative studies and animal models. *Perspectives on Psychological Science* 10, 202–212. http://dx.doi.org/10.1177/1745691614564876.
- Capitanio, J.P., Hawkley, L.C., Cole, S.W., Cacioppo, J.T. (2014) A behavioral taxonomy of loneliness in humans and rhesus monkeys (*Macaca mulatta*). *PLoS ONE* 9(10), e110307. http://dx.doi.org/10.1371/journal.pone.0110307.
- Coe, C.L., Franklin, D., Smith, E.R., Levine, S. (1982) Hormonal responses accompanying fear and agitation in the squirrel monkey. *Physiology and Behavior* 29, 1051–1057. http://dx.doi.org/10.1016/0031-9384 (82)90297-9.
- Cohen, S. and Wills, T.A. (1985) Stress, social support, and the buffering hypothesis. *Psychological Bulletin* 98, 310–357. http://dx.doi.org/10.1037/0033-2909.98.2.310.
- Conger, J.J., Sawrey, W.L., Turrell, E.S. (1958) The role of social experience in the production of gastric ulcers in hooded rats placed in a conflict situation. *The Journal* of Abnormal and Social Psychology 57, 214–220. http://dx.doi.org/10.1037/h0041533.
- Cozolino, L. (2006) The Neuroscience of Human Relationships. WW Norton & Co., New York, USA.
- Da Costa, A.P., Leigh, A.E., Man, M.S., Kendrick, K. M. (2004) Face pictures reduce behavioural, autonomic, endocrine and neural indices of stress and fear in sheep. *Proceedings of the Royal Society of London B: Biological Sciences* 271, 2077–2084. http://dx.doi. org/10.1098/rspb.2004.2831.
- Davitz, J. and Mason, D.J. (1955) Socially facilitated reduction of fear response in rats. *Journal of Comparative and Physiological Psychology* 48, 149–151. http://dx.doi.org/10.1037/h0046411.
- DeVries, A.C., Craft, T.K., Glasper, E.R., Neigh, G.N., Alexander, J.K. (2007) 2006 Curt P. Richter award winner: Social influences on stress responses and health. *Psychoneuroendocrinology* 32, 587–603. http://dx.doi.org/10.1016/j.psyneuen.2007.04.007.
- DeWall, C.N., MacDonald, G., Webster, G.D., Masten, C.L., Baumeister, R.F., et al. (2010) Acetaminophen reduces social pain: Behavioral and neural evidence. Psychological Science 21, 931–937 http://dx.doi.org/10.1177/0956797610374741.

- Ditzen, B. and Heinrichs, M. (2014) Psychobiology of social support: The social dimension of stress buffering. Restorative Neurology and Neuroscience 32, 149–162.
- Dreschel, N.A. and Granger, D.A. (2005) Physiological and behavioral reactivity to stress in thunderstorm-phobic dogs and their caregivers. *Applied Animal Behaviour Science* 95, 153–168. http://dx.doi.org/10.1016/j.applanim.2005.04.009.
- Dronjak, S., Gavrilović, L., Filipović, D., Radojčić, M. B. (2004) Immobilization and cold stress affect sympatho–adrenomedullary system and pituitary–adrenocortical axis of rats exposed to long-term isolation and crowding. *Physiology & Behavior* 81, 409–415. http://dx.doi.org/10.1016/j.physbeh.2004.01.011.
- Edgar, J., Held, S., Paul, E., Pettersson, I., Price, R. I. A., et al. (2015) Social buffering in a bird. *Animal Behaviour* 105, 11–19. http://dx.doi.org/10.1016/j.anbehav.2015.04.007.
- Eisenberger, N.I. (2012) The neural bases of social pain: Evidence for shared representations with physical pain. *Psychosomatic Medicine* 74, 126–135. http://dx.doi.org/10.1097/PSY.0b013e3182464dd1.
- Ethgen, O., Vanparijs, P., Delhalle, S., Rosant, S., Bruyere, O., et al. (2004) Social support and health-related quality of life in hip and knee osteoarthritis. *Quality of Life Research* 13, 321–330. http://dx.doi.org/10.1023/B:QURE.0000018492.40262.d1.
- Febo, M., Numan, M., Ferris, C.F. (2005) Functional magnetic resonance imaging shows oxytocin activates brain regions associated with mother–pup bonding during suckling. *Journal of Neuroscience* 25, 11637–11644. http://dx.doi.org/10.1523/JNEUROSCI. 3604-05.2005.
- Feeney, B.C. and Collins, N.L. (2015) A new look at social support: A theoretical perspective on thriving through relationships. *Personality and Social Psychology Review* 19, 113–147. http://dx.doi. org/10.1177/1088868314544222.
- Feuerbacher, E.N. and Wynne, C.D. (2015). Shut up and pet me! Domestic dogs (*Canis lupus familiaris*) prefer petting to vocal praise in concurrent and single-alternative choice procedures. *Behavioural Processes* 110, 47–59. http://dx.doi.org/10.1016/j.beproc.2014.08.019.
- Galindo, F., Newberry, R.C., Mendl, M. (2018) Social conditions. In: Appleby, M.C., Olsson, I.A.S., Galindo, F. (eds.) Animal Welfare, 3rd edn. CAB International, Wallingford, UK, pp. 271–293. http://dx.doi.org/10.1079/ 9781786390202.0271.
- Gilbert, P., McEwan, K., Mitra, R., Franks, L., Richter, A., et al. (2008) Feeling safe and content: A specific affect regulation system? Relationship to depression, anxiety, stress, and self-criticism. Journal of Positive Psychology 3, 182–191. http://dx.doi.org/10.1080/17439760801999461.
- González, M., Averós, X., Beltrán de Heredia, I., Ruiz, R., Arranz, J., et al. (2013) The effect of social buffering on fear responses in sheep (Ovis aries). Applied

- Animal Behaviour Science 149, 13–20. http://dx.doi.org/10.1016/j.applanim.2013.09.011.
- Grippo, A.J., Cushing, B.S., Carter, C.S. (2007) Depression-like behavior and stressor-induced neuroendocrine activation in female prairie voles exposed to chronic social isolation. *Psychosomatic Medicine* 69, 149–157. http://dx.doi.org/10.1097/PSY.0b013e31802f054b.
- Hawkley, L.C., Cole, S.W., Capitanio, J.P., Norman, G.J., Cacioppo, J.T. (2012) Effects of social isolation on glucocorticoid regulation in social mammals. *Hormones and Behavior* 62, 314–232. http://dx.doi.org/10.1016/j. yhbeh.2012.05.011.
- Helgeson, V.S. (2003) Social support and quality of life. Quality of Life Research 12(Suppl. 1), 25–31. http://dx.doi.org/10.1023/A:1023509117524.
- Hennessy, M.B., Kaiser, S., Sachser, N. (2009) Social buffering of the stress response: Diversity, mechanisms, and functions. *Frontiers in Neuroendocrinology* 30, 470–482. http://dx.doi.org/10.1016/j. yfrne.2009.06.001.
- Hermes, G.L., Rosenthal, L., Montag, A., McClintock, M.K. (2006) Social isolation and the inflammatory response: Sex differences in the enduring effects of a prior stressor. American Journal of Physiology — Regulatory, Integrative and Comparative Physiology 290, 273–282. http://dx.doi.org/10.1152/ajpregu.00368.2005.
- Hostinar, C.E. and Gunnar, M.R. (2015) Social support can buffer against stress and shape brain activity. AJOB Neuroscience 6, 34–42. http://dx.doi.org/10.10 80/21507740.2015.1047054.
- Hostinar, C.E., Sullivan, R.M., Gunnar, M.R. (2014) Psychobiological mechanisms underlying the social buffering of the HPA axis: A review of animal models and human studies across development. *Psychological Bulletin* 140, 256–282. http://dx.doi.org/10.1037/a0032671.
- Howard B. (2008) Swiss law orders pet buddy system. Available at: http://veterinarybusiness.dvm360.com/ swiss-law-orders-pet-buddy-system (accessed 3 January 2019).
- Kay, R. and Hall, C. (2009) The use of a mirror reduces isolation stress in horses being transported by trailer. Applied Animal Behaviour Science 116, 237–243. http://dx.doi.org/10.1016/j.applanim.2008.08.013
- Kikusui, T., Winslow, J.T., Mori, Y. (2006) Social buffering: Relief from stress and anxiety. *Philosophical Transactions of The Royal Society of London Series B – Biological Sciences* 361, 2215–2228.
- Kiyokawa, Y., Honda, A., Takeuchi, Y., Mori, Y. (2014) A familiar conspecific is more effective than an unfamiliar conspecific for social buffering of conditioned fear responses in male rats. *Behavioural Brain Research* 267, 189–193. http://dx.doi.org/10.1016/j.bbr.2014.03.043
- Liddell, H. (1949) Some specific factors that modify tolerance for environmental stress. Research publications-Association for Research in Nervous and Mental Disease 29, 155–171.

- MacDonald, G. and Leary, M.R. (2005) Why does social exclusion hurt? The relationship between social and physical pain. *Psychological Bulletin* 131, 202–223. http://dx.doi.org/10.1037/0033-2909.131.2.202.
- McGowan, R.T., Rehn, T., Norling, Y., Keeling, L.J. (2014) Positive affect and learning: exploring the 'Eureka Effect' in dogs. *Animal Cognition* 17, 577–587. http://dx.doi.org/10.1007/s10071-013-0688-x.
- McMillan, F.D. (2016) The psychobiology of social pain: Evidence for a neurocognitive overlap with physical pain and welfare implications for social animals with special attention to the domestic dog (*Canis familiaris*). *Physiology & Behavior* 167, 154–171. http://dx.doi.org/10.1016/j.physbeh.2016.09.013.
- Mendoza, S.P., Coe, C.L., Lowe, E.L., Levine, S. (1978) The physiological response to group formation in adult male squirrel monkeys. *Psychoneuroendocrinology* 3, 221–229. http://dx.doi.org/10.1016/0306-4530(78)90012-4.
- Mounier, L., Veissier, I., Andanson, S., Delval, E., Boissy, A. (2006) Mixing at the beginning of fattening moderates social buffering in beef bulls. *Applied Animal Behaviour Science* 96, 185–200. http://dx.doi.org/10.1016/ j.applanim.2005.06.015.
- Neumann ID. (2009) The advantage of social living: Brain neuropeptides mediate the beneficial consequences of sex and motherhood. *Frontiers in Neuroendocrinology* 30, 483–496. http://dx.doi.org/10.1016/j.yfrne.2009.04.012.
- Norman, G.J., Karelina, K., Morris, J.S., Zhang, N., Cochran, M., et al. (2010) Social interaction prevents the development of depressive-like behavior post nerve injury in mice: A potential role for oxytocin. Psychosomatic Medicine 72, 519–526. http://dx.doi. org/10.1097/PSY.0b013e3181de8678.
- Ortigue, S., Bianchi-Demicheli, F., Patel, N., Frum, C., and Lewis, J. (2010) Neuroimaging of love: fMRI meta-analysis evidence towards new perspectives in sexual medicine. *Journal of Sexual Medicine* 7, 3541–3552. http://dx.doi.org/10.1111/j.1743-6109.2010.01999.x.
- Ozer, E.J., Best, S.R., Lipsey, T.L., Weiss, D.S. (2003) Predictors of posttraumatic stress disorder and symptoms in adults: A meta-analysis. *Psychological Bulletin* 129, 52–73. http://dx.doi.org/10.1037/0033-2909.129.1.52.
- Panksepp, J. (1998) Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, New York, USA.
- Panksepp, J. (2001) The long-term psychobiological consequences of infant emotions: Prescriptions for the 21st century. *Neuropsychoanalysis* 3, 149–178. http://dx.doi.org/10.1080/15294145.2001.10773353.
- Panksepp, J. (2011) The neurobiology of social loss in animals: Some keys to the puzzle of psychic pain in humans. In: MacDonald, G. and Jensen-Campbell, L.A. (eds.) Social Pain: Neuropsychological and Health Implications of Loss and Exclusion. American Psychological Association, Washington, DC, USA, pp. 11–51.

- Pop, D., Rusu, A.S., Pop-vancia, V., Papuc, I., Constantinescu, R., et al. (2014) Physiological effects of human-animal positive interaction in dogs – Review of the literature. Bulletin UASVM Animal Science and Biotechnologies 71, 102–110.
- Proudfoot, K. and Habing, G. (2015) Social stress as a cause of diseases in farm animals: Current knowledge and future directions. *Veterinary Journal* 206, 15–21. http://dx.doi.org/10.1016/j.tvjl.2015.05.024.
- Rasmussen, E.W. (1939) Social facilitation. *Acta Psychologica* 4, 275–291. http://dx.doi.org/10.1016/S0001-6918(39)90009-0.
- Rault, J.L. (2012) Friends with benefits: Social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science* 136, 1–14. http://dx.doi. org/10.1016/j.applanim.2011.10.002.
- Robinson, L.M., Altschul, D.M., Wallace, E.K., Úbeda, Y., Llorente, M., et al. (2017) Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. Applied Animal Behaviour Science 191, 90– 97. http://dx.doi.org/10.1016/j.applanim.2017.02.008.
- Rørvang, M.V. and Christensen, J.W. (2018) Attenuation of fear through social transmission in groups of same and differently aged horses. *Applied Animal Behaviour Science* 209, 41–46. http://dx.doi.org/10.1016/j.applanim. 2018.10.003.
- Ruis, M.A.W., Te Brake, J.H.A., Buwalda, B., De Boer, S.F., Meerlo, P., et al. (1999) Housing familiar male wildtype rats together reduces the long-term adverse behavioural and physiological effects of social defeat. Psychoneuroendocrinology 24, 285–300. http://dx.doi.org/10.1016/S0306-4530(98)00050-X.
- Seeman, T.E. and McEwen, B.S. (1996) Impact of social environment characteristics on neuroendocrine regulation. *Psychosomatic Medicine* 58, 459–471. http:// dx.doi.org/10.1097/00006842-199609000-00008.
- Segerstrom, S.C. (2008). Social networks and immunosuppression during stress: Relationship conflict or energy conservation? *Brain, Behavior, and Immunity* 22, 279–284. http://dx.doi.org/10.1016/j.bbi.2007.10.011.
- Siedlecki, K.L., Salthouse, T.A., Oishi, S., Jeswani, S. (2014) The relationship between social support and subjective well-being across age. Social Indicators Research 117, 561–576. http://dx.doi.org/10.1007/ s11205-013-0361-4.
- Smith, A.S. and Wang, Z. (2014) Hypothalamic oxytocin mediates social buffering of the stress response. *Biological Psychiatry* 76, 281–288. http://dx.doi.org/10.1016/j.biopsych.2013.09.017.
- Stanton, M.E., Patterson, J.M., Levine, S. (1985) Social influences on conditioned cortisol secretion in the squirrel monkey. *Psychoneurendocrinology* 10, 125–134. http://dx.doi.org/10.1016/0306-4530(85) 90050-2.
- Sullivan, R.M. and Perry, R.E. (2015) Mechanisms and functional implications of social buffering in infants: Lessons from animal models. Social Neuroscience

- 10, 500–511. http://dx.doi.org/10.1080/17470919. 2015.1087425.
- Takeda, K., Sato, S., Sugawara, K. (2003) Familiarity and group size affect emotional stress in Japanese Black heifers. Applied Animal Behaviour Science 82, 1–11. http://dx.doi.org/10.1016/S0168-1591(03)00039-X.
- Taylor, G.T. (1981) Fear and affiliation in domesticated male rats. *Journal of Comparative and Physiological Psychology* 95, 685–693. http://dx.doi.org/10.1037/ h0077817.
- Taylor, S.E., Dickerson, S.S., Klein, L.C. (2005) Toward a biology of social support. In: Snyder, C.R. and Lopez, S.J. (eds.) *Handbook of Positive Psychology*. Oxford University Press, Oxford, UK, pp. 556–569.
- Thoits, P.A. (2011) Mechanisms linking social ties and support to physical and mental health. *Journal of Health and Social Behavior* 52, 145–161. http://dx.doi.org/10.1177/0022146510395592.
- Tuber, D.S., Hennessy, M.B., Sanders, S., Miller, J.A. (1996) Behavioral and glucocorticoid responses of adult domestic dogs (*Canis familiaris*) to companionship and social separation. *Journal of Comparative Psychology* 110, 103–108. http://dx.doi.org/10.1037/ 0735-7036.110.1.103.
- Uchino, B.N. (2006) Social support and health: A review of physiological processes potentially underlying links

- to disease outcomes. *Journal of Behavioral Medicine* 29, 377–387. http://dx.doi.org/10.1007/s10865-006-9056-5.
- Uchino, B.N., Cacioppo, J.T., Kiecolt-Glaser, J.K. (1996) The relationship between social support and physiological processes: a review with emphasis on underlying mechanisms and implications for health. Psychological Bulletin 119, 488–531. http://dx.doi.org/10.1037/0033-2909.119.3.488.
- Weiss, R.S. (1973) Loneliness: The Experience of Emotional and Social Isolation. MIT Press, Cambridge, Massachusetts. USA.
- Wittig, R.M., Crockford, C., Weltring, A., Langergraber, K.E., Deschner, T., et al. (2016) Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. Nature Communications 7, 13361. http://dx.doi.org/10.1038/ ncomms13361.
- Young, C., Majolo, B., Heistermann, M., Schulke, O., Ostner, J. (2014) Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proceedings of the National Academy of Sciences of the United States of America* 111, 18195–18200. http://dx.doi.org/10.1073/pnas.1411450111.
- Zajonc, R.B. (1965) Social facilitation. *Science* 149, 269–274. http://dx.doi.org/10.1126/science.149.3681.269.

9

Subjective Well-being, Happiness, and Personality in Animals

ALEXANDER WEISS AND LAUREN M. ROBINSON

Department of Psychology, The University of Edinburgh, Edinburgh, UK; Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, Vienna, Austria

9.1 Background and Overview

In many societies, and for some time, the lives of most people have no longer been characterized by an existential struggle to feed, house, and clothe oneself and one's family, but by a pursuit of happiness (Inglehart, 2018). More recently, in fact in some people's living memory, there has been a growing concern for the happiness and well-being of others, including unrelated individuals living in different countries and animals (Pinker, 2011; Inglehart, 2018).

The question of how best to ensure the happiness – whether we define it as welfare, subjective wellbeing, or some other term (see Chapter 2, this volume, for a discussion) - of animals under our care is a pressing and relatively recent concern. This development is remarkable considering that the desire to ensure animal happiness extends not just to animals with whom we share a recent common ancestor, such as chimpanzees and the other great apes, or a home, as with companion animals. The human desire for animals to be happy extends to distantly related species, animals in the wild, animals in the entertainment industry, animals that we use to learn more about ourselves and our world, animals that help us cure diseases, and even to farmed animals that many of us eat.

It is hard to imagine how this strong impulse to care for the well-being of species other than our own could have arisen if it were not possible for us to perceive where individual animals stand on a psychological continuum ranging from suffering to contentedness. Of course, it is possible that we are fooling ourselves. We may be seeing emotions that are not there or mistaking the display of one emotion for another. However, it is our view that the

evidence suggests that, when we perceive an animal to be happy, sad, or 'fair to middling', we are more likely than not to be accurate in our appraisal.

In this chapter we will evaluate a subset of the evidence that our perceptions of animal happiness are accurate and that the 'happiness' that we see in other animals is much like the happiness that we see in other humans or experience ourselves. This evidence consists of work on the relationships between personality traits and subjective well-being, both of which are psychological constructs, a notion that we will define early on. We will then - perhaps too briefly – discuss the implications of these findings with regard to what they say about the evolution of happiness, the practical implications of these findings, and what they say about how one might be able to better understand the physiological bases of happiness. That said, we will not engage in a defense of or promote the use of ratings by humans to measure happiness, or personality for that matter, in animals. We will also abstain from cataloging, comparing, or ranking all the methods for measuring subjective well-being and personality in animals.

9.2 Psychological Constructs and Nomological Networks

Determining any given human or animal's level of happiness or standing on some personality trait differs from determining its height or weight. In the latter case, the measure is a more or less 'direct' measure of a physical property that is being measured. In the case of happiness, however, there is not a direct correspondence between our measure of happiness and happiness itself. Instead, our measure in this instance is based on a theory of how the

thing that we wish to measure is represented by things that we can measure in the world.

The lack of a one-to-one correspondence between measures of any psychological construct and the measure itself is true whether one is interested in studying subjective well-being, personality, or any other psychological trait or state (Cronbach and Meehl, 1955). It is also true regardless of whether the measures we use are behavioral observations, behavioral tests, ratings by knowledgeable informants, or blood tests. Consequently, when measuring any psychological construct, it is important to establish the construct validity of a measure for, by doing so, one is better able to rule out the possibility that something other than the construct of interest is being measured (Cronbach and Meehl, 1955). This may sound straightforward, but it is not because in most cases there is no direct measure of the construct that can serve as a criterion. Contrast this with the case for weight: if we wanted to develop a new means of assessing weight, we could check whether it measures weight by examining the relationship between our new measure and the weight indicated by a scale. In short, so-called 'objective' and 'subjective' measures of psychological constructs stand on the same shaky ground.

We expect that it may surprise some people that the degree to which a measure is rooted in what can be seen and counted is not informative with regards to whether it is a good measure of what one wishes to measure. Moreover, the question of how, given this situation, one goes about studying things like subjective well-being or personality in animals (or even humans), is probably vexing to some. It is thus worth illustrating this point with a historical example, particularly because this example points toward a solution.

In the 1940s researchers became interested in locating the part of the brain that made people feel like they had had enough to eat. An obvious way to have identified this satiety center would have been an experiment in which human volunteers either experienced some kind of 'sham surgery' control or had a part of their brain removed. After enough studies, one of the experimental groups would report being insatiable when compared to the sham surgery group. Of course, there are ethical problems with this kind of study, and so experimenters turned to the next best thing at the time: rats. These studies of rats eventually did find an area – the ventromedial nucleus of the hypothalamus – that seemed to be the satiety center of the brain. Although

the rats could obviously not tell the researchers how hungry or full they felt, compared to rats in the control group the rats in the experimental group ate constantly, and consequently, became obese. Similar results were produced by lesioning this area of the brain in other animals and similar behavior was described in humans who had tumors affecting that part of the brain (Brobeck, 1946 cited in Miller *et al.*, 1950).

Not surprisingly, these researchers concluded that the ventromedial nucleus of the hypothalamus was the brain's satiety center. Not everybody was convinced, however, that the behavior displayed by subjects with these lesions were expressions of hunger. A series of experiments by Miller et al. (1950) showed that this skepticism was justified. They found that, unlike rats without lesions, rats with lesions did not seem as motivated to eat: their rate of bar pressing to receive food rewards did not increase as much as a function of food deprivation, they did not run down an alley toward a food reward as quickly or pull harder to get a food reward, they consumed less food than the nonlesioned rats when they had to lift a heavy lid to obtain a food reward, and they were less likely to eat food that had been made to taste bitter.

This side story from the history of psychology tells us that to measure something like happiness or a personality trait – entities that do not have corresponding criteria in the physical world – we need to use multiple indicators of multiple traits that we do and do not expect to be manifestations of that which we wish to measure (Campbell and Fiske, 1959). Doing so is a sort of triangulation that enables us to identify whether the psychological construct underlying these measures is the one that we think underlies these measures (see Fig. 9.1). Conversely, this means that we infer the presence of a psychological construct by the relationships among our measures.

We offer here one further elaboration. To be able to claim that one's measures do 'tap' the construct of interest requires setting one's measures within a 'nomological network'. This means theoretically deriving and testing predictions about how constructs impinge on measures and other constructs, and testing predictions about the relationships between constructs and things in the 'real world' (Cronbach and Meehl, 1955).

For our purposes, in the next section we will describe a measure of nonhuman animal happiness. Claiming that one has a measure of 'happiness' for a nonhuman species is still controversial. It was

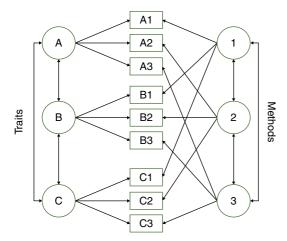


Fig. 9.1. By gathering data on multiple traits, each measured with a set of methods, one can isolate the variance related to the trait from that related to how the trait was measured and vice versa. Circles represent variance related to either traits (e.g., subjective well-being, cognitive ability, and self-control) or the methods used to measure those traits (e.g., behavioral tests, questionnaires, and behavioral observations). Boxes represent observations in a study, such as the score on a behavioral test that purportedly measures subjective well-being. (Figure by the authors and licensed under the terms of the Creative Commons Attribution 4.0 International License.)

thus probably a good thing that this measure was initially developed to measure happiness in chimpanzees, since, in our personal experience, people are more willing to forgive studying such fanciful things in our closest nonhuman relatives. We will then show that, although happiness' nomological network started small, its 'roots' (Cronbach and Meehl, 1955) have since entwined more and more constructs and things in the real world and have spread to other species. Personality played a key role in these developments.

9.3 Chimpanzee Happiness

The study of personality in nonhuman primates, including by using ratings, can be traced back to at least the 1930s (Whitman and Washburn, 2017). However, although researchers had developed and studied animal, including primate, models of negative affective states, such as depression (see, e.g., Harlow and Suomi, 1974) for some time, studies of happiness originated much later. The first (so far as we are aware) notable study was by King and

Landau (2003). Looking at 128 zoo-housed chimpanzees, King and Landau measured the happiness of their subjects by obtaining ratings on a four-item questionnaire from zookeepers and staff who knew the individual chimpanzees, often for many years. Versions of this questionnaire can be found at: http://extras.springer.com/2011/978-1-4614-0175-9.

There are multiple definitions of human subjective well-being and each of the items that King and Landau devised was designed to operationalize one of the more common definitions. The first item concerned the balance of positive and negative affect, and asked raters to do the following:

Estimate the amount of time the chimpanzee is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the chimpanzee is unhappy, bored, frightened, or otherwise in a negative mood.

The second item asked about the degree of positive versus negative affect that a chimpanzee experienced from social interactions:

Estimate the extent to which social interactions with other chimpanzees are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the chimpanzee. Use as many social interactions that you can recall as a basis for your judgment.

The third item was less straightforward than the first two. It asked raters to estimate the degree of control that a chimpanzee had over its life:

Estimate, for this chimpanzee, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the enclosure. Keep in mind that each chimpanzee will presumably have its own set of goals that may be different from other chimpanzees.

The last item was an attempt to get raters to gauge the chimpanzee's overall life satisfaction. In a sense, it was asking raters to indicate how one of the English-speaking chimpanzees from the movie *Planet of the Apes* (the 1968 version, of course) would respond if he or she were asked 'How happy are you?'.

Imagine how happy you would be if you were that chimpanzee for a week. You would be exactly like that chimpanzee. You would behave the same way as that chimpanzee, would perceive the world the same way as that chimpanzee, and would feel things the same way as that chimpanzee.

The overarching goal of King and Landau's study was to determine the extent to which chimpanzee happiness, as defined by ratings on this questionnaire, was surrounded by a nomological network like that which surrounds human measures of happiness. They thus addressed five questions, all bearing upon whether a consistent set of findings from the human happiness literature would be present in chimpanzees. These findings from the human literature included the correlation between individuals' self-reports of happiness and reports of their happiness by others; the positive intercorrelations of happiness measures, which suggest the presence of a single underlying factor; the rank order stability of happiness; and the relationships between happiness and personality whereby individuals who are higher in extraversion, lower in neuroticism, and higher in conscientiousness tend to be happier (Pavot et al., 1991; Sandvik et al., 1993; DeNeve and Cooper, 1998). They also asked a fifth question, which was whether their measure of chimpanzee happiness was related to independently assessed behaviors.

King and Landau did find evidence for a humanlike pattern of relationships. First, across the four questionnaire items, there was a respectable level of agreement between independent ratings. Second, the four subjective well-being items were intercorrelated and a principal components analysis indicated that a single dimension accounted for just over 70% of their variance. Third, in a subsample of chimpanzees that were rated twice with an average of 4.6 years separating the ratings, there was very little difference in the level of happiness and the stability of the ratings was high, that is, a chimpanzee's level of happiness relative to other chimpanzees was consistent over time. Fourth, there was a meaningful pattern of correlations between a set of ratings-based personality factors obtained as part of a previous study and happiness. Specifically, the sum of the four items from the subjective wellbeing scale was related to higher dominance, higher extraversion, and higher dependability (since Weiss et al., 2009, we have referred to this factor as 'conscientiousness'). Higher ratings on the balance of positive and negative affect, the pleasure derived from social interactions, and global life satisfaction (the first, second, and fourth items, respectively) were related to higher dominance and extraversion. Higher ratings on the degree of control chimpanzees had over their lives and their ability to achieve their goals (the third item) were related to higher dominance and higher dependability. They also did not find significant associations between any of the items or the total score and either agreeableness, emotionality (since Weiss *et al.*, 2009, we have referred to this factor as 'neuroticism'), or openness. Fifth, again in a subsample of chimpanzees, there was a negative correlation between behaviors related to submissiveness, and especially avoidance, which is consistent with the just-described relationship between higher dominance and happiness.

Before moving onwards, it is worth pointing out that although the personality-happiness relationships mostly resembled those found in humans, there was a clear difference, too. Neuroticism was not significantly related to lower chimpanzee happiness (King and Landau, 2003). Instead, dominance, a personality domain that is apparently not represented by a single factor in humans (Digman, 1990), had the strongest relationship with happiness. This should strike the reader as odd. After all, there is a consistent and strong relationship between human happiness and low neuroticism (DeNeve and Cooper, 1998; Steel et al., 2008). Although we will revisit this matter later, the likely explanation has to do with the items that defined dominance and neuroticism in chimpanzees. The neuroticism measure was based on the results of an earlier study, which showed that chimpanzee neuroticism was defined by lower ratings on two items – one denoting stability and one denoting unemotionality - and higher ratings on one item denoting excitability (King and Figueredo, 1997). Higher dominance, on the other hand, was not just defined by items indicating competitive prowess or agonistic interactions with others, but by lower ratings on items relating to dependence, fearfulness, timidity, and cautiousness (King and Figueredo, 1997). Putting it another way, dominance may have possessed more traits related to those aspects of neuroticism related to lower well-being.

9.4 Chimpanzee Happiness Revisited

The chimpanzee study described in the previous section was followed by three follow-on studies that also examined the extent to which the nomological network that captured human subjective well-being applied to its chimpanzee counterpart. The first study had two goals: (i) to test whether variation in

chimpanzee happiness was partly attributable to genetic differences between chimpanzees; and (ii) to determine the extent to which genes for personality were also genes for subjective well-being. The goal of the second study was to determine whether features of captive chimpanzees' physical or social environments contributed to their happiness. The goal of the third study was to determine whether the relationship between chimpanzee personality and subjective well-being was present in an independent sample.

The first study was conducted by Weiss et al. (2002) and was motivated by two previous studies of subjective well-being. One of these was Lykken and Tellegen's (1996) classic study of human happiness, in which twins were administered twice, several years apart, a personality questionnaire that included a subjective well-being scale (the Multidimensional Personality Questionnaire; Tellegen, 1982). This study had three noteworthy findings. First, 44-52% of the variability in subjective well-being was attributable to genetic differences. Second, around 80% of the variability of the stable component of subjective well-being was attributable to genetic differences between individuals. In other words, among these participants, most of the differences in happiness that were not attributable to fluctuations around an individual's average happiness were genetic in origin. Third, only a small proportion of differences in individuals' subjective well-being was attributable to things shared by people raised in the same family, or demographic indicators, such as socioeconomic status, education level, and marital status. The second foundational study determined that among 145 zoo-housed chimpanzees, differences in the personality factor dominance were the result of genetic differences; the other five factors were not 'heritable' (Weiss et al., 2000). The study by Weiss et al. (2002) used the 128 chimpanzees featured in King and Landau's (2003) study and found that about 40% of the variation in chimpanzee subjective well-being was heritable (Weiss et al., 2002), which is consistent with the average of heritability estimates derived from previous and later studies of human happiness (Bartels and Boomsma, 2009). Moreover, this study found that nearly all the shared variation between chimpanzee dominance and subjective well-being was attributable to common genetic effects. Since the publication of this study, research on happiness in humans (Weiss et al., 2008, 2016; Hahn et al., 2013, 2016) and

orangutans (Adams *et al.*, 2012) have yielded similar results concerning the genetic bases of the personality–happiness relationship.

The second follow-on study found little to no evidence that the physical (e.g., population density) or social (e.g., how related an individual was to group mates) characteristics of the enclosure contributed to subjective well-being over and above the effects of sex, age, and personality (Weiss and King, 2006). Thus, much like Lykken and Tellegen's results, demographic factors relating to the environment did not appear to contribute to chimpanzee happiness either. Work in humans that has been conducted since these studies suggests that the early pessimism about environmental effects may have been premature. However, because these new findings will take some time to describe and are useful for pointing out new directions for work on animal happiness, we will return to these matters in the concluding section of this chapter.

The purpose of the third study was to determine whether the personality and subjective well-being relationships described by King and Landau could be found in an independent sample. This study of 146 chimpanzees by Weiss et al. (2009) differed from King and Landau's study in two ways. First, to measure personality, this study used the Hominoid Personality Questionnaire (HPQ; Weiss, 2017), an extended version of the questionnaire developed for King and Figueredo's 1997 study. The HPQ includes 11 additional items to better represent traits related to neuroticism, openness, and conscientiousness. Second, the chimpanzees were housed in either Japanese zoos, the Kyoto University Primate Research Institute, or, what is now known as Kumamoto Sanctuary. As such, this study tested whether the relationships between personality and subjective well-being generalized when raters were from a different culture. The results of this study of chimpanzees in Japan demonstrated two points of consistency with the results of King and Landau's study of chimpanzees in zoos in the United States and Australia. One was that the four subjective well-being items defined a single component. The other was that dominance and extraversion were related to higher ratings on each of the subjective well-being scale's items and the sum of these items, the latter representing the construct. However, there were also important differences: conscientiousness was not related to any of the subjective well-being measures; neuroticism, as one would expect based on human studies (DeNeve and Cooper, 1998; Steel

et al., 2008), was related to lower ratings on all the measures; agreeableness was related to higher ratings on the items and the sum score; and openness was related to all the measures save the item relating to the ability to achieve goals. Because of some procedural and data analytic differences between this study and that of King and Landau, it is impossible to determine whether the differences reflect cultural differences in how raters interpreted some questionnaire items or the procedural and data analytic differences mentioned above.

The results of these studies are encouraging and add further support to the notion that the 'happiness' construct measured in chimpanzees has a nomological network resembling that of human happiness. One finding that was especially encouraging was the identification of a biological explanation for the relationship between chimpanzee personality and happiness, which was subsequently found in humans and orangutans. Nevertheless, like all psychological constructs, establishing construct validity will continue to be a work in progress. This reflects two characteristics of psychological constructs and nomological networks. First, there are near infinite ways that one can measure a construct. Second, nomological networks grow and their connections may change with new observations and a better understanding of the construct (Cronbach and Meehl, 1955). As we shall discuss in the next two sections, this is true for subjective well-being regardless of the species in which it is measured.

9.5 Other Species

As hinted at in the previous section, the work based on the human conception of happiness has included studies of other species. To prevent confusion in this section, it is worth pointing out two things to readers who are not familiar with the animal personality literature. First, the set of personality dimensions possessed by a given species tends to differ to varying degrees from those possessed by other species. Second is the so-called 'jingle jangle' problem: different researchers often have different naming conventions for what are probably the same personality traits and/or affix the same name to what are probably different personality traits (Thorndike, 1904; Kelley, 1927, both cited in Block, 1995). As such, although we will introduce more than a few different personality domain labels, the reader should bear in mind the degree to which they might be aligned with the human domains that tend to be associated with subjective well-being.

Published research in nonhuman primates has examined at least one species belonging to great apes, Old World monkeys, and New World monkeys (no work has been conducted on prosimians, such as ring-tailed lemurs). As in studies of subjective well-being in humans (Pavot *et al.*, 1991; Sandvik *et al.*, 1993) and chimpanzees (King and Landau, 2003; Weiss *et al.*, 2009; Robinson *et al.*, 2017), the items used to measure subjective well-being items in these studies defined a single subjective well-being factor.

Among great apes, other than chimpanzees the only report of correlations between personality and subjective well-being was in 140 zoo-housed orangutans (Weiss *et al.*, 2006). Orangutans were found to have five personality domains and of these, higher extraversion, higher agreeableness, and lower neuroticism were associated with being rated higher in subjective well-being.

A study of semi-free ranging rhesus macaques living on Cayo Santiago found correlations between the six personality domains identified in this study and subjective well-being. The relationships between subjective well-being and higher confidence, higher friendliness, and lower anxiety were significant regardless of whether these constructs were measured at the same time or at two different times between 13.9 and 18 months apart (Weiss *et al.*, 2011).

A study of 66 brown capuchin monkeys in research centers also found evidence for prospective, that is, cross-time, associations between personality and subjective well-being. The personalities of these monkeys were assessed as part of an earlier study, which identified five personality dimensions (Morton *et al.*, 2013). Two of these dimensions, assertiveness and sociability, were positively associated with subjective well-being (Robinson *et al.*, 2016).

These associations were also examined in 77 common marmosets, another New World monkey species, housed in a laboratory colony in Japan (Inoue-Murayama *et al.*, 2018). This study identified three personality domains of which two, sociability and neuroticism, were, respectively, positively and negatively related to subjective well-being.

So far as we are aware, questions about the associations between personality and subjective well-being have only been investigated in one other taxonomic group: felids. These studies found that the four or five subjective well-being items were

intercorrelated in such a way as to define a single dimension. The first of these studies was of 25 Scottish wildcats living in zoos (Gartner and Weiss, 2013) and found that of three personality domains, self-control was consistently related to higher subjective well-being. The second study examined these associations in 16 clouded leopards, 17 snow leopards, and 21 African lions, all of which lived in zoos (Gartner et al., 2016). In all three species, higher neuroticism was related to lower subjective well-being. Moreover, in the clouded leopards, higher subjective well-being was also related to higher scores on a personality domain that was a blend of agreeableness and openness, and in African lions, impulsiveness was related to lower subjective well-being.

Overall, these findings indicate that personality domains related to being gregarious, sociable, and active are associated with higher subjective well-being and that those related to being impulsive, fearful, and vigilant are related to lower subjective well-being. In short, the links in the nomological net between subjective well-being and personality are consistent across distantly related species of nonhuman primates and between primates and another mammalian order.

The studies reviewed here and in the previous section only focused on a part of the nomological net that supports the construct validity of happiness (and personality) as measured in nonhuman primates and felids. In the next section we will discuss other connections in this net, including how and whether they support the construct validity of subjective well-being.

9.6 Other Connections

As should be evident by now, one question when considering the construct validity of the subjective well-being measure is whether it is associated with other purported measures of happiness or similar constructs. Other measures hypothesized to be related to the relative happiness (or unhappiness) of nonhuman animals, and in some cases, humans, include welfare questionnaires, cognitive bias tests, motor stereotypies, and corticosteroid levels. There have been tests for associations between these measures; however, when it comes to tests of associations between subjective well-being ratings and these measures, the research has been sparse. This is regrettable for it means there are few strong tests

for the construct validity of subjective well-being ratings and these other measures.

One exception to this lack of studies is the case of welfare and subjective well-being. A broad definition of welfare focuses on the so-called 'Five Freedoms' hypothesis, that is, freedom from hunger and thirst; freedom from discomfort; freedom from pain, injury, or disease; freedom to express normal behavior; and freedom from fear and distress (Farm Animal Welfare Council, 1979). Using this framework, animal welfare measures have often focused on using behavioral and physiological outputs as indicators of negative welfare states (Broom, 1991). More recently, researchers have recognized the need to focus not just on suffering, but on thriving, and have put forward ways to measure positive welfare states (Boissy et al., 2007; Yeates and Main, 2008). In addition to the recognition that one needs to study positive welfare states there has been an increasing interest in studying whether the needs that matter to an individual animal are being satisfied, a notion known as the animal's quality of life (McMillan, 2000, 2005).

It would be surprising if a measure of subjective well-being was not related to measures of positive welfare or quality of life. If this were found, it would cast doubt upon whether these were measures of these constructs. To examine this, Robinson et al. (2016) developed a 12-item scale, since expanded into a 16-item scale (Robinson et al., 2017), to assess quality of life and a few aspects of the five freedoms in captive nonhuman primates. This scale, available at https://www.drlaurenrobinson.com/ surveysdesigned, targeted people who had been working with individual animals, such as care staff and researchers in laboratories, and was created with the principle that welfare ranges from very bad to very good (Boissy et al., 2007; Yeates and Main, 2008). The key section of this questionnaire included items that reflected traditional conceptions of animal welfare (Broom, 1991; Broom and Johnson, 1993) and factors identified as relating to quality of life (McMillan, 2005). As such, these questions were about mental stimulation, health, social relationships, stress, and the control of the social and physical environment. For example, one question was 'How frequently is this individual stressed? Stress being an unpleasant emotional experience in response to a threatening event that potentially harms the individual's health.' Another question was 'How often does the individual display signs of positive welfare?'. In addition to these questions, Robinson *et al.* (2016) included one question that incorporated quality of life into assessments of welfare (see Green and Mellor, 2011):

In this individual's life, would you say he/she experiences: A. considerably more negative experiences than positive experiences.

B. more negative experiences than positive experiences. C. equal amounts of negative and positive experiences. D. more positive experiences than negative experiences. E. considerably more positive experiences than negative experiences.

In both the brown capuchin monkeys and the chimpanzees studied by Robinson et al. in 2016 and 2017, respectively, ratings on the welfare scale were highly correlated (>0.9) with the subjective well-being items scale. Not surprisingly, principal components analyses in these two studies found that all the items from both scales loaded onto a single component. Both studies then examined the relationships between this component and personality. In brown capuchin monkeys, higher component scores were associated with higher sociability and assertiveness and lower neuroticism and attentiveness. In chimpanzees, higher component scores were associated with higher extraversion and lower neuroticism. Finally, the study of chimpanzees also tested for association between this component and several behaviors. In doing so, it found that the component was related to less frequent regurgitation, coprophagy (eating feces), urophagy (drinking urine), and increased proximity to neighboring chimpanzees. These findings provide strong and direct evidence in favor of the construct validity of subjective well-being or happiness in these species. The construct that the subjective well-being scale assesses is nearly identical to that of welfare measured using a very different scale, and the combination of these scales is related to personality and behaviors in ways that one would expect.

Along with this direct evidence, there is also indirect evidence for the construct validity of subjective well-being. This evidence, some of which we discuss below, is in the form of associations between other purported measures of well-being or similar constructs, such as positive affect, and personality traits related to subjective well-being.

Cognitive bias tests were developed for use in laboratory rodents (Harding *et al.*, 2004) and have since been applied across animals ranging from honeybees (Bateson *et al.*, 2011) to

chimpanzees (Bateson and Nettle, 2015) and animals housed in different environments, including on farms (Baciadonna and McElligott, 2015) and in zoos (Clegg, 2018). The test procedure is as follows. First, each animal is trained in a discrimination task in which one stimulus signals the presence of a food treat and the other signals the absence of a food treat. For example, a rat would be presented with several trials in which a food is hidden behind a white card and no food is hidden behind a black card. In each trial, the rat is given the treat if it approaches the white card and is not given a treat if it approaches the black card. After several trials the rat learns to approach only the white card. Then comes the crucial test. The rat is presented with a stimulus that is intermediate in value. In our example, the rat would be presented with a gray card. An animal - our hypothetical rat – that approaches this ambiguous stimulus is said to be 'optimistic' in that it is acting as if it expects the food reward to be behind the stimulus. An animal that does not approach this stimulus is said to be 'pessimistic'. The construct validity of the cognitive bias test has amassed considerable support, including evidence indicating that animals reared in poor environments or that are made to experience a stressor are more likely to make pessimistic decisions than those animals reared in good environments (Mendl et al., 2009; Baciadonna and McElligott, 2015). These findings mirror studies of humans that show, for example, that people with major depressive disorder perceive neutral events as more threatening than do people without major depressive disorder (for a review, see Gotlib and Joormann, 2010).

One study which provides evidence that performance on the cognitive bias test may be related to subjective well-being comes from a study of three chimpanzees - one adult female and two adult males - by Bateson and Nettle (2015). Of the three chimpanzees, the more dominant of the males showed the least pessimism, measured by the latency to touch the intermediate stimulus, the other male showed an intermediate amount of pessimism, and the female showed the most pessimism. These findings are consistent with findings from studies based on ratings that show a relationship between higher ratings of dominance and higher subjective well-being in chimpanzees (King and Landau, 2003; Weiss et al., 2009; but see Robinson et al., 2017).

A study of 31 dogs by Barnard *et al.* (2018) also provides indirect evidence that subjective well-being is related to cognitive bias. Choices reflecting an optimistic bias were associated with dogs that exhibited greater sociability, one of five traits measured by the Dog Mentality Assessment test, a behavioral assay (Svartberg and Forkman, 2002), and owner ratings reflecting higher nonsocial fear and excitability, two of the six dimensions on the Canine Behavioral Assessment and Research Questionnaire (Hsu and Serpell, 2003). A pessimistic bias was associated with higher dimensions derived by owner ratings for dog-directed aggression, dog-directed fear, and separation-related problems.

Motor stereotypes are seemingly functionless behaviors that are repetitive and unchanging (Mason, 1991; Mason and Latham, 2004). A study of over 4000 rhesus macagues examined whether demographic factors, early rearing, animal housing, and personality traits were associated with motor stereotypies and self-biting (Gottlieb et al., 2013). Personality in this study was measured in infancy using ratings and behavioral tests. The authors found that along with several demographic, rearing, and housing factors, monkeys were at greater risk of developing motor stereotypies if they displayed an 'active temperament', that is, were less 'gentle', more likely to display activity in response to a human intruder, and made more contact with novel objects.

Cortisol (a corticosteroid) levels are related to activation of the hypothalamic-pituitary-adrenal (HPA) axis, which aids the organism in coping with stress. High cortisol levels may indicate chronic activation of the axis, which can have harmful effects on the organism. There thus should be an association between chronic levels of stress, lower well-being, and cortisol levels. In a review, Koolhaas et al. (1999) described a clustering of behavioral and physiological characteristics in rodents referred to as coping styles. Proactive coping styles were related to low attack latencies, protecting one's territory, and low levels of flexibility. Reactive coping styles were related to more defensive behaviors, withdrawal responses, and higher levels of flexibility. Koolhaas et al. also reported that these coping styles were related to, respectively, lower and higher HPA axis activation.

Work that examines relationships between behavioral traits and cortisol in primates is mostly consistent with the work on coping styles, and offers indirect evidence linking personality and subjective

well-being. One of these studies measured brown capuchin monkey personality using behavioral observations and ratings, and found that higher basal blood cortisol and cortisol reactivity were associated with an inhibited and fearful personality (Byrne and Suomi, 2002). Another study found that basal serum cortisol levels in rhesus macaques were negatively associated in the afternoon with excitability and positively associated in the morning with level of confidence, respectively (Capitanio et al., 2004). A third study did not find a relationship between subjective well-being ratings and hair cortisol levels (Inoue-Murayama et al., 2018). Moreover, contrary to what one might expect, this study of marmosets found an association between higher cortisol levels and sociability.

What, then, may be concluded from what has been presented so far, both about subjective well-being as a construct and its probable genetic association with personality? In addition, and more importantly for some readers, what conclusions may be drawn regarding what can or cannot be done to improve the happiness of animals in our care? We discuss these matters, and consider future directions for research, in the final section.

9.7 Concluding Remarks

If anything, the research outlined here as well as that which we did not cite on subjective well-being and related constructs in nonhuman primates and other animals should convey a single point. There is at least as much scientific evidence to support the existence of something like human subjective wellbeing or happiness in at least some species of nonhuman animals as there is in support of the existence of this construct in humans. In addition, the parallels between human and animal subjective well-being, including how and why they are related to personality, suggests that the constructs are similar across species. Consequently, the experience of happiness or subjective well-being along with its links to personality are almost certainly evolutionarily old. To test this, that is to rule out alternative evolutionary scenarios such as convergent evolution, however, requires more work. Large phylogenetic studies, such as those used to study other traits (MacLean et al., 2014) would go some way to achieve this aim.

More critically for captive animals is the question of how do these findings inform best practice? We expect that some readers will come away pessimistic. After all, subjective well-being in humans, chimpanzees, orangutans, and probably other species is influenced by genes, including those genes related to personality variation. But such pessimism would reflect a misunderstanding about what heritability estimates mean. Heritability estimates indicate the degree to which differences between individuals are influenced by genes and not the degree to which individuals are influenced by genes (Falconer and Mackay, 1996). In other words, if an environmental intervention, such as a new enclosure, raised every individual's happiness by a roughly equal amount, the heritability of happiness would be roughly the same. That is because the differences between individuals would still be present and likely related to their genetic background.

But, then, is it possible to change happiness by means of environmental interventions? We think so and studies of animals and humans support this view. Contrary to earlier thinking on the matter, human happiness can be adversely affected over long periods of time by events such as divorce, unemployment, or widowhood (Diener et al., 2006). Likewise, animal rearing and husbandry practices can make a difference (Clay et al., 2018). Moreover, a study of human happiness in 52 countries found that happiness in 45 of the countries increased from 1981 to 2007 and that the rate of increase was related to economic development, democratization, and greater tolerance, all of which contributed to a sense that individuals had free choice (Inglehart et al., 2008). These findings suggest that some current views about role of free choice on animal welfare and the actions to take (Kagan et al., 2015) are on the right track. More importantly, perhaps, they show just how much we can potentially learn about animal happiness from studying it in humans, and vice versa.

9.8 References

- Adams, M.J., King, J.E. Weiss, A. (2012) The majority of genetic variation in orangutan personality and subjective-well being is nonadditive. *Behavior Genetics* 42, 675–686. http://dx.doi.org/10.1007/s10519-012-9537-y.
- Baciadonna, L. and McElligott, A.G. (2015) The use of judgement bias to assess welfare in farm livestock. *Animal Welfare* 24, 81–91.
- Barnard, S., Wells, D.L., Milligan, A.D.S., Arnott, G., Hepper, P.G. (2018) Personality traits affecting judgement bias task performance in dogs (*Canis familiaris*). *Scientific Reports* 8, 6660. http://dx.doi.org/10.1038/ s41598-018-25224-y.

- Bartels, M. and Boomsma, D.I. (2009) Born to be happy? The etiology of subjective well-being. *Behavior Genetics* 39, 605–615. http://dx.doi.org/10.1007/s10519-009-9294-8.
- Bateson, M. and Nettle, D. (2015) Development of a cognitive bias methodology for measuring low mood in chimpanzees. *PeerJ* 3, e998. http://dx.doi. org/10.7717/peerj.998.
- Bateson, M., Desire, S., Gartside, S.E., Wright, G.A. (2011) Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology* 21, 1070–1073. http://dx.doi.org/10.1016/j.cub.2011.05.017.
- Block, J. (1995) A contrarian view of the five-factor approach to personality description. *Psychological Bulletin* 117, 187–215. http://dx.doi.org/10.1037/ 0033-2909.117.2.187.
- Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., et al. (2007) Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior* 92, 375–397. http://dx.doi.org/10.1016/j. physbeh.2007.02.003.
- Brobeck, J.R. (1946) Mechanism of the development of obesity in animals with hypothalamic lesions. *Physiological Reviews* 26, 541–559. http://dx.doi.org/10.1152/physrev.1946.26.4.541.
- Broom, D.M. (1991) Animal welfare: Concepts and measurement. *Journal of Animal Science* 69, 4167–4175. http://dx.doi.org/10.2527/1991.69104167x.
- Broom, D.M. and Johnson, K.G. (1993) Stress and Animal Welfare. Springer, Dordrecht, The Netherlands. http://dx.doi.org/10.1007/978-94-024-0980-2.
- Byrne, G. and Suomi, S.J. (2002) Cortisol reactivity and its relation to homecage behavior and personality ratings in tufted capuchin (*Cebus apella*) juveniles from birth to six years of age. *Psychoneuroendocrinology* 27, 139–154. http://dx.doi.org/10.1016/S0306-4530 (01)00041-5.
- Campbell, D.T. and Fiske, D.W. (1959) Convergent and discriminant validation by the multitrait-multimethod matrix. *Psychological Bulletin* 56, 81–105. http://dx. doi.org/10.1037/h0046016.
- Capitanio, J.P., Mendoza, S.P., Bentson, K.L. (2004) Personality characteristics and basal cortisol concentrations in adult male rhesus macaques (*Macaca mulatta*). Psychoneuroendocrinology 29, 1300–1308. http://dx.doi.org/10.1016/j.psyneuen.2004.04.001.
- Clay, A.W., Bard, K.A., Bloomsmith, M.A. (2018) Effects of sex and early rearing condition on adult behavior, health, and well-being in captive chimpanzees (*Pan troglodytes*). *Behavioural Processes* 156, 58–76. http://dx.doi.org/10.1016/j.beproc.2017.06.011.
- Clegg, I.L.K. (2018) Cognitive bias in zoo animals: An optimistic outlook for welfare assessment. *Animals* 8, 104. http://dx.doi.org/10.3390/ani8070104.
- Cronbach, L.J. and Meehl, P.E. (1955) Construct validity in psychological tests. *Psychological Bulletin* 52, 281–302. http://dx.doi.org/10.1037/h0040957.

120 A. Weiss and L.M. Robinson

- Deneve, K.M. and Cooper, H. (1998) The happy personality: A meta-analysis of 137 personality traits and subjective well-being. *Psychological Bulletin* 124, 197–229. http://dx.doi.org/10.1037/0033-2909.124.2.197.
- Diener, E., Lucas, R.E., Scollon, C.N. (2006) Beyond the hedonic treadmill: Revising the adaptation theory of well-being. *American Psychologist* 61, 305–314. http://dx.doi.org/10.1037/0003-066X.61.4.305.
- Digman, J.M. (1990) Personality structure: Emergence of the Five-Factor Model. Annual Review of Psychology 41, 417–440. http://dx.doi.org/10.1146/annurev.ps.41. 020190.002221.
- Falconer, D.S. and Mackay, T.F.C. (1996) *Introduction to Quantitative Genetics*. Longman, Harlow, UK.
- Farm Animal Welfare Council (1979) Press Statement. Available at: http://webarchive.nationalarchives.gov.uk/20121010012427/http://www.fawc.org.uk/freedoms.htm (accessed 25 July 2019).
- Gartner, M.C. and Weiss, A. (2013) Scottish wildcat (*Felis silvestris grampia*) personality and subjective wellbeing: Implications for captive management. *Applied Animal Behaviour Science* 147, 261–267. http://dx.doi.org/10.1016/j.applanim.2012.11.002.
- Gartner, M.C., Powell, D.M., Weiss, A. (2016) Comparison of subjective well-being and personality assessments in the clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and African lion (*Panthera leo*). Journal of Applied Animal Welfare Science 19, 294–302. http://dx.doi.org/10.1080/10888705.2016.1141057.
- Gotlib, I.H. and Joormann, J. (2010) Cognition and depression: Current status and future directions. *Annual Review of Clinical Psychology* 6, 285–312. http://dx.doi.org/10.1146/annurev.clinpsy.121208.131305.
- Gottlieb, D.H., Capitanio, J.P., McCowan, B. (2013) Risk factors for stereotypic behavior and self-biting in rhesus macaques (*Macaca mulatta*): Animal's history, current environment, and personality. *American Journal of Primatology* 75, 995–1008. http://dx.doi.org/10.1002/ aip.22161.
- Green, T.C. and Mellor, D.J. (2011) Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. *New Zealand Veterinary Journal* 59, 263–271. http://dx.doi.org/10.1080/00480 169.2011.610283.
- Hahn, E., Johnson, W., Spinath, F.M. (2013) Beyond the heritability of life satisfaction – The roles of personality and twin-specific influences. *Journal of Research* in Personality 47, 757–767. http://dx.doi.org/10.1016/j. jrp.2013.07.003.
- Hahn, E., Gottschling, J., König, C.J., Spinath, F.M. (2016) The heritability of job satisfaction reconsidered: Only unique environmental influences beyond personality. *Journal of Business and Psychology* 31, 217–231. http://dx.doi.org/10.1007/s10869-015-9413-x.
- Harding, E.J., Paul, E.S., Mendl, M. (2004) Animal behaviour: Cognitive bias and affective state. *Nature* 427, 312. http://dx.doi.org/10.1038/427312a.

- Harlow, H.F. and Suomi, S.J. (1974) Induced depression in monkeys. *Behavioral Biology* 12, 273–296. http:// dx.doi.org/10.1016/S0091-6773(74)91475-8.
- Hsu, Y. and Serpell, J.A. (2003) Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. *Journal of the American Veterinary Medical Association* 223, 1293–1300. http://dx.doi.org/10.2460/javma.2003.223.1293.
- Inglehart, R.F. (2018) Cultural Evolution: People's Motivations Are Changing, and Reshaping the World. Cambridge University Press, Cambridge, UK. http:// dx.doi.org/10.1017/9781108613880.
- Inglehart, R., Foa, R., Peterson, C., Welzel, C. (2008)
 Development, freedom, and rising happiness.

 Perspectives on Psychological Science 3, 264–285.
 http://dx.doi.org/10.1111/j.1745-6924.2008.00078.x.
- Inoue-Murayama, M., Yokoyama, C., Yamanashi, Y., Weiss, A. (2018) Common marmoset (Callithrix jacchus) personality, subjective well-being, hair cortisol level, and AVPR1a, OPRM1, and DAT genotypes. Scientific Reports 8, 10255. http://dx.doi.org/10.1038/ s41598-018-28112-7.
- Kagan, R., Carter, S., Allard, S. (2015) A universal animal welfare framework for zoos. *Journal of Applied Animal Welfare Science* 18, S1–S10. http://dx.doi.org/10.108 0/10888705.2015.1075830.
- Kelley, T.L. (1927) Interpretation of Educational Measurements. World Book, Yonkers-on-Hudson, New York, USA.
- King, J.E. and Figueredo, A.J. (1997) The Five-Factor Model plus dominance in chimpanzee personality. *Journal of Research in Personality* 31, 257–271. http://dx.doi.org/10.1006/jrpe.1997.2179.
- King, J.E. and Landau, V.I. (2003) Can chimpanzee (Pan troglodytes) happiness be estimated by human raters? Journal of Research in Personality 37, 1–15. http://dx.doi.org/10.1016/S0092-6566(02)00527-5.
- Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., et al. (1999) Coping styles in animals: Current status in behavior and stressphysiology. Neuroscience and Biobehavioral Reviews 23, 925–935. http://dx.doi.org/10.1016/S0149-7634 (99)00026-3.
- Lykken, D. and Tellegen, A. (1996) Happiness is a stochastic phenomenon. *Psychological Science* 7, 186–89. http://dx.doi.org/10.1111/j.1467-9280.1996.tb00355.x.
- MacLean, E.L., Hare, B., Nunn, C.L., Addessi, E., Amici, F., et al. (2014) The evolution of self-control. Proceedings of the National Academy of Sciences of the United States of America 111, E2140–E2148. http://dx.doi.org/10.1073/pnas.1323533111.
- Mason, G.J. (1991) Stereotypies: A critical review. Animal Behaviour 41, 1015–1037. http://dx.doi.org/10.1016/ S0003-3472(05)80640-2.
- Mason, G.J. and Latham, N.R. (2004) Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare* 13, S57–S69.

- McMillan, F.D. (2000) Quality of life in animals. *Journal of the American Veterinary Medical Association* 216, 1904–1910. http://dx.doi.org/10.2460/jayma.2000.216.1904.
- McMillan, F.D. (2005) The concept of quality of life in animals. In: McMillan, F.D. (ed.) *Mental Health and Well-Being in Animals*. Blackwell Publishing, Ames, Iowa, USA, pp. 183–200. http://dx.doi.org/10.1002/9780470384947.ch13.
- Mendl, M., Burman, O.H.P., Parker, R.M.A., Paul, E.S. (2009) Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science* 118, 161– 181. http://dx.doi.org/10.1016/j.applanim.2009.02.023.
- Miller, N.E., Bailey, C.J. Stevenson, J.A.F. (1950) Decreased 'hunger' but increased food intake resulting from hypothalamic lesions. *Science* 112, 256–259.
- Morton, F.B., Lee, P.C., Buchanan-Smith, H.M., Brosnan, S.F., Thierry, B., et al. (2013) Personality structure in brown capuchin monkeys (Sapajus apella): Comparisons with chimpanzees (Pan troglodytes), orangutans (Pongo spp.), and rhesus macaques (Macaca mulatta). Journal of Comparative Psychology 127, 282–298. http://dx.doi.org/10.1037/a0031723.
- Pavot, W., Diener, E., Colvin, C.R. Sandvik, E. (1991) Further validation of the Satisfaction with Life Scale Evidence for the cross-method convergence of well-being measures. *Journal of Personality Assessment* 57, 149–161. http://dx.doi.org/10.1207/s15327752jpa5701_17.
- Pinker, S. (2011) The Better Angels of Our Nature: The Decline of Violence In History and Its Causes. Allen Lane, London, UK.
- Robinson, L.M., Waran, N.K., Leach, M.C., Morton, F.B., Paukner, A., et al. (2016) Happiness is positive welfare in brown capuchins (Sapajus apella). Applied Animal Behaviour Science 181, 145–151. http:// dx.doi.org/10.1016/j.applanim.2016.05.029.
- Robinson, L.M., Altschul, D., Wallace, E., Úbeda, Y., Llorente, M., et al. (2017) Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. Applied Animal Behaviour Science 191, 90– 97. http://dx.doi.org/10.1016/j.applanim.2017.02.008.
- Sandvik, E., Diener, E. Seidlitz, L. (1993) Subjective well-being: The convergence and stability of self-report and non-self-report measures. *Journal of Personality* 61, 317–342. http://dx.doi.org/10.1111/j.1467-6494.1993.tb00283.x
- Steel, P., Schmidt, J. Shultz, J. (2008) Refining the relationship between personality and subjective wellbeing. *Psychological Bulletin* 134, 138–161. http:// dx.doi.org/10.1037/0033-2909.134.1.138.
- Svartberg, K. and Forkman, B. (2002) Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science* 79, 133–155. http://dx.doi.org/10.1016/S0168-1591(02)00121-1.
- Tellegen, A. (1982) *Brief Manual for the Multidimensional Personality Questionnaire*. University of Minnesota, Minneapolis, Minnesota, USA.

- Thorndike, E.L. (1904) An Introduction to the Theory of Mental and Social Measurements. Teacher's College, Columbia University, New York, USA. http://dx.doi. org/10.1037/13283-000.
- Weiss, A. (2017) Exploring factor space (and other adventures) with the Hominoid Personality Questionnaire. In: Vonk, J., Weiss, A., Kuczaj, S. (eds.) Personality in Nonhuman Animals. Springer, Cham, Switzerland, pp. 19–38. http://dx.doi.org/10.1007/ 978-3-319-59300-5_2.
- Weiss, A. and King, J.E. (2006) Searching for the genetic and environmental contributions to personality and happiness in chimpanzees (*Pan troglodytes*). In: Canli, T. (ed.) *Biology of Personality and Individual Differences*. Guilford Press, New York, USA, pp. 407–426.
- Weiss, A., King, J.E., Figueredo, A.J. (2000) The heritability of personality factors in chimpanzees (*Pan troglodytes*) *Behavior Genetics* 30, 213–221. http://dx.doi.org/10.1023/A:1001966224914.
- Weiss, A., King, J.E., Enns, R.M. (2002) Subjective well-being is heritable and genetically correlated with dominance in chimpanzees (*Pan troglodytes*). *Journal of Personality and Social Psychology* 83, 1141–1149. http://dx.doi.org/10.1037/0022-3514.83.5.1141.
- Weiss, A., King, J.E., Perkins, L. (2006) Personality and subjective well-being in orangutans (*Pongo pyg-maeus* and *Pongo abelii*). *Journal of Personality* and *Social Psychology* 90, 501–511. http://dx.doi. org/10.1037/0022-3514.90.3.501.
- Weiss, A., Bates, T.C., Luciano, M. (2008) Happiness is a personal(ity) thing: The genetics of personality and well-being in a representative sample. *Psychological Science* 19, 205–210. http://dx.doi.org/10.1111/j.1467-9280.2008.02068.x.
- Weiss, A., Inoue-Murayama, M., Hong, K.-W., Inoue, E., Udono, S., et al. (2009) Assessing chimpanzee personality and subjective well-being in Japan. American Journal of Primatology 71, 283–292. http://dx.doi.org/10.1002/ajp.20649.
- Weiss, A., Adams, M.J., Widdig, A., Gerald, M.S. (2011) Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal* of Comparative Psychology 125, 72–83. http://dx.doi. org/10.1037/a0021187.
- Weiss, A., Baselmans, B.M.L., Hofer, E., Yang, J., Okbay, A., et al. (2016) Personality polygenes, positive affect, and life satisfaction. Twin Research and Human Genetics 19, 407–417. http://dx.doi.org/10.1017/thg.2016.65.
- Whitman, W. and Washburn, D A. (2017) A history of animal personality research. In: Vonk, J., Weiss, A., Kuczaj, S. (eds.) *Personality in Nonhuman Animals*. Cham, Switzerland: Springer.
- Yeates, J.W. and Main, D.C.J. (2008) Assessment of positive welfare: A review. *The Veterinary Journal* 175, 293–300. http://dx.doi.org/10.1016/j.tvjl.2007.05.009.

122

10 Fostering Mental and Behavioral Wellness During Upbringing and Throughout Life

DANIEL Q. ESTEP AND SUZANNE HETTS

Animal Behavior Associates, Sun City, Arizona, USA

Historically, concern for the welfare of animals has focused on the relief of suffering through the prevention and treatment of physical illness and the provision of environmental and social necessities such as food, water, shelter, and companionship. Much progress has been made in understanding. alleviating, and preventing animal suffering. But it has only been recently that scientists and animal welfare advocates have begun to address the positive side of animal welfare – how a good quality of life can be facilitated for animals. As McMillan (2002) points out, good mental health is more than just the absence of suffering: it is the attainment of positive emotional states such as happiness and contentment. Research in this area is evolving, and we still do not know as much as we need to about how best to facilitate good animal mental health. In this chapter we will review what is known about how mental health may be influenced - for the better and for the worse - and how that research can be used to create programs that can improve and perhaps even optimize mental health.

We will take a developmental approach because it is known that experiences early in life can have significant effects on behavior and well-being in animals well into adulthood. Positive mental health programs instituted in these early stages of life hold promise to improve long-term well-being efficiently and economically.

10.1 Definitions and Terminology

There is no consensus in the definitions of terms such as mental (or psychological) wellness, well-being, quality of life, mental health, or stress as they apply to nonhuman animals (hereafter referred to as animals). Clark *et al.* (1997) argue that '...arriving at a universally acceptable definition of animal wellbeing is probably impossible because the way people define quality of nonhuman animal life depends on their personal experiences, views and values'. For many people, welfare and well-being are synonymous. Among the general public, welfare often means well-being, happiness, health, prosperity, comfort, or a state of faring well. Clark *et al.* (1997) and McMillan (2000) also see quality of life as equivalent to or very close to well-being (for a more extensive discussion of terminology, see Chapter 2, this volume).

10.1.1 Mental health

Our working definition of mental health is that it is a variable condition of the animal characterized by the constantly changing combination of pleasant and unpleasant emotions and variations in the functioning of various mental (cognitive) processes including learning, thinking, remembering, and perceiving. Mental health exists along a continuum from very good to very poor. For our purposes we consider mental health, mental wellness, mental well-being, and mental quality of life as synonymous. We agree with Duncan and Fraser (1997) that any consideration of general welfare must include assessment of mental wellness in addition to those of health and longevity. We assume mental wellness to be just one component of overall wellness.

Mental health is dynamic, not static, and obviously varies and changes over time. For that reason,

the time frame for assessments of mental health should be specified. Is it just over a few days in the early development of the animal, just during her declining senior years, or over the entire lifespan? This is rarely specified in the research and writings about mental wellness and is one source of confusion in the evaluation of mental wellness.

10.1.2 Behavioral health and mental health

Behavioral health and mental health are often used interchangeably. The interrelationships among subjective experiences, physiologic processes, and behavior are complex, where each one seems to be influenced by the others. However, animal subjective experiences are not directly accessible to people, and many physiological measures of mental well-being are not available to most people, leaving behavior as the chief indicator of internal states and mental health. Even though behavior is not always a perfect reflection of internal physiological and subjective states, we will use the terms mental health and behavioral health interchangeably for the purposes of this chapter.

10.1.3 Stress and stressors

Stress is another term frequently used in discussions of well-being and is used to describe various physiological and/or behavioral responses to environmental stimulation. It too has no commonly agreed-upon definition. We will use McEwen's (2000) 'stress response', defined as a physiological and/or behavioral response to a perceived threat to homeostasis. Stress responses that are damaging to the animal are called distress and those that are beneficial are called eustress. The environmental stimulus that elicits the stress response is known as the stressor and the outcome of the stress response for the animal is known as coping. Coping can vary from good to poor depending on the change in the animal. McMillan (2005) has discussed the close relationship between stress and emotions, especially distress and negative emotions such as fear and depression. It is not uncommon for researchers and others to use the terms fear and stress (or distress) interchangeably when describing the reactions of animals to certain aversive stimuli. Our working definitions may differ from others.

10.2 Welfare and the Concept of Needs

It has long been recognized that good welfare depends on good health. Good health in turn is dependent, in part, on certain physical needs, such as food, water, and protection from the physical elements, being met. Since the 1980s, research has made clear that mental as well as physical needs must be met to insure good mental well-being and overall welfare. Poole (1992) first directly addressed the idea of behavioral needs, providing a list of five needs for mammals: stability and security in the environment, environmental complexity, some novelty and unpredictability in the environment, opportunities to achieve goals, and companionship. McMillan (2002) and Hetts et al. (2004) incorporated and expanded on Poole's original list. There is considerable overlap in the lists of McMillan and Hetts et al. although they frame the needs in slightly different ways, including labeling needs behavioral as compared to mental. For the sake of simplicity, in this discussion we will follow McMillan's (2002) categorization and describe points of departure from Hetts et al. We will use Poole's and Hetts' label of behavioral needs rather than mental needs.

It should be obvious that there are species and individual differences (including age and sex) in the importance of specific needs and in the particulars of how they can be satisfied. For example, some breeds of dogs need a great deal of exercise in the form of running and walking, others do not. A 6-month-old foal may have a greater need for social play than a 25-year-old senior horse.

10.2.1 Avoiding negative emotional states

Perhaps the most basic behavioral need is to escape, avoid, or minimize fear, discomfort, boredom, and depression. These unpleasant emotional states can arise from illness such as a cat suffering from arthritis of the hips, an adverse physical environment such as a dog in a hot yard without shade or water, or from social conflict such as a house cat that is repeatedly stalked by a dog or grabbed by a young child. The first two examples overlap with the physical needs of food, water, and a safe environment, but these become behavioral needs when they involve strong emotions in the animal.

D.Q. Estep and S. Hetts

10.2.2 Social companionship

The second behavioral need is a need for social companionship. This might be members of the animal's own species, another nonhuman species, or people. A playful young cat may find a persistent young child a good playmate while an old arthritic cat may find the same child unbearable. The quality of the social experience will differ with the identity of the companion, the context in which the companion is presented, the behaviors exhibited by the companion, and prior experiences of the animal. A dog that has been the victim of an attack by another dog, for example, may be frightened of dogs resembling the attacker. As we will see later, puppies and kittens that have had no experience with people at a young age can find people very frightening during the animals' adolescence and adulthood. This probably holds true for most other domesticated and wild animals.

10.2.3 Mental stimulation

A third need is for mental stimulation. Most mammals and birds have a self-rewarding curiosity for exploring new places and things that sometimes even extend to the regular re-exploration of familiar places and things. Monotonous, uniform environments with nothing new to see, hear, smell, or feel can create boredom and depression. Giving animals opportunities for foraging for food, the manipulation of food puzzles, or opportunities for investigating novel things are examples of ways to increase mental stimulation.

10.2.4 Predictability

A fourth behavioral need is predictability in both the physical and social environment. Having a predictable mealtime or a predictably friendly social partner can reduce anxiety and create positive anticipation of the coming of the event or individual, which is rewarding and creates positive emotions. Frequent unpredictability in the environment or in behavior of others can create anxiety and distress and make otherwise tolerable situations intolerable. However, a degree of unpredictability in the environment, especially if it involves positively reinforcing events, can enhance mental health by relieving or preventing boredom. Examples can be special walks for a suburban-living dog or unscheduled play for an indoor cat. These events

create positive emotions that may relieve boredom and depression.

10.2.5 Controllability

Related to predictability is the ability to exert a degree of control over the environment. Animals that have control over certain variables in their lives such as a dog that can choose when to go outside or stay indoors, can create their own predictability in changing environments. The ability to control the environment and particularly to make choices is very important for many species (for reviews, see Mineka and Hendersen, 1985, and Chapter 6, this volume).

10.2.6 Pleasurable experiences

The sixth behavioral need is the need to generate pleasurable experiences. These experiences may include displaying species-typical behaviors such as opportunities for cats to scratch, for dogs to use their olfactory abilities in scent work, or simply opportunities for social and object play for most species of animals. These actions are self-reinforcing and create their own positive emotions. Other pleasurable experiences may be generated through opportunities to engage in learned behaviors that result in externally delivered reinforcement, such as a cat meowing for food or a dog barking at the back door to go outside. Animals that are prevented from showing sufficient species-typical behaviors, either by punishment delivered by caretakers or because the environment does not facilitate them, often become frustrated and the needs get expressed in behaviors people find unacceptable. This leads to further restrictions or punishment, all resulting in a decrement in mental well-being.

10.3 Development and Mental Welfare

Two classes of factors determine the developmental trajectory of an animal. The first is genetic predispositions and the second is environmental influences. These factors interact from conception and throughout life to create the physical structures, physiological processes, and behavioral actions that comprise the living animal. Both the mental and physical health of an animal are determined by these interactions.

10.3.1 Genetic predispositions

Historically, much more attention has been paid to environmental influences on welfare than on genetic influences. Until very recently, knowledge about how genes influenced behavior and welfare was lacking, and it was easier to study and manipulate environmental factors. The genetic constitution of the animal influences every aspect of structure, physiology, and behavior, and therefore has indirect effects on mental welfare. Genes influence behaviors. emotions, and mental processes that impact welfare in people as well as other animals (see review in Plomin et al., 2008). Behavioral genetic research has begun to examine the interactions and co-actions of genes with environmental factors in the expression of behavior, including mental illnesses. Kim-Cohen et al. (2006) showed that in children a gene involved in the regulation of neurotransmitters interacted with childhood maltreatment to effect antisocial behavior and, consequently, mental health.

In animals it is known that genes can influence a variety of behaviors that either directly contribute to mental wellness or that are indicators of mental wellness. One of the best examples in companion animals is seen in the work of Murphree and colleagues (Murphree et al., 1967; Dykman et al., 1979). They selectively bred two lines of pointer dogs, one for normal or stable behavior and the other for nervous or unstable behavior. In a very few generations the dogs in the nervous line were consistently much more fearful of people than those in the normal line. The finding that the behavior responded to directional selection indicated a genetic influence. From a young age the nervous dogs were fearful of people, and as they got older the fear became more prominent. They were terrified to be in close proximity to people and would freeze statue-like for minutes at a time. Because of their fear, these dogs likely had reduced well-being compared to their nonfearful counterparts.

Mills et al. (1997) point out that genetic selection for or against traits that influence welfare such as fearfulness and adaptability to changing environments may be a powerful way to improve animal well-being. Such change would come slowly if left to traditional selective breeding. In the future, with newer gene splicing and editing techniques (along with a well-developed understanding of gene actions and interactions) very specific changes to an animal's anatomy and physiology could be quickly made that could improve well-being.

10.3.2 The Development of altricial mammals

Altricial animals are born in a state of relative physical and behavioral under-development. They cannot feed themselves, their abilities to thermoregulate and eliminate are poorly developed, they cannot see or hear, and are capable of very little movement. They are completely dependent upon their mother for survival in the early days after birth. For most altricial mammals, the process of development from conception to adulthood can be divided into several phases:

- prenatal phase, from conception to birth;
- neonatal phase, from birth to the opening of the eyes and ears and coordinated movement;
- socialization phase, from the end of the neonatal phase to around the time of weaning or several days afterwards; and
- adolescent or juvenile phase, which starts at the end of the socialization phase and ends at sexual maturity and young adulthood.

Because different species develop at different rates, the length of each phase varies from species to species.

10.4 Environmental Influences on Behavior During Early Development

What happens to animals during behavior development not only influences their welfare at the time but often has life-long impacts. Much more is known about environmental influences that produce negative effects on welfare than is known about how to maximize or optimize welfare. We will provide a sampling of this research. Both Serpell et al. (2017) and Dietz et al. (2018) reviewed the development of the behavior of dogs and the effects of early experiences on the development of behavior problems in dogs. Bradshaw et al. (2012) have provided a review of the development of behavior in cats. Historically, it has been thought that events occurring during the socialization phase were critically important for normal social development (Scott and Fuller, 1965). More recent research suggests that environmental and social stimulation during other phases are important in influencing later social behavior and adaptation to environmental challenges.

10.4.1 Prenatal phase

In dogs and cats the gestation or the prenatal phase, is about 63 days long. In rats and mice the

D.Q. Estep and S. Hetts

development is even faster, with the prenatal phase lasting between 19 and 21 days for domestic mice and 21 and 23 days for domestic rats.

Research on the effects of prenatal influences on behavior has received very little attention in dogs and cats but studies of laboratory rats, mice, and primates have shown significant (though often conflicting) results. In his review of the behavioral results of aversive stimuli on pregnant female rats and mice, Weinstock (2008) found that seven of 14 studies found increases in pup fear later in life, but five found no effects, and two found decreases in fearfulness. Six of 11 studies found that aversive stimulation of pregnant female rats and mice produced deficits in learning and memory, but three others found no effects, and two actually saw improvements in offspring learning and memory.

There were significant differences among the studies in the species and breeds used as well as test methodology. It is thought that the results could be influenced by genetic predispositions, the kind and duration of aversive experience, the timing of the adversity during pregnancy, the behavioral measures taken, and the age at testing of the offspring (Weinstock, 2008).

So, while some prenatal experiences aversive to pregnant females adversely affect the behavior of offspring, others seem to have no effects or even seem to improve later coping abilities and learning and memory. These effects persist at least into adolescence and probably into adulthood.

10.4.2 Neonatal phase

The neonatal phase extends from birth to about 3 weeks of age in dogs and to 2 weeks of age in cats. In rats this phase begins at birth and ends at weaning at about 5 to 6 weeks of age.

There is a rich body of research on the effects of exposure of neonatal animals to various kinds of stimulation including handling and separations from mother and littermates (Serpell *et al.*, 2017). These and other experiences have produced a variety of effects (Wilson *et al.*, 1965; Gazzano *et al.*, 2008a), many of which are contradictory.

Overall, gentle handling results in animals that are less fearful and possibly with enhanced learning ability (Fox, 1978). Handling and mildly aversive stimulation, such as brief social separations, sometimes result in increased resilience to aversive situations and reduced fearfulness in novel situations (de Azevedo *et al.*, 2010). But in other cases, these

experiences can sensitize animals to fearful reactions when adults (see review in Serpell *et al.*, 2017).

A variety of variables may influence the results, but the intensity and kind of stimulation seem to be two important ones. Mild stimulation seems to lead to greater resilience to adverse conditions, whereas more intense or longer lasting stimuli seem to have the opposite effect. Resilience to fear-provoking stimuli would appear to contribute positively to welfare in that resilient animals are better able to cope with challenging and aversive environments. Likewise, chronically fearful animals are more likely to have reduced welfare.

It also seems obvious that the quality of maternal care can affect the later behavior of young animals. In general, good maternal care has positive effects on offspring (Foyer *et al.*, 2016; Guardini *et al.*, 2016). Maternal and prenatal experiences have been shown to interact (Wakshlak and Weinstock, 1990). Postnatal handling of rats attenuated the effects of maternal prenatal aversive stimulation when offspring were tested at 8 weeks of age for fearful behavior in an open field and in a maze test.

While a large number of studies have evaluated the effects of prenatal and postnatal experiences on offspring during behavior development, most did not measure effects into adulthood.

10.4.3 Socialization phase in dogs

This developmental period has received the most research attention and arguably has the potential to have greater influence on adult behavior, welfare, and mental health than any other developmental phase. The socialization phase in dogs is from about 3–12 weeks of age and from 2–7 weeks in cats. Research has not defined a socialization phase in rats and mice that corresponds to that of dogs and cats.

Scott and Fuller (1965) included an additional phase for dogs, the transitional phase, between the neonatal phase and the socialization phase that covers several days from about 2 weeks of age and is characterized by rapid physical changes such as opening of the eyes and ears and rapid changes in locomotor abilities. This phase has not been consistently recognized in other altricial mammals.

Research has shown that during the socialization phase it is easiest for young animals to learn their species identity, develop both interspecific and intraspecific social relationships, and practice speciestypical behaviors. The preferences for particular types of social partners that have begun during this time are long-lasting. The first attachments young animals form, often referred to as primary socialization, is to their mother and littermates. Because it is so easy for social relationships to form during this phase, young animals readily become attached to most any individuals they spend time with (Cairns and Werboff, 1967).

In a classic study of dog socialization, Freedman *et al.* (1961) determined that the sensitive period for socialization was between 2.5 and 9–13 weeks of age. Puppies who had no experience with people before 14 weeks of age were fearful of people, uncooperative, and described as 'wild'.

The onset of fear responses is thought to be the mechanism that ends the sensitive period for socialization in dogs and other species. Genetic differences may influence the timing of sensitive periods in puppies. Morrow *et al.* (2015) compared the development of fear responses in German shepherd, Yorkshire terrier, and Cavalier King Charles spaniel puppies from 2–12 weeks of age. The onset of increasing fear in Cavalier King Charles spaniels was 2 weeks later than that of German shepherds. Clearly more research is needed to examine individual and breed differences in the timing of sensitive periods.

10.4.4 Socialization phase in cats

Based on results from selectively handling kittens at varying ages prior to 8 weeks of age, the sensitive period for socialization for cats seems to be between 2 and 7 weeks of age (Karsh, 1983; Karsh and Turner, 1988; McCune, 1995). This has practical significance because many cats are weaned between 6 and 8 weeks of age, at the end of the sensitive period. It has been argued that to take advantage of this time of rapid social learning, those who breed or care for neonatal cats should begin socialization experiences while the young are still in their care, prior to weaning.

McCune (1995) found that genetics could interact with social experiences to affect the outcome of early handling during the sensitive period of cats. Kittens born of a father that was friendly to people and that were handled daily from 2–12 weeks of age were more attracted to and friendlier to people than kittens that were handled for the same time but were sired by an unfriendly father. These results may help to explain why some animals remain fearful of people even when they have had good

experiences at what would appear to be ideal ages for socialization.

10.4.5 Broader meaning of 'socialization'

The classic literature on 'socialization' refers to social attachments. Scott and Fuller (1965) speculated that location attachment may also develop during this time. For this and other reasons the term 'socialization' has come to have a broader meaning referring to animals' abilities to readily adapt to unfamiliar circumstances and a broad array of events, stimuli, and social interactions. This greatly confuses the communication about the early development of behavior.

From this broader definition have come recommendations that young animals should be exposed to as many unique experiences as possible in order to increase their resilience and adaptability. Yet this assumption has not been generally tested. In one study a group of purpose-bred service dog puppies were provided additional visual, auditory, tactile, and human interaction experiences beyond the broad array already included as part of their enriched rearing environment (Vaterlaws-Whiteside and Hartmann, 2017). At 8 months of age when this group was compared to other dogs who did not receive the enhanced experiences, they were less distressed when left alone, displayed less overall anxiety, and were less distractible.

Some recommendations for socialization experiences advise exposing animals to circumstances they will likely encounter as adults. However, the benefits of this have not been empirically supported. One study provides evidence that adaptation and stimulus generalization can occur as a result of sound exposure during the socialization phase. Chaloupkova et al. (2018) reported that exposing prospective police dog puppies to radio programs daily for the first part of the socialization phase resulted in animals that responded more favorably to loud, sudden sounds when tested at 8 weeks of age. A survey of dog owners in Finland examined the maternal care and early experiences of dogs in relation to behavior problems (Tiira and Lohi, 2015). They reported that dogs that had poor maternal care or fewer early socialization experiences were more likely to later exhibit fears of people and things.

The age at which pups should be removed from their natal home and placed in their new homes is a subject of controversy and conflicting data. Scott

128 D.Q. Estep and S. Hetts

and Fuller (1965) recommended rehoming between 7 and 8 weeks of age. Pierantoni *et al.* (2011) reported that dogs homed between 4 and 5.5 weeks of age were more likely to be fearful and have other behavior problems, including excessive attention-seeking, possessiveness (for food and toys), destructiveness, and excessive barking than those homed at 8.5 weeks of age. Slabbert and Rasa (1993) found pups rehomed at 6 weeks had higher mortality and morbidity and more signs of separation distress than those rehomed at 12 weeks. Conversely, a Finnish study (Jokinen *et al.*, 2017) found dogs homed between 13 and 16 weeks of age showed more fearful and aggressive behavior than those homed from 6–8 weeks old.

Based on the research literature, it is hard to identify a single 'best time' for weaning and rehoming dogs. Obvious questions arise about the variations in the breeding environment, maternal care, and genetic differences already discussed. More research is needed but it appears rehoming too early, sometime before 7 weeks, or too late, sometime after 9 weeks, could increase the risks of behavior problems for dogs acquired as pets.

10.4.6 Adolescent phase in dogs

In dogs, the adolescent phase lasts from approximately 12 weeks of age to the time of sexual maturity, which occurs between 6 months to over 2 years of age depending upon the breed of dog and rearing conditions. The adolescent phase in cats is quite variable in length with sexual maturity occurring from about 4 months to a year of age.

The effects of specific experiences on later behavior and welfare have not been as well studied for this phase for dogs and cats, although there are a number of studies of rats and mice. This paucity of research is surprising given the significant physical and behavioral changes that occur during this phase, including the onset of sexual maturity. Based on their clinical experience, professionals from a variety of backgrounds who work with behavior problems in dogs believe that limited social interactions during this phase can contribute to fearful and aggressive behavior directed toward unfamiliar people and dogs, even when the dogs were exposed to other dogs and people during the socialization phase.

Appleby et al. (2002) compared the early histories and environments of dogs with avoidance and aggression problems to those with other behavior

problems that had been brought to a clinical animal behavior service. The dogs with avoidant and aggressive behaviors were more likely to have come from pet stores or large commercial breeders and to not have been raised in urban environments between the ages of 3 and 6 months. Their hypothesis was that dogs raised in these environments probably missed important social interactions with people and other animals.

McMillan (2017) reviewed seven studies concerning the adult behavior of dogs born at large commercial breeding facilities. The results indicated a higher than expected frequency of emotional and behavioral problems in dogs from those facilities compared with dogs from other sources. The problems included aggression toward the dog owner's family members, unfamiliar people, and other dogs, as well as fears of people, other dogs, and nonsocial things and events. There are a number of reasons why dogs from these commercial facilities might have more problems, including genetic predispositions, prenatal aversive events, inadequate maternal care, inadequate socialization experiences, early weaning and maternal separation, events related to transport and sale of the dogs, as well as inadequate owner-related knowledge and care.

A survey of Australian pet owners (Wormald et al., 2016) revealed the average age of exposure of pet dogs to unfamiliar people and other dogs was 13 weeks of age. But the longer owners waited to expose their dogs to other dogs, the lower the probability their dog would show dog-to-dog aggression. They also reported no relationship between the number of other dogs that subject dogs had met and the amount of time spent with other dogs and inter-dog aggression. This appears to be counter to the conventional wisdom that the earlier the exposure to other dogs and the more dogs encountered, the less the likelihood of dog-to-dog aggression problems. One possible explanation is that the more encounters a dog has, the more likely at least one of them will result in a conflict with persisting effects on behavior.

10.4.7 Adolescent phase in rats and mice

There is a body of research investigating the effects of experiences during this phase on the neuroendocrine system and behavior of laboratory rats and mice. Certain experiences during this time, as in the earlier phases, can also produce long-lasting effects on behavior (reviewed in Buwalda *et al.*, 2011).

Providing an enriched environment for several weeks to adolescent rats who had been prenatally stressed could attenuate their stress-induced depression during social play (Morley-Fletcher *et al.*, 2003). Social play seems to be important in many species for normal development of adult social skills and behavior.

Adolescent environmental enrichment can compensate for early life adversity, such as repeated maternal separations of neonatal rats (Francis et al., 2002). When neonatally separated rats were evaluated in open-field tests for fear, enriched rats showed significantly less fear than unenriched rats.

Rather than negatively impacting welfare, stressful experiences during adolescence may help animals cope with stressors later in life. Adolescent rats were exposed to several weeks of various aversive stimuli, from tilting their cages, to flashing lights and sounds, to exposures to the smells or sounds of potential predators (Chaby et al., 2015). As adults these rats and their untreated controls were exposed to a mildly aversive foraging test (an open field box with hidden food in a darkened room) and a more aversive one (an open field box with hidden food in a brightly lit room with the sight and sound of a hawk, a predator). The rats did not differ in their performance in the low-stress foraging test, but the rats exposed to adolescent stressors performed better than the controls in the high stress test. The researchers concluded that some kinds of stressful experiences may be beneficial by helping young animals prepare for more stressful environments in the future. While these results cannot be directly applied to other species, popular ideas about the necessity for a 'stress free' life for pets and other animals should be critically examined. It is possible that certain unpleasant experiences during this phase can actually enhance resilience to other challenges later in life.

10.5 Recommendations for Improving the Mental Health of Young and Older Companion Animals

10.5.1 Development of realistic expectations

To start, caretakers need to have realistic expectations about what they can reasonably expect from their relationships with their pets in order to avoid disappointment, frustration, and from setting goals for their pets' behaviors that will never be attainable. When it comes to people—pet relationships,

unrealistic expectations stem from a lack of understanding of the pets' physical and behavioral needs and normal behavior as well as a failure to correctly read the behavioral signs of emotional states, especially those of negative emotions. Pet owners have long had access to information about the physical needs of companion animals from veterinarians and other pet professionals as well as from books, videos, and online resources. This education has undoubtedly improved the physical health of pets. What has been lacking until very recently is good information that allows pet caretakers to develop an understanding of normal pet behavior and to recognize the emotional states and behavioral needs of pets.

10.5.2 Understanding normal behavior

Despite the wealth of information available on pet behavior, incomplete and incorrect information about normal pet behavior is still widespread. Many people do not know enough about normal dog or cat elimination behavior to know the best way to housetrain a new dog or how to set up a litterbox that will be regularly used by a new cat. Some people wrongly believe that behaviors seen in pets left home alone, such as destructiveness and house soiling, are motivated by spite. Pet caretakers cannot hope to provide the best quality of life for their animals without a good understanding of normal pet behavior.

10.5.3 Recognizing emotional states

Research has found that pet parents have difficulty identifying signs of fear, depression, and other negative emotions in their dogs (Mariti *et al.*, 2012). Pet professionals with little experience also have been found to have difficulty recognizing fearful behaviors in dogs (Wan *et al.*, 2012). An inability to correctly identify an animal's emotional states makes it difficult to meet its needs and promote mental health. It follows that caretakers who can read the emotions of their pets can better meet their pets' behavioral needs and promote better welfare.

10.5.4 Meeting behavioral needs

It is reasonable to assume that minimizing pain, fear, and discomfort, and providing for social companionship, mental stimulation, predictability, and controllability in the environment should generate

D.Q. Estep and S. Hetts

more positive emotions for animals and improve their mental health. Precisely how these worthy goals can be accomplished is neither as simple nor straightforward as it might seem. As we stated in the review of early development research, it is hard to know which experiences are going to be the most helpful for any given animal at any specific time. Genetic predispositions and prior experiences can influence the relative importance of behavioral needs and thus the effectiveness of particular environmental interventions.

Dogs that have had only a narrow range of enjoyable experiences with other dogs and in new situations when young are more likely to be fearful in unfamiliar contexts and when meeting unfamiliar animals. Such dogs are more likely to respond to the social overtures of others with avoidance, escape, threats, or aggression, and are more likely to avoid novelty. The result is limited opportunities for experiencing new sources of social contact and mental stimulation and the positive emotions associated with them. Conversely, well socialized dogs who have had a variety of pleasant experiences with people, other animals, and new situations early in life are more likely to enjoy social overtures by others. Their openness to social contact and opportunities for social play and mental stimulation can then expand, as can the frequency of positive emotions associated with them.

Thus, the needs for social contact and mental stimulation will be very different for animals who enjoy them compared to those who do not. New social contacts and new places will be a source of rewards and positive emotions for better socialized dogs, but they will be sources of aversiveness and negative emotions for the others.

The needs to predict changes in the social and physical environment and to control some aspects of their environments will be important regardless of socialization status, but the specifics are likely to be different. Poorly socialized dogs will likely find unpredictable and uncontrollable environments more aversive and more emotionally unpleasant than better socialized and adaptable dogs who can tolerate and even enjoy more unpredictability and uncontrollability in life.

Clearly, these six behavioral needs are interrelated. In general, having needs met for social contact, mental stimulation, predictability, and controllability will create or increase positive emotions, while not having those needs met will create or increase negative emotions. The specifics of how those needs are best met for individual animals will be dependent on individual characteristics and will typically vary over time and circumstances.

10.5.5 Limitations of specific recommendations

What this means is that generalized recommendations for meeting behavioral needs cannot be expected to be a good fit for all animals. While some puppies or kittens may benefit from meeting as many unfamiliar people as possible, or being exposed to a wide variety of novel situations, too many of these experiences may be counterproductive for other animals. Any general guidelines about how to meet the needs of dogs or cats must be tempered by a recognition that the needs of each animal will be different and management and training should be tailored to those individual needs. To further complicate matters, behavioral needs will change with age. The need for control of the environment by a 4-week old puppy will not be the same as for that same dog at 4 or 10 years of age. Pet owners should be reminded that their pets' needs will change over time and will need to be re-evaluated.

10.5.6 Discovering what creates or enhances positive emotions

Given the variability in the behavioral needs of animals and what little we know of how those needs are affected by experiences during development and later, one of the most important things that caretakers can do is to continually be aware of what their pets find rewarding and what they find aversive. Steps can then be taken to facilitate the former and diminish the latter. That can be best achieved by carefully observing – and understanding – the animal's body language associated with positive and negative emotional states.

Another way to determine what pets find reinforcing is by giving the animal choices, that is, doing informal preference tests to see which experiences, items, or events they prefer or actively choose over others. Would the family cat prefer the cat perch placed next to the window where he can look out, or in the corner of the living room where he can see what most of the family is doing? Placing the perch in each location for a few days and capturing the duration or frequency of use by the cat will give one indication of preference. A check sheet such as the one in Fig. 10.1 can help caretakers and pet professionals identify the

A Check Sheet for Making Your Pet Happy (Giving Her a Good Quality of Life)

How to use this Check Sheet

Providing a good quality of life (QOL) for your pets is more than just providing food, water and shelter, good health care, and protecting them from undue fear and stress. QOL also means providing for their behavioral needs for exercise, mental and social stimulation, opportunities to control parts of their environment and having safe, pleasant places to rest and sleep. It also means trying to maximize their opportunities to obtain rewards and experience pleasant emotions while trying to minimize the opportunities for unpleasant emotions such as pain, anxiety, uncertainty, and fear. To do this, the first steps are to recognize and attend to the emotions your pets are experiencing. Try to review this check sheet for your pets every few months, because their behaviors and likes and dislikes may change as they age, as they acquire new life experiences, and even when their physical surroundings change from season to season or if you move. If you're having trouble completing this check sheet, discuss it with the pet professional who gave it to you.

	Can you recognize the behaviors and postures associated with these emotions in your pet? Write down what they are for your pet. (think about what your pet looks like and what she does)
	_ Happiness
	Contentedness
	_ Sadness _ Depression
	_ Fear or Anxiety
	If you're not sure, talk to the professional that gave you this list about how to read the emotions in your pet.
	What activities or situations make your pet happy or give her joy? Make a list. It might be playing fetch or chasing a toy, for example. How often do you provide these for your pet?
	What objects, activities or situations make your pet contented or relaxed and tranquil? Examples might be napping in the sun or sleeping with you. How often do you provide these for your pet?
	How are you meeting your pet's need for regular exercise? _ Describe what you do
	How are you meeting your pet's need for mental stimulation? _ Describe what you do
	How are you meeting your pet's need for pleasant social contact with other animals and people? Describe what you do.
	How are you meeting your pet's need to express species-typical behavior such as investigation, scratching, digging or chewing? _ Describe what you do.
Fig	. 10.1. A check sheet for making your pet happy (continued on next page).

having ways to ask you for treats, walks or pets? Describe what you do.
How are you meeting your pet's need for safe, comfortable rest and sleep spots? _ Where are they?
How are you meeting your pet's needs to avoid, escape or minimize things or experiences that cause pain, fea threats or discomfort? (such as pesky children, fireworks or confinement to a small crate) Describe what you do.
Do you provide a reasonably predictable environment for your pet? (Such as having consistent rules for her to follow, consistent times for feeding, play and exercise) Describe what you do.

Fig. 10.1. Continued.

emotions of the animals in their care and determine if they are meeting the behavioral needs of the animals.

Creating an environment that is largely predictable, but with 'pleasant surprises' from time to time, will probably be sufficient for many animals. Feeding times, play and exercise times, and bedtime should be fairly consistent, but extra walks on occasion, a new puzzle toy, or a short ride in the car with the family may break up routines and create more positive emotions. Monitoring the animal's emotional responses to these unpredictable surprises will help the caretaker identify the ones that are pleasant and the ones that are not.

Giving pets choices in other ways may help give them a better sense of control, especially with experiences that are aversive. Caretakers should avoid forcing the animal to experience things that are clearly aversive, except when it is necessary for the well-being of the animal or others. Dogs should not be allowed to choose not to make a necessary visit the veterinarian or groomer, for example. But many times the emotional valence of currently aversive events can be changed so that they become at least more tolerable and maybe even enjoyable. Experienced behavior consultants and trainers can accomplish these changes with behavior modification techniques such as counterconditioning and desensitization.

10.5.7 The limits to giving choices

Giving animals control and choices in their lives, especially over aversive conditions, is important to

helping them achieve good mental health. However, this approach has its limits, because animals (and people) do not always make the best choices for their long-term mental and physical health or take into consideration the consequences of their choices on others (McMillan, 2002). Some animals will eat to the point of obesity if allowed to do so, shortening their lives and limiting their opportunities to generate more positive emotions. Some choices by animals may create problems for caretakers or others in the community. For example, dogs who chase bicycles and cars cannot be allowed to exercise this choice because of the danger it presents to others. Accordingly, giving animals control to make their own choices should always involve a weighing of the effects of those choices on the animal's short-term well-being against the animal's long-term well-being and the well-being of others.

10.6 How Professionals Can Help

There are many opportunities for pet professionals to provide expert advice to pet caretakers about expectations, normal behavior, behavioral needs, and recognizing emotional states to pet parents. This sort of education should be part of many, if not all, points of contact between pet caretakers and pet professionals. Ideally, veterinarians and technicians, behavioral consultants, trainers, breeders, groomers, day care and boarding kennel staff, shelters, breeders, and more

should be well educated on these topics, but misinformation is still far too common.

10.6.1 The benefits of caretaker education, environmental enrichment, and resilience training

One source of education for caretakers and training and enrichment for their pets is puppy classes and kitten kindergartens. These are classes that are conducted with groups of adolescent puppies or kittens to provide them with controlled, safe, and positive exposures to stimuli they are likely to experience throughout their lives. Examples include vacuum cleaners, unfamiliar people, and conspecifics. Many of these classes also teach basic manners for dogs such as walking on a loose leash or sitting on cue. Most of them also provide education for new caretakers in basic pet behavior and care. One study of the effectiveness of puppy classes found short-term improvement in cued learning (such as sit or stay) but no long-term effects on handling or in responsiveness to novel stimuli or to new social situations (Seksel et al., 1999). A survey by Cutler et al. (2017) found that puppies that attended classes were reported to have fewer fears than those that did not attend classes.

Another way to provide information to caretakers is during veterinary visits or in separate classes for caretakers. One study by Gazzano *et al.* (2008b) found that new dog owners that attended an expert lecture on dog behavior and care reported reduced incidences of aggression, barking, house soiling, and begging for food when surveyed 1 year later.

Enrichment and resilience training hold promise in preventing or attenuating the effects of early deficits or even boosting the quality of life for some animals over the 'normal' environments in which they are usually raised. Herron and Buffington (2010) have recommended that cats living exclusively indoors be provided with environmental enrichments that address many of the behavioral needs discussed here. While there is little direct empirical evidence to support their specific recommendations, addressing the behavioral needs of animals living in restricted environments is especially important. Environmental enrichment may even help older animals. Sampedro-Piquero et al. (2016) found exposing very old rats to 2 months of an enriched environment reduced their fear in a novel enclosure.

Resilience training has not become a common procedure in the care of companion animals. However, it is gaining popularity in human psychotherapy and has been the subject of research in human and nonhuman animals for a number of years. Liu et al. (2018, p.326) pointed out that, 'The term "resilience" refers to the ability to adapt successfully to stress, trauma and adversity, enabling individuals to avoid stress-induced mental disorders such as depression, posttraumatic stress disorder (PTSD) and anxiety.' The study by Chaby et al. (2015) described in Section 10.4.7 demonstrated how adolescent exposure to distressing conditions improved their foraging performance under different distressing situations later in life. Much research remains to be done to show the applicability and effectiveness of such treatments to companion animals.

At this point in time animal caretakers should be cautious in implementing enrichment programs or resilience training. The differences among the studies cited here are multiple, including differences in species and breeds, the nature of the early experiences, their intensity, duration, and timing during development, how and when the animals are tested, and the specific measures taken. Puppy and kitten classes may be beneficial to pets and owners, but expert information may be just as helpful. It is not yet clear precisely which elements of enrichment, resilience training, and puppy/kitten classes are beneficial and which are not. More research is needed to sort it all out.

10.6.2 Prevention of behavior problems

Just as prevention of disease can improve physical health, prevention of behavior problems can improve mental health. We have discussed already the roles of genetics and early experiences in influencing mental health. We have also talked about the information animal caretakers need to prevent and correct poor mental health including having realistic expectations, having the ability to recognize the emotional states of their animals, and addressing the behavioral needs of their animals.

But there are specific pet behaviors and life changes that create problems for caretakers and reduce the mental health of the animals. It is possible to prevent many of these problems with the right information when these behaviors occur or when life changes are expected in a family. Preparing pets for the arrival of a new baby, or creating a plan

D.Q. Estep and S. Hetts

Informational Topics on Dog and Cat Behavior

Dog Behavior

Introducing a Family Dog to a New Baby Introducing a Family Dog to a New Dog Introducing a Family Dog to a New Cat Dog Threats or Aggression to People Dog Threats or Aggression to Other Dogs Dog Threats or Aggression to Other Animals Helping Children and Dogs Get Along □ Excessive Barking Destructive Behavior Fears and Phobias in Dogs The Dog That Cannot Be Left Alone House Training Dogs **Elimination Behavior Problems** Socializing Dogs ☐ Using Rewards (Positive Reinforcement) To Change Behavior Cautions on Using Punishment to Change Behavior Reading Your Dog's Emotions Dogs That are Intolerant of Handling Dogs That Become Overly Excited Guidelines For Choosing a Dog Trainer **Cat Behavior** Introducing a New Cat to Family Cats Introducing a New Cat to Family Dogs Cat Threats or Aggression to People Cat Threats or Aggression to Other Cats Cat Aggression to Other Animals Helping Children and Cats Get Along □ Cat Excessive Vocalizations Cat Destructive Behavior Cat Elimination Behavior Problems Socializing Cats ☐ Using Rewards (Positive Reinforcement) to Change Behavior Cautions on Using Punishment to Change Behavior Reading Your Cat's Emotions Cats That are Intolerant of Handling

Fig. 10.2. Informational topics on dog and cat behavior.

to help them adjust to a move to a new home can prevent fear, aggression, house soiling, or other negative behavioral reactions to these events.

Research suggests that expert advice provided to new pet parents can reduce the incidence of some kinds of behavior problems that can harm human-animal relationships and have a negative influence on the mental health of animals (Gazzano *et al.*, 2008b). For example, even 5 minutes of education about housetraining techniques for owners adopting a dog from a shelter significantly increased house-training success and reduced the use of punishment (Herron *et al.*, 2007). This proactive approach is

preferable to reactively having to solve problems that have already had a detrimental effect on the pet's mental health and weakened the family's bond with the pet.

A list of informational topics related to dog and cat behavior that may help prevent behavior problems can be found in Fig. 10.2. Hetts *et al.* (2004, 2005) have urged the creation of educational handouts for caretakers that provide protocols or strategies to help prevent specific behavior problems. Such educational materials can be found in veterinary behavior textbooks such as Landsberg *et al.* (2013) and on professional websites such as the ASPCA

Pet Care pages (https://www.aspca.org/pet-care) and the University of California, Davis, College of Veterinary Medicine website (www.vetmed.ucdavis.edu/hospital/animal-health-topics#B).

10.6.3 Resolving behavior problems

Resolving animal behavior problems and life change issues such as those listed in Fig. 10.2 can help improve the mental health of companion animals. Routine assessments of behavior and mental health of animals by veterinarians at all nonemergency appointments can help to identify problems early before they become serious. Hetts et al. (2004) discuss protocols for such assessments, and examples of brief behavior screens can be found online at AnimalBehaviorAssociates.com (dog behavior screen http://animalbehaviorassociates. com/quiz_dog.htm; cat behavior screen http://animalbehaviorassociates.com/quiz_cat.htm). Once problems have been identified, providing behavior consulting services at the veterinary hospital or by referring the client to a qualified animal behavior consultant should be made.

Some problems can be addressed with environmental changes, such as changing the characteristics of a litterbox to address a cat's house soiling behavior. In other cases, more complex behavior modification procedures are needed to change behavior, such as counterconditioning and desensitization when a dog is afraid of children. Psychoactive medications will also be helpful in some of these cases, such as serious fears and aggression problems. Textbooks such as Landsberg *et al.* (2013) provide details concerning treatment of specific behavior problems.

10.7 Concluding Remarks

In summary, our knowledge of the development of behavior and well-being states, the interactions of the different variables influencing them, and the wide inter-individual variation is too incomplete to permit the formulation of highly specific rules or protocols for fostering the mental health of animals. The recommendations in this chapter have therefore been general in nature. And because even general recommendations will vary between individual animals, caretakers will need to adjust their care to account for these individual differences.

Genetic predispositions and experiences early in life can have profound effects on later behavior and mental health. Many kinds of aversive experiences in early life as well as restriction of some kinds of experiences have deleterious effects on behavior and, we assume, on mental health. Some kinds of extra or enriching experiences seem to promote more healthy behavior and presumably improve mental health.

To improve the mental health of animals regardless of age, caretakers should maximize their pleasant experiences and minimize unpleasant ones. To do that successfully, caretakers must understand the normal behavior of their animals, especially body language, so that they can recognize positive and negative emotional states. Caretakers must also understand the behavioral needs of their animal so that they can meet those needs and maximize positive emotions.

Meeting behavioral needs is closely tied to environmental enrichment. Some enrichment experiences may even attenuate the effects of aversive experiences or limited experiences during development. Training that promotes resilience to common life challenges may also promote better mental health.

Behavior problems can be the result of needs not being met, or when animals use behaviors that are unacceptable to people in order to get their needs met. Consequently, preventing and resolving problems have great potential to improve mental health. The earlier problems, or warning signs of potential problems, are identified, the sooner intervention and even prevention can occur. Behavior screenings, much like depression screening questionnaires now used by a variety of health care providers in human medicine from physicians to physical therapists, should become the norm. They can be administered by veterinarians, groomers, trainers, and any other appropriately trained professionals. Preventing and treating behavior, or mental health, problems is just as important as preventing and treating physical health problems.

In order to accomplish all of the above tasks, pet parents and pet professionals can obtain help and information from experts well-versed in the scientific principles of animal behavior. It is essential for animal well-being that this evidence-based approach come to replace reliance on enduring myths and misinformation that in the Internet age have become far too easily spread.

D.Q. Estep and S. Hetts

10.8 References

- Appleby, D.L., Bradshaw, J.W.S., Casey, R.A. (2002) Relationship between aggressive and avoidance behaviour by dogs and their experience in the first six months of life. *Veterinary Record* 150, 434–438. http://dx.doi.org/10.1136/vr.150.14.434.
- Bradshaw, J.W.S., Casey, R.A., Brown, S.L. (2012) *The Behaviour of the Domestic Cat*, 2nd edn. CAB International, Boston, Massachusetts, USA. http://dx.doi.org/10.1079/9781845939922.0000.
- Buwalda, B., Geerdink, M., Vidal, J., Koolhaas, J.M. (2011) Social behavior and social stress in adolescence: A focus on animal models. *Neuroscience and Biobehavioral Reviews* 35, 1713–1721. http://dx.doi.org/10.1016/j.neubiorev.2010.10.004.
- Cairns, R.B. and Werboff, J. (1967) Behavior development in the dog: An interspecific analysis. *Science* 158, 1070–1072. http://dx.doi.org/10.1126/science. 158.3804.1070.
- Chaby, L.E., Sheriff, M.J., Hirrlinger, A.M., Braithwaite, V.A. (2015) Does early stress prepare individuals for a stressful future? Stress during adolescence improves foraging under threat. *Animal Behaviour* 105, 37–45. http://doi.org/10.1016/j.anbehav.2015.03.028.
- Chaloupkova, H., Svobodova, I., Vapenik, P., Bartos, L. (2018) Increased resistance to sudden noise by audio stimulation during early ontogeny in German shepherd puppies. *PLoS ONE* 13(5), e0196553. https:// doi.org/10.1371/journal.pone.0196553.
- Clark, J.D., Rager, D.R., Calpin, J.P. (1997) Animal well-being. I. General considerations. *Laboratory Animal Science* 47, 564–570.
- Cutler, J.H., Coe, J.B., Niel, L. (2017) Puppy socialization practices of a sample of dog owners from across Canada and the United States. *Journal of the American Veterinary Medical Association* 251, 1415–1423. http://dx.doi.org/10.2460/javma.251.12.1415
- de Azevedo, M.S., de Souza, F.L., Fagundes Donadio, M.V., Lucion, A.B., Giovenardi, M. (2010) Interventions in the neonatal environment in rats and their relationship to behavior in adulthood and maternal behavior. *Psychology & Neuroscience* 3, 73–78. http://dx.doi. org/10.3922/j.psns.2010.1.009.
- Dietz, L., Arnold, A-M.K., Goerlich-Jansson, V.C., Vinke, C.M. (2018) The importance of early life experiences for the development of behavioural disorders in domestic dogs. *Behaviour* 155, 83–114. http://dx.doi. org/10.1163/1568539X-00003486.
- Duncan, I.J.H. and Fraser, D. (1997) Understanding animal welfare. In: Appleby, M.C. and Hughes, B.O. (eds.) *Animal Welfare*. CAB International, New York, USA, pp. 19–31.
- Dykman, R.A., Murphree, O.D., Reese, W.G. (1979) Familial anthropophobia in pointer dogs? Archives of General Psychiatry 36, 988–983. http://dx.doi.org/ 10.1001/archpsyc.1979.01780090074008.

- Fox, M.W. (1978) The Dog Its Domestication and Behavior. Krieger Publishing Company, Malabar, Florida, USA, pp. 189–196.
- Foyer, P., Wilsson, E., Jensen, P. (2016) Levels of maternal care in dogs affect adult offspring temperament. *Nature.com/Scientific Reports* 6, 19253. http:// dx.doi.org/10.1038/srep19253.
- Francis, D.D., Diorio, J., Plotsky, P.M., Meaney, M.J. (2002) Environmental enrichment reverses the effects of maternal separation on stress reactivity. *The Journal of Neuroscience* 22, 7840–7843. http://dx.doi.org/10.1523/JNEUROSCI.22-18-07840.2002.
- Freedman, D.G., King, J.A., Elliot, O. (1961) Critical period in the social development of dogs. *Science* 133, 1016–1017. http://doi.org/10.1126/science.133. 3457.1016.
- Gazzano, A., Mariti, C., Notari, L., Sighieri, C., McBride, E.A. (2008a) Effects of early gentling and early environment on emotional development of puppies. *Applied Animal Behavior Science* 110, 294–304. http://dx.doi.org/10.1016/j.applanim.2007.05.007.
- Gazzano, A., Mariti, C., Alvares, S., Cozzi, A., Tognetti, R., Sighieri, C. (2008b) The prevention of undesirable behaviors in dogs: Effectiveness of veterinary behaviorists' advice given to puppy owners. *Journal of Veterinary Behavior* 3, 125–133. http://dx.doi.org/ 10.1016/j.jveb.2008.04.004.
- Guardini, G., Mariti, C., Bowen, J., Fatjó, J., Ruzzante, S., et al. (2016) Influence of morning maternal care on the behavioural responses of 8-week-old beagle puppies to new environmental and social stimuli. Applied Animal Behaviour Science 181, 137–144. http://dx.doi.org/10.1016/j.applanim.2016.05.006.
- Herron, M.E. and Buffington, C.A. (2010) Environmental enrichment for indoor cats. *Compendium for Continuing Veterinary Education* 32, E4. https://www.ncbi.nlm.nih.gov/pmc/PMC3922041.
- Herron, M.E., Lord, L.K., Hill, L.N., Reisner, I.R. (2007) Effects of preadoption counseling for owners on house-training success among dogs acquired from shelters. *Journal of the American Veterinary Medical Association* 231, 558–562. http://dx.doi.org/10.2460/ javma.231.4.558.
- Hetts, S., Estep, D., Marder, A.R. (2005) Psychological well-being in animals. In: McMillan, F.D. (ed.) *Mental Health and Well-Being in Animals*. Blackwell Publishing Company, Ames, Iowa, USA, pp. 211–220. http://dx.doi.org/10.1002/9780470384947.ch15.
- Hetts, S., Heinke, M.L., Estep, D.Q. (2004) Behavior wellness concepts for general veterinary practice. *Journal of the American Veterinary Medical Association* 225, 506–513. http://dx.doi.org/10.2460/ javma.2004.225.506.
- Jokinen, O., Appleby, D., Sandbacka-Saxén, S., Appleby, T., Valros, A. (2017) Homing age influences the prevalence of aggressive and avoidance-related behaviour in adult dogs. Applied Animal Behaviour

- Science 195, 87–92. http://dx.doi.org/10.1016/j.applanim.2017.06.003.
- Karsh, E.B. (1983) The effects of early handling on the development of social bonds between cats and people. In: Katcher, A.H. and Beck, A.M. (eds.) New Perspectives on Our Lives With Companion Animals, University of Pennsylvania Press, Philadelphia, Pennsylvania, USA, pp. 22–28.
- Karsh, E.B. and Turner, D.C. (1988) The human cat relationship. In: Turner, D.C. and Bateson, P. (eds.) *The Domestic Cat: The Biology of Its Behaviour*, 1st edn. Cambridge University Press, New York, USA, pp. 159–177.
- Kim-Cohen, J., Caspi, A., Taylor, A., Williams, B., Newcombe, R., et al. (2006) MAOA, maltreatment, and gene-environment interaction predicting children's mental health: New evidence and a meta-analysis. Molecular Psychiatry 11, 903–913. http://dx.doi. org/10.1038/si.mp.4001851.
- Landsberg, G., Hunthausen, W., Ackerman, L. (2013) Behavior Problems of the Dog and Cat, 3rd edn. Saunders Elsevier, New York, USA, pp. 385–413.
- Liu, H., Zhang, C., Ji, Y., Yang, L. (2018) Biological and psychological perspectives of resilience: Is it possible to improve stress resistance? Frontiers In Human Neuroscience 12, 326. http://dx.doi.org/10.3389/ fnhum.2018.00326.
- Mariti, C., Gazzano, A., Moore, J.L., Baragli, P., Chelli, L., et al. (2012) Perception of dogs' stress by their owners. *Journal of Veterinary Behavior* 7, 213–219. http://dx.doi.org/10.1016/j.jveb.2011.09.004.
- McCune, S. (1995) The impact of paternity and early socialization on the development of cats' behaviour to people and novel objects. *Applied Animal Behaviour Science* 45, 109–124. http://dx.doi.org/10.1016/ 0168-1591(95)00603-P.
- McEwen, B.S. (2000) The neurobiology of stress: From serendipity to clinical relevance. *Brain Research* 886, 172–189. https://doi.org/10.1016/S0006-8993(00) 02950-4.
- McMillan, F.D. (2000) Quality of life in animals. *Journal of the American Veterinary Medical Association* 216, 1904–1910. http://dx.doi.org/10.2460/javma.2000. 216.1904.
- McMillan, F.D. (2002) Development of a mental wellness program for animals. *Journal of the American Veterinary Medical Association* 220, 965–972. http://dx.doi.org/10.2460/javma.2002.220.965.
- McMillan, F.D. (2005) Stress, distress, and emotion: Distinctions and implications for mental well-being. In: McMillan, F.D. (ed.) *Mental Health and Well-Being in Animals*. Blackwell Publishing Company, Ames, Iowa, USA, pp. 93–111.
- McMillan, F.D. (2017) Behavioral and psychological outcomes for dogs sold as puppies through pet stores and/or born in commercial breeding establishments:

- Current knowledge and putative causes. *Journal of Veterinary Behavior* 19, 14–26. http://dx.doi.org/10.1016/j.jveb.2017.01.001.
- Mills, A.D., Beilharz, R.G., Hocking, P.M. (1997) Genetic selection. In: Appleby, M.C. and Hughes, B.O. (eds.) Animal Welfare. CAB International, New York, USA, pp. 219–231.
- Mineka, S. and Hendersen, R.W. (1985) Controllability and predictability in acquired motivation. *Annual Review of Psychology* 36, 495–529. https://doi. org/10.1146/annurev.ps.36.020185.002431.
- Morley-Fletcher, S., Rea, M., Maccari, S., Laviola, G. (2003). Environmental enrichment during adolescence reverses the effects of prenatal stress on play behaviour and HPA axis reactivity in rats. *European Journal of Neuroscience* 18, 3367–3374. https://doi.org/10.1111/j.1460-9568.2003.03070.x.
- Morrow, M., Ottobre, J., Ottobre, A., Neville, P., St-Pierre, N., et al. (2015) Breed-dependent differences in the onset of fear-related avoidance behavior in puppies. Journal of Veterinary Behavior 10, 286–294. http://dx.doi.org/10.1016/j.jveb.2015.03.002.
- Murphree, O.D., Dykman, R.A., Peters, J.E. (1967) Genetically-determined abnormal behavior in dogs. Results of behavioral tests. *Conditioned Reflex* 2, 199–205.
- Pierantoni, L., Albertini, M., Pirrone, F. (2011) Prevalence of owner-reported behaviours in dogs separated from the litter at two different ages. *Veterinary Record* 169, 468–473. http://dx.doi.org/10.1136/vr.d4967.
- Plomin, R., DeFries, J.C., McClearn G.E., McGuffin, P. (2008) *Behavioral Genetics*, 5th edn. McMillan Publishers, New York, New York, USA.
- Poole, T.B. (1992) The nature and evolution of behavioural needs in mammals. *Animal Welfare* 1, 203-220. https://www.ingentaconnect.com/content/ufaw/aw/1992/00000001/00000003/art00006.
- Sampedro-Piquero, P., Castilla-Ortega, E., Zancada-Menendez, C., Santín, L.J., Begega, A. (2016) Environmental enrichment as a therapeutic avenue for anxiety in aged Wistar rats: Effect on cat odor exposition and GABAergic interneurons. *Neuroscience* 330, 17–25. https://doi.org/10.1016/j.neuroscience. 2016.05.032.
- Scott, J.P. and Fuller, J.L. (1965) Genetics and Social Behavior of the Dog. University of Chicago Press, Chicago, Illinois, USA, pp. 84–116.
- Seksel, K., Mazurski, E.J., Taylor, A. (1999) Puppy socialisation programs: Short and long term behavioural effects. Applied Animal Behaviour Science 62, 335–349. http://dx.doi.org/10.1016/S0168-1591(98) 00232-9.
- Serpell, J., Duffy, D.L., Jagoe, J.A. (2017) Becoming a dog: Early experience and the development of behavior. In: Serpell, J. (ed.) *The Domestic Dog. Its Evolution, Behavior and Interactions with People*, 2nd edn. Cambridge University Press, Cambridge, UK, pp. 93–117.

138 D.Q. Estep and S. Hetts

- Slabbert, J.M. and Rasa, O.A. (1993) The effect of early separation from the mother on pups in bonding to humans and pup health. *Journal of the South African Veterinary Association* 64, 4–8.
- Tiira, K. and Lohi, H. (2015) Early life experiences and exercise associate with canine anxieties. *PLoS ONE* 10(11), e0141907. https://doi.org/10.1371/journal.pone.0141907.
- Vaterlaws-Whiteside, H. and Hartmann, A. (2017) Improving puppy behavior using a new standardized socialization program. *Applied Animal Behaviour Science* 197, 55–61. http://dx.doi.org/10.1016/j.applanim.2017.08.003.
- Wakshlak, A. and Weinstock, M. (1990) Neonatal handling reverses behavioral abnormalities induced in rats by prenatal stress. *Physiology & Behavior* 48, 289–292. http://dx.doi.org/10.1016/0031-9384(90)90315-U.

- Wan, M., Bolger, N., Champagne, F.A. (2012) Human perception of fear in dogs varies according to experience with dogs. *PLoS ONE* 7(12), e51775. https:// doi.org/10.1371/journal.pone.0051775.
- Weinstock, M. (2008) The long-term behavioural consequences of prenatal stress. Neuroscience and Biobehavioral Reviews 32, 1073–1086. http://dx.doi.org/10.1016/j.neubiorev.2008.03.002.
- Wilson, M., Warren, J.M, Abbott, L. (1965) Infantile stimulation, activity and learning in cats. *Child Development* 36, 843–853. http://dx.doi.org/10.1111/j.1467-8624. 1965.tb05343.x.
- Wormald, D., Lawrence, A.J., Carter, G., Fisher, A.D. (2016) Analysis of correlations between early social exposure and reported aggression in the dog. *Journal* of Veterinary Behavior 15, 31–36. http://dx.doi.org/ 10.1016/j.jveb.2016.08.071.

1 1 What Is Distress? A Complex Answer to a Simple Question

FRANKLIN D. McMILLAN

Best Friends Animal Society, Kanab, Utah, USA

Few concepts exhibit a wider disparity between their importance for well-being and their definitional clarity than distress. Despite its frequent use among researchers and scholars, the term is not only encumbered with a variety of meanings, but many of the meanings directly contradict one another. For example, distress is often used both interchangeably with stress (National Research Council, 2008; Overall, 2019) and distinguished from stress (Committee on Pain and Distress in Laboratory Animals, 1992; Koolhaas et al., 2011), is commonly equated to suffering (National Research Council, 2008; Ledger and Mellor, 2018) but is also distinguished from suffering (DeGrazia, 1996), and has been frequently conceived as something caused by stress (Moberg, 1987) but also considered to be a form of stress (Moberg, 1987).

Historically, few attempts have been made to understand distress on a systematic and scientific basis (Committee on Pain and Distress in Laboratory Animals, 1992) and there is currently no universally accepted definition of distress in any species, nonhuman animal (hereafter animal) or human (Clark, 2007; National Research Council, 2008). A standard and generally representative dictionary definition of distress is 'extreme anxiety, sorrow, or pain' (Oxford Dictionaries, 2019a), and numerous medical dictionaries define distress as 'mental or physical anguish or suffering' (e.g., Dorland's Medical Dictionary for Health Consumers, 2007; Saunders Comprehensive Veterinary Dictionary, 2007; The American Heritage Medical Dictionary, 2007).

Descriptions are offered for various characteristics of distress, such as its causes, circumstances surrounding its occurrence, and manifestations. However, in so doing current definitions often fail to distinguish 'what *is* distress' from 'what *indicates* distress'. A useful analogy here is gravity. The force

of gravity is well-described in terms of the physics and mathematics of its actions between two objects (i.e., it is directly proportional to the product of their masses and inversely proportional to the square of the distance between them), how it explains the orbits of celestial bodies, and its contribution to the nature of black holes. In addition, gravity can be measured with extreme accuracy by determining the strength of attraction between two bodies. But none of this answers the question, what *is* gravity? This is the current status of understanding distress.

11.1 Current Conceptualizations of Distress

The foremost challenge in developing a unified understanding of distress is the variation in the ways that the concept is characterized. The following are the most common, but not necessarily the only, conceptualizations of distress.

11.1.1 Distress is extreme unpleasantness

This view is in line with the Oxford Dictionaries (2019a) definition, in which distress is defined with terms indicating an unpleasant experience of substantial severity. The key element here is that of *intensity*, where intensity refers to magnitude and/or duration of the adversity, or, stated differently, the 'quantity' of adversity. This conceptualization of distress involves a *threshold* of unpleasantness, above which is regarded as distress and below which is not. This would exclude minor aversive experiences, such as a twinge of anxiety, a slight pain, a hint of sadness, or minor thirst. This does not mean that there cannot be mild distress, just that even the mild forms exceed the threshold.

This view of distress can be found in scientific and daily discourse. This is the view of distress that is most consistent with the notion that distress and suffering are the same thing (to be discussed in Section 11.7).

11.1.2 Distress is any unpleasantness

Distress has also been commonly conceived as unpleasantness of any intensity or severity. In common usage, people often speak of things such as 'watching the news these days is distressing' and 'I don't want to cause you any distress, so I'll give this assignment to someone else'. This view of distress is also used in scientific fields; for example, Mosby's Medical Dictionary (2009) defines distress – without reference to intensity – as 'an emotional or physical state of pain, sorrow, misery, suffering, or discomfort'. Tomkins (1963) used distress to indicate an affective experience of not greater aversiveness ('toxicity'), but rather to be a relatively lower intensity affect. In the animal literature, Rushen (1990, p.8) wrote that 'Distress, or aversion, as measured by aversion learning techniques, can be considered as the common, negative emotional component that underlies a diverse range of more specific mental states such as fear, pain, anxiety and frustration', and Russell and Burch (1959) stated that 'any degree' of visceral ill health may be assumed to entail a measurable amount of distress.

11.1.3 Distress is any severity of certain mental disorders

This conceptualization of distress is a more specialized version of the previous view and the one used most often in the context of human health, psychology, and well-being. Here, the term (often spoken of as psychological distress) describes an array of types of psychopathology, of any severity. Cromby et al. (2013) uses the term distress 'to refer to just the same kinds of phenomena that textbooks of this kind usually call mental illness or psychopathology. We use distress to mean all of the different kinds of difficult or unusual experiences associated with the hundreds of psychiatric diagnoses currently employed.' Psychological distress is defined by some authors as depression and anxiety (e.g., Kessler, 1979; Mirowsky and Ross, 2003) and by others as also including other states such as burnout, irritability, worrying, problems concentrating, and, more broadly, psychological maladjustment and negative mental health states (Holahan and Moos, 1981; Veit and Ware, 1983; de Haes *et al.*, 1990; Dyrbye *et al.*, 2006).

11.1.4 Distress is a specific, discrete, or basic emotion

Distress has frequently been conceived of as a specific emotion. For example, Izard (1977) wrote that 'distress is the most common negative emotion' and that 'distress and sadness are generally considered synonymous'. This view is often expressed as a list in which distress is included as an emotion comparable to other specific emotions, such as Roseman *et al.* (1994) describing their experimental design with 'The emotions studied were fear, sadness, distress, frustration, disgust, dislike, anger, regret, guilt, and shame.'

11.2 Key Considerations in Conceptualizing Distress

Discussions of distress have involved several key issues; the following seem to be among the most fundamental for understanding the concept.

11.2.1 The issue of consciousness

On the basis of the intuitive or commonsense conceptualization, the experiential aspect comprises the very essence of distress, for which consciousness is clearly a requirement. This view is not recent; 60 years ago, Russell and Burch (1959) wrote that 'It is assumed that to be in a state of distress an animal must be in a certain state of consciousness, which may be eliminated by, for instance, deep general anesthesia.' More recently, the National Research Council (2008) similarly pointed out that distress could be prevented in laboratory animals by using a general anesthetic and Karas and Silverman (2014) stated that 'While under general anesthesia an animal cannot consciously perceive the presence of a negative state, and thus distress is prevented by loss of consciousness.'

However, some research has questioned the notion that conscious awareness is essential for distress. Schultheiss and Wirth (2018), for example, have noted that researchers in the fields of biopsychology, neuropsychology, psychopharmacology, and social psychology have reached the conclusion that consciousness may not be a necessary prerequisite

for goal-directed, reward-seeking behavior (the connection between distress and motivation will be addressed in Section 11.5).

11.2.2 The intensity/threshold question

As described above, two mutually exclusive conceptualizations of distress hinge on the question of whether or not distress involves intensity and a threshold of any kind. Clearly, distress being equated with any degree of unpleasantness makes the recognition (or diagnosis) of distress easier, as it is either present or not; no measurement is required to establish whether an intensity has reached a particular level. However, this presents its own problems, as exemplified by the array of empirical referents and 'distress scales' that have been developed and utilized in humans to determine whether individuals are experiencing psychological distress (reviewed by Ridner, 2004). The necessity of such testing attests to the peculiarity of a person being unaware that she is experiencing distress until informed by the person scoring the test.

11.2.3 The question of whether distress is anything more or different than intense negative affect¹ (NA): whether distress differs qualitatively or only quantitatively from less intense NA

The nature of distress can be thought of in two ways. The first is that distress is nothing more than intense NA; that is, distress differs quantitatively, but not qualitatively, from less intense NA. In this view, as NA - e.g., fear, nausea, pain, anxiety, loneliness - intensifies, we simply label the experience distress when it becomes highly aversive. An analogy here is the term discomfort. Discomfort has multiple definitions, but one common usage is as a description for any mild NA. A mild itch is a discomfort, as is the first sensation of a filling bladder, the feeling in one's buttocks from sitting too long in one position, the uneasiness of being in an eerie place, chapped lips, the bright sun as one exits a movie theater, and so on. Yet the discomfort here is not something in and of itself - it is simply a descriptive label applied to any mildly unpleasant feeling and the change in feeling is considered to be 'increasing discomfort' – staying simply a descriptor – as the intensity of the unpleasant affect grows. Distress may be the same thing with unpleasant feelings, so that 'increasing distress' is (and remains) strictly a descriptive label.

The second possible nature of distress is that it in some way differs qualitatively, not just quantitatively, from less intense NA. In this case, as pain or fear rises in intensity, a new experience is 'added onto' the intensifying NA (which, of course, remains present). An analogy here would be a simple alarm system. The type of threat and the affect it elicits (e.g., pain, fear, thirst, loneliness) remain the same, but have increased in magnitude whereby the animal is informed – by the 'added on' affective experience of distress – of a state of emergency and need for urgent action.

These two different natures of distress involve the threshold concept discussed above. We can reason that if there is no qualitative difference between distress and intense NA, then there is no threshold. Conversely, if there *is* a threshold then there *is* a qualitative difference, as something different than simply increasing intensity of NA emerges.

Related to this question is the idea that distress is severe stress. This is a common notion among the general public as well as the scientific community. For example, Moberg (1987) proclaimed in the simplest terms that the most severe form of stress is distress. This view is also expressed in language that describes stress becoming distress, such as in the National Research Council's (2008) report 'Recognition and Alleviation of Distress in Laboratory Animals', where mention is made of 'the transition of stress to distress', and when Wolfensohn *et al.* (2018) refer to the 'point where [stress] will develop into distress'.

There is evidence to challenge the idea that distress is severe stress. For example, it is possible for severe stress to occur without distress emerging. One example of this is in humans and animals rendered unconscious by general anesthesia. The stress response to surgery (specifically, the tissue trauma) is characterized by increased secretion of pituitary hormones and activation of the sympathetic nervous system. The increase in plasma concentrations of adrenocorticotropic hormone (ACTH) and cortisol can be measured within minutes of the start of surgery and, in general, the magnitude and duration of the response are proportional to the surgical injury (Desborough, 2000). More evidence of stress mechanisms in the (presumed) absence of consciousness is that pronounced physiological stress responses occur - (presumably) without distress - in many invertebrate species, including mollusks and insects

(Adamo, 2012). A second line of evidence is that in sentient animals there are potential threats to homeostasis, such as tumor growth, that will elicit stress responses even though the individual may never be conscious of and hence experience no distress from the threats (Carstens and Moberg, 2000).

11.3 Why is it Important to Clarify our Understanding of Distress?

The absence of a unified definition affects the evaluation of distress and its impact on individual well-being of, in particular, animals in veterinary, scientific, and legislative contexts (National Research Council, 2008). Even the most basic foundations of research are undermined by the polysemous nature of distress. For example, if two separate studies measured the number of times per day people reported experiencing distress (or researchers were identifying distress in animals), without clear definitions of distress there would be no way to tell if the studies were measuring the same thing. In addition, understanding how, when, and why distress arises and subsides is critical to developing methods to prevent its emergence and to facilitate its resolution.

11.4 Limitations of Current Research-based Operational Definitions

Scientific investigations of distress require operational definitions, i.e., definitions that prescribe measurable criteria. In humans this is frequently done by self-reports of experiencing distress; since these methods are unavailable in animals, measurable criteria have included pathological effects (Selye, 1974; Kopin et al., 1988; Clark et al., 1997) and abnormal behavior (Kopin et al., 1988; Clark et al., 1997). Before discussing operational definitions of distress appearing in the literature, some important points need to be made. Because operational definitions are trying to achieve something measurability – that is not (necessarily) the objective of 'regular' definitions, none of these definitions should be deemed 'right' or 'wrong'. Relatedly, scrutinizing the accuracy of operational definitions is fraught with challenges. Consider if an analysis were to suggest that operational definition A could not be true since distress could occur 'outside' this definition. A problem is immediately evident in the question, What definition of distress is one using to dispute A? If A defines distress using specific criteria, then distress is, by definition, that which meets these criteria. With that caveat in mind, let us look at some operational definitions.

11.4.1 Distress is the state that occurs when an individual's ability to cope or adapt to an aversive condition or event is exceeded

One of the most widely accepted themes regarding the nature of distress is that it is based on one's ability to cope or adapt, and that it emerges once this ability has been exceeded or overcome (Kitchen et al., 1987; Kopin et al., 1988; Committee on Pain and Distress in Laboratory Animals, 1992; Clark et al., 1997; Clark, 2007; National Research Council, 2008). Karas and Silverman (2014) encapsulated this concept in stating that 'When the effort required to adapt to some stressors, or the aversive nature of the stressor, increases and reaches a point where the animal fails to be able to adapt adequately, this is considered by some authors to represent distress.' A more specific example is evident where The National Research Council (2008) proposed that the distinguishing feature between stress and distress is that the latter reflects 'an animal's ability or inability to cope or adapt to changes in its immediate environment and experience'. Minor variations in wording place the emphasis on the inability to cope or adapt to stressors (Kitchen et al., 1987; Committee on Pain and Distress in Laboratory Animals, 1992; Clark et al., 1997; Clark, 2007; National Research Council, 2008; Karas and Silverman, 2014), the inability to maintain homeostasis (Clark et al., 1997; National Research Council, 2008) or adaptive equilibrium (Committee on Pain and Distress in Laboratory Animals, 1992), or that coping mechanisms are overwhelmed (Moberg, 2000; Clark, 2007).

Most problematic for the linking of distress with the inability to adapt is that this view conceptualizes distress exclusively as a failing/failed – a maladaptive – state, exemplified by the Committee on Pain and Distress in Laboratory Animals' (1992) statement: 'Stressors do not pose a threat to the animal as long as it can maintain an adaptive equilibrium. When that is no longer possible, the animal enters a state of distress, in which its behavior and physiology become maladaptive.' Similarly, Clark *et al.* (1997) stated that a maladaptive state of distress occurs when an animal fails to adapt, cope, habituate to a challenging stimulus, and 'Progression into the maladaptive state [of distress] may be due to a severe or prolonged stressor or

multiple cumulative stressful insults with deleterious effects on the animal's welfare.' This provides a logical explanation as to how the phrase 'leads to distress' has come to mean something exclusively bad.

There are several problems with the view that distress is the result of a failed or overwhelmed ability to cope or adapt, evident by examining the three main implications of this view: (i) if adaptation (or the more specific coping) is successful then distress will not be present; (ii) its converse, whenever distress is present the individual is failing (or has failed) to adapt; and (iii) distress cannot occur before adaptation processes have begun to fail. Current evidence seems able to discount all of these implications. Most importantly, distress and successful coping frequently coexist: distress is often present during fully successful adaptation or coping attempts (Committee on Pain and Distress in Laboratory Animals, 1992; Tiefenbacher et al., 2005; National Research Council, 2008). For example, during the course of an illness caused by an infection (such as the influenza virus) to which the body is successfully responding, there can be considerable distress (as anyone who has suffered a bad case of the flu can attest). If distress is (only) the result of failing adaptation, distress should not occur since adaptation is succeeding, albeit slowly. The same is true during the time that the body is successfully healing burned skin: distress from pain is present while the adaptation is proceeding (in fact, one of the main features of burn pain is that its duration often exceeds healing time [Latarjet and Choinère, 1995]).

11.4.2 Distress is the state that exists when stress responses lead to pathologic changes

Numerous literature discussions of distress have suggested that a reliable indicator of distress is the development of pathologic changes. For example, Carstens and Moberg (2000) stated that 'Certainly the presence of pathologies such as disease, self-mutilation, or death are obvious indicators of distress,' and the Committee on Pain and Distress in Laboratory Animals (1992) wrote that when pathologic changes, such as gastric ulcers, occur, it can be said that the animal is not only stressed, but distressed. However, upon scrutiny it becomes evident that pathology may not be a reliable indicator of distress. The most concise argument here can be stated as such: pathology can exist without distress and distress can exist without pathology.

First, disease processes may arise and progress wholly outside the individual's awareness. As noted by Karas and Silverman (2014): 'a poor physiologic state does not always mean that distress is present: an animal may have cancer or other disease for some time and not be "aware" or affected by its body's efforts or inability to cope and ... from the standpoint of health, it is not (yet) distressed'. The National Research Council (2008) made a similar observation, suggesting that it is possible for an animal to be in a state of poor health that does not impinge on its emotional state and that this condition may even last for some time without the animal's conscious awareness; the authors used the example of an animal having but being unaware of a life-threatening aneurysm and therefore have no experience of a negative emotional state.

Other types of evidence argue against the idea that distress is the state when pathology develops. One is that the 'development of pathology' is not at all a precise and recognizable event. For example, not all adverse stress-induced health changes become manifest immediately; pathologic changes may appear at a much later time in the individual's life. In addition, pathological changes may consist of an increased susceptibility to or risk for, as opposed to overt expression, of pathology. Evidence from studies of humans (reviewed by Fagundes et al., 2013; Miller et al., 2011) and animals (reviewed by Miller et al., 2011) indicates that early life adversity (ELA) shows strong correlations to the development of psychopathology later in life. For instance, several rodent and primate models of ELA, including those that model maternal separation or loss, abuse, neglect, and social deprivation, have demonstrated that these types of early stressful experiences are associated with long-term alterations in neuroendocrine responsiveness to stress, emotional and behavioral regulation, coping style, cognitive function, quality of social affiliations and relationships, and expression levels of nervous system genes shown to be associated with anxiety and mood disorders (Sanchez et al., 2001; Cohen et al., 2006). In humans, severe stress early in life, such as child abuse, increased the risk of anxiety and depressive mood disorders (Heim et al., 2002; Chapman et al., 2004; Shea et al., 2005) and of developing posttraumatic stress disorder (PTSD) in response to major stressors (Brewin et al., 2000) later in life. In all, there is consistent evidence linking early stress and later physical and mental health disorders in humans and animals, and that in animals this is a

causal link (Miller et al., 2011). The key point here is that if adverse health effects (pathology) are used to operationally define distress, delayed effects and increased risk of pathology would both require that the confirmation of current distress could only be made retrospectively. In such cases an individual enduring adversity could not be determined at present to be experiencing distress, even for humans assessing their own mental state. This raises the unusual possibility of a person currently enduring some form of adversity being asked 'Are you experiencing distress?' and the person responding, 'I don't know. I guess I'll find out when I'm older'.

11.4.3 Distress is the state that exists when adversity leads to abnormal and maladaptive behaviors

One of the most prominently proposed indicators of distress in animals is the occurrence of abnormal or atypical behavior. For example, the Committee on Pain and Distress in Laboratory Animals (1992) has written that 'When an animal is experiencing distress, maladaptive behaviors result, varying in range and severity with increasing distress' and that the appearance of such behaviors marks the point where distress arises.

However, this view also has difficulty standing up to scrutiny. First, as noted by the National Research Council (2008), it is unclear at this time whether any or all abnormal behaviors qualify as indicators of distress, and distress may not manifest itself with recognizable maladaptive behaviors. Second, not all abnormal behavior during severe adversity is pathological or maladaptive; some abnormal behaviors can (and often do) represent homeostatic processes of adapting to the stress (Committee on Pain and Distress in Laboratory Animals, 1992; Tiefenbacher et al., 2005; National Research Council, 2008). Research shows that in some humans and nonhuman primates, even more serious forms of abnormal and self-injurious behavior may function to reduce arousal (Tiefenbacher et al., 2005) and it has been suggested by those who favor the arousal reduction hypothesis as an explanation for stereotypic behavior that such behavior may serve to calm the animal and thereby avoid distress (Mason, 1991). For instance, in rhesus monkeys bouts of selfinjurious biting were associated with reduced indices of physiological stress (Novak et al., 2006) and several studies have demonstrated that some

individuals exhibiting a high degree of stereotypic behavior appear to cope better than nonstereotypic conspecifics (reviewed by the Committee on Pain and Distress in Laboratory Animals, 1992; Mason and Latham, 2004).

11.4.4 But is distress a negative, maladaptive, failed state?

The definitional characterization of distress as a maladaptive, failed state must be questioned. The evidence in the previous sections indicate that distress is not a uniformly failed state; animals (and people) can successfully cope and recover from this experience. Resolving this question comes by reconceptualizing distress as a state that can have either an adaptive (successful) outcome or a maladaptive (unsuccessful) outcome, to which we will return later.

But if it is a misconception to view distress as indicative of failure to cope and maladaptive outcomes, why did this view become so prominent? The explanation may be in the confusion surrounding the concurrence of events at the point when distress arises. As the intensity of unpleasantness increases in response to an aversive stimulus, the events that occur include abnormal behavior (e.g., extreme, forceful, frantic, disorganized, illogical, counterproductive, harmful, futile), pathological changes, an intensified physiological stress response, and impaired welfare (including the related concepts of well-being, quality of life, and happiness). The temporal relationship among these events gives the impression of causal correlations and the assumption that, for example, distress leads to abnormal behavior and/or a decrease in well-being. However, there is insufficient justification for these assumptions; for example, rather than being an effect of distress, abnormal behavior may emerge along with distress as a mechanism for coping with the distress, and the threatened well-being could arise independently where the co-occurring distress is the organism's response to the threat, i.e., the distress arises to help alleviate the threat to well-being. With the co-occurrence of distress and harm, it is easy to view distress as the cause of that harm, but once it is recognized that distress often has a successful outcome, then the co-existence of distress and harm is uncoupled and causality is no longer assumed to run from distress to the various adverse changes.

11.5 Homeostasis, Stress, and Distress

Deviations from homeostasis represent a threat to and reduced chances for fitness; hence, animals have evolved effective mechanisms for detecting and correcting such deviations (Panksepp, 1998). The CNS assesses the importance of stimuli to homeostasis and, for those stimuli representing a meaningful threat, organizes and initiates the responses necessary to maintain or restore biological equilibrium (Panksepp, 1998). It is now well recognized that defensive responses on the part of the organism cannot be random or generalized in type and intensity; rather, responses must be both specific and proportional to the stimulus or situation that elicits them (Selye, 1974; Rolls, 2000; National Research Council, 2008). For most threats, the simplest and frequently the most biologically cost-effective response for an animal is to alter its behavior in a way that alleviates the threat (e.g., scratch an itch, curl up when cold, move away from a source of heat, cough to clear an airway irritant, step away from a cliff edge). This may involve only the CNS and voluntary muscle activity, and there may be little or no sympathetic or glucocorticoid response (Moberg, 1985; Clark et al., 1997). When a threat is not alleviated by a specific but minor behavioral response, as when the disturbances are more intense and/or persistent, other behavioral, physiologic, and biochemical responses and arousal mechanisms are required to neutralize the threat: these are the stress responses (Clark et al., 1997).

Expanding on Selye's (1936) original distinction between selective (and normally adequate) responses to minor challenges and nonselective (emergency) responses to major challenges which can be termed stressors, Day (2005) suggested that stress is the body's multi-system response to any challenge that overwhelms, or is judged likely to overwhelm, selective homeostatic response mechanisms. A crucial point here is that when stimuli are aversive or otherwise threatening enough to activate a stress response, the primary defense mechanisms are assisted by, but not replaced by, the stress response.

11.6 Affect and Motivation as the Core Elements of Distress

Affective states are considered to be psychophysiological constructs that vary along three principal dimensions: valence, arousal, and motivational

intensity (Harmon-Jones et al., 2013). As expressed concisely by Schultheiss and Wirth (2018), 'Motivation is, at its very core, about affect ... [and] attaining a pleasurable incentive (reward) or at avoiding an aversive disincentive (punishment)' is its hallmark. Abundant evidence suggests that affective states are proximate mechanisms which serve as motivational guides to facilitate behavior that is, at the ultimate level, beneficial to reproductive fitness and to discourage behavior contrary to these goals (Bindra, 1978; Committee on Pain and Distress in Laboratory Animals, 1992; Barnard and Hurst, 1996; Panksepp, 1998, 2011; Duncan, 2004; Leknes and Tracey, 2008; Edwards, 2010; Harmon-Jones et al., 2012). Additionally, in general, the strength of motivation is correlated with the intensity of the affect, so that as the intensity of affect increases, so too does the intensity of motivation (MacDonald and Shaw, 2005; Leknes and Tracey, 2008; Webster, 2011). Together, these elements construct a function for distress that departs widely from the view of a failed, maladaptive state.

When primary responses are inadequate to address a homeostatic challenge, a stress response is activated. This mechanism, honed over millions of years of natural selection, is highly effective in restoring homeostasis; however, in some cases the stress response generates inadequate changes in the behavioral and physiologic homeostatic systems (National Research Council, 2008). When faced with the possibility that current coping methods are insufficient, the individual has four choices:

- 1. The individual could continue to do the same thing it has been doing. However, as Wechsler (1995) has pointed out, 'If an animal can neither escape from nor remove an aversive stimulus, it is not adaptive to repeat these coping strategies over and over again.' In this way, continuing current coping methods would have a high likelihood that in terms of adaptation, *insufficient* progresses to *failing* and then to *failed* (with some exceptions, as explained below).
- **2.** The individual could continue current coping efforts, but carry them out more forcefully ('try harder' [Crombez *et al.*, 2008]).
- **3.** The individual could do something different.
- 4. The individual could cease coping efforts, i.e., 'shut down', originally described by Engel and Schmale (1972) as the conservative-withdrawal response and characterized behaviorally primarily by immobility.

For choices 1 and 4, successful adaptation could be achieved, in essence, by waiting the stressor out. If the stressor abates, both strategies can pay off, and in the case of choice 4, the individual preserves resources in the process. Additionally, a successful outcome could result for both strategies if, while being carried out, habituation were to occur. For both choices, however, there is also substantial risk of a catastrophic outcome. Because of the high risk, only in extraordinary circumstances would it make evolutionary sense to use choices 1 or 4, leaving choices 2 and 3 as the most likely to be successful when coping is perceived to be insufficient and at risk of failing at the level of the stress responses. In selecting choice 2 (try harder) or 3 (do something different), a crucial need is motivation. The affect of the original response serves to alert the animal, focus attention, and motivate behavior (Panksepp, 1998). At the stage where defense systems are unable to adequately meet the demands created by the threat, a situation of different biological importance is reached (Broom, 2008). The motivational component in a potentially failing situation instills a determination in the individual's pursuit of the goal (in this case the alleviation of NA), which may historically have proven successful in overcoming obstacles and preventing the premature disengagement from a primary goal (Rothermund, 2006). All of this argues for requiring a higher degree of motivation - a motivation boost or amplification in order to initiate the more demanding efforts in the face of potential coping failure.

There have been relatively few specific mentions in the literature of behavior and distress consistent with a motivational function of distress to meet the objective of successful adaptation. Russell and Burch (1959) wrote that 'one of the best criteria for distress is that of serving as motivation', while Clark *et al.* (1997) wrote that avoiding distress is one of the main objectives motivating learning. Tomkins (1963) proposed that distress motivates the individual to take action necessary to reduce, remove the source of, or change his relationship to the cause of the distress; however, distress in Tomkins' view is an affect of relatively low aversiveness (Tomkins 1963, 1984).

This suggests that, in direct contrast to the view of distress as a failed, maladaptive state, it is instead a highly adaptive, 'rescue' process for an animal who perceives itself in grave danger. But because intensified affect is itself highly motivating, this still does not answer the fundamental question about the nature of distress: is distress merely an intense NA or something 'added to' the original affect; that is, as NA rises in intensity (recall that intensity consists of magnitude and/or duration), does this *become* distress or *elicit* distress? What it does do, however, is allow us to add a third possibility: that distress is the *amplification of* the primary NA.

In accordance with this view of distress, the following definition is proposed. Distress may be conceived of as a conscious, negatively valenced, intensified affective motivational state that occurs in response to a perception that current coping mechanisms (involving, in part, physiologic stress responses) are at risk of failing to alleviate the aversiveness of the current situation in a sufficient and timely manner.

11.7 Comparing Distress and Suffering

Suffering and distress are closely related concepts, and as mentioned at the beginning of this chapter, they have been distinguished by some authors (DeGrazia, 1996) while equated by others (National Research Council, 2008; Ledger and Mellor, 2018). When descriptions of the nature of suffering are examined it becomes evident that many attributes appear to apply very similarly to both suffering and distress (see Chapter 12, this volume, for an extended discussion on suffering in animals). Drawing from the (relatively scant) literature on the two concepts, a direct comparison can be made.

11.7.1 Definitions

Reflecting the challenge of describing subjective phenomena, only a few attempts have been made in the scientific literature at a definition for suffering. Barnard (2007) made note of this when he wrote that suffering 'is a putative negative subjective state that is rarely defined, either in terms of what it comprises or of where on a presumably sliding scale of negativity it lies'. Definitional elements of distress and suffering overlap extensively; within the general as well as scientific literature distress is commonly defined in terms of suffering (see Section 11.1.2), and suffering in terms of distress. For example, suffering is defined by Oxford Dictionaries (2019b) as 'The state of undergoing pain, distress, or hardship' and by physician Eric Cassell (2004) as 'the state of severe distress'. Philosopher David DeGrazia (1996) defined suffering as 'a highly unpleasant emotional state associated with

more-than-minimal pain or distress', adding that although suffering is not the same as distress, great distress is a form of suffering. Dawkins (1980, 1990, 2006) suggested that suffering refers to a wide range of intense and unpleasant subjective states of people or animals while emphasizing the intense nature of the unpleasantness, as have Ledger and Mellor (2018), who wrote that 'There are numerous negative subjective affects that animals are likely to experience where the impact of their character, intensity, and/or duration can be sufficiently aversive or extreme for them to be described in terms of suffering.' It seems difficult to find definitions of suffering that would not equally apply to distress, and vice versa.

11.7.2 Specific characteristics

Extreme unpleasantness and identifying a cut-off point

As noted in the above definitions and earlier discussion on distress, both suffering and distress are widely conceived as intensely unpleasant. Related to this, both concepts share the problem of determining what quantity or level of an unpleasant experience qualifies as the state in question, i.e., distress or suffering. Dawkins (1980) notes, for example, that not all unpleasant affect is a suffering and that a major difficulty with any definition of suffering is to decide how much (i.e., how intense, or how prolonged) of an unpleasant emotional state constitutes, or is associated with, suffering.

Function

The adaptive survival functions of distress-related NA were discussed earlier and prominently involve motivation, but also include an alert function as well as a focusing of attention on the threat (Panksepp, 1998). In addition, as the unpleasantness increases in intensity, these functions all correspondingly increase. In this way, the individual is increasingly compelled to focus on the threat and not on matters less relevant (at that moment) to survival (Panksepp, 1998). This functional description has long been applied to suffering. For example, as related by Dawkins (1980), in the late nineteenth century Spencer (1880)

saw disagreeable feelings of pain or other kinds of suffering as a sort of internal stimulus, causing the animal to move away and find some other environment. Animals that experienced suffering when they found themselves in conditions which were harmful to their well-being and took steps to find somewhere else, he said, would survive better than those that derived pleasure from the harmful environment and stayed in it.

Several authors have concurred with this strong view of the adaptiveness of suffering, adding that the capacity for suffering is a product of natural selection (Cabanac, 1979; Dawkins, 1980, 1990; Broom, 1986; Barnard and Hurst, 1996), helps to restore physiological deficits resulting from the animal's natural environment (Cabanac, 1979; Broom, 1986), enhances the animal's capacity to learn from past experience (Dawkins, 1980), and enables an animal to cope with the conflict and often eventually to resolve it (Olsson *et al.*, 2011).

The proposed alert function of suffering has been addressed by Barnard and Hurst (1996), who discussed suffering as a generalized subjective 'state of emergency' that is geared to avoiding deleterious circumstances. The motivation function as it specifically relates to the state of suffering has recently received increasing attention; Dawkins (1990, 2006) has been at the forefront of this discussion. The main premise of Dawkins' view is that animals often suffer in situations in which they are prevented from doing something that they are highly motivated to do (Dawkins, 1990). From the perspective of ultimate causes of behavior, suffering occurs when unpleasant subjective feelings are acute or continue for a long time as a result of the animal being unable to carry out the actions that would normally reduce risks to life and reproduction in those circumstances (Dawkins, 1990). Based on this hypothesized association between motivation and suffering, Dawkins has suggested that suffering may be measurable by using the intensity of motivation as a proxy. Such a quantification is made by measuring how hard an animal will work to obtain a particular outcome, and Dawkins (1990, 2006) contends that if the degree of work an animal will perform to obtain or to escape from something is as hard as or harder than it will work to obtain food, an essential for health and welfare, then we can presume that that effort stems from a motivation to alleviate a state so unpleasant as to constitute suffering. There appear to be limitations on the evolutionary value of suffering, however, as Broom (2008) noted when he wrote that extreme suffering is 'probably not adaptive'.

Eliciting affects retain their original character

As presented earlier, it appears that a rising intensity of NA at some point becomes associated with a state of distress while the specific NA itself remains present. This same process has been proposed for suffering. Ledger and Mellor (2018) wrote

note that when specific negative affects approach their extreme, they are not transformed into an experience of 'suffering'; rather, they retain their original character so that, for example, intense breathlessness continues to be experienced as breathlessness. The same is true for thirst, hunger, pain, nausea, anxiety, fear, panic, or depression, as these and all other such negative experiences also retain their individual character when they are present at high intensities.

Proposed causes

The proposed causes of distress and suffering are indistinguishable. For example, the major causes of suffering have been specified as physical injury, pain, disease, lack of water, lack of food, temperatures that are too low or too high, not enough space to move around in, fear, anxiety, depression, lack of stimulation, helplessness, hopelessness, social isolation, and loss of loved ones (Cassell, 2004; Dawkins, 2005; Panksepp, 2011; Tossani, 2013) – all identified by others as causes of distress (National Research Council, 2008).

The connection with a sense of control

It is now well supported that for humans and nonhuman animals, in the presence of an aversive stimulus, control - defined as the perception that one has a response available that can affect the aversiveness of the event - bestows to the individual the sense that he/she can, at will, terminate the event, make it less probable or less intense, or change its duration or timing, each of which can increase the individual's ability to tolerate the unpleasant stimulus (Thompson, 1981; Foa et al., 1992). A large body of literature has demonstrated that those who perceive that they have the ability to affect the outcomes they receive experience reduced intensity and harmful effects of physiologic and emotional stress in humans (Dantzer, 1989; Sapolsky, 1994; Mench, 1998; Bollini et al., 2004) and in animals (Joffe et al., 1973; Hanson

et al., 1976; Videan et al., 2005), and cope better with a stressful situation in humans (Thompson and Spacapan, 1991) and in animals (Weiss, 1972; Seligman, 1975; Broom, 1986; Korte, 2001; Manteuffel, 2002; Reiche et al., 2004). Conversely, the perception of uncontrollability over aversive events produces a constellation of persistent cognitive, motivational, and emotional deficits (Seligman, 1972; Abramson et al., 1978; Crombez et al., 2008).

With this robust buffering effect on NA it is not surprising that many researchers believe that there is a strong relationship between distress and perceived control (National Research Council, 2008). In humans, Steptoe and Poole (2016) stated that 'It is generally found that distress is associated with a perception that events are uncontrollable' and Lundberg and Frankenhaeuser (1978) have argued that how much a task can be controlled is a major determinant of the degree of distress experienced. The relationship between perceived control and distress in specific human populations (e.g., patients with particular diseases, people in certain occupations) has been widely studied. Unfortunately, almost without exception these studies either omit any definition of distress or use the term consistent with 'psychological distress' as defined in Section 11.1.3, making direct comparisons of these studies problematic. This work has shown that in people with chronic pain (Crisson and Keefe, 1988), women with breast cancer (Barez et al., 2009), firefighters (Brown et al., 2002), and teachers (Leung et al., 2000), the greater the sense of personal control (internal locus of control), the lower the level of psychological distress. Other studies have found positive effects of perceived control on distress in response to electric shock and loud noises (reviewed by Thompson, 1981). A series of studies of torture survivors by Başoğlu and colleagues (1994, 1997, 2007) demonstrated that the subjective appraisal of the torture event as being uncontrollable and unpredictable was associated with higher perceived distress during torture and that the greater ability to exercise control over torture stressors was associated with less perceived distress.

In animals, Russell and Burch (1959) referred to the research setting when suggesting that 'serious distress may not be present in experiments where an animal has already learned to eliminate a painful stimulus in advance – e.g. by turning a wheel or pressing a lever'. In its report 'Recognition and Alleviation of Distress in Laboratory Animals', the National Research Council (2008) wrote

predictability and controllability (i.e., the ability of the animal to control its environment) are important determinants in 'the transition of stress to distress'. Numerous studies indicate that, in animals that can predict the onset of a stressful stimulus or control its duration, the behavioral and physiological impacts of stressor exposure are attenuated. Notable among these studies are findings that rats exposed to inescapable shock develop clear signs of distress, whereas yoked rats that can terminate shock exposure do not, despite subjection to the same intensity and duration of shock experience (Maier and Watkins, 2005).

Discussions of control and suffering have closely paralleled those for control and distress (see Chapter 12, this volume, for coverage of the relationship between control, agency, and suffering). An anecdotal relationship between suffering and the perception of control has been described by Cassel (1982, 2004), who wrote that people in pain frequently report suffering from the pain when they do not believe that the pain can be controlled and that the suffering of patients with terminal cancer can often be relieved by demonstrating that their pain can in fact be controlled. He writes: 'Patients who have been rolling in agony, believing their pain beyond relief, will often tolerate the same severe pain without complaint after they have been shown that it can be controlled' (Cassell, 2004). Knowledge about the source of the pain conceived by some as a form of control (Averill, 1973) - also exerts an effect. Cassel wrote that 'patients can writhe in pain from kidney stones and by their own admission not be suffering, because they "know what it is"; they may also report considerable suffering from apparently minor discomfort when they do not know its source'. This kind of effect, when expanded to include pain but without specific reference to suffering, has been extensively studied (Thompson, 1981; Toomey et al., 1991; Pellino and Ward, 1998; Walder et al., 2001) and found in most cases to exhibit a negative correlation between perception of control and self-reported pain.

The question as to whether suffering differs qualitatively or only quantitatively from less intense NA

This most basic of questions about distress has been raised earlier (see Section 11.2.3). The same

question has been applied to suffering. For example, DeGrazia (1996) wrote:

Suffering is a highly unpleasant emotional state associated with more-than-minimal pain or distress. The words 'associated with' bypass the difficult conceptual and scientific issue of whether more-than-minimal pain and distress *cause* or *are forms of* suffering. (italics in the original)

It appears that for both distress and suffering, intensifying NA can either *become* distress or suffering (the intense affect is simply described as 'distress' or 'suffering') or *elicit* distress or suffering (in which case a qualitatively different affective experience emerges 'on top' of the intensifying affect). Or, as suggested for distress (see Section 11.5), suffering may refer to an amplifying process for the primary NA.

11.8 Concluding Remarks

The question in the title of this chapter must be currently answered with the classic but nonhelpful response of 'Depends on whom you ask.' Unfortunately, this imposes major constraints on the research and understanding of arguably the most important aspects of animal and human wellbeing: the highly unpleasant experiences of distress and suffering. Two of the greatest challenges we face are to bring together the disparate conceptualizations of distress into a more unified view and to determine whether distress (and suffering) are only descriptive labels or, rather, actual mental experiences themselves. For now, there can be no argument that regardless of the specifics of the nature of distress, making every effort we can to protect animals from this state is the overriding concern in animal care.

Note

¹ Affect is often regarded as the feeling experienced in connection to an emotion or mood, but the definition used in the present chapter is the broader interpretation of Fredrickson (2001), who wrote that affect 'refers to consciously accessible feelings. Although affect is present within emotions (as the component of subjective experience), it is also present within many other affective phenomena, including physical sensations, attitudes, moods, and even affective traits. In this chapter the use of negative affect (NA) will be taken to mean any unpleasant feeling, and is equated to aversiveness.

11.9 References

- Abramson, L.Y., Seligman, M.E., Teasdale, J.D. (1978) Learned helplessness in humans: Critique and reformulation. *Journal of Abnormal Psychology* 87, 49–74. http://dx.doi.org/10.1037/0021-843X.87.1.49.
- Adamo, S.A. (2012) The effects of the stress response on immune function in invertebrates: An evolutionary perspective on an ancient connection. *Hormones and Behavior* 62, 324–330. http://dx.doi.org/10.1016/j.yhbeh.2012.02.012.
- Averill, J.R. (1973) Personal control over aversive stimuli and its relationship to stress. *Psychological Bulletin* 80, 286–303. http://dx.doi.org/10.1037/h0034845.
- Barez, M., Blasco, T., Fernández-Castro, J., Viladrich, C. (2009) Perceived control and psychological distress in women with breast cancer: A longitudinal study. *Journal of Behavioral Medicine* 32, 187–196. http:// dx.doi.org/10.1007/s10865-008-9180-5.
- Barnard, C. (2007) Ethical regulation and animal science: Why animal behavior is special. *Animal Behaviour* 74, 5–13. http://dx.doi.org/10.1016/j.anbehav.2007. 04 002.
- Barnard, C.J. and Hurst, J.L. (1996) Welfare by design: The natural selection of welfare criteria. *Animal Welfare* 5, 405–433.
- Başoğlu, M., Paker, M., Paker, O., Ozmen, E., Marks, I., et al. (1994) Psychological effects of torture: A comparison of tortured with nontortured political activists in Turkey. American Journal of Psychiatry 151, 76–81.
- Başoğlu, M, Mineka, S., Paker, M., Aker, T., Livanou, M., et al. (1997) Psychological preparedness for trauma as a protective factor in survivors of torture. Psychological Medicine 27, 1421–1433. http://dx.doi.org/10.1017/S0033291797005679.
- Başoğlu, M., Livanou, M., Crnobaric, C. (2007) Torture vs other cruel, inhuman, and degrading treatment: Is the distinction real or apparent? Archives of General Psychiatry 64, 277–285. http://dx.doi.org/10.1001/ archpsyc.64.3.277.
- Bindra, D. (1978) How adaptive behavior is produced: A perceptual-motivational alternative to responsereinforcement. *Behavioral and Brain Sciences* 1, 41–52. http://dx.doi.org/10.1017/S0140525X00059380.
- Bollini, A.M., Walker, E.F., Hamann, S., Kestler, L. (2004) The influence of perceived control and locus of control on the cortisol and subjective responses to stress. *Biological Psychology* 67, 245–260. http://dx.doi.org/10.1016/j.biopsycho.2003.11.002.
- Brewin, C.R., Andrews, B., Valentine, J.D. (2000) Metaanalysis of risk factors for posttraumatic stress disorder in trauma-exposed adults. *Journal of Consulting* and Clinical Psychology 68, 748–766. http://dx.doi. org/10.1037/0022-006X.68.5.748.
- Broom, D.M. (1986) Indicators of poor welfare. *British Veterinary Journal* 142, 524–526.

- Broom, D.M. (2008) Welfare assessment and relevant ethical decisions: Key concepts. *Annual Review of Biomedical Sciences* 10, T79–T90. http://dx.doi.org/10.5016/1806-8774.2008.v10pT79.
- Brown, J., Mulhern, G., Joseph, S. (2002) Incident-related stressors, locus of control, coping, and psychological distress among firefighters in Northern Ireland. *Journal of Traumatic Stress* 15, 161–168. http://dx.doi.org/10.1023/A:1014816309959.
- Cabanac, M. (1979) Sensory pleasure. Quarterly Review of Biology 54, 1–29. http://dx.doi.org/10.1086/410981.
- Carstens, E. and Moberg, G.P. (2000) Recognizing pain and distress in laboratory animals. *ILAR Journal* 41, 62–71. http://dx.doi.org/10.1093/ilar.41.2.62.
- Cassel, E.J. (1982) The nature of suffering and the goals of medicine. New England Journal of Medicine 306, 639–645. http://dx.doi.org/10.1056/ NEJM198203183061104.
- Cassell, E.J. (2004) The Nature of Suffering and the Goals of Medicine, 2nd edn. Oxford University Press, Oxford, UK. http://dx.doi.org/10.1093/acprof:oso/ 9780195156164.001.0001.
- Chapman, D.P., Whitfield, C.L., Felitti, V.J., Dube, S.R., Edwards, V.J., et al. (2004) Adverse childhood experiences and the risk of depressive disorders in adulthood. *Journal of Affective Disorders* 82, 217–225. http://dx.doi.org/10.1016/j.jad.2003.12.013.
- Clark, J.D., Rager, D.R., Calpin, J P. (1997) Animal well-being II. Stress and distress. *Laboratory Animal Science* 47, 571–579.
- Clark, J.M. (2007) Does distress matter? In: Proceedings of the 6th World Congress on Alternatives and Animal Use in the Life Sciences, Tokyo, Japan. *AATEX* 14, Special Issue: 93–95. Available at: http://altweb.jhsph.edu/wc6/paper93.pdf (accessed 11 April 2019).
- Cohen, H., Matar, M.A., Richter-Levin, G., Zohar, J. (2006) The contribution of an animal model toward uncovering biological risk factors for PTSD. *Annals of* the New York Academy of Sciences 1071, 335–350. http://dx.doi.org/10.1196/annals.1364.026.
- Committee on Pain and Distress in Laboratory Animals. (1992) Recognition and Alleviation of Pain and Distress in Laboratory Animals. National Academy Press, Washington, DC, USA.
- Crisson, J.E. and Keefe, F.J. (1988) The relationship of locus of control to pain coping strategies and psychological distress in chronic pain patients. *Pain* 35, 147–154. http://dx.doi.org/10.1016/0304-3959(88) 90222-9.
- Crombez, G., Eccleston, C., De Vlieger, P., Van Damme, S., De Clercq, A. (2008) Is it better to have controlled and lost than never to have controlled at all? An experimental investigation of control over pain. *Pain* 137, 631–639. http://dx.doi.org/10.1016/j.pain.2007. 10.028.
- Cromby, J., Harper, D., Reavey, P. (2013) *Psychology, Mental Health and Distress*. Palgrave Macmillan,

- London, UK. http://dx.doi.org/10.1007/978-1-137-29589-7.
- Dantzer, R. (1989) Neuroendocrine correlates of control and coping. In: Steptoe, A. and Appels, A. (eds.). Stress, Personal Control and Health. Wiley, New York, USA, pp. 640–696.
- Dawkins, M.S. (1980) Animal Suffering. Chapman and Hall, London, UK. http://dx.doi.org/10.1007/978-94-009-5905-7.
- Dawkins, M.S. (1990) From an animal's point of view: Motivation, fitness, and animal welfare. *Behavioral and Brain Sciences* 13, 1–61. http://dx.doi.org/10.1017/S0140525X00077104.
- Dawkins, M.S. (2005) The science of suffering. In: McMillan, F.D. (ed.) *Mental Health and Well-being in Animals*. Blackwell Publishing, Ames, Iowa, USA, pp. 47–55. http://dx.doi.org/10.1002/9780470384947. ch4.
- Dawkins, M.S. (2006) The scientific basis for assessing suffering in animals. In: Singer, P (ed.) *In Defense of Animals: The Second Wave*. Blackwell Publishing, Malden, Massachusetts, USA, pp. 26–39.
- Day, T.A. (2005) Defining stress as a prelude to mapping its neurocircuitry: No help from allostasis. *Progress In Neuro-Psychopharmacology & Biological Psychiatry* 29, 1195–1200. http://dx.doi.org/10.1016/j.pnpbp.2005. 08.005.
- DeGrazia, D. (1996) Taking Animals Seriously. Cambridge University Press, Cambridge, UK. http:// dx.doi.org/10.1017/CBO9781139172967.
- de Haes, J.C.J.M., van Knippenberg, F.C.E., Neijt, J.P. (1990) Measuring psychological and physical distress in cancer patients: Structure and application of the Rotterdam Symptom Checklist. *British Journal of Cancer* 62, 1034–1038. http://dx.doi.org/10.1038/ bic.1990.434.
- Desborough, J.P. (2000) The stress response to trauma and surgery. *British Journal of Anaesthesia* 85, 109–117. http://dx.doi.org/10.1093/bja/85.1.109.
- Dorland's Medical Dictionary for Health Consumers. (2007) Distress. Available at: http://medical-dictionary. thefreedictionary.com/distress (accessed 11 April 2019).
- Duncan, I.J.H. (2004) A concept of welfare based on feelings. In: Benson, G.J and Rollin, B.E. (eds.) The Well-Being of Farm Animals. Blackwell Publishing, Ames, Iowa, USA, pp. 85–101. http://dx.doi.org/ 10.1002/9780470344859.ch5.
- Dyrbye, L.N., Thomas, M.R., Shanafelt, T.D. (2006) Systematic review of depression, anxiety, and other indicators of psychological distress among U.S. and Canadian medical students. *Academic Medicine* 81, 354–373. http://dx.doi.org/10.1097/00001888-20060 4000-00009.
- Edwards, L.N. (2010) Animal well-being and behavioural needs on the farm. In: Grandin, T (ed.) *Improving Animal Welfare: A Practical Approach*. CAB International, Wallingford, UK, pp. 139–159.

- Engel, G.L. and Schmale, A.H. (1972) Conservation withdrawal: A primary regulatory process for organic homeostasis. In: Ciba Foundation (ed.) *Physiology, Emotions and Psychosomatic Illness*. Associated Scientific Publishers, Amsterdam, The Netherlands, pp. 57–85.
- Fagundes, C.P., Glaser, R., Kiecolt-Glaser, J.K. (2013) Stressful early life experiences and immune dysregulation across the lifespan. *Brain Behavior and Immunity* 27, 8–12. http://dx.doi.org/10.1016/j.bbi. 2012.06.014.
- Foa, E.B., Zinbarg, R., Rothbaum, B.O. (1992) Uncontrollability and unpredictability in post-traumatic stress disorder: An animal model. *Psychological Bulletin* 112, 218–238. http://dx.doi.org/10.1037/0033-2909.112.2.218.
- Fredrickson, B.L. (2001) The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American Psychologist* 56, 218–226. http://dx.doi.org/10.1037/0003-066X. 56,3,218.
- Hanson, J.D., Larson, M.E., Snowdon, C.T. (1976) The effects of control over high intensity noise on plasma cortisol levels on Rhesus monkeys. *Behavioral Biology* 16, 333–340. http://dx.doi.org/10.1016/ S0091-6773(76)91460-7.
- Harmon-Jones, E., Gable, P.A., Price, T.F. (2012) The influence of affective states varying in motivational intensity on cognitive scope. Frontiers in Integrative Neuroscience 6, 83–87. http://dx.doi.org/10.3389/ fnint.2012.00073.
- Harmon-Jones, E., Gable, P.A., Price, T.F. (2013) Does negative affect always narrow and positive affect always broaden the mind? Considering the influence of motivational intensity on cognitive scope. *Current Directions In Psychological Science* 22, 301–307. http://dx.doi.org/10.1177/0963721413481353.
- Heim, C., Newport, D.J., Wagner, D., Wilcox, M.M., Miller, A.H., et al. (2002) The role of early adverse experience and adult stress in the prediction of neuroendocrine stress reactivity in women: A multiple regression analysis. *Depression and Anxiety* 15, 117–125. http://dx.doi.org/10.1002/da.10015.
- Holahan, C.J. and Moos, R.H. (1981). Social support and psychological distress: A longitudinal analysis. *Journal of Abnormal Psychology* 90, 365–370. http:// dx.doi.org/10.1037/0021-843X.90.4.365.
- Izard, C.E. (1977) Human Emotions. Plenum Press, New York, USA. http://dx.doi.org/10.1007/978-1-4899-2209-0.
- Joffe, J.M., Rawson, R.A., Mulick, J.A. (1973) Control of their environment reduces emotionality in rats. *Science* 180, 1383–1384. http://dx.doi.org/10.1126/ science.180.4093.1383.
- Karas, A.Z. and Silverman, J. (2014) Pain and distress. In: Silverman, J, Suckow, M.A., Murthy, S. (eds.) *The IACUC Handbook*, 3rd edn. CRC Press, Boca Raton,

- Florida, USA, pp. 317–375. http://dx.doi.org/10.1201/b16915-17.
- Kessler, R.C. (1979) Stress, social status, and psychological distress. *Journal of Health and Social Behavior* 20, 259–272. http://dx.doi.org/10.2307/2136450.
- Kitchen, H., Vanderlip, J.E., Aronson, A.L., Bittle, J.L., McPherson, C.W., et al. (1987) Panel report on the colloquium on recognition and alleviation of animal pain and distress. Journal of The American Veterinary Medical Association 191, 1186–1191.
- Koolhaas, J.M., Bartolomucci, A., Buwalda, B., de Boer, S.F., Flügge, G., et al. (2011). Stress revisited: A critical evaluation of the stress concept. Neuroscience and Biobehavioral Reviews 35, 1291–1301. http:// dx.doi.org/10.1016/j.neubiorev.2011.02.003
- Kopin, I. J., Eisenhofer, G., Goldstein, D. (1988) Sympathoadrenal medullary system and stress. In: Chrousos, G.P., Loriaux, D.L., Gold, P.W. (eds.) Mechanisms of Physical and Emotional Stress. Plenum Press, New York, USA, pp. 11–23. http://dx.doi.org/10.1007/978-1-4899-2064-5_2.
- Korte, S.M. (2001) Corticosteroids in relation to fear, anxiety, and psychopathology. *Neuroscience and Biobehavioral Reviews* 25, 117–142. http://dx.doi. org/10.1016/S0149-7634(01)00002-1.
- Latarjet, J. and Choinère, M. (1995) Pain in burn patients. *Burns* 21, 344–348. http://dx.doi.org/10.1016/0305-4179 (95)00003-8.
- Ledger, R.A. and Mellor, D.J. (2018) Forensic use of the five domains model for assessing suffering in cases of animal cruelty. *Animals* 8, 101. http://dx.doi. org/10.3390/ani8070101.
- Leknes, S. and Tracey, I. (2008) A common neurobiology for pain and pleasure. *Nature Reviews Neuroscience* 9, 314–320. http://dx.doi.org/10.1038/nrn2333.
- Leung, T., Siu, O., Spector, P.E. (2000) Faculty stressors, job satisfaction, and psychological distress among university teachers in Hong Kong: The role of locus of control. *International Journal of Stress Management* 7, 121–138. http://dx.doi.org/10.1023/A:1009584202196.
- Lundberg, U. and Frankenhaeuser, M. (1978) Psychophysiological reactions to noise as modified by personal control over noise intensity. *Biological Psychology* 6, 51–59. http://dx.doi.org/10.1016/0301-0511(78)90006-6.
- MacDonald, G. and Shaw, S. (2005) Adding insult to injury: social pain theory and response to social exclusion. In: Williams, K., Forgas, J., von Hippel, W. (eds.) The Social Outcast: Ostracism, Social Exclusion, Rejection, and Bullying. Psychology Press, New York, USA, pp. 77–90.
- Maier, S.F. and Watkins, L.R. (2005) Stressor controllability and learned helplessness: The roles of the dorsal raphe nucleus, serotonin, and corticotropin-releasing factor. Neuroscience and Biobehavioral Reviews 29,

- 829–841. http://dx.doi.org/10.1016/j.neubiorev. 2005.03.021.
- Manteuffel, G. (2002) Central nervous regulation of the hypothalamic-pituitary-adrenal axis and its impact on fertility, immunity, metabolism and animal welfare. *Archiv Tierzucht* 45, 575–595.
- Mason, G. (1991) Stereotypies: A critical review. Animal Behaviour 41, 1015–1037. http://dx.doi.org/10.1016/ S0003-3472(05)80640-2.
- Mason, G.J. and Latham, N. (2004) Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare* 13, S57–S69.
- Mench, J.A. (1998) Thirty years after Brambell: Whither animal welfare science? *Journal of Applied Animal Welfare Science* 1, 91–102. http://dx.doi.org/10.1207/s15327604jaws0102 1.
- Miller, G.E., Chen, E., Parker, K.J. (2011) Psychological stress in childhood and susceptibility to the chronic diseases of aging: Moving towards a model of behavioral and biological mechanisms. *Psychological Bulletin* 137, 959–997. http://dx.doi.org/10.1037/a0024768.
- Mirowsky, J. and Ross, C.E. (2003) Social Causes of Psychological Distress, 2nd edn. Aldine Transaction, New Brunswick, New Jersey, USA.
- Moberg, G. (2000) Biological response to stress: implications for animal welfare. In: Moberg, G. and Mench, J.A. (eds.) The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare. CAB International, Wallingford, UK, pp. 1–22. http://dx.doi.org/10.1079/9780851993591.0000.
- Moberg, G.P. (1985) Biological responses to stress: key to assessment of animal well-being? In: Moberg, G.P. (ed.) Animal Stress. American Physiological Society, Bethesda, Maryland, USA, pp. 27–49.
- Moberg, G.P. (1987) Problems defining stress and distress in animals. *Journal of The American Veterinary Medical Association* 191, 1207–1211.
- Mosby's Medical Dictionary, 9th edn. (2009) Distress. Available at: http://medical-dictionary.thefreedictionary.com/distress (accessed 11 April 2019).
- National Research Council. (2008) Recognition and Alleviation of Distress in Laboratory Animals. National Academies Press, Washington, DC, USA.
- Novak, M.A., Meyer, J.S., Lutz, C., Tiefenbacher, S. (2006) Deprived environments: developmental insights from primatology. In: Mason, G., Rushen, J. (eds) Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare, 2nd edn. CAB International, Wallingford, UK, pp. 153–189.
- Olsson, I.A.S., Wurbel, H., Mench, J.A. (2011) Behaviour. In: Appleby, M.C., Mench, J.A., Olsson, I.A.S, Hughes, B.O. (eds) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK, pp. 138–154.
- Overall, K.L. (2019) Evidence-based paradigm shifts in veterinary behavioral medicine. *Journal of the American Veterinary Medical Association* 254, 798–807. http://dx.doi.org/10.2460/javma.254.7.798.

- Oxford Dictionaries. (2019a) Distress. Available at: www.oxforddictionaries.com/definition/english/distress (accessed 10 April 2019).
- Oxford Dictionaries. (2019b) Suffering. Available at: https://dictionary.cambridge.org/us/dictionary/english/suffering (accessed 10 April 2019).
- Panksepp, J. (1998) Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, New York, USA.
- Panksepp, J. (2011) The basic emotional circuits of mammalian brains: Do animals have affective lives? Neuroscience and Biobehavioral Reviews 35, 1791–1804. http://dx.doi.org/10.1016/j.neubiorev. 2011.08.003.
- Pellino, T.A. and Ward, S.E. (1998) Perceived control mediates the relationship between pain severity and patient satisfaction. *Journal of Pain and Symptom Management* 15, 110–116. http://dx.doi.org/10.1016/S0885-3924(97)00255-8.
- Reiche, E.M.V., Nunes, S.O.V., Morimoto, H.K. (2004) Stress, depression, the immune system, and cancer. *Lancet Oncology* 5, 617–625. http://dx.doi.org/10.1016/S1470-2045(04)01597-9.
- Ridner, S.H. (2004) Psychological distress: Concept analysis. *Journal of Advanced Nursing* 45, 536–545.
- Rolls, E.T. (2000) Precis of *The Brain and Emotion*. Behavioral and Brain Sciences 23, 177–234. http://dx.doi.org/10.1017/S0140525X00002429.
- Roseman, I.J., Wiest, C., Swartz, T.S. (1994) Phenomenology, behaviors, and goals differentiate discrete emotions. *Journal of Personality and Social Psychology* 67, 206. http://dx.doi.org/10.1037/ 0022-3514.67.2.206.
- Rothermund, K. (2006) Hanging on and letting go in the pursuit of health goals: Psychological mechanisms to cope with a regulatory dilemma. In: De Ridder, D. and De Wit, J. (eds.) *Self-regulation in Health Behavior*. Wiley, Chichester, UK, pp. 217–242.
- Rushen, J. (1990) Use of aversion-learning techniques to measure distress in sheep. *Applied Animal Behaviour Science* 28, 3–14. http://dx.doi.org/10.1016/0168-1591(90)90043-D.
- Russell, W.M.S. and Burch, R.L. (1959) The Principles of Humane Experimental Technique. Methuen, London, UK.
- Sanchez, M.M., Ladd, C.O., Plotsky, P.M. (2001) Early adverse experience as a developmental risk factor for later psychopathology: Evidence from rodent and primate models. *Developmental Psychopathology* 13, 419–449. http://dx.doi.org/10.1017/S09545794 01003029.
- Sapolsky, R.M. (1994) Why Zebras Don't Get Ulcers: A Guide to Stress, Stress-Related Diseases, and Coping. W.H. Freeman and Company, New York, USA.

- Saunders Comprehensive Veterinary Dictionary, 3rd edn. (2007) Distress. Available at: http://medical-dictionary.thefreedictionary.com/distress (accessed 11 April 2019).
- Schultheiss, O.C., Wirth, M.M. (2018) Biopsychological aspects of motivation. In: Heckhausen, J. and Heckhausen, H. (eds.) *Motivation and Action*, 3rd edn. Cambridge University Press, New York, New York, pp. 407–451. http://dx.doi.org/10.1007/978-3-319-65094-4_10.
- Seligman, M.E. (1972) Learned helplessness. *Annual Review of Medicine* 23, 407–415. http://dx.doi.org/10.1146/annurev.me.23.020172.002203.
- Seligman, M.E. (1975) *Helplessness: On Depression, Development, and Death.* W.H. Freeman and Company, San Francisco, California, USA.
- Selye, H. (1936) A syndrome produced by diverse nocuous agents. *Nature* 138, 32. http://dx.doi.org/10.1038/138032a0.
- Selye, H. (1974) Stress Without Distress. Signet, New York, USA.
- Shea, A., Walsh, C., Macmillan, H., Steiner, M. (2005)
 Child maltreatment and HPA axis dysregulation:
 Relationship to major depressive disorder and post-traumatic stress disorder in females.

 Psychoneuroendocrinology 30, 162–178. http://dx.doi.org/10.1016/j.psyneuen.2004.07.001.
- Spencer, H. (1880) *Principles of Psychology*, 3rd edn. Longmans, London, UK.
- Steptoe, A. and Poole, L. (2016) Control and stress. In: Fink, G. (ed.) Stress: Concepts, Cognition, Emotion, and Behavior. Academic Press, Cambridge, Massachusetts, USA, pp. 73–80. http://dx.doi.org/10.1016/B978-0-12-800951-2.00008-X.
- The American Heritage Medical Dictionary. (2007) Distress.

 Available at: http://medical-dictionary.thefreedictionary.

 com/distress (accessed 11 April 2019).
- Thompson, S.C. (1981) Will it hurt less if I can control it?
 A complex answer to a simple question. *Psychological Bulletin* 90, 89–101. http://dx.doi.org/10.1037/0033-2909.90.1.89.
- Thompson, S.C. and Spacapan, S. (1991) Perceptions of control in vulnerable populations. *Journal of Social Issues* 47, 1–21. http://dx.doi.org/10.1111/j.1540-4560.1991.tb01831.x.
- Tiefenbacher, S., Novak, M.A., Lutz, C.K., Meyer, J.S. (2005) The physiology and neurochemistry of selfinjurious behavior: A nonhuman primate model. Frontiers In Bioscience 10, 1–11. http://dx.doi. org/10.2741/1500
- Tomkins, S.S. (1963) Affect Imagery Consciousness: Volume II: The Negative Affects. Springer Publishing Company, New York, USA.
- Tomkins, S.S. (1984) Affect theory. In: Scherer, K.R. and Ekman, P. (eds.) Approaches to Emotions. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA, pp. 163–195.

- Toomey, T.C., Mann, D., Abashian, S., Thompson-Pope, S. (1991) Relationship between perceived self-control of pain, pain description and functioning. *Pain* 45, 129–133. http://dx.doi.org/10.1016/0304-3959(91) 90177-Y.
- Tossani, E. (2013) The concept of mental pain. *Psychotherapy and Psychosomatics* 82, 67–73. http://dx.doi.org/10.1159/000343003.
- Veit, C.T. and Ware, J.E. (1983) The structure of psychological distress and well-being in general populations. *Journal of Consulting and Clinical Psychology* 51, 730–742. http://dx.doi.org/10.1037/0022-006X. 51.5.730.
- Videan, E.N., Fritz, J., Schwandt, M.L., Smith, H.F., Howell, S. (2005) Controllability in environmental enrichment for captive chimpanzees (*Pan troglo-dytes*). *Journal of Applied Animal Welfare Science* 8, 117–130. http://dx.doi.org/10.1207/s15327604 jaws0802 4.

- Walder, B., Schafer, M., Henzi, I., Thramer, M.R. (2001) Efficacy and safety of patient-controlled opioid analgesia for acute postoperative pain. A quantitative systematic review. ACTA Anaesthesiologica Scandinavica 45, 795–804. http://dx.doi.org/10.1034/ j.1399-6576.2001.045007795.x.
- Webster, J. (2011) Husbandry and animal welfare. In: Webster, J. (ed.) *Management and Welfare of Farm Animals*. Wiley-Blackwell, Chichester, UK, pp. 1–30.
- Wechsler, B. (1995) Coping and coping strategies: A behavioural view. *Applied Animal Behavior Science* 43, 123–134. http://dx.doi.org/10.1016/0168-1591(95)00557-9.
- Weiss, J.M. (1972) Psychological factors in stress and disease. *Scientific American* 226, 104–113. http://dx.doi.org/10.1038/scientificamerican0672-104.
- Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., et al. (2018) Assessment of welfare in zoo animals: Towards optimum quality of life. Animals 8, 110. http://dx.doi.org/10.3390/ani8070110.

12 Suffering, Agency, and the Bayesian Mind¹

DANIEL M. WEARY

University of British Columbia, Animal Welfare Program, Faculty of Land and Food Systems, Vancouver, British Columbia, Canada

12.1 Introduction

Suffering is a central issue of animal welfare, and the alleviation and prevention of suffering is a core moral responsibility to those for whom we care. One motivation in writing this chapter is to serve as a reminder of the fundamental importance of this concept and responsibility it carries. The rapid emergence of the field of animal welfare science has led to many important advances, including the development of improved assessment methods for negative affective states like pain and fear, and a more recent focus on positive affective states. Clearly a better understanding of how animals feel is important to assess and improve animal welfare, as is a sense of how positive experiences may somehow compensate for negative ones to contribute to the animal's overall sense of well-being (Webb et al., 2019). But let not the merely important distract us from the fundamental; prevention and alleviation of suffering lies at the very heart of our duties toward animals under our care. The overall aim of this chapter is to contribute to the still embryonic body of scholarly work explicitly addressing the issue of animal suffering.

One reason for the reluctance of scholars to seriously address the issue of animal suffering may be that they are still influenced by the charming but outdated notion that the job of the scientist is to study the 'facts', and leave the difficult discussions around 'values' to others. The term suffering is infused with moral loading, explaining why it is often used in the rhetoric of animal advocates and in criminal law, and this moral loading has likely led academics to shy away from the concept. In the following section I briefly review how the term has been used in the academic literature, and compare this with what I argue is a more meaningful usage found in the human clinical literature.

12.2 Academic Usage of the Term 'Suffering'

In the scientific literature on animal welfare the word 'suffering' is typically used in conjunction with the experience of some negative affective state. Most often this affective state is pain, and this is the state I focus on in most of the examples I use this chapter.

As illustrated in Table 12.1, the simplest usage of the term is adjunctive, as in 'pain and suffering', without attempt to distinguish the two ideas. This renders the term decorative.

A second usage of the term 'suffer' adds some value in that it suggests that the animal must consciously experience the negative state. It is this sense of the word that is used by authors interested in the conscious experience of pain in invertebrates (Elwood, 2011) and other animals for which there may be some questions about the animal's level of sentience. Used in this way the word makes no claims about the quality or magnitude of pain, only that the pain is in some way felt by the animal. The search for methods that allow for strong inferences about the extent to which affective states like pain are consciously felt by animals is still ongoing (Weary et al., 2017). For academic usage I suggest that this distinction is too important to obfuscate by using the term 'suffer', unless specifically defined it this way. Moreover, to apply this technical meaning of 'any felt negative affective state' would seem to strain the boundaries of common usage of the word. One might say, for example, that 'I felt the prick of the injection when I went for my flu shot', but it would seem theatrical to call this 'suffering'.

A stronger usage of suffering considers the magnitude and duration of unpleasant affective experiences. For example, Dawkins (1980, p.76) states 'Not all

Table 12.1. Usage of the term suffering in the academic literature. Included are the top six relevant peer-reviewed journal publications from Google Scholar when using the search terms "animal*" AND "suffer*", sorted using Google's algorithm for relevance. Examples are provided with my categorization of usage as defined in the body of the chapter as (i) decorative; (ii) consciously felt; or (iii) exceeding some threshold of severity and/or duration.

Usage category	Phrase illustrating usage
Decorative	'may serve to stimulate the release of brain opioids which may reduce pain and suffering in stressed animals' (Hughes and Duncan, 1988, p.1704)
Consciously felt	'There is also still the problem of relating changed physiological state to the animal's subjective feelings of distress. Animals may suffer before any physiological disturbances are detected' (Dawkins, 1977, p.1035)
	Anatomical, pharmacological and behavioural data suggest that affective states of pain, fear and stress are likely to be experienced by fish This implies that fish have the capacity to suffer' (Chandroo et al., 2004, p.225)
	'Can invertebrates suffer? Or, how robust is argument-by-analogy?' (Sherwin, 2001, p.103) 'Well-fed Labrador Retrievers may never suffer from hunger but are likely to develop heart problems from being over-weight' (Fraser, 2008, p.3)
Exceeding some threshold	'Withholding conditions or commodities for which an animal shows "inelastic demand" is very likely to cause suffering' (Dawkins, 1990, p.1)

fear, frustration or conflict indicates suffering. But prolonged or intense occurrences of these same states may indicate great suffering.' Later in her book, Dawkins acknowledges the difficulty in establishing a clear line where suffering begins: 'There is a subjective element, for example, in deciding how much fear, conflict etc. constitutes "suffering". Dawkins' academic usage comes closer to what might be considered common usage, such as that captured in the phrase 'Last month I suffered from severe back pain.' That said, even in this example there is some redundancy (how does the term 'suffer' add to the sentence given that we already know that the pain was severe?). We could instead say 'Last month I suffered from back pain,' thus using the term 'suffer' to mean 'experience severe pain', but the meaning would be clearer if the sentence simply specified the magnitude (and duration) directly. In addition, the use of 'suffer' to quantify the level of negative affect to be above some (unspecified) cutoff for severity and duration would seem to miss any additional, qualitative aspects that the moral imperative of the term connotes.

12.3 Human Descriptions of Suffering

A more nuanced understanding of suffering can be found in the academic literature describing human self-reports. As with the work on nonhuman animals described above, this literature on humans illustrates the importance of experiencing a negative subjective state of some considerable magnitude or

duration. In addition, this literature points to other factors that are also important in conceptions of suffering.

In the classic paper in this field, Cassell (1982) recounts that one patient required 'small doses of codeine' for pain when she thought that this pain was due to sciatica, but required much higher doses when she found out that the cause was cancer. This and other examples suggest that when pain is associated with fear the likelihood of suffering increases: fear that the pain will increase to the extent that it can no longer be controlled with analgesics, fear that it will last forever, fear of becoming overwhelmed by the pain, or fear that the pain is a sign of a serious disease.

Another factor associated with suffering is that the patients are no longer able to do those things that are most important to them. Snyder (2004) states 'Pain is a physical sensation of discomfort, whereas suffering taps the degree to which a person has let the pain prevent him or her from doing the important things in life.' Anhedonia, a sign of depression, can be considered both a reduction in the motivation to access a reward and a reduction in the pleasure that is experienced from that reward (Treadway and Zald, 2011). Thus, reduced rates of activities can be both a cause of suffering (as in the first example of a person so incapacitated by pain that they can no longer perform an activity they previously enjoyed) and a sign of suffering (if the person is sufficiently depressed to show signs of anhedonia).

Loss of control is a recurrent theme in studies of human suffering. As described by Cassell (1999), 'Suffering can start with anguish over the possibility that if the symptom continues, the patient will be overwhelmed or lose control — "I won't be able to take it".' Loss of control is sometimes characterized as loss of the essence of who you consider yourself to be as a person, perhaps related to being able to do those things that you enjoy or believe to be important. The importance of loss of 'personhood' to the concept of suffering can be seen even in the definition of torture as an attempt to 'obliterate the personality of the victim or to diminish his physical or mental capacities, even if they do not cause physical pain' (Organization of American States, 1985).

The lack of access, or inability to cognitively process, environmental cues important to effective decision making may contribute to the feeling of being overwhelmed or losing control. One example of this importance of cognitive control comes from how patients understand the meaning of their pain. This is illustrated in relation to fear of catastrophic consequences in the cancer example discussed earlier. In addition, people sometimes report positive meanings to their pain, such as that associated with childbirth, and even pain that is self-inflicted as in attempts at 'spiritual cleansing' (Cassell, 1982). Thus, pain that is not perceived to have value, or is associated with other negative outcomes, is more likely to be perceived as suffering.

I conclude from these examples that control, in all its forms and effects, is key to understanding suffering. Control includes being able to take action, for example to avoid pain, as well as the ability to access and understand information to predict the occurrence, duration, and severity of the pain (for more on the benefits of control to wellbeing, see Chapter 6, this volume). These factors fall under the concept of agency. The literature on agency as a component of animal welfare has advanced greatly over the past few years. In the section below I will briefly review some of the key ideas from this literature, and discuss how these can be applied to better understand suffering in animals.

12.4 Agency

Research on quality of life in humans illustrates that assessments of our own well-being are only partially related to what we have. Our sense of agency (how we gain access to the things we value, including our ability to learn about different outcomes and to make informed choices) is also critical (Higgins, 2012). Recent thinking in the animal welfare literature has begun to argue that such processes are central to the welfare of nonhuman animals as well (Špinka and Wemelsfelder, 2011; Franks and Higgins, 2012; Špinka, 2019).

Špinka and Wemelsfelder (2011) defined agency as 'the propensity of an animal to engage actively with the environment with the main purpose of gathering knowledge and enhancing its skills for future use', and added that this will include 'goaloriented behavioural sequences such as foraging, mate seeking and predator avoidance' as well as 'agency-based patterns such as exploration and play'. As further explained by Špinka and Wemelsfelder, the ability to express these aspects of agency may be beneficial to welfare by improving feelings of competence and allowing animals to improve their success in dealing with environmental and social challenges. These authors also discussed how the lack of opportunity to express agency can be negative for animal welfare, for example by inducing feelings of boredom (increasingly recognized as a welfare harm; see Meagher, 2019) and even affecting measures of health. Most importantly from the perspective of the current chapter, they linked diminished agency with increased negative affect. For example, they argued that 'declining agency may affect welfare ... through the consequences of underdeveloped competence, such as heightened fear and anxiety and compromised social coping', and that 'animals from impoverished backgrounds may be overwhelmed by events when they arise, fail to cope and experience intense fear or anxiety'. The sense of being overwhelmed, failing to cope, and experiencing intense fear and anxiety correspond with how human patients characterize suffering as discussed in the previous section.

Špinka and Wemelsfelder (2011) also suggested that keeping animals in low agency conditions can result in them becoming 'less well able to classify and evaluate perceived environmental stimuli, and will be less ready to deal with challenges once they arise'. I will return to ideas about the perceptual and cognitive capacities in the next section.

Špinka (2019) proposed four categories of agency:

passive/reactive (animal being behaviourally passive or purely reactive), action-driven (animal behaviourally pursuing current desirable outcomes), competence building (animal engaging with the environment to gain skills and information for future

D.M. Weary

use), and aspirational (the animal achieving longterm goals through planning and autobiographical reflection).

The passive/reactive category includes the simplest and arguably most fundamental aspects of agency, and the aspirational category includes the autobiographical component that juxtaposes well with concerns about sense of self described in the human suffering literature. Also convenient is that the intermediate categories (action and competence building) link with the conceptions of Franks and Higgins (2012) ('control effectiveness' and 'truth effectiveness', respectively), as described below.

Franks and Higgins (2012) center their ideas around the concept of 'effectiveness', suggesting that 'animals want to be successful in having desired results (value effectiveness), establishing what is real (truth effectiveness), and managing what happens (control effectiveness)'. They conclude that high welfare results 'when these three domains work together to create organizational effectiveness'.

The first of these domains (value effectiveness) is the easiest to grasp as it fits neatly into traditional conceptions of well-being as in having what you want. This will include access to suitable housing, food and water, social companionship, etc., as well as having pleasurable experiences and avoiding painful or otherwise unpleasant experiences.

The second domain (truth effectiveness) is the motivation for information and understanding about the physical and social environment; this helps the animal avoid confusion and develop a sense of confidence in their knowledge of the world around them. Truth effectiveness is established, in humans at least (Higgins, 2012), by asking questions like 'What is that?', 'Why did this happen?', 'Is this what I expected?', and 'Are my beliefs consistent with those of my group mates?', questions that correspond well with the Bayesian framework discussed in the next section of this chapter. Franks and Higgins (2012) provide many examples showing how animals appear motivated to learn and acquire information about their world, even about features that may be fearinducing or dangerous.

The third domain (control effectiveness) relates to the animal's motivation to exert control over themselves (e.g., perform the behaviors they are motivated to perform) and over the physical and social environment in which they live (e.g., where they sleep, what they eat, and whom they interact with). As with the other domains, exerting control effectiveness may be a way of getting what you want (i.e., achieving value effectiveness, in this case a comfortable bed, a good meal, and some time with a friend), but it is also considered inherently important. Thus, animals may be motived to exert some choice, regardless of whether this provides them access to better options. Animals may also be motivated to work for access to options, even if they can have access to the same options for free (called 'contrafreeloading').

In Section 12.3 on human descriptions of suffering I reviewed how the inability to perceive or process information from the world around us can be an important contributor to suffering in our species, and how the experience of severe negative affective states like pain and fear can reduce our ability to sense and comprehend environmental cues. In the current section on agency I have reviewed the related conceptions of 'competencebuilding agency' (Špinka, 2019) and 'truth effectiveness' (Franks and Higgins, 2012), which argue that animals are inherently motivated to perceive and learn from environmental cues and to use this information to inform their actions (i.e., 'control effectiveness' and 'action-driven agency'), and to ultimately obtain the things they desire (i.e., 'value effectiveness'). Together, these ideas indicate that a reduced ability to perceive and make sense of new information, and use this to inform our actions, contributes to the experience of suffering.

12.5 The Bayesian Mind

12.5.1 Bayes' theorem and its application to pain

Over the past decade an important idea has begun to transform the way we think about cognitive processes in humans and other animals: the way we perceive and understand cues from our environment is affected by our expectations, and vice versa (Clark, 2015). In this section I will briefly introduce Bayes' theorem and its influence on the way we think about animal cognition in general and pain perception in particular.

According to Bayes' theorem, our belief about the probability of an event is based on prior expectations, updated by any new data that are available. To illustrate the power of this simple idea, consider the example of a coin toss. If you were to take a coin and toss it five times and each time the coin came up 'heads', how certain would you be that the coin had 'heads' on both sides? To be sure, five out of five heads is a rare result with a fair coin, and would only be expected to occur by chance about 3% of the time. But in addition to considering the results of this specific test, the Bayesian would ask about 'priors'; that is to say, their belief that the coin was fair before they received the results of the coin toss. Say that for this type of coin it was known that only one in a million were two-headed. According to Bayes' theorem, this prior should be considered in combination with the test result; the combined probability is still small, showing that despite the unusual sequence of heads it is still unlikely that the coin is two-headed.

Humans or other animals do not routinely calculate exact probabilities, but this is not required of Bayesian conceptions of cognition (Sanborn and Chater, 2016). The important point is that we do not simply respond to our bottom-up perceptions. Our top-down expectations affect what we perceive and how we make sense of these perceptions, and our experiences contribute to future expectations. This process is described by Ongaro and Kaptchuk (2019) as follows:

The nervous system is constantly dealing with a continuous and potentially overwhelming stream of varying signals coming from our body and senses. For the sake of adaptation, the brain must turn this confused play of sensory inputs and neural firings into a reliable perception of the world. Debate in cognitive science has revolved around how exactly the brain accomplishes this task. While previous theories, in line with the current biomedical model of disease, viewed perception mostly as a bottom-up readout of sensory signals, emerging Bayesian models suggest, instead, that perception is cognitively (mostly nonconsciously) modulated, and might be best viewed as a process of prediction, based on an integration of sensory inputs, prior experience, and contextual cues.

The value of this Bayesian perspective is well illustrated with examples from the pain literature. In one experiment on human subjects, Kessner *et al.* (2014) trained some participants to believe that a (placebo) cream was an effective analgesic, and others that the same cream was ineffective. When these participants were later re-tested with a 'new' (placebo) cream, those with positive experiences rated the cream as providing superior analgesic effects. In another elegant experiment, Hoskin *et al.* (2019) showed that expectations regarding both the magnitude and variance in pain stimuli affect perceptions.

In the words of Wiech and Tracey (2013) 'the prospect of pain relief' strengthens the placebo effect for patients with positive experiences, and more generally explains why placebo effects occur at all (i.e., the expectations of benefit help drive the perception of a benefit). The opposite case to the placebo effect (i.e., when expectations that pain will be bad make the perception painful, even in the absence of afferent inputs that would normally be considered nociceptive) is of equal interest. As explained by Ongaro and Kaptchuk (2019), 'In a condition of chronic pain, the brain may nonconsciously initiate visceral sensations (e.g., stomach tension) that match the hypothesis of being in pain.' In this case the Bayesian brain works to 'conform inputs to predictions, even if at the detriment of subjective well-being'. (For a review of the placebo effect in animals, see McMillan, 1999.)

12.5.2 Learning about pain

If expectations are driven at least in part by our previous experiences then understanding how and what animals learn from these experiences is important. A number of basic ideas from learning theory can help explain how bad experiences (such as those associated with pain) may be made worse (see Vlaeyen, 2015 for review). As a simple example, take the process of stimulus generalization (i.e., that responses will be similar to similar stimuli). The adaptive value of this process is clear: it helps reduce the risk that animals will fail to respond appropriately to biologically similar stimuli. For example, following an unsuccessful charge from a lion the potential prey animal would benefit from learning to fear not just that specific lion, but also others like it (e.g., other lions, other large cats, etc.). However, in captive settings at least, it is easy to see how stimulus generalization may also be detrimental for animals. For example, following a procedure in which a cow is restrained and vaccinated by the herd veterinarian, the animal may become more fearful not just of that veterinarian, but also others like her (e.g., all women, all people wearing blue coveralls, etc.), such that the animal experiences fear in many situations for which there is no real risk to the animal.

Fear conditioning is another example of a learning process that can make a bad experience worse. In the classic case of 'Little Albert' (Watson and Rayner, 1920), the human infant subject (Albert) at first showed no fear when presented with a rat or

160 D.M. Weary

other animals, but cried when he heard the sound of a loud clang (produced by hitting a metal bar with a hammer). Albert was then exposed to the clang every time that he was shown the rat. After just a few pairings Albert began to show fear responses to the rat. This conditioned fear response also generalized so that Albert became fearful of a range of other animals. Practically this is important because conditioned fear responses make otherwise innocuous stimuli fearful. For example, if the first time a beef calf is introduced to a squeeze chute it is castrated or dehorned, then it is likely to develop a conditioned fear response of the chute. Thus, the animal is likely to show a fear response to (and aversion to enter) the chute on future occasions, so even when the chute is used for other reasons it is likely to be perceived as negative by the calf.

For group living animals, a particularly salient cue is the behavior of group mates. Given that animals are highly motivated to acquire information from relevant environmental cues, following Spinka's (2019) conceptions of 'competence-building agency' and Franks and Higgins' (2012) conception of 'truth effectiveness', the presence of group mates is likely to be considered positive. Moreover, from a Bayesian perspective the presence of certain social partners will also affect expectations. For example, when animals are with group mates with whom they have had a long history of socio-positive interactions their expectations are likely to be positive (and vice versa).

Unknown animals are sometimes considered a social threat and in this case their presence would be likely to induce negative expectations, accentuating the animal's perception of pain and other negative affective states. Consistent with this idea, Langford *et al.* (2011) found that when male mice were exposed to mild social stress via proximity to an unknown male they showed stronger responses to pain stimuli. Another way to consider social threat is that the social partner intends to harm them. Peeters and Vlaeyen (2011) showed that when human participants believed that a social partner intended to cause them harm they rated a pain stimulus as more painful.

These examples show how an understanding of learning processes, like generalization, fear conditioning, and attention to social cues, can help account for how animals form their beliefs about the world. According to the Bayesian perspective, these beliefs will in turn affect how the animal is likely to perceive pain. The Bayesian perspective

also requires that animals update their expectations based upon their ongoing experiences, requiring they attend to and process important inputs coming from their own bodies and the external world. Unfortunately, as discussed in the next section, the experience of pain can interfere with perception and other cognitive processes in important ways.

12.5.3 The effects of pain on perception and cognition

Pain is known to interfere with perception and cognition (Eccleston and Crombez, 1999). This 'interruptive' function of pain is likely of considerable value under many circumstances. For example, upon feeling a sudden pain in your toe, it is generally a good idea to stop walking and make sure you have not stepped on a sharp object. But here again we see the influence of expectations. For example, patients who express greater fear of their pain are more likely to be distracted by painful experiences (Crombez et al., 2013), and individuals who possess especially negative beliefs about pain (i.e., those likely to catastrophize their symptoms) are less able to disengage from the pain and attend to other things (Van Damme et al., 2004). These results suggest that the distracting effect of pain is likely to be especially severe for individuals who have negative expectations around pain.

The cognitive demand of pain interferes with the ability to attend to and comprehend other cues. Wiech and Tracey (2013) argue that our attentional capacity is limited such that pain may 'engage full capacity in relevant processing and leave no spare capacity to other processes' and that these effects are likely to be more 'prominent the higher the pain intensity and the more difficult the task'. From this perspective, feelings of pain (perhaps combined with associated fear) can be seen as squeezing out other perceptual inputs and preventing cognitive processing; this perceptual and cognitive 'shutting down' may then interfere with the Bayesian process of updating priors (i.e., our beliefs and expectations about future events).

If the act of learning about the world (i.e., 'competence-building agency'/truth effectiveness') is in itself a highly motivated component of welfare, and the lack of this knowledge undermines other important aspects of agency (including the ability to make good decisions and thus direct behaviors in ways that they are likely to be effective), then we can see how these processes can

combine with the potential of having a much greater impact on the animal's welfare.

12.5.4 Suffering, agency, and the Bayesian mind

The examples discussed above show how Bayesian priors (positive in the case of placebos and negative in the case of chronic pain) can result in nociceptive inputs being perceived as neutral and neutral inputs being perceived as painful. We also saw how learning mechanisms, essential to updating priors, can mitigate and compound painful experiences, sometimes making these much worse. Finally, we learned how painful experiences can interfere with perception and other cognitive processes. In the section that follows I will argue that this Bayesian conception of pain experiences, together with a recognition of the importance of agency to considerations of animal welfare and human well-being, can help us understand how pain becomes suffering.

Let us start where we left off at the end of the previous section: with the idea that the experience of intense pain can cause a type of perceptual and cognitive shutting down. We saw earlier the argument that the Bayesian mind relies upon constant updating to build and maintain useful priors, perhaps explaining why animals are so motivated to learn about the world as we reviewed in the section on agency. Thus, taken together, an animal experiencing pain that is sufficiently intense to reduce perceptual and other cognitive processing experiences the double harm of the pain itself and the reduced ability to update beliefs. The Bayesian mind may find this lack of updates especially distressing, perhaps directly but also because it undermines confidence in the belief structure that is needed to make sense of new inputs. More contentiously, perhaps the loss of cognitive processing reduces the animal's ability to even access or make sense of any existing priors, undermining its sense of self.

Imagine an animal in conditions of much reduced agency, for example, with limited ability to escape (due to a high level of confinement), to learn about the world (because information is withheld or not presented in a way that makes it easy to learn from), and to act on this information (with little opportunity to exert choice). Imagine that this animal is also experiencing pain in ways that compound the negative experience (e.g., via fear condition and in conjunction with social actors

that they believe wish to cause them harm). Imagine that the pain is sufficiently intense that it begins to limit cognitive functioning, including the ability to sense new inputs, to learn from these, and perhaps undermines the animal's ability to access and make sense of any pre-existing beliefs, even undermining the animal's sense of self. Put these elements together intentionally and we seem to have the Organization of American States' (1985) definition of torture encountered earlier in this chapter: an attempt to 'obliterate the personality of the victim or to diminish his physical or mental capacities'. Following this logic, I suggest that it is this combination of factors that should be considered in attempts to distinguish the experience of pain, fear, and other negative affect from the experience of suffering (Table 12.2).

One real-world example of a management practice in which these factors are intentionally combined to undermine the personality of an animal is the process of *phajaan*, or 'breaking' of young elephants. According to Kontogeorgopoulos (2009), the elephant calf is separated from its mother, restrained in a crush or shackled by the legs, and goaded by the mahout using an ankus or other tools to inflict pain, with the explicit intention of removing the will of the animal to act independently. A Western example that arguably includes similar elements is the traditional practice of 'breaking' horses.

There are also more common examples where these factors come together, potentially putting animals at risk of suffering. Animals are often restrained for painful procedures, with little opportunity to avoid these. Sometimes handling involves blinds or other tools so that the animal is unable to see or understand what the handler is doing, further interfering with the animal's ability to respond. Animals are often removed from their social group when subjected to painful procedures on farms; even companion animals may be removed from their owners when undergoing painful procedures at a veterinary clinic. This combination may turn a relatively innocuous procedure into an event that is much more distressing for the animal, and this may be especially likely for procedures associated with more severe and sustained pain (like surgery and the resulting post-operative pain). Such effects can be expected to increase if animals experience the noxious event repeatedly, as the animal is likely to develop learned fear responses to the people and facilities associated with the procedure.

D.M. Weary

Table 12.2. Factors likely to contribute to sensations of suffering in animals.

Factor	Description
Agency ^a	
Passive/reactive	Unable to escape harm
Competence building	Unable to learn about potential threats
Action drive	Unable to pursue desirable/avoid undesirable outcomes
Aspirational	Unable to plan or reflect
Bayesian	
Updating priors ^b	Unable to perceive and interpret relevant cues
Accessing priors ^c	Unable to access pre-existing beliefs
Learning	· · ·
Fear conditioning	Learnt associations between harm and previously neutral cues such that these too become fear inducing
Social factors	Lack of social support/presence of social threat

^aAs defined by Špinka (2019); see also Franks and Higgins (2012) for related conceptions but using a different terminology.

12.6 Assessing Suffering in Animals

The checklist in Table 12.2 provides a useful starting point in considering what types of situations are more likely to result in animal suffering. But this list of factors is likely incomplete, and at this stage there is little research available to determine which of these should be considered necessary or sufficient. Also, in many cases we may be unsure of the history of the case, making it more difficult to know if the animal understands its capacity to escape or respond to a threat, whom it perceives as providing social support or posing a social threat, the extent to which it has developed conditioned fear responses, etc. For these reasons, it is necessary to consider what scientific tools could be used to identify cases of animal suffering.

Suffering is often associated with reports of low mood in human patients. In recent years a number of approaches have been developed for identifying low mood in animals including judgment bias testing (Mendl et al., 2009; Roelofs et al., 2016), assessing depression-like forms of inactivity (including that associated with learned helplessness; Fureix and Meagher, 2015), anhedonia testing (i.e., reduced motivation to consume rewards and less pleasure in their consumption; Treadway and Zald, 2011), and reductions in anticipatory behavior (van der Harst and Spruijt, 2007) (see also Chapter 23, this volume). All types of response can be seen as reflective of a general decline in previously motivated behaviors. The animal behavior literature provides a wide range of methods to record the frequency and duration of behaviors and to assess changes in motivation to express these behaviors and access desirable resources (Fraser and Nicol, 2011). Thus, evidence of any of these responses in conjunction with a painful experience may be seen as indicative of suffering. That said, it is important to distinguish between behaviors that decline as a direct result of the pain (i.e., because performing the behavior is now painful) and those behaviors that reduce in frequency as a result of changes in mood indicative of depression; the latter (i.e., pain accompanied by evidence of depression) provides stronger evidence of suffering.

In addition to these general indicators of low mood, the literature on Bayesian conceptions of pain can be used to generate a variety of additional approaches. As reviewed earlier, a considerable body of literature on pain in humans illustrates the importance of expectations on our experiences. Similar work is now required to better understand how animals develop priors regarding painful experiences, and how these expectations are updated and used by animals in directing their perception, learning, and behavioral choices. One obvious prediction is that animals conditioned to have positive expectations regarding pain will show less evidence of pain response, and vice versa. Relatedly, when painful situations have also become fear inducing (via fear conditioning), pain responses are likely to increase.

Given that more intense experiences of pain are expected to cause a decline in perceptual processing and other cognitive functioning, future studies could specifically seek to document these cognitive

^bRelated to the 'competence-building' agency defined in Section 12.4.

[°]Related to both the 'competence-building' and 'aspirational' agency defined in Section 12.4.

declines. Specifically, this work could determine which types of painful experiences are associated with a decline in the animal's ability to sense and attend to environmental cues, to perform cognitively demanding tasks, and to learn new associations. One value of this approach is that it may provide a type of qualitative threshold, in that it could distinguish pain that interferes with normal cognitive functioning versus pain that does not.

Relatedly, new work could specifically examine memory recall, as the ability to access one's beliefs about the world is essential to any Bayesian reasoning and perhaps encompasses at least part of what can be considered a sense of self. Given the importance of the latter concept to considerations of agency (especially aspirational agency; Špinka, 2019), and that threats to this sense of self are an important element in human descriptions of suffering, developing innovative methods of addressing sense of self in animals would be of value. One idea is to examine changes in affiliative behaviors and social relationships. Specifically, animals with a diminished sense of self may no longer distinguish between novel and familiar pen mates, or even novel and previously preferred social partners (a lack of interest in affiliative social relationship could also be a sign of anhedonia). More speculatively, a more complete destruction of this sense of self may result in changed personality traits, and the development of new social relationships (perhaps including with the persons who inflicted the suffering, as occurs in Stockholm syndrome; see Cantor and Price, 2007).

The ideas listed above should not be considered complete. Rather, these provide a cautious starting point for new research explicitly formulated to address concerns about animal suffering. I began this chapter with what I hope is an uncontentious claim: the alleviation and prevention of suffering is one of our core responsibilities to the animals in our care. The combination of a list of factors to consider if an animal is at risk of suffering, as provided in Table 12.2, and the development of scientific approaches to better assess if indeed an animal is suffering, will I hope provide some practical basis to meeting this responsibility.

12.7 Concluding Remarks

 The existing literature in animal welfare science uses the term suffering in three ways: as an

- embellishment when we describe negative affect in animals, to imply conscious experience of negative affect, and to identify negative affect that is severe or prolonged.
- In contrast, human patients most commonly characterize their condition as suffering when negative affective states are combined or interact when this undermines a person's sense of self, and when this is associated with low mood.
- Agency is now considered an important component of animal welfare. The concept of agency extends from simply the ability to avoid noxious stimuli, to learn about the environment, to plan and take actions, and to reflect about individual beliefs in a way that contributes to a sense of self.
- Our understanding of how animals experience pain has been transformed by Bayesian conceptions of animal cognition. The key element is that perceptions are driven not simply by current afferent inputs, but also by the animal's expectations that direct attention and change the way that bottom-up inputs are evaluated.
- Taken together, a consideration of animal agency and Bayesian pain processing provide a novel basis for understanding animal suffering. Specifically, painful experiences in combination with low agency conditions and conditions which interfere with Bayesian processing are more likely to result in suffering.
- I have proposed a number of scientific approaches to assessing suffering in animals. In combination with evidence of pain, these include low mood, reduced cognitive functioning, and perhaps threats to the animal's sense of self.

Acknowledgments

I am grateful to Lucia Amendola, Thomas Ede, Benjamin Lecorps, Julia Lomb, and Frank McMillan for comments on earlier drafts of the manuscript. I also gratefully acknowledge NSERC for funding my research related to this topic via a Discovery grant (RGPIN-2016-04620).

Note

¹ This chapter is a revision and elaboration of ideas first addressed in 'What is suffering in animals?' (Weary, 2014); here I develop the idea that the lack of relevant agency, and expectancies regarding negative affective experiences, contribute to the experience of suffering.

D.M. Weary

12.8 References

- Cantor, C. and Price, J. (2007) Traumatic entrapment, appeasement and complex post-traumatic stress disorder: Evolutionary perspectives of hostage reactions, domestic abuse and the Stockholm syndrome. Australian and New Zealand Journal of Psychiatry 41, 377–384. http://dx.doi.org/10.1080/00048670701 261178.
- Cassell, E.J. (1982) The nature of suffering and the goals of medicine. *New England Journal of Medicine* 306, 639–645. http://dx.doi.org/10.1056/NEJM198203183 061104.
- Cassell, E.J. (1999) Diagnosing suffering: A perspective. Annals of Internal Medicine 131, 531–534. http://dx.doi.org/10.7326/0003-4819-131-7-199910050-00009.
- Chandroo, K.P., Duncan, I.J.H., Moccia, R.D. (2004) Can fish suffer? Perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science* 86, 225–250. http://dx.doi.org/10.1016/j. applanim.2004.02.004.
- Clark, A. (2015) Surfing Uncertainty: Prediction, Action, and the Embodied Mind. Oxford University Press, Oxford, UK.
- Crombez, G., Viane, I., Eccleston, C., Devulder, J., Goubert, L. (2013) Attention to pain and fear of pain in patients with chronic pain. *Journal of Behavioral Medicine* 36, 371–378. http://dx.doi.org/10.1007/s10865-012-9433-1.
- Dawkins, M. (1977) Do hens suffer in battery cages? Environmental preferences and welfare. *Animal Behaviour* 25, 1034–1046. http://dx.doi.org/10.1016/0003-3472(77)90054-9.
- Dawkins, M.S. (1980) Animal Suffering: The Science of Animal Welfare. Chapman and Hall, New York, USA. http://dx.doi.org/10.1007/978-94-009-5905-7.
- Dawkins, M. (1990) From an animal's point of view: Motivation, fitness, and animal welfare. *Behavioral and Brain Sciences* 13, 1–9. http://dx.doi.org/10.1017/S0140525X00077104.
- Eccleston, C., and Crombez, G. (1999) Pain demands attention: A cognitive-affective model of the interruptive function of pain. *Psychological Bulletin* 125, 356–366. http://dx.doi.org/10.1037/0033-2909. 125.3.356.
- Elwood, R.W. (2011) Pain and suffering in invertebrates? ILAR Journal 52, 175–184. http://dx.doi.org/10.1093/ilar.52.2.175.
- Franks, B. and Higgins, E.T. (2012) Effectiveness in humans and other animals: A common basis for well-being and welfare. *Advances in Experimental Social Psychology* 46, 285–346.
- Fraser, D. (2008) Understanding animal welfare. *Acta Veterinaria Scandinavica* 50, S1. http://dx.doi.org/10.1186/1751-0147-50-S1-S1.
- Fraser, D. and Nicol, C.J. (2011) Preference and motivation research. In: Appleby, M.C., Mench, J.A., Olsson,

- I.A.S., Hughes, B.O. (eds.) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK, pp. 183–199. http://dx.doi.org/10.1079/9781845936594.0183.
- Fureix, C. and Meagher, R.K. (2015) What can inactivity (in its various forms) reveal about affective states in non-human animals? A review. *Applied Animal Behaviour Science* 171, 8–24. https://doi.org/10.1016/j.applanim.2015.08.036.
- Higgins, E.T. (2012) Beyond Pleasure and Pain: How Motivation Works. Oxford University Press, New York, USA.
- Hoskin, R., Berzuini, C., Acosta-Kane, D. El-Deredy, W. Guo, H., et al. (2019) Sensitivity to pain expectations: A Bayesian model of individual differences. Cognition 182, 127–139. http://dx.doi.org/10.1016/j.cognition. 2018.08.022.
- Hughes, B.O. and Duncan, I.J.H. (1988) The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour* 36, 1696–1707. http://dx. doi.org/10.1016/S0003-3472(88)80110-6.
- Kessner, S., Forkmann, K., Ritter, C., Wiech, K., Ploner, M., et al. (2014) The effect of treatment history on therapeutic outcome: Psychological and neurobiological underpinnings. PLoS ONE 9, e109014. https://doi.org/10.1371/journal.pone.0109014.
- Kontogeorgopoulos, N. (2009) The role of tourism in elephant welfare in northern Thailand. *Journal of Tourism* 10. 1–19.
- Langford D.J., Tuttle, A.H., Briscoe, C., Harvey-Lewis, C., Baran, I., et al. (2011) Varying perceived social threat modulates pain behavior in male mice. The Journal of Pain 12, 125–132. http://dx.doi.org/10.1016/j.jpain. 2010.06.003.
- McMillan, F.D. (1999) The placebo effect in animals. Journal of the American Veterinary Medical Association 215, 992–999.
- Meagher, R.K. (2019) Is boredom an animal welfare concern? Animal Welfare 28, 21–32. http://dx.doi.org/10.7120/09627286.28.1.021.
- Mendl, M., Burman, O.H.P., Parker, R.M.A., Paul, E.S. (2009) Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science* 111, 161–181. http://dx.doi.org/10.1016/j.applanim.2009. 02.023.
- Ongaro, G. and Kaptchuk, T.J. (2019) Symptom perception, placebo effects, and the Bayesian brain. *Pain* 160, 1–4. http://dx.doi.org/10.1097/j.pain. 00000000000001367.
- Organization of American States. (1985) Inter-American Convention to Prevent and Punish Torture, *OAS Treaty Series*. Available at: http://www.oas.org/juridico/english/treaties/a-51.html (accessed 30 March 2019).
- Peeters, P.A.M. and Vlaeyen, J.W.S. (2011) Feeling more pain, yet showing less: The influence of social threat on pain. *The Journal of Pain* 12, 1255–1261. http:// dx.doi.org/10.1016/j.jpain.2011.07.007.

- Roelofs, S., Boleij, H., Nordquist, R., van der Staay, F.J. (2016) Making decisions under ambiguity: Judgment bias tasks for assessing emotional state in animals. Frontiers in Behavioral Neuroscience 10, 119. http:// dx.doi.org/10.3389/fnbeh.2016.00119.
- Sanborn, A.N. and Chater, N. (2016) Bayesian brains without probabilities. *Trends in Cognitive Sciences* 20, 883–893. http://dx.doi.org/10.1016/j.tics.2016.10.003.
- Sherwin, C.M. (2001) Can invertebrates suffer? Or, how robust is argument-by-analogy? *Animal Welfare* 10, 103–118.
- Snyder, C.R. (2004) Physical pain ≠ suffering: A personal commentary on coping. *Journal of Loss and Trauma* 10, 51–71. http://dx.doi.org/10.1080/1532502049089065.
- Špinka, M. (2019) Animal agency, animal awareness and animal welfare. *Animal Welfare* 28, 11–20. http://dx.doi.org/10.7120/09627286.28.1.011.
- Špinka, M. and Wemelsfelder, F. (2011) Environmental challenge and animal agency. In: Appleby, M.C., Mench, J.A., Olsson, I.A.S., Hughes, B.O. (eds.) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK, pp. 27–43. http://dx.doi.org/10.1079/9781845936594.0027.
- Treadway, M.T. and Zald, D.H. (2011) Reconsidering anhedonia in depression: Lessons from translational neuroscience. Neuroscience and Biobehavioral Reviews 35, 537–555. http://dx.doi.org/10.1016/j. neubiorev.2010.06.006.
- Van Damme, S., Crombez, G., Eccleston, C. (2004) Impaired disengagement from pain: The role of

- catastrophic thinking about pain. *Pain* 107, 70–76. http://dx.doi.org/10.1016/j.pain.2003.09.023.
- van der Harst, J.E. and Spruijt, B.M. (2007) Tools to measure and improve animal welfare: Reward-related behaviour. *Animal Welfare* 16, 67–73
- Vlaeyen, J.W.S. (2015) Learning to predict and control harmful events: Chronic pain and conditioning. *Pain* 156, S86–S92. http://dx.doi.org/10.1097/j.pain. 00000000000000107.
- Watson, J.B. and Rayner, R. (1920) Conditioned emotional reactions. *Journal of Experimental Psychology* 3, 1–14. http://dx.doi.org/10.1037/h0069608.
- Weary, D.M. (2014) What is suffering in animals? In: Appleby, M.C., Weary, D.M., Sandøe, P. (eds.) Dilemmas in Animal Welfare. CAB International, Wallingford, UK, pp. 188–202. http://dx.doi.org/10.1079/ 9781780642161.0188.
- Weary, D.M., Droege, P., Braithwaite, V.A. (2017) Behavioural evidence of felt emotions: Approaches, inferences and refinements. Advances in the Study of Behavior 49, 27–48. https://doi.org/10.1016/bs. asb.2017.02.002.
- Webb, L.E., Veenhoven, R., Harfeld, J.L., Jensen, M.B. (2019) What is animal happiness? *Annals of The New York Academy Of Sciences* 1438, 62–76. http://dx.doi.org/10.1111/nyas.13983.
- Wiech K. and Tracey, I. (2013) Pain, decisions, and actions: A motivational perspective. Frontiers in Neuroscience 7, 46. http://dx.doi.org/10.3389/fnins. 2013.00046.

D.M. Weary

Mental Illness in Animals: Diagnostic Considerations Using Selected Mental Disorders

KAREN L. OVERALL

Biology Department, University of Pennsylvania, Philadelphia, Pennsylvania, USA and Atlantic Veterinary College, University of Prince Edward Island, Charlottetown, Prince Edward Island, Canada

13.1 Approaching Complex Situations

Diagnoses are not diseases; correlation is not causality. Conditions for which there is putative etiologic and pathophysiologic heterogeneity (multifactorial disorders) are complex, and nowhere is this truer than for the topic of fears, phobias, and anxieties. Diagnosis and treatment will be, by definition, complex. For example, fear and anxiety are probably closely related, but may not be identical at the neurophysiological level.

When one diagnoses a problem related to fear, anxiety, or aggression one is doing so at the level of the phenotypic or functional diagnosis; when medication is used such conditions are treated at the neurophysiological level. Diagnoses based on phenotype, function, and phenomenology will – when carefully constructed – allow us to ask about mechanisms at all subsequent levels, which will lead to better understanding for, screening of, treatment for, and prevention of behavioral conditions.

Some of the more reductionistic mechanistic or causal levels can be tested to some extent using treatment (the rare, very specific pharmacologic agents), but few phenotypic diagnoses can be specifically tested using behavior modification. Regardless, the logic for using very specific phenomenological diagnoses is to (i) assess and identify the particular behavioral manifestation that needs to be altered or assessed, and (ii) to identify areas where specific behavioral intervention can be useful (Overall, 1997a,b, 2013).

13.2 What is a Diagnosis?

Cautious and discrete use of terminology will lead to clear thinking. Phenotypic diagnoses are useful because they cluster together patients whose pathologies are more similar than they are different, but that differ from other pathologies in some major aspect of form or context. Phenotypic diagnoses may comprise a varying mechanistic population. For example, fear can be caused by neurodevelopmental delays that affect amygdala and hippocampal volume (Kim and Diamond, 2002; Mahar *et al.*, 2014; Schoenfeld *et al.*, 2017) or by some genetic change in a neurotransmitter that putatively affects how receptors and neurotransmitters interact (Campbell *et al.*, 2019).

The main problem in understanding behavioral conditions involves the fact that the act of exhibiting the behavior alters other mechanistic levels that then go on to alter the phenotype (Table 13.1; Fig. 13.1). The dynamism of behavior means that the pathology one sees now may not be the pathology that was seen last week. We know that many behavioral conditions in humans, rodents, and dogs progress if left untreated. How these conditions progress may depend on mechanism and endophenotypes. As we move toward precision medicine, these differences will become apparent and should shift how we group diagnoses. For us to benefit from emergent science we need to acknowledge that clear use of terminology helps to make apparent the parts of phenotypic diagnoses that are consistent, so that

Table 13.1. Understanding patterns of behavior within levels of a mechanistic approach. None of these levels is independent; the first four are very dynamic – actions that originate at any level may then affect the other levels, and the extent to which the levels interact is a function of the genetic response surface and learning. All levels other than phenotypic interact to produce mechanistic grouping of phenomenological diagnoses.

- A. Phenomenological, phenotypic, functional diagnoses: must meet diagnostic criteria that link clinical signs more in a way that this diagnostic grouping contains members whose behaviors are more similar, as a diagnostic group, to each other than they are to those with other diagnoses in some salient manner
 - B. Neuroanatomical/regional diagnoses
 - C. Neurochemical/neurophysiological diagnoses
 - D. Molecular/cellular diagnoses
 - E. Genetic diagnoses

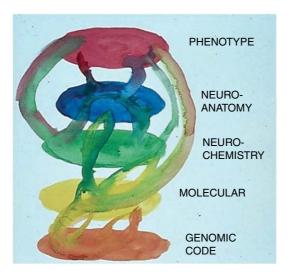


Fig. 13.1. Schematic showing how the levels of mechanistic diagnosis interact in a dynamic way to produce behavioral phenotypes.

we can understand and separate them from those that are more complex.

Behavioral diagnoses are made largely on the basis of constellations of nonspecific signs. Signs or descriptors are often erroneously or carelessly used as a diagnosis. By viewing a diagnosis mechanistically as a hypothesis to be tested it is possible to begin to define and understand abnormal behaviors at a variety of levels that include, but are not restricted to, the phenotypic, functional, and phenomenological diagnoses that are most commonly employed. The first step in this process is to define the criteria necessary for making the diagnosis by using the patterns of nonspecific signs in a contextual manner. Most canine and feline conditions are functional anxiety disorders, and this subset of psychiatric/behavioral pathologies across species is

sensitive to changes in external physical, social, and behavioral contexts. Accordingly, some diagnoses need to reflect these contextual contributions.

Separate clusters of phenotypes that are characterized by shared nonspecific signs may be 'endophenotypes' (Gottesman and Shields, 1972). For example, once the definitional criteria are met, condition A could sort into two phenotypic groups based on treatment response. In human psychiatry, assessments for the number of categories to which the patient responds and/or the intensity of the response have been used as one form of biomarker, particularly as they respond to treatment (Perlis, 2011). In the simplest scenario, group 1 responds only to drug 1 and group 2 responds only to drug 2, although behaviorally the groups are indistinguishable. A pattern like this would hint that two underlying mechanisms are functioning (Fig. 13.2). Condition B may also have a group that responds only to drug 2 and although these are different conditions, these two variants may be endophenotypes, sharing an underlying mechanism.

In another variant of this example, the definitional criteria are met, but group 1 most commonly displays signs 1–3 and group 2 displays signs 3–5. The question now becomes whether shared or separate mechanisms contribute to these clusters (Fig. 13.2). If these clusters are truly wholly separate at all levels of mechanism, one could rationally argue that these are two truly phenotypically separate diagnostic conditions, and that sign 3 is a truly nonspecific, noninformative sign for this level of inquiry.

When we know little about the mechanisms linking all levels of diagnosis we have broader, more inclusive diagnoses. To take the example of cognitive impairment in humans and cognitive dysfunction in dogs and cats, the list of potential pathological changes at levels below the phenotypic include plaque and tangle formation, vascular pathologies,

168 K.L. Overall

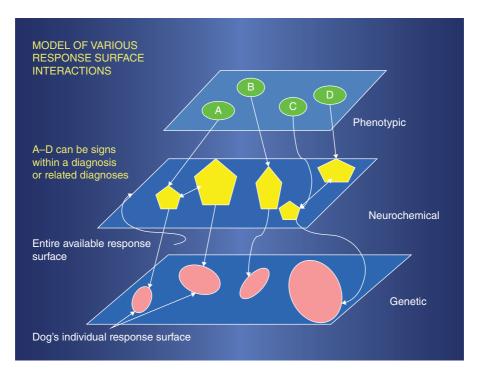


Fig. 13.2. Putative causal mechanistic patterns in signs or populations.

neurochemical deficits, cellular injury, inflammation, oxidative stress, mitochondrial changes, changes in genomic activity, synaptic dysfunction, disturbed protein metabolism, and disrupted metabolic homeostasis (Stephan et al., 2012). Some of these factors drive the behavior we see - e.g., the confusion, the decrease in problem solving ability - while some drive the accompanying physical factors we see - e.g., the locomotor and elimination changes. Finally, some of these factors may drive the neurodegeneration affecting these other changes. The situation is further complicated because some of what we see are simply derivative signs of damage due to disease progression. Such complexity renders an understanding of how behavioral signs interact with each other essential and also how tests of mechanisms are important. Few somatic diagnostic domains are so plastic and dynamic.

The genetic study of these behavioral and biological intermediate phenotypes/endophenotypes can identify patterns of behaviors that may act as markers for later pathology. For example, a group of 'high reactive' human male infants can be characterized by specific patterns of reactivity to visual, olfactory, and auditory stimuli. When these individuals are followed through time, subsequent complex social

behaviors including shyness or fearful interactions with strangers become apparent. There must be a mechanistic link between the earlier 'reactivity' and the later social fears, and in this example, the reactivity affects functioning of the amygdala (Schwartz et al., 2012). Yet we do not know if the altered functioning of the amygdala is due to changes in migration of neurons, altered pruning or arborization of the neurons, or altered synaptic spine density that then leads to decreases in synaptic density (Brennand et al., 2012). All of these processes have been implicated in autism spectrum disorder (ASD) in humans, and there is evidence for all of them causing one or more morphs of ASD. If these link to an intermediate functional endophenotype, we can more finely parse our phenotypic diagnosis in a way that short cuts how we seek treatment. If not, we may be able to develop a further series of diagnostic tests that suggests some treatment or prevention strategies are better than others for some subsets of patients with the diagnosis.

The implementation of 'necessary and sufficient' criteria, using the terms as they are used in logical and mathematical applications, is a refinement over descriptive definitions of terms. These act as

qualitative, and potentially quantitative, exclusion criteria, allowing for uniform and unambiguous assessment of aberrant, abnormal, and undesirable behaviors. A *necessary* criterion or condition is one that must be present for the listed diagnosis to be made. A *sufficient* criterion or condition is one that will stand alone to singularly identify the condition. Sufficiency is an outcome of knowledge: the more we learn about the genetics, molecular responses, neurochemistry, and neuroanatomy of any condition as well as its behavioral correlates, the more succinctly and accurately we will be able to define a sufficient condition.

These criteria are not synonymous with a compendium of signs associated with the condition, as discussed. The number of signs present and their intensity may be a gauge for the severity of the condition, or act as a flag when there can be variable, nonoverlapping presentations of the same condition. The pattern by which the signs cluster will help in defining heterogeneity of the underlying afflicted population, may identify endophenotypes, and will permit epidemiological studies and tests of underlying mechanisms to be conducted.

Implicit in this approach is that there is no known underlying somatic (physical/physiological) reason for the behavioral problem and that somatic 'causes' have been ruled out. It is also important to remember that classifications as discussed here represent diagnoses of problem behaviors, not just descriptions of a behavioral event (i.e., impulse control aggression can only be a diagnosis for an abnormal behavior, but 'protective aggression' can be both a diagnosis and description). The proposed terminology represents an attempt to create a terminology that is internally consistent, easily used because of its descriptive utility, and informative because of the manner in which it allows data (e.g., demography, associated nonspecific signs, etc.) to be collected and used to test ideas about various levels of mechanism, while concurrently avoiding psychological jargon. This is harder than it sounds.

This approach is actually similar to that taken by the American Psychiatric Association for the Diagnostic and Statistical Manual, and for the World Health Organization and International Classification of Diseases diagnostic guidelines. The required criteria for human psychiatric diagnoses are embedded within the descriptions of the conditions. Because large numbers of patients are seen in human psychiatry, subgroups of patients can be characterized by nonspecific signs, demography, treatment responses, etc., often within the diagnostic criteria. These groupings have

increasingly become the basis for diagnosis, without consideration of the original criteria. In other words, many diagnoses in human psychiatry are now actually based on nonspecific signs, and then assigned a label that may not reflect the biological reality. This failure is due, at least in part in the USA, to the need to have a diagnostic code to receive payment for health care or disability, and it is one reason that genome scans utilizing diagnostic codes have produced so little useful information. This failure in human psychiatry has led many researchers to suggest that we refocus on precision medicine, endophenotypes (Castellanos and Tannock, 2002), stratified diagnoses, and a research domain criteria (RDoC) approach that focuses on integrated response and presentation clusters (Insel et al., 2010; Kapur et al., 2012; Insel, 2014)

In the world view presented here, diagnosis and treatment is about both understanding the neurochemical changes that occur with learning and repeated exposure, and about becoming humane. To do this, we must begin to see the world from our animal patient's point of view, which requires that we understand normal ethology and behavioral ontogeny of that species. Heuristically, this approach minimally requires that we let go of labels which may say more about us and our needs than they do about the behavior. As the field of veterinary behavioral medicine advances we should become more mindful of terminology, issues, and approaches which can inadvertently do more harm than good.

The unclear distinction between normal aggression (the aggressor is truly threatened and aggressive behavior is adaptive) and abnormal aggression (there is no realistic threat to the aggressor) exists, and is a function of our lack of knowledge about how behavioral conditions develop. The extent to which an animal deviates from 'normal' in aggression or any other suite of behaviors may depend on ontogeny, multiple gene effects, and pleiotropic environmental effects. If anxiety-based aggression has a causal pattern similar to other anxiety-based conditions like obsessive-compulsive disorder (OCD), both a familial or genetic 'predisposition' and a social stressor play roles in the development of the aggression (Overall and Dunham, 2002).

13.3 Understanding Different Levels of Mechanistic Interaction

Identification of a diagnosis using definitional criteria represents an algorithmic approach that clusters

170 K.L. Overall

behaviors of patients that are more similar to each other and separates them from those less similar. This clustering, or labeling as a diagnosis, does not mean that patients will be equally afflicted, or that they are all exhibiting the same underlying pathology even if their behavior is the same (see Table 13.2). This approach acknowledges variability in cause, variability in presentation, and that there may not be a unitary causal mapping.

The value of a phenotypic diagnosis should be to help the clinician and client alike to understand the provocative circumstances that can induce a worsening or an improvement in the behavior and the distress that goes with it. Examples for four sets of conditions – canine impulse control aggression, canine separation anxiety, canine noise reactivity and phobia, and canine and feline OCD – will make clear the value of these approaches (Table 13.3). There are now sufficient data for these conditions so that we can examine patterns of pathology for at least one other level than the phenotypic one, and for some putative endophenotypes.

13.3.1 The evolving story of impulse control aggression

Aggression is best defined as an appropriate or inappropriate, interspecific or intraspecific challenge, threat, or contest resulting in deference or in combat and resolution (Overall, 1997a). The importance of context cannot be over emphasized in any evaluation of aggression.

Most abnormal aggressions are the result of underlying anxiety (Overall, 1997a, 2000; King *et al.*, 2000). Some of the best data for aberrant or abnormal

aggression involve one of the most controversial canine behavioral diagnoses: impulse control aggression (formerly called 'dominance aggression' and sometimes now called 'conflict aggression' or 'aggression to humans'; [Luescher and Reisner, 2008]). Impulse control aggression is about control, or access to control, in direct social situations involving humans. This discrete definition has the advantage of not coupling the challenge to food (food-related aggression), toys (possessive aggression), or space (territorial aggression). These types of aggression can all be correlates of impulse control aggression and when associated with it may be indicative of a more severe situation. This diagnosis cannot be made on the basis of a one-time event.

This approach is a radical departure from the common descriptions of this aggression that specify that the dog will often react to being pushed on, to being corrected with a leash, or to being pushed from a sofa or a person. The number of situations in which the dog reacts inappropriately or the intensity with which he or she reacts do not affect the necessary and sufficient conditions, although these factors may affect the ability to treat the condition, the risk to people, and the prognosis.

The range of behaviors manifest in this condition includes postural threats and stares to sudden stiffening and bites. This is the primary category of canine aggression in which little to no obvious warning is given (Borchelt, 1983). Careful observation may reveal pupil dilation and a slight stiffening immediately prior to the aggression. The classically afflicted dog growls, lunges, snaps, or bites if they are stared at, physically manipulated – often when reaching over their head to put on a leash, physically

Table 13.2. Example for consideration of interaction of phenotypic level of mechanism with others. In this example two variants in the condition are due to some difference in environmental response. This could be a purely phenotypic effect (abnormal variant B). Alternatively, the effect could be due to learning and long-term potentiation (in which case the molecular level is affected – abnormal variant A); this molecular effect also affects neurochemistry. The effect could also be one of a shift in neurochemistry, without affecting the molecular level in any kind of meaningful way (abnormal variant C). Finally, one could have an abnormal variant due to a genetic polymorphism (abnormal variant D; phenotype E). Phenotypes A, B, C, and E all look the same and different from D without provocative tools (tests or biomarkers) to identify them.

	Α	В	С	D	E
Behavioral phenotype	Abnormal Variant A	Abnormal Variant B	Abnormal Variant C	Normal Variant D	Abnormal
Neuroanatomical phenotype	I	1	I	1	
Neurochemical phenotype	а	b	а	b	а
Molecular/cellular phenotype	ľ	II'	II'	II'	ľ
Genotype	b'	b'	b'	b'	a'

Table 13.3. Necessary and sufficient conditions for selected behavioral diagnoses discussed in the text (adapted from Overall, 1997b, 2013):

Behavioral diagnosis	Necessary conditions	Sufficient conditions	
Impulse control aggression (canine)	Abnormal, inappropriate, out-of-context aggression (threat, challenge, or attack) consistently exhibited by the dog toward people under any circumstance involving passive or active control of the dog's behavior or the dog's access to the behavior	Intensification of any offensive aggressive response from the dog upon any passive or active correction, interruption, or control of the dog's behavior or the dog's access to the behavior	
Separation anxiety (canine)	Physical or behavioral signs of distress exhibited by the animal <i>only</i> in the absence of, or lack of access to, the client	Consistent, intensive destruction, elimination, vocalization, or salivation exhibited <i>only</i> in the virtual or actual absence of the client. Behaviors are most severe close to the time of separation, and many anxiety-related behaviors (autonomic hyperactivity, increased motor activity, and increased vigilance and scanning) may become apparent as the client exhibits behaviors associated with leaving	
Noise phobia/noise reactivity (canine)	Sudden and profound, nongraded, extreme response to noise, manifested as intense, active avoidance, escape, or anxiety behaviors associated with the activities of the sympathetic branch of the autonomic nervous system. Behaviors can include catatonia or mania concomitant with decreased sensitivity to pain or social stimuli; repeated exposure results in an invariant pattern of response. Dogs who are continuously and characteristically distressed when exposed to specified noises, including storms, but who do not meet the criteria for a 'phobia' may be classified as 'reactive'		
Obsessive-compulsive disorder (canine and feline)	Repetitive, stereotypic motor, locomotory, grooming, ingestive, or hallucinogenic behaviors that occur out-of-context to their 'normal' occurrence, or in a frequency or duration that is in excess of that required to accomplish the ostensible goal	The behavior interferes with the animal's ability to otherwise function in his or her social environment	

disrupted, or moved from a resting site – no matter how gently this is done, and when they are physically or verbally 'corrected'.

Within the population of dogs manifesting the behavior at social maturity, at least two phenotypic groups have been identified: (i) those dogs that are not able to function using the social cues in the human environment and become explosive when they reach their stimulus threshold (the truly impulsive dogs); and (ii) those dogs that are uncertain of the human social environment and provoke it to gain information about what expected social responses and consequences could be (the dogs who use control as a tool) (Overall, 1997a). Both phenotypes of this condition are forms of internalized rule structures that have gone wrong. Keys to treatment include replacement with rule structures that clearly and humanely specify expectations, as well as the use of anti-anxiety medications.

As for most other behavioral conditions, this aggression commonly fully develops during social maturity when neurochemistry undergoes changes that will result in the individual's adult neurochemical profile. However, dogs exhibiting this behavioral abnormality at social maturity tend to be male, whereas affected females exhibit the behavioral pathology in puppyhood, suggesting that this is a multi-factorial disorder with different underlying mechanisms leading to similar phenotypes (Overall, 1995; Overall and Beebe, 1997).

Using either ante-mortem imaging or postmortem neuroanatomical or cytoarchitectural studies, little work has been done on impulse control aggression or impulsivity, *per se*, although limbic system structures in general have been related to impulsive risk-taking, behavioral timing, and time judgments (Nedergaard *et al.*, 2002).

172 K.L. Overall

The serotonin system has been implicated in both canine impulse control aggression and in human impulsivity. Affected dogs in one study (Reisner et al., 1996), but not in a better controlled, replicate study (Mertens, 2000), had lower cerebrospinal fluid (CSF) levels of 5-hydroxyindol acetic acid (5-HIAA) and homovanillic acid (HVA), metabolites of serotonin and dopamine, respectively, post-mortem than did control dogs. Although there is evidence that CSF HVA level may be a function of breed, CSF 5-HIAA levels appear to be decreased irrespective of breed. Afflicted dogs differ from all other aggressive dogs based on data from urinary metabolic screens: these dogs consistently manifest excretion of glutamine, the metabolite of the excitatory amino acid glutamate (Overall, 2013). Further refinement of amino acid identification is still needed to interpret these findings.

The data on associations with the serotonin system may be affected by genetics, although this link has been inadequately studied. Purebred affected dogs for whom a family history is available often come from family lines where approximately 50% the dogs are afflicted by social maturity. Once identified within a breed or familial line the condition appears each generation. Breeds that have been commonly represented in specific populations include American cocker spaniels, Dalmatian, English springer spaniel, golden retriever, German shepherd, Labrador retriever, and rottweiler (Overall, 1997a) in the USA, English cocker spaniels in the UK (Podberscek and Serpell, 1996, 1997), and golden retrievers in Europe. Genetic polymorphisms for other neurotransmitter systems have been associated with breed risk for fear and noise reactivity in multiple breeds, but with considerable variation across breeds (Bellamy et al., 2018).

Finally, these dogs respond to treatment with tricyclic anti-depressants (TCAs) and selective serotonin reuptake inhibitors (SSRIs) when combined with behavior modification. Neuroimaging studies suggest at least one mechanism for these improvements. In a series of studies using single photon emission computed tomography (SPECT; Peremans et al., 2003, 2005), there was a significantly higher 5-HT2A binding index in all cortical regions studied (the frontal, temporal, and occipital cortices) in untreated dogs with impulse control aggression than in unaffected dogs. With treatment with the SSRI citalopram, 5-HT2A receptor binding decreased and clinical signs significantly improved. As an SSRI, citalopram exerts its action through

serotonin transporter (SERT) blockade. SERT transfers monoamine neurotransmitters from the synaptic cleft to the relevant presynaptic receptor, causing a recycling of the neurotransmitter and making it unavailable for further neurotransmission, ultimately resulting in a thermostatic process when the transport of more of the monoamine is then inhibited (down-regulation). This process is one way to explain the effects of citalogram on decreasing 5-HT2A receptor binding: SSRIs block the downregulation process and make more serotonin available for neurotransmission. It is also possible that with increased amounts of serotonin available, fewer 5-HT2A receptors are available for ligand binding, a downstream sequela to the re-uptake inhibition. Regardless of the molecular mechanism, these studies show that blocking cortical SERT improves signs in impulse control aggression, suggesting at least one set of consistently linked neuroanatomical and neuromolecular phenotypic mechanisms.

13.3.2 Separation anxiety and noise reactivity/phobia

Anxiety disorders are among the most common health concerns in human medicine (Narrow *et al.*, 2002), as they are for pet dogs. Like humans, dogs with one anxiety-related diagnosis frequently have other anxiety-related diagnoses (Overall *et al.*, 2001; Overall and Dunham, 2002; Storengen and Lingaas, 2015; Tiira *et al.*, 2016), suggesting the existence of some putative genetic or neurochemical liability (Smoller and Tsuang, 1998; Insel *et al.*, 2010).

Neuroanatomical studies of panic disorder are closely linked to those pertaining to fear and to peripheral responses. The extent to which learning and memory play roles in fear, anxiety, phobias, and OCD has been poorly studied because it is difficult to do so given the complexity of the neurochemical systems involved. What is known is that: (i) a functioning amygdala is required to learn fear; (ii) a functioning forebrain is required to unlearn fear (i.e., to effect habituation); and (iii) many human abnormalities involving fear appear to be the result of the inability to inhibit a fear response.

Accordingly, it has been hypothesized that fear is, in part, due to chronic amygdala over-reaction and/or failure of the amygdala to turn off after the threat has passed. The specific neuroanatomy of a fear response involves the locus ceruleus (LC), the principal norepinephrinergic (noradrenergic) nucleus in the brain. Dysregulation of the LC appears to lead

to panic and phobias in humans (Charney and Heninger, 1986). The LC directly supplies the limbic systems and may be responsible for many correlated 'limbic' signs. Patients with true panic and phobic responses are more sensitive to pharmacologic stimulation and suppression of the LC than are controls (Ko *et al.*, 1983; Charney and Heninger, 1986; Pyke and Greenberg, 1986).

Although there are few quantitative clinical studies on anxious dogs, those focusing on noise reactivity (Overall et al., 2001; Storengen and Lingaas, 2015), separation anxiety (Overall et al., 2001), and OCD (Overall and Dunham, 2002) have shown that a high percentage of affected patients experience other, comorbid anxiety disorders (~90% and 75%, respectively, for the separation anxiety and OCD studies cited). Similar patterns have been identified in large survey studies where clients evaluate their dogs using a standardized screen. These are not clinical cases and lack the same information that such cases provide, but instead provide some prevalence estimate across populations (Blackwell et al., 2013; Tiira and Lohi, 2014; Tiira et al., 2016).

Heightened noise reactivity/fear as a young dog may be hypothesized to predispose the individual to the later development of separation anxiety. If so, this strongly suggests that associations between various anxiety conditions may be the result of increased risk that is either the direct result of a shared underlying cause of the initial disorder or the indirect result of neurochemical/molecular changes that occur because of the initial disorder. Similar patterns have been noted for noise reactivity in humans (Wallhäusser-Franke et al. 2013; Milenković and Paunović, 2015). In one clinical study (Overall et al., 2001), separation anxiety occurred significantly more often as a solitary diagnosis than would be expected under random conditions, and noise phobias occur significantly less often as a solitary diagnosis under the same conditions. These findings support the concept that although they share nonspecific signs, the diagnoses are separate entities.

Furthermore, the finding that the observed frequency of a diagnosis of separation anxiety + thunderstorm phobia and of separation anxiety + noise phobia was significantly lower than expected were they independent, but that the observed frequency of a diagnosis of thunderstorm phobia + noise phobia and of separation anxiety + noise phobia + thunderstorm phobia is significantly higher than expected

were the diagnoses independent, supports two important conclusions. First, noise and thunderstorm phobia are different from each other and affect the frequency and intensity of related behaviors in comorbid diagnoses differently. Second, the interaction of multiple pathological responses to noise likely either reflects an altered, dysfunctional, underlying neurochemical substrate, or is the result of one.

The conditional probability that a canine patient with noise phobia also has separation anxiety is high (88%) and approximately the same as if they have thunderstorm phobia (87%). Almost identical proportions were reported for a large, online study conducted in the general population (Tiira *et al.*, 2016). However, the probability that a patient with separation anxiety also has noise phobia is higher (74%) than the probability that they have thunderstorm phobia (61%).

These data, combined with the finding that the probability of having a noise phobia given a thunderstorm phobia is not equivalent to the converse (90% versus 76%) supports the hypothesis that neurochemical responses to nonstorm noise are different from those to thunderstorms, if the behavioral phenotypes or endophenotypes are manifestations of repeated exposure and long-term potentiation. Such findings suggest heterogeneity of triggers and possible neurochemical/neuromolecular phenotypes within one diagnostic class. The properties of unpredictability and uncertainty associated with thunderstorms may have a role in shaping the neurochemical and behavioral responses to anxiety provoking situations, suggesting future areas of exploration for understanding anxiety-related responses in dogs. Acoustic startle amplitude is considered a graded reflex that depends on the characteristics of the provocative stimulus (Davis, 1989). It is likely that different noises have different salience values for different dogs and are processed differently depending on the noise characteristics (Belojevic et al., 2003; Manikandan et al., 2006; Banis and Lorist, 2012), and may affect the structural and functional cellular and molecular changes associated with the condition found in the hippocampus and amygdala (Kraus and Canlon, 2012).

With respect to the clinical signs seen in these conditions, the nonspecific signs of anxiety are shared across conditions. This does not mean that they are equally experienced across all diagnoses or populations, and the extent to which they are expressed may, again, shed light on underlying mechanisms.

174 K.L. Overall

The most common signs clients report for their dogs with noise reactivity/phobia are remarkably consistent across survey studies (Blackwell et al., 2013; Tiira et al., 2016). Crowell-Davis et al. (2003) found that 94% of the afflicted clinical canine patients panted, 88% trembled, 88% became clingy or sought physical proximity to humans, 86% paced, and 81% hid. Korpivaara et al. (2017) reported that the most common reported signs for patients were, from most to least common: trembling, panting, pacing, seeking people, and trying to hide, with 79% to 94% of dogs studied displaying these signs. It is important to remember that clients commonly recognize only the easiest to visualize signs of canine anxiety (Mariti et al., 2012). The consistency among studies suggests that some shared mechanism is involved in the production of these suites of signs. The most common signs listed are affected by the central nucleus of the amygdala, supporting amygdala dysfunction as part of the pathology.

Performance in cognitive test situations may provide insight into endophenotypes. Mendl *et al.* (2010) examined dogs with separation anxiety using cognitive bias to test the hypothesis that such a diagnosis was accompanied by 'negative affect'. The scores for the separation-related behaviors correlated with performance on the cognitive bias test, with high scores resulting in lower performance. These results suggest that such tests could help parse some of the effects of the diagnosis and act as test for phenotypic diagnosis. (For a more detailed discussion, see Chapter 23, this volume.)

Overall et al. (2019) tested dogs who were and were not noise reactive in a 13-item problemsolving test battery. The final test involved response to a custom-made recording. Prior to testing, all dogs were screened for behavioral patterns using a standardized questionnaire about exposure and responses used clinically and in clinical studies. All dogs who reacted to the recording were identified as noise reactive, but not all identified noise reactive dogs reacted to the recording. Dogs who reacted to the recording had statistically significantly higher Anxiety Intensity Rank (AIR) scores, calculated on the number and intensity of signs, than did the noise reactive dogs who did not respond adversely to the recording. Accelerometer data revealed that noise reactivity dogs had more periods of stillness, more erratic and less consistent movement, and higher deviations from the mean in extreme movements when engaged in testing than did non-noise reactive dogs. A statistically significant number of dogs who were noise reactive could not complete 2/3 replications of another test, the puzzle box test, a rare event for non-noise reactive dogs. When noise reactive dogs did complete the puzzle box test they did so, on average, more slowly, and comprised a greater proportion of the slowest dogs.

These results suggest that such tests may identify informative endophenotypes like those associated with problem solving outcomes and movement patterns. Exploration of such endophenotypes may link phenotypic diagnoses with underlying neuro-anatomical and neuromolecular ones.

Other studies (Overall et al., 2016; Bellamy et al., 2018) have suggested genetic liabilities for noise reactivity/phobia. By working across these diagnostic levels and examining endophenotypes shared across related anxiety disorders, we could make substantial progress in early risk assessment that would allow anticipatory guidance, early treatment, novel treatment, and genetic counseling.

13.3.3 Obsessive-compulsive disorder in dogs and cats – a case study in variation and the emergent story of putative underlying mechanisms

The symptomology and pathophysiology of OCD are striking in humans and domestic animals. OCD, which is often called compulsive disorder (CD) in dogs and cats, is characterized by repetitive, ritualistic behaviors in excess of any required for normal function, the execution of which interferes with normal daily activities and functioning. Inherent in this description is a behavior that is exaggerated in form as well as duration.

In the human patient, the behavior can be self-perceived as abnormal and may be controlled to the extent that the behavior is performed only minimally, or not at all, in the presence of others. This pattern seems true also for domestic animals. In humans, obsessions are unwanted, repetitive thoughts that are manifest in ways often related to what are perceived to be uniquely human experiences. However, the fears and intrusive thoughts for which humans are known may be reflected in dogs by *how* they perform their OCDs.

Dogs who flank suck or tail chase may, after frequent reprimands and corrections, remove themselves from view, then commit the behavior elsewhere. Upon approach, the behavior ceases, to be begun again when no one is watching or when the animal removes himself from view. The existence of this evasive behavior pattern (Overall and Dunham, 2002) suggests that the problem involves higher level processes than the behavior alone may indicate (i.e., higher level cognitive mechanisms not only control the behavior, but allow the dog to recognize the circumstances when inhibition of the behavior is at least temporarily indicated). Furthermore, such examples support the notion that obsessions are a valid component of OCD. We evaluate obsessions in humans by asking them about ruminant, invasive thoughts. The verbal or written component of the response is a translation of the rumination - it is not identical to the ruminant thought itself. It is inappropriate to apply a set of criteria to one species that has a divergent phylogeny that prohibits the use of that tool or criteria, and to then assume that such phenomenology does not exist.

However, it is important to note that not all dogs and cats fit a volitional pattern where they can at least temporarily stop their compulsive behaviors. Some patients exhibit continuous stereotypic and ritualistic behavior regardless of training, distraction, or canine, feline, or human companionship.

It is not necessary that the behavior be continuously witnessed for the animal to have OCD, but it is requisite that the offending behavior substantially interfere with normal functioning in the absence of physical restraint. If the desire to exhibit the behavior is present despite physical restraint (e.g., from punishment, training, or physical incarceration), the condition is present. The key is that if such control is removed and the animal could commit the behavior, he will commit the behavior. Ignoring this crucial point will result in underdiagnosis of OCD and under-estimation of its frequency in canine and feline populations.

OCD in humans frequently appears in adolescence, at the onset of social maturity, and continues through mid-life. Human patients are generally clustered into four major groups: washers, checkers, ruminators, and an indistinct group of primary obsessive slowness. In dogs and cats, the only clinical survey study published to date suggests that OCD also appears during this indistinct period of social maturity (range for dogs: 12–36 months, average ~18–24 months; range for cats: 24–48 months, average ~30–36 months). Left untreated, whether by behavioral or pharmacologic intervention, the condition worsens (Overall and Dunham,

2002). Given the relatively early age at which this condition develops and the probability of profound deterioration when left untreated, young animals should be routinely screened for OCD and receive early appropriate treatment. Dogs and cats with a known familial history of OCD should be carefully watched for the appearance of any repetitive behaviors, as the condition could occur in the same – or different – form as that which was exhibited by their relatives.

Of 23 cats studied, ten manifested their particular form of OCD after some physical trauma or social upheaval, and the OCD in these cases may have occurred with intercat aggression or elimination complaints (Overall and Dunham, 2002). Most cats affected with OCD exhibit self-mutilation or excessive grooming. No cats were reported to hallucinate; however, 'hallucinations' may have been associated with feline tail chasing. Most clients with these cats reported that the cats acted as if something was on or near their tail which they were trying to chase or escape from. Accordingly, feline hallucinations may not have been adequately identified in this study.

Unlike cats, few dogs were reported to exhibit OCD following trauma or social/situational distress or upheaval, but as they improved, such stresses were associated with recidivism. The two cases of trauma involved abusive training: hanging by a choke chain collar. That 2% of this self-selected population of patients for whom clients were seeking treatment for OCD was subject to such abuse should give us all pause.

Of the 103 dogs, few (~10%) had a putative neurological disorder, physical condition, or potentially painful disorder associated with their OCD, which could either be primary or secondary to the OCD. One dog had a diagnosis of 'irritable bowel syndrome', a diagnosis which may be simply a nonspecific sign of an anxiety-related condition (Bécuwe-Bonnet *et al.*, 2012).

These findings support the hypothesis that OCD in dogs is based in some primary neurochemical/neurogenetic dysfunction, and that mechanisms driving OCD may differ between dogs and cats.

OCD affects at least 2% of the human population, and this is believed to be an under-estimate (Karno *et al.*, 1988). Some forms of OCD have a familial genetic component (Grados *et al.*, 2001); however, most instances of human OCDs appear to be sporadic (Hirschtritt *et al.*, 2017; Dougherty *et al.*, 2018). The development of

176 K.L. Overall

specific breeds and the practice of inbreeding within those breeds may be contributing to a higher incidence of OCDs in dogs than that reported for human beings.

The breeds of dogs in which OCD appears to run in family lines may include at least Great Danes, German short-haired pointers, German shepherd dogs, bull terriers (Moon-Fanelli and Dodman, 1998), Jack Russell terriers, Dalmatians, Bouvier de Flanders, salukis, cairn terriers, basset hounds, and soft-coated wheaten terriers. The close correlations between canine breeds and forms of OCD (e.g., German shepherds: tail chasing; rottweilers, Dalmatians, bulldogs: hallucinations) strongly supports a genetic basis, albeit, in part, as the result of genetic canalization for OCD associated with breed.

As mentioned above, first degree relatives usually have a different manifestation of OCD than does the proband (the same is true for humans). These features support the above hypotheses of a neurochemical basis for OCD. That 50% of the dogs in the 2002 study for whom familial data were known had a relative affected with some form of OCD strongly suggests two important points: (i) purebred dogs appear to have a high incidence of OCD, perhaps higher than that in the human population, and (ii) a larger number of canine family members are affected than appears true for humans. This frequency of familial occurrence strongly suggests a genetic component of OCD that should be further investigated.

Recent research strongly suggests that OCD in humans is the result of genetically controlled dysfunction of genes involving regulatory systems (Dougherty et al., 2018). Such complex regulatory functions that have a genetic, heritable basis have also been reported for dogs with narcolepsy (Mignot, 2001), dogs with noise reactivity/phobia (Overall et al., 2016), and in polymorphisms suggesting a role for dopaminergic function (Bellamy et al., 2018). Genome-wide associational studies in humans and laboratory animal models for OCD have provided convergent evidence implicating genes involved in glutamatergic neurotransmission and synaptic function (Dougherty et al., 2018). Dodman et al. (2010, 2016) have identified a gene region involved in flank/blanket sucking behavior in dobermans, using 92 cases and 68 controls. One region on canine chromosome 7 containing genes encoding for the adhesion molecule, CDH2, was found predominantly in affected dogs. CDH2/cadherin and other neuronal adhesion protein polymorphisms that mediate synaptic activity are involved in both human OCD and ASDs (Wang et al., 2009). Furthermore, dogs with multiple behaviors associated with OCD/canine compulsive disorder (CCD) had a higher frequency of the risk allele than did dogs who were less affected (60% versus 43%), both of which were higher than risk allele frequency in unaffected dogs (22%). This pattern of symptom frequency appears similar to that reported for noise reactivity in dogs (Bellamy et al., 2018; Overall et al., unpublished data), suggesting that frequency and intensity of signs may themselves act as an endophenotype for some putative shared mechanisms. It is also interesting that the genes identified as risk factors for canine noise reactivity (Overall et al., 2016) and those associated with canine OCD/CCD almost all flag neuronal regulatory proteins as foci of interest.

On the basis of human studies in which brain structural abnormalities have been associated with OCD, Ogata et al. (2013) compared brain structure in eight dobermans with OCD/CCD and eight unaffected controls. Dogs with OCD/CCD had higher total brain and gray matter volumes and lower dorsal anterior cingulate cortex (dACC) and right anterior insula gray matter densities than did the controls. Dogs with OCD/CCD also had higher fractional anisotropy in the splenium of the corpus callosum. Fractional anisotropy is thought to reflect white matter fiber density, axonal diameter, and extent of myelination, all of which can affect neurotransmission. The degree of the anisotropy function correlated with the severity of the behavioral phenotype.

The lower levels dACC grey matter volume in affected dogs may affect movement, since the localized region of impairment is adjacent to the cingulate sulcus and abnormalities in this region can affect both repetitive movement and functional connectively driving executive control. Schlösser et al. (2010) reported abnormal functional connectivity between the dorsolateral prefrontal cortex and dACC, which has been negatively associated with OCD symptom severity in humans. Lower levels of dACC grey matter density has also been reported across human anxiety disorders (Radua et al., 2010), again suggesting a suite of related pathologies and endophenotypes conferring risk.

Interestingly, OCD in humans is no longer considered an 'anxiety disorder' since not all patients show signs of anxiety. There appear to be roles for fear and/or anxiety in subpopulations of human

OCD that correlate with the form the OCD takes (Dougherty et al., 2018). This pattern is likely true for dogs, too, and many clients with dobermans with flank sucking do not identify patterns associated with anxiety or distress. One should then ask whether our assessments are sufficiently sensitive to identify the range of anxious or fearful behaviors and whether, if regions associated with these are identified as involved in imaging studies, the lack of any fearful or anxious response is real or a functional mismatch. The mechanistic implications of such questions are not trivial, but we lack the combined functional, molecular, and phenotypic studies for most canine mental illnesses.

Regardless, the treatment approaches to OCD in humans and dogs still focus on anxiolysis, and cases are overwhelmingly treated with TCAs and SSRIs. Given the findings of Peremans *et al.* (2003, 2005) that blocking cortical SERT ameliorates signs of anxiety involved with impulsivity and impulsive aggression, one must assume that mechanisms of cortical integration and inhibition are also implicated in OCD.

13.4 Concluding Remarks

In this chapter I have discussed how to think about behavioral conditions and their diagnostic criteria. Additionally, I have provided examples of four broad sets of conditions that emphasize how important discrete diagnoses are, how reliance on nonspecific signs can be treacherous, and how interactions of conditions can allow both to go unnoticed unless we are rigorous and use detailed, standardized, objective assessment tools. Such pursuits may lead to better or more targeted treatments.

Symptom severity has been shown to correlate with (i) problem solving ability in a puzzle box and movement pattern in noise reactivity (Overall et al., 2019); (ii) extent and type of signs of separation anxiety in dogs also affected with noise reactivity/ phobia (Overall et al., 2001); (iii) allele frequency in OCD/CCD (Dodman et al., 2010) and noise reactivity (Bellamy et al., 2018); and (iv) anisotropy in the splenium of the corpus callosum (Ogata et al., 2013). Whether this suggests a suite of shared endophenotypes at the neuroanatomical, neuromolecular, or genomic level underlining mental disorders or whether it suggests shared neuroanatomical x neuromolecular regional complexes in these disorders can only be determined using wellcontrolled studies that evaluate behavioral phenotype and at least two levels of functional phenotype (e.g., neuromolecular × genomic levels; neuroanatomical × neuromolecular levels).

Because what we call something affects how we think about it, mishandling terminology can do considerable harm. The association between labels and thought processes is considerably less damaging for traditional somatic conditions where we can all recognize a hole in the heart, an intestinal worm, or a broken bone. When what is broken is intangible, dynamic, and affects all other organ system responses, our terminology can blind us to what we need to know and stop us from acknowledging what we do not know. Paradigms that appear to work for purely 'somatic' conditions rarely work for behavioral ones, in part because of changes in neuronal function that are induced by the behavior itself. As we learn more, we will see that these diagnostic and treatment paradigms really work only for the most obvious of medical conditions. By exploring the complex response surface interactions that define neurobehavioral genetics we may also be able to shed archaic paradigms and introduce an understanding of complexity and mechanism into all areas of medicine. In veterinary behavioral medicine, in particular, this paradigm shift may also represent our last best chance to become more humane.

13.5 References

Banis, S. and Lorist, M.M. (2012) Acute noise stress impairs feedback processing. *Biological Psychology* 91, 163–171. http://dx.doi.org/10.1016/j.biopsycho. 2012 06 009

Bécuwe-Bonnet, V., Bélanger, M.C., Frank, D., Parent, J., Hélie, P. (2012) Gastrointestinal disorders in dogs with excessive licking of surfaces. *Journal of Veterinary Behavior: Clinical Applications and Research* 7, 194–204. http://dx.doi.org/10.1016/j.jveb. 2011.07.003.

Bellamy, K.K., Storengen, L.M., Handegård, K.W., Arnet, E.F., Prestrud, K.W., et al. (2018) DRD2 is associated with fear in some dog breeds. Journal of Veterinary Behavior: Clinical Applications and Research 27, 67–73. http://dx.doi.org/10.1016/j.jveb.2018.07.008.

Belojevic, G., Jakovljevic, B., Slepcevic, V. (2003) Noise and mental performance: Personality attributes and noise sensitivity. *Noise and Health* 6, 77.

Blackwell, E.J., Bradshaw, J.W., Casey, R.A. (2013) Fear responses to noises in domestic dogs: Prevalence, risk factors and co-occurrence with other

178 K.L. Overall

- fear related behaviour. *Applied Animal Behaviour Science* 145, 15–25. http://dx.doi.org/10.1016/j.applanim. 2012.12.004.
- Borchelt, P.L. (1983) Aggressive behavior of dogs kept as companion animals: Classification and influence of sex, reproductive status and breed. *Applied Animal Ethology* 10, 45–61. http://dx.doi.org/10.1016/0304-3762(83)90111-6.
- Brennand, K.J., Simone, A., Tran, N., Gage, F.H. (2012) Modeling psychiatric disorders at the cellular and network levels. *Molecular Psychiatry* 17, 1239–1253. http://dx.doi.org/10.1038/mp.2012.20.
- Campbell, N.G., Shekar, A., Aguilar, J.I., Peng, D., Navratna, V., et al. (2019) Structural, functional, and behavioral insights of dopamine dysfunction revealed by a deletion in SLC6A3. Proceedings of the National Academy of Sciences 201816247. http://dx.doi.org/10.1073/pnas.1816247116.
- Castellanos, F.X. and Tannock, R. (2002) Neuroscience of attention-deficit/hyperactivity disorder: The search for endophenotypes. *Nature Reviews Neuroscience* 3, 617–628. http://dx.doi.org/10.1038/nrn896.
- Charney, D.S. and Heninger, G.R. (1986) Abnormal regulation of noradrenergic function in panic disorders: Effects of clonidine in healthy subjects and patients with agoraphobia and panic disorder. *Archives of General Psychiatry* 43, 1042–1054. http://dx.doi.org/10.1001/archpsyc.1986.01800110045006.
- Crowell-Davis, S.L., Seibert, L.M., Sung, W., Parthasarathy, V., Curtis, T.M. (2003) Use of clomipramine, alprazolam, and behavior modification for treatment of storm phobia in dogs. *Journal of the American Veterinary Medical Association* 222, 744–748. http://dx.doi.org/10.2460/javma.2003.222.744.
- Davis, M. (1989) Neural systems involved in fear-potentiated startle. Annals of the New York Academy of Sciences 563, 165–183. http://dx.doi.org/10.1111/j.1749-6632. 1989.tb42197.x.
- Dodman, N.H., Karlsson, E.K., Moon-Fanelli, A., Galdzicka, M., Perloski, M., et al. (2010) A canine chromosome 7 locus confers compulsive disorder susceptibility. Molecular Psychiatry 15, 8–10. http:// dx.doi.org/10.1038/mp.2009.111.
- Dodman, N.H., Ginns, E I., Shuster, L., Moon-Fanelli, A.A., Galdzicka, M., Zheng, J., et al. (2016) Genomic risk for severe canine compulsive disorder, a dog model of human OCD. International Journal of Applied Research in Veterinary Medicine 14, 1.
- Dougherty, D.D., Brennan, B.P., Stewart, S.E., Wilhelm, S., Widge, A.S., et al. (2018) Neuroscientifically informed formulation and treatment planning for patients with obsessive-compulsive disorder: A review. JAMA Psychiatry 75, 1081–1087. http://dx.doi.org/10.1001/ jamapsychiatry.2018.0930.
- Gottesman, I.I. and Shields, J. (1972) Schizophrenia and Genetics: A Twin Study Vantage Point. Academic Press, New York, USA.

- Grados, M.A., Riddle, M.A., Samuels, J.F., Liang, K.Y., Hoehn-Saric, R., et al. (2001) The familial phenotype of obsessive-compulsive disorder in relation to tic disorders: The Hopkins OCD family study. *Biological Psychiatry* 50, 559–565. http://dx.doi.org/10.1016/ S0006-3223(01)01074-5.
- Hirschtritt, M.E., Bloch, M.H., Mathews, C.A. (2017) Obsessive-compulsive disorder: Advances in diagnosis and treatment. *JAMA* 317, 1358–1367. http://dx.doi.org/10.1001/jama.2017.2200.
- Insel, T.R. (2014) The NIMH Research Domain Criteria (RDoC) Project: Precision medicine for psychiatry. American Journal of Psychiatry 171, 395–397. http:// dx.doi.org/10.1176/appi.ajp.2014.14020138.
- Insel, T., Cuthbert, B., Garvey, M., Heinssen, R., Pine, D.S., et al. (2010) Research Domain Criteria (RDoC): Toward a new classification framework for research on mental disorders. *American Journal of Psychiatry* 167, 748–751. http://dx.doi.org/10.1176/appi.ajp.2010.09091379.
- Kapur, S., Phillips, A.G., Insel, T.R. (2012) Why has it taken so long for biological psychiatry to develop clinical tests and what to do about it? *Molecular Psychiatry* 17, 1174–1179. http://dx.doi.org/10.1038/mp.2012.105.
- Karno, M., Golding, J.M., Sorenson, S.B., Burnam, M.A. (1988) The epidemiology of obsessive-compulsive disorder in five US communities. Archives of General Psychiatry 45, 1094–1099. http://dx.doi.org/10.1001/ archpsyc.1988.01800360042006.
- Kim, J.J. and Diamond, D.M. (2002) The stressed hippocampus, synaptic plasticity and lost memories. *Nature Reviews Neuroscience* 3, 453. http://dx.doi. org/10.1038/nrn849.
- King, J.N., Simpson, B.S., Overall, K.L., Appleby, D., Pageat, P., et al. (2000) Treatment of separation anxiety in dogs with clomipramine: Results from a prospective, randomized, double-blind, placebocontrolled, parallel-group, multicenter clinical trial. Applied Animal Behaviour Science 67, 255–275. http://dx.doi.org/10.1016/S0168-1591(99)00127-6.
- Ko, G.N., Elsworth, J.D., Roth, R.H., Rifkin, B.G., Leigh, H., et al. (1983) Panic-induced elevation of plasma MHPG levels in phobic-anxious patients: Effects of clonidine and imipramine. Archives of General Psychiatry 40, 425–430. http://dx.doi.org/10.1001/ archpsyc.1983.01790040079011.
- Korpivaara, M., Laapas, K., Huhtinen, M., Schöning, B., Overall, K. (2017) Dexmedetomidine oromucosal gel for noise-associated acute anxiety and fear in dogs a randomised, double-blind, placebo-controlled clinical study. *Veterinary Record* 180, 1–7. http://dx.doi. org/10.1136/vr.104045.
- Kraus, K.S. and Canlon, B. (2012) Neuronal connectivity and interactions between the auditory and limbic systems. Effects of noise and tinnitus. *Hearing Research* 288, 34–46. http://dx.doi.org/10.1016/j. heares.2012.02.009.

- Luescher, A.U. and Reisner, I.R. (2008) Canine aggression toward familiar people: A new look at an old problem. Veterinary Clinics of North America: Small Animal Practice 38, 1107–1130.
- Mahar, I., Bambico, F.R., Mechawar, N., Nobrega, J.N. (2014) Stress, serotonin, and hippocampal neurogenesis in relation to depression and antidepressant effects. *Neuroscience & Biobehavioral Reviews* 38, 173–192. http://dx.doi.org/10.1016/j.neubiorev.2013.11.009.
- Manikandan, S., Padma, M.K., Srikumar, R., Parthasarathy, N.J., Muthuvel, A., et al. (2006) Effects of chronic noise stress on spatial memory of rats in relation to neuronal dendritic alteration and free radical-imbalance in hippocampus and medial prefrontal cortex. Neuroscience Letters 399, 17–22. http://dx.doi.org/10.1016/j.neulet.2006.01.037.
- Mariti, C., Gazzano, A., Moore, J.L., Baragli, P., Chelli, L., et al. (2012) Perception of dogs' stress by their owners. Journal of Veterinary Behavior: Clinical Applications and Research 7, 213–219. http://dx.doi.org/10.1016/j. jveb.2011.09.004.
- Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., et al. (2010) Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. Current Biology 20, R839–R840. http://dx.doi.org/10.1016/j. cub.2010.08.030.
- Mertens, P. (2000) CSF metabolites don't correlate with aggression. In: Proceedings of Annual Clinical Animal Behavior Conference. American Veterinary Society of Animal Behavior, Salt Lake City, Utah, USA.
- Mignot, E. (2001) A commentary on the neurobiology of the hypocretin/orexin system. *Neuropsychopharmacology* 25, S5–S13. http://dx.doi.org/10.1016/ S0893-133X(01)00316-5.
- Milenković, S. and Paunović, K. (2015) Noise sensitivity, handedness, and the occurrence of high perceived anxiety and depression in young adults. *Personality* and *Individual Differences* 83, 158–163. http://dx. doi.org/10.1016/j.paid.2015.04.004.
- Moon-Fanelli, A.A. and Dodman, N.H. (1998) Description and development of compulsive tail chasing in terriers and response to clomipramine treatment. *Journal of the American Veterinary Medical Association* 212, 1252–1257.
- Narrow, W.E., Rae, D.S., Robins, L.N., Regier, D.A. (2002) Revised prevalence estimates of mental disorders in the United States: Using a clinical significance criterion to reconcile 2 surveys' estimates. *Archives of General Psychiatry* 59, 115–123. http:// dx.doi.org/10.1001/archpsyc.59.2.115.
- Nedergaard, M., Takano, T., Hansen, A.J. (2002) Beyond the role of glutamate as a neurotransmitter. Nature Reviews Neuroscience 3, 748–755. http:// dx.doi.org/10.1038/nrn916.
- Ogata, N., Gillis, T.E., Liu, X., Cunningham, S.M., Lowen, S.B., et al. (2013) Brain structural abnormali-

- ties in doberman pinschers with canine compulsive disorder. *Progress in Neuro-Psychopharmacology and Biological Psychiatry* 45, 1–6. http://dx.doi.org/10.1016/j.pnpbp.2013.04.002.
- Overall, K. L. (1995) Sex and aggression. *Canine Practice* 20, 16–18.
- Overall, K.L. (1997a) Clinical Behavioral Medicine for Small Animals. Mosby, St. Louis, Missouri, USA.
- Overall, K.L. (1997b) Terminology in behavioral medicine: Diagnosis, necessary and sufficient conditions, and mechanism. In: *Proceedings of the First International Conference on Veterinary Behavioural Medicine*. European Society of Veterinary Clinical Ethology, Birmingham, UK, pp. 14–19.
- Overall, K.L. (2000) Dogs as 'natural' models of human psychiatric disorders: Assessing validity and understanding mechanism. *Progress in Neuro-Psychopharmacology* & Biological Psychiatry 24, 727–776. http://dx.doi.org/10.1016/S0278-5846(00)00104-4.
- Overall, K.L. (2013) Manual of Clinical Behavioral Medicine. Elsevier, St. Louis, Missouri, USA.
- Overall, K.L. and Beebe, A.D. (1997) Dominance aggression in young female dogs: What does this suggest about the heterogeneity of the disorder? In: *Proceedings of the First International Conference on Veterinary Behavioural Medicine*. European Society of Veterinary Clinical Ethology, Birmingham, UK, pp. 58–63.
- Overall, K.L. and Dunham, A.E. (2002) Clinical features and outcome in dogs and cats with obsessive-compulsive disorder: 126 cases (1989–2000). *Journal of the American Veterinary Medical Association* 221, 1445–1452. http://dx.doi.org/10.2460/javma.2002.221.1445.
- Overall, K.L., Dunham, A.E., Frank, D. (2001) Frequency of nonspecific clinical signs in dogs with separation anxiety, thunderstorm phobia, and noise phobia, alone or in combination. *Journal of the American Veterinary Medical Association* 219, 467–473. http://dx.doi.org/10.2460/javma.2001.219.467.
- Overall, K.L., Dunham, A.E., Juarbe-Diaz, S.V. (2016) Phenotypic determination of noise reactivity in 3 breeds of working dogs: A cautionary tale of age, breed, behavioral assessment, and genetics. *Journal of Veterinary Behavior: Clinical Applications and Research* 16, 113–125. http://dx.doi.org/10.1016/j.jveb.2016.09.007.
- Overall, K.L., Dunham, A.E., Scheifele, P., Sonstrom Malowski, K. (2019) Fear of noises affects canine problem solving behavior and locomotion in standardized cognitive tests. *Applied Animal Behaviour Science* (revised).
- Peremans, K., Audenaert, K., Coopman, F., Blanckaert, P., Jacobs, F., et al. (2003) Estimates of regional cerebral blood flow and 5-HT2A receptor density in impulsive, aggressive dogs with 99m Tc-ECD and 123 I-5-I-R91150. European Journal of Nuclear

180 K.L. Overall

- Medicine and Molecular Imaging 30, 1538–1546. http://dx.doi.org/10.1007/s00259-003-1250-x.
- Peremans, K., Audenaert, K., Hoybergs, Y., Otte, A., Goethals, I., et al. (2005) The effect of citalopram hydrobromide on 5-HT 2A receptors in the impulsive–aggressive dog, as measured with 123 I-5-I-R91150 SPECT. European Journal of Nuclear Medicine and Molecular Imaging 32, 708–716. http://dx.doi.org/10.1007/s00259-005-1772-5.
- Perlis, R.H. (2011) Translating biomarkers to clinical practice. *Molecular Psychiatry* 16, 1076–1087. http:// dx.doi.org/10.1038/mp.2011.63.
- Podberscek, A.L. and Serpell, J.A. (1996) The English cocker spaniel: Preliminary findings on aggressive behaviour. *Applied Animal Behaviour Science* 47, 75–89. http://dx.doi.org/10.1016/0168-1591(95) 01012-2.
- Podberscek, A.L. and Serpell, J.A. (1997) Aggressive behaviour in English cocker spaniels and the personality of their owners. *Veterinary Record* 141, 73–76. http://dx.doi.org/10.1136/vr.141.3.73.
- Pyke, R.E. and Greenberg, H.S. (1986) Norepinephrine challenges in panic patients. *Journal of Clinical Psychopharmacology* 6, 279–285. http://dx.doi.org/10.1097/00004714-198610000-00004.
- Radua, J., van den Heuvel, O.A., Surguladze, S., Mataix-Cols, D. (2010) Meta-analytical comparison of voxel-based morphometry studies in obsessive-compulsive disorder vs other anxiety disorders. *Archives of General Psychiatry* 67, 701–711. http://dx.doi.org/10.1001/archgenpsychiatry.2010.70.
- Reisner, I.R., Mann, J.J., Stanley, M., Huang, Y.Y., Houpt, K.A. (1996) Comparison of cerebrospinal fluid monoamine metabolite levels in dominant-aggressive and non-aggressive dogs. *Brain Research* 714, 57–64. http://dx.doi.org/10.1016/0006-8993(95)01464-0.
- Schlösser, R.G., Wagner, G., Schachtzabel, C., Peikert, G., Koch, K., et al. (2010) Fronto-cingulate effective connectivity in obsessive compulsive disorder: A study with fMRI and dynamic causal modeling. *Human Brain Mapping* 31, 1834–1850. http://dx.doi.org/10.1002/ hbm.20980.

- Schoenfeld, T.J., McCausland, H.C., Morris, H.D., Padmanaban, V., Cameron, H.A. (2017) Stress and loss of adult neurogenesis differentially reduce hippocampal volume. *Biological Psychiatry* 82, 914–923. http://dx.doi.org/10.1016/j.biopsych.2017.05.013.
- Schwartz, C.E., Kunwar, P.S., Greve, D.N., Kagan, J., Snidman, N.C., et al. (2012) A phenotype of early infancy predicts reactivity of the amygdala in male adults. Molecular Psychiatry 17, 1042–1050. http:// dx.doi.org/10.1038/mp.2011.96.
- Smoller, J.W. and Tsuang, M.T. (1998) Panic and phobic anxiety: Defining phenotypes for genetic studies. *American Journal of Psychiatry* 155, 1152–1162. http://dx.doi.org/10.1176/ajp.155.9.1152.
- Stephan, B.C.M., Hunter, S., Harris, D., Llewellyn, D.J., Siervo, M., et al. (2012) The neuropathological profile of mild cognitive impairment (MCI): A systematic review. Molecular Psychiatry 17, 1056–1076. http:// dx.doi.org/10.1038/mp.2011.147.
- Storengen, L.M. and Lingaas, F. (2015) Noise sensitivity in 17 dog breeds: Prevalence, breed risk and correlation with fear in other situations. *Applied Animal Behaviour Science* 171, 152–160. http://dx.doi.org/10.1016/j.applanim.2015.08.020.
- Tiira, K. and Lohi, H. (2014) Reliability and validity of a questionnaire survey in canine anxiety research. Applied Animal Behaviour Science 155, 82–92. http://dx.doi.org/10.1016/j.applanim.2014. 03.007.
- Tiira, K., Sulkama, S., Lohi, H. (2016) Prevalence, comorbidity, and behavioral variation in canine anxiety. *Journal of Veterinary Behavior: Clinical Applications and Research* 16, 36-44. http://dx.doi.org/10.1016/j. jveb.2016.06.008.
- Wallhäusser-Franke, E., Schredl, M., Delb, W. (2013) Tinnitus and insomnia: Is hyperarousal the common denominator? Sleep Medicine Reviews 17, 65–74. http://dx.doi.org/10.1016/j.smrv.2012.04.003.
- Wang, K., Zhang, H., Ma, D., Bucan, M., Glessner, J.T., et al. (2009) Common genetic variants on 5p14. 1 associate with autism spectrum disorders. *Nature* 459, 528–533. http://dx.doi.org/10.1038/nature07999.

14 Psychological Trauma and Posttraumatic Psychopathology in Animals

FRANKLIN D. McMILLAN

Best Friends Animal Society, Kanab, Utah, USA

14.1 Introduction

The knowledge that severe adversity can cause longterm psychological and physiological problems in humans has been recognized for centuries. 'Trauma', the ancient Greek word meaning 'to wound' or 'pierce', first referred to the bodily injury suffered by soldiers from the piercing of their armor (Spiers and Harrington, 2001). In the more recent use of the term, particularly in the human psychological and psychiatric literature, trauma is now understood as a wound inflicted upon the mind as well as the body (Ray, 2008). Despite the longstanding recognition of stress-induced changes, the characteristic syndrome of psychological trauma only attained formal recognition when, in 1980, the American Psychiatric Association included in the Diagnostic and Statistical Manual of Mental Disorders (DSM-III) a new category, called posttraumatic stress disorder (PTSD) (Nayback, 2009). From a retrospective viewpoint, the disorder that is now known as PTSD first appeared in the official nomenclature when the first edition of the DSM in 1952 described the syndrome under the name 'gross stress reaction' (Andreasen, 2010).

In general, physical and psychological processes of an organism return to a baseline state of homeostasis after disruption. Recent studies in humans and nonhuman animals (hereafter animals) have shown that following experiences of severe psychological stress a homeostatic psychological state may not be reestablished, especially with diversity that is prolonged or repetitive in nature (Wilson, 2004). Rather than return to homeostasis the mind-body undergoes persistent dysfunction, often continuing to operate as if the trauma were perpetual and ongoing in daily life (Wilson, 2004). The different forms that this enduring

dysfunction can take are what constitute posttraumatic psychopathology.

14.1.1 Indistinct concepts and terminology

A major problem pervades the field of psychological trauma: the inherently indistinct lines between the most fundamental concepts, including pathological versus nonpathological, adaptive versus maladaptive, normal versus impaired function, and clinically significant versus not clinically significant changes (Marshall *et al.*, 1998; Wakefield and Horwitz, 2010; Joseph, 2011). Questions persist as to whether firm lines exist to distinguish these basic concepts or if they each constitute a dimensional continuum.

14.1.2 What is psychological trauma?

In both scientific and everyday usage, psychological trauma has had two meanings. It is used to refer to the stressful stimulus or event, such as 'the dog was *exposed to* trauma', or to the *response to* the stressful stimulus or event, such as 'the dog *experienced* psychological trauma'. This double meaning conflates the injury with the incident. When an event is deemed 'traumatic', the assumption is that the event, by definition, results in injury (Gist and Devilly, 2010). However, the well-established fact that multiple individuals exposed to the same aversive stimulus or event will experience a diverse array of psychological outcomes (Ruscio *et al.*, 2002) demonstrates that trauma is not the event, but rather the response of individuals to that event. In this context it is

important to stipulate that the aversive, stressful events are *potentially* traumatic and that trauma is what occurs within an individual during and after exposure to the event (O'Donnell *et al.*, 2010). In this chapter the term 'potentially traumatic event' (PTE) will be used to maintain clarity that the event itself is not traumatic and the reactions of those exposed may for some individuals never reach a pathologic level of intensity or duration (Gist and Devilly 2010), and 'trauma' will be used to denote the response, not the stressor.

14.1.3 Psychological trauma: Considerations when comparing humans and animals

A large body of research has demonstrated that despite the influence of higher cognitive functions in humans, basic emotional processes are shared by humans and other mammals (Panksepp, 1998). Strong evidence also indicates commonalities across species in psychopathological processes. Brain structures and neuroendocrine mechanisms implicated in mood and anxiety disorders are shared across a wide range of vertebrates, and vulnerability, risk, and protective factors for stress- and trauma-related psychopathology also appear to operate similarly among higher animals (Panksepp, 1998). Nevertheless, despite the shared brain structures and emotional processes, a number of factors must be taken into consideration when comparing psychopathology in humans and animals.

Language and cognitive barriers

Among the most formidable challenges we encounter in our attempts to understand psychological processes in nonhuman species involve the limitations in the animals' capacities for introspection of their subjective experiences and the language barrier, which impair their ability to convey the content of their thought processes (and/or our ability to interpret their communications). These barriers greatly impair our ability to acquire two types of information highly relevant to the assessment of psychological trauma in any species: historical information and information about one's subjective experiences. From a comparative perspective, the same challenge occurs in very young children, where research has shown that because of limited verbal expression capabilities, assessment criteria need to be more behaviorally anchored (Scheeringa, 2016).

Historical information

The histories of companion animals are almost always incomplete, since unless the current caregiver raised the animal from birth, the experiences that that animal was exposed to or deprived of may be omitted from the animal's records or unknown altogether. This is true not just for the obvious cases of stray and shelter animals, but also for animals purchased as pets from reputable sources, since some stressful event may have occurred prior to the purchase, including the first 8 weeks of life. Moreover, due to the abundant research on the effects of maternal stress on the prenatal neuroendocrine development of mammalian fetuses (Braastad, 1998), an accurate history of adversity needs to also include maternal experiences throughout pregnancy.

The deficiencies in historical information create two major diagnostic problems. First, as will be discussed in more detail later, inadequate socialization¹ in early life may result in later behaviors - predominantly fear-based - that often closely resemble those resulting from psychological trauma. Second, the diagnoses of certain trauma- and stressor-related disorders is contingent on historical information before and after a stressful event to distinguish pre-existing conditions from effects. Specifications in the diagnostic criteria, in particular 'not present before trauma' or 'beginning after the traumatic event(s) occurred' (American Psychiatric Association, 2013), cannot be met when the individual's history prior to such an event is unknown. Child psychology research has shown that there is no feasible way to obtain information about traumatic events from the victims themselves if the children are too young to verbalize experiences (Scheeringa, 2016).

Information about subjective experiences

The current 'gold standard' for the diagnosis of posttraumatic disorders in humans is the diagnostic criteria set forth in the fifth edition of the DSM, which rely heavily on patients' subjective reports of their experiences and internal states (Pitman *et al.*, 2012). Clearly, the subjective experiences of some symptoms such as recurrent, involuntary, and intrusive distressing memories of the traumatic event(s); dissociative flashbacks; nightmares; and an inability to remember important aspects of the traumatic event(s) cannot be confirmed (or modeled) in animals and may only be inferred from nonverbal behavioral and other measures (e.g., physiological

measurements, brain imaging) (Foa et al., 1992; Whitaker et al., 2014; Richter-Levin et al., 2018). This, as for incomplete histories, is not exclusive to animals, for although inaccessibility to subjective states applies to all animals it also applies to some humans, such as infants, some mentally disabled individuals, and persons with dementia (Ferdowsian et al., 2011).

14.2 Adaptive Fear Responses

The emotion of fear – consisting of physiological, perceptual, and psychological elements - elicits highly adaptive behavioral responses when real or perceived threats endanger the life or well-being of the individual (Rosen and Schulkin, 1998). Behavioral responses are traditionally grouped into three categories: flight, fight, or freeze (Wiedenmayer, 2004). Lang (1977) has described the concept of a fear structure, which is conceived of as a neural program for escape or avoidance behavior containing information about the feared stimulus, the behavioral responses, and the appraised meanings of both stimulus and responses. Activation of a fear structure occurs when the animal perceives environmental cues that correspond to information represented in the structure, which coordinates and monopolizes brain resources for the purpose of enhancing the animal's ability to defend against a challenge (LeDoux, 2012). When a fear structure accurately represents threats in the world it serves as a blueprint for effective action, which, in conjunction with its motivational function, results in the production of self-protective behavior (Rosen and Schulkin, 1998; Cahill and Foa, 2007; LeDoux, 2012).

Fears are either innate (hard-wired) or learned. Most relevant to the phenomenon of psychological trauma is the latter, for, as we will see, trauma commonly (though not always) occurs as a result of a fearful experience and then manifests as a fear or anxiety disorder. Evidence indicates that the evolutionary development of fear-learning mechanisms was guided by the fact that the likelihood of injury or death is strongly linked to the speed, strength, and duration of learned fears. In situations where the animal perceives a high risk of injury, subsequent exposure to this stimulus or situation could have fatal consequences and therefore fast-learning mechanisms that can immediately alter behavioral responses, as occurs in one-trial learning, are of high fitness priority (Wiedenmayer, 2004). In a recent review of research on the formation of learned fears in animals, Wiedenmayer (2004) presented findings from studies with rats demonstrating that a single aversive experience may alter synaptic transmission in components of the fear pathway such as the amygdala, hippocampus, and periaqueductal gray, and profoundly affect an animal's behavioral, psychological, and physiological responsivity. Such neural alterations may persist for extended periods of time and appear to underlie long-term behavioral changes after the threat.

The paradigm of fear conditioning has become the first choice for studying the neural basis of fear learning and, more recently, the memory-related aspects of PTSD-like symptoms (Siegmund and Wotjak, 2006). In this particular form of classical conditioning, a biologically neutral stimulus (conditioned stimulus, CS) acquires threat status when it occurs in association with a biologically significant threat (unconditioned stimulus, US) (LeDoux, 2012).

Crucial for the understanding of psychological trauma is that the learning involved with an aversive experience involves two processes: generalization and sensitization. In fear conditioning neural connections form to associate not only the CS, but also the contextual cues of the environment, with the US (Wiedenmayer, 2004). The process of generalization accounts for how traumatic reactions can broaden to involve not only stimuli clearly related to the traumatic event (trauma-related cues, TRCs), but also to stimuli seemingly unrelated (Monson et al., 2007). Sensitization, on the other hand, is a nonassociative form of learning that refers to an increased responsivity after an aversive event to the TRCs and in some cases to other, even harmless, stimuli (Wiedenmayer, 2004). Through sensitization, the animal becomes more reactive each time a nonthreatening stimulus is encountered, which can result in problematic responses such as hyperexcitability and exaggerated fear responses (Mills, 2009). Both generalization and sensitization appear to contribute to the emotional disturbances in posttraumatic distress (Parsons and Ressler, 2013).

For situations and stimuli which continue to pose a potential risk for an individual, retention of fear memories and responses is adaptive. However, when the risk subsides it is biologically costly to retain highly reactive fear responses for nonthreats, and in such situations memory-modulating mechanisms – e.g., fear extinction, habituation, de-sensitization, or forgetting – serve to restrict the duration of memory storage and ensure that only relevant features are retained (Wiedenmayer, 2004). Memory-modulating

mechanisms may allow animals to gradually trade off threat-related behaviors with other activities more relevant to current needs. The phenomenology and neurocircuitry of fear conditioning and extinction are highly conserved among humans and many other animal species (Bonne *et al.*, 2004; LeDoux, 2012; VanElzakker *et al.*, 2014).

14.3 Posttraumatic Psychopathology in Humans and Animals

The changed behavior elicited by normal fear responses is of clear survival value in protecting animals from danger. However, fear mechanisms, like any other biological process, are vulnerable to dysfunction. When this occurs, adaptive, nonpathological responses cross over to become maladaptive and pathological. What is not at all clear is at what 'level' this occurs; that is, where any line might exist that distinguishes pathologic behavior and adaptive, high levels of fear (Marshall et al., 1998; Wakefield and Horwitz, 2010). In addition, many gaps remain in our understanding of how traumatic events produce the changes constituting longer-lasting and pathologic sequelae, including reduced thresholds for activation and hyperexcitability in fear circuits and disruption of memory-modulating mechanisms regulating the balance between learning and forgetting, resulting in an emotional event being stored for an excessive period of time (Rosen and Schulkin, 1998; Wiedenmayer, 2004). The work in this area will be discussed in the section on the pathophysiology of PTSD.

Acknowledging the indeterminacy of any line separating normal from pathological fear, Foa and Kozak (1986) have proposed criteria for such a distinction. They suggested that a fear structure is pathological or maladaptive when the following characteristics are present: (i) associations among stimulus elements are inaccurate or unrealistic; (ii) harmless stimuli and response elements are erroneously associated with threat meaning; (iii) physiological and escape/avoidance responses are evoked by harmless stimuli; and (iv) excessive and easily triggered response elements interfere with normal, adaptive behavior.

Transitioning from a discussion on pathological fear to posttraumatic psychopathology in general requires a brief explanation. Historically, a large proportion of pathophysiology research on psychological trauma, and in particular PTSD, has focused on fear mechanisms, and hence there is much overlap between fear research and PTSD research. However,

as Friedman *et al.* (2007b) have noted, since other emotions, such as sadness, grief, anger, guilt, shame, and disgust, are also associated with PTSD, it would be inappropriate to conceptualize this disorder entirely within the context of fear-based appraisals and reactions. Reflecting the emphasis of the trauma literature on fear, the discussions of psychological trauma in this chapter will be predominantly about this particular emotion. Throughout, however, it bears keeping in mind that while pathological fear constitutes much of posttraumatic psychopathology, the two phenomena are not equivalents.

The challenge of identifying lines between adaptive and pathologic fear can be broadened to psychopathology in general. As is the case for fear specifically, while a definitive line dividing non-pathological and pathological may be not be possible for mental disorders as a whole, there is little debate that at some point nonpathological crosses over to pathological. The DSM-5 (American Psychiatric Association, 2013) approaches this by defining mental disorder as:

a syndrome characterized by clinically significant disturbance in an individual's cognition, emotion regulation, or behavior that reflects a dysfunction in the psychological, biological, or developmental processes underlying mental functioning. Mental disorders are usually associated with significant distress or disability in social, occupational, or other important activities. (p. 20)

The formal recognition of PTSD (defined below) in 1980 was accompanied by the realization that PTSD fell short of capturing the full range of posttraumatic responses and psychological injuries, which vary in both type and severity. Epidemiological studies have shown that PTSD symptoms are not the only, indeed not even the most likely, type of posttraumatic reactions; other types include specific phobia, generalized anxiety disorder (GAD), and mood disorders (O'Donnell et al., 2004; Rosen et al., 2010a). It is now accepted that the reactions to overwhelming psychological stressors are best understood as a spectrum of conditions rather than as a single disorder (Herman, 1997; Briere and Spinazzola, 2005; Bryant, 2010), and in this chapter 'spectrum' will refer to this array of different types of posttraumatic pathologic responses.

14.3.1 Posttraumatic stress

In addition to the diagnosis of PTSD referring to just one *type* of response to trauma, it also represents

only one *level of severity*, namely, very severe. This de-emphasizes, if not ignores, the less severe forms of this particular type of posttraumatic response (Norris and Slone, 2007). On this issue of severity, a major point of debate is whether PTSD is a dimensional condition differing only quantitatively from milder and normal reactions to stressful events or whether it is a discrete syndrome qualitatively different from less severe and normative stress reactions (Ruscio et al., 2002). It is known that not everyone exposed to a PTE will develop the full complement of symptoms of PTSD, but most people will develop some emotional distress following the adversity (Joseph, 2011). To address this question Ruscio et al. (2002) conducted multiple taxometric procedures in a large sample of male combat veterans to determine the latent structure of PTSD. They found that PTSD was best characterized as a dimensional disorder rather than as a categorical structure that views PTSD as a qualitatively distinct clinical syndrome served by a dichotomous diagnostic breakdown of 'PTSD' and 'no PTSD' (Ruscio et al., 2002).

This dimensional view suggests that posttraumatic distress symptoms are distributed along a mildto-severe continuum and individuals who meet current PTSD diagnostic criteria generally represent those affected most severely (Briere and Spinazzola, 2005; Friedman et al., 2007b). However, there would be no distinct line that would qualitatively separate these individuals from those exhibiting less severe signs (see Fig. 14.1). It has been proposed that this continuum be referred to by the term posttraumatic stress (PTS, and will be used in this chapter), and that once posttraumatic stress reaches a certain level of intensity the individual experiencing it is said to have PTSD (Joseph, 2011). This chapter will espouse the dimensional interpretation of PTS and PTSD, and will use the term PTSD when referring to research that has used a categorical view. In addition, 'continuum' will refer to the gradations of severity of PTS responses as depicted in Fig. 14.1.

New terminology to describe the forms of PTS exhibited by victims who experience substantial psychological impairment and distress but fall below the diagnostic threshold of PTSD is not consistent among researchers; the terms include *subthreshold*, subsyndromal, and partial PTSD (Bergman et al., 2017). In a recent review, Bergman et al. (2017) found that the majority of articles used the term subthreshold PTSD, which will be used in this chapter. As the term implies, subthreshold PTSD denotes a condition consisting of the presence of some symptoms of PTSD, but the number and intensity of the symptoms fail to reach the diagnostic threshold for the disorder as described in the DSM (Ruscio et al., 2002; Cukor et al., 2010). In contrast to subthreshold forms of PTS, the condition in which all the diagnostic criteria have been met is referred to most commonly as simply PTSD, but has also been termed full and full-threshold PTSD (Friedman et al., 2007b; American Psychiatric Association, 2013) as well as full-blown PTSD (Bergman et al., 2017). Other methods of describing the PTS continuum have been used, such as the notion that subthreshold PTSD be considered an 'intermediate phenotype' of the disorder, and individuals would be 'affected, intermediate, and non-affected' (Richter-Levin et al., 2018).

The validity and clinical relevance of subthreshold PTSD has been questioned since it was first used with the Vietnam veteran population (Cukor *et al.*, 2010), but lending credence to the concept is the clinically significant difference between those with PTSD, subthreshold PTSD, and no symptoms (Cukor *et al.*, 2010). By multiple measures – functional impairment, severity of symptoms, wanting or needing

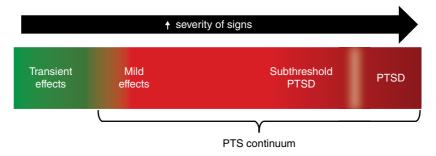


Fig. 14.1. Dimensional view of posttraumatic stress. PTS, posttraumatic stress; PTSD, posttraumatic stress disorder. (Adapted from Herman [1997]; Briere and Spinazzola [2005]; Joseph [2011].)

treatment, healthcare utilization, distress, psychological well-being, psychological impairment, and quality of life – subthreshold PTSD falls between full PTSD and having no disorder (Norris and Slone, 2007; Cukor *et al.*, 2010; Brancu *et al.*, 2016; Bergman *et al.*, 2017).

Subthreshold PTSD consists of different conditions and courses. Subthreshold PTSD groups may include individuals with PTSD who have partially remitted to subthreshold status, vulnerable patients whose symptoms will develop into late-onset full PTSD, and individuals who will remain at chronic, subthreshold levels (Cukor *et al.*, 2010; Brancu *et al.*, 2016; Bergman *et al.*, 2017).

Studies investigating the prevalence of subthreshold PTSD have been hampered by the variability of diagnostic criteria among researchers, but it is clear that subthreshold PTSD is prevalent among PTEexposed individuals (Cukor et al., 2010; Brancu et al., 2016). Norris and Slone (2007) summarized the epidemiology of PTSD by noting that at any one point of time there are at least one to two times as many individuals in the current population with severe subthreshold PTSD as those with full PTSD. The recognition of the concept of subthreshold PTSD has engendered ongoing debate among human mental health professionals, as the concern about the possibility that creating a subthreshold diagnosis may pathologize normal responses to extreme adversity must be continually weighed against the possibility of ignoring the needs of a crucial subpopulation of individuals who experience significant psychopathology and functional impairment (Cukor et al., 2010; Bergman et al., 2015).

Posttraumatic stress disorder

Posttraumatic stress disorder is one of the most severe outcomes of exposure to a severely aversive event. At present, PTSD is not a well-defined disorder. The definition and diagnosis of PTSD in humans is based on behavioral symptoms and self-reports, without any objective parameters (Richter-Levin *et al.*, 2018). PTSD is not defined by or composed of the immediate responses to trauma exposure: it is rather a disorder of the more chronic, lingering symptoms.

The clinical diagnosis of PTSD is made only if an individual exhibits a certain number of symptoms from each of four well-defined symptom clusters for a certain period of time. As specified in the DSM-5 (American Psychiatric Association, 2013),

in addition to the history of exposure to actual or threatened death, serious injury, or sexual violence, the four symptom clusters that distinguish PTSD from other posttraumatic psychological disturbances are unwanted intrusions of memories of the traumatic event, often in the form of dissociation, flashbacks, and nightmares; avoidance of anything reminiscent of the traumatic event; negative alterations in cognition and mood; and alterations in arousal and reactivity, including hyperarousal symptoms such as hypervigilance and increased startle response. Additional diagnostic elements include: the components within these symptom clusters must begin or worsen after the traumatic event(s) occurred, the duration of symptoms is greater than 1 month, and the disturbance causes clinically significant distress or impairment in social, occupational, or other important areas of functioning. On the basis of several decades of research demonstrating that children and adolescents can develop PTSD (Scheeringa et al., 2003), the fifth edition of the DSM has introduced a set of diagnostic criteria for children 6 years of age and younger, which require fewer and slightly recategorized symptoms than is set forth for humans over 6 years of age. Generally speaking, the diagnosis of PTSD is used in children and adolescents when intrusive memories, avoidance, and arousal symptoms are serious, continue, and interfere with daily functioning (Fairbank et al., 2007). Table 14.1 summarizes the criteria for children 6 years of age or less and is given the most attention in this chapter because of the similar challenges in animals and very young humans regarding documenting adult symptoms, such as the problem of obtaining reliable verbal self-reports.

Interindividual variability of PTSD symptom profiles is characteristic for the disorder in humans (Wilson, 2004). For example, in some individuals avoidance reactions may predominate, while others may experience mostly hyperarousal and reactivity. Any one symptom prominent in one individual may be minor or even absent in another.

The course of posttraumatic distress has been well characterized in humans. For the large majority of the population the distress after exposure to a PTE is limited to an acute, transient disturbance followed by complete recovery as neurobiological effects extinguish over time (Marshall *et al.*, 1998; Friedman *et al.*, 2007a; Rosen *et al.*, 2010a; Sherin and Nemeroff, 2011). However, a substantial minority of traumatized individuals do not fully recover but go on to develop clinical problems that

F

Table 14.1. Summary view of the DSM-5 diagnostic criteria for posttraumatic stress disorder in children 6 years of age and younger (American Psychiatric Association, 2013).

Criterion Specified criteria for children 6 years of age and younger

- A The child has been exposed to an event involving real or threatened death, serious injury, or sexual violence in at least one of the following ways:
 - **1.** Directly experienced the event.
 - 2. Personally witnessed another person, especially a primary caregiver, experience the event (not including events appearing on television, in movies, or other images).
 - 3. Learned that a primary caregiver experienced the event.
- B The child has at least one of the following intrusive symptoms that are associated with the event and first appeared after the event occurred:
 - 1. Spontaneous, recurring, involuntarily, and intrusive memories of the event which cause distress (but may not appear distressing to observers and may be expressed in forms of play).
 - 2. Event-related dreams which are recurring and distressing (however, clearly associating the fearful dream with the traumatic event may not be possible).
 - 3. Episodes in which the child feels and/or acts as if the event were happening again, which may be through flashbacks or other dissociative reactions (this may occur in the context of play reenactment).
 - 4. Intense and enduring emotional distress when encountering internal or external reminders of the event.
 - 5. Pronounced physiological reactions when encountering internal or external reminders of the event.
- C The child has at least one of the following six event-related symptoms involving either persistent avoidance or disturbing cognitions and mood, first appearing or worsening after the event.

Persistent avoidance of stimuli

- 1. Actual or attempted avoidance of places, activities, or other physical reminders of the traumatic event.
- 2. Actual or attempted avoidance of people, conversations, or interpersonal situations that elicit memories of the event.

Negative alterations in cognitions

- 3. More frequent experiences of negative emotions, such as fear, anxiety, sadness, or quilt.
- 4. Substantially diminished desire to participate in activities or endeavors that prior to the traumatic event were meaningful to the child.
- 5. Withdrawal from social activities and interactions.
- 6. Diminished expression of positive emotions, such as joy.
- D The child experiences at least two of the following event-related changes in arousal levels and reactivity to stimuli, first appearing or worsening after the event.
 - 1. Irritable, angry, or aggressive behavior toward other individuals or inanimate objects, which may include extreme temper tantrums.
 - 2. Hypervigilance.
 - 3. Exaggerated startle response.
 - 4. Having difficulties maintaining concentration or focus.
 - 5. Disturbances of sleep, such as restless sleep or problems falling or staying asleep.
- E Symptoms must be present for at least 1 month.
 - Symptoms must have resulted in clinically significant distress or disturbances in social relationships or school-related behavior.
- G Symptoms are not accounted for by another medical condition or by the use of substances such as drugs or alcohol.

create ongoing distress of varying severity. Studies in human populations exposed to a PTE have been relatively consistent in showing that the incidence of PTSD falls between 15% and 35% for most types of trauma, including sexual assault, military combat, natural disaster, motor vehicle accident, captivity, or witnessing the death or serious injury of another individual (Santiago et al., 2013; VanElzakker et al., 2014). Thus, there are two trajectories following traumatic stress: normal transient distress (i.e., resilience; successful coping response) or chronic clinical morbidity/distress (unsuccessful or partially successful coping response). This does not mean that the transiently affected individuals are completely free of long-term effects, as memories of the event are likely to remain, but these memories do not significantly impair the individual's functioning and enjoyment of life.

NEUROBIOLOGY AND PATHOPHYSIOLOGY OF PTSD The neurobiological mechanisms underlying PTSD are incompletely understood and have been recently reviewed (Southwick *et al.*, 2007; Sherin and Nemeroff, 2011; Shalev *et al.*, 2017). The following is a brief synopsis of some of the disorder's key dysfunctional elements currently known or hypothesized.

Shalev *et al.* (2017) have suggested that four brain functions play a prominent role in the psychopathology of PTSD: (i) threat detection; (ii) contextual processing; (iii) fear learning; and (iv) emotion regulation and executive function. It is well accepted that, broadly conceived, the primary dysfunction in the disorder involves fear mechanisms; fear conditioning as well as fear sensitization and generalization processes contribute to both the development and maintenance of the disorder (Thoeringer and Wotjak, 2013; VanElzakker *et al.*, 2014).

Classical fear conditioning has been a leading paradigm for research on the neural processes of PTSD. Fear conditioning is a normal learning process critical for animal survival, and its use in modeling PTSD is based on the assumption that the underlying neurobiology of PTSD is similar in principle to that of classical fear conditioning, only more intense (Richter-Levin *et al.*, 2018). However, until this assumption is confirmed it remains possible that that PTSD is a result of the failure of the normal fear responses following exposure to a severe stressor, resulting in the development of an alternative, pathological process (Richter-Levin *et al.*, 2018). Accordingly, Richter-Levin *et al.* (2018) have stressed

the importance of efforts to differentiate the mechanisms underlying adaptive fear memory formation from those that contribute to the development of pathology.

Evidence indicates that disturbances in PTSD occur in several interacting brain regions involved in the regulation and integration of stress and fear responses, including the amygdala, hippocampus, anterior cingulate cortex, and prefrontal cortical regions (Heim and Nemeroff, 2009; Shalev *et al.*, 2017). The pathophysiology of PTSD involves both sustained hyperactivity of the sympathetic branch of the autonomic nervous system and dysregulation and sensitization of the hypothalamic–pituitary–adrenocortical (HPA) axis (Friedman *et al.*, 2007b; Heim and Nemeroff, 2009). The dysfunction in this system may be associated with changes in perception, memory, motivation, personality, cognitive processing, and interpersonal relations (Wilson, 2004).

A major conceptualization of PTSD highlights the role of the amygdala in processing threatening or fearful stimuli. The amygdala in PTSD becomes hyperresponsive to stimuli (trauma-related as well as non-trauma-related) and this excessive activation is accompanied by an abnormally low response in the brain regions, such as the medial prefrontal cortex, that exert inhibitory control on amygdala activity (Charney, 2004; Yehuda and LeDoux, 2007; VanElzakker et al., 2014). These changes are supported by neuroimaging studies in human patients with PTSD, which demonstrate that structures involved in fear expression over-activate while structures involved in fear inhibition under-activate or deactivate (VanElzakker et al., 2014). For most individuals, extinction learning causes fear responses to trauma-related stimuli to diminish over time, such that repeated exposure to TRCs in the absence of threat forms a new and less excitatory association that competes with the original fear memory (Quirk, 2002). However, in individuals with PTSD the extinction deficit associated with the inhibition failure of the amygdala permits conditioned fears, and the symptoms they elicit, to persist for months or years beyond the point that they would normally be extinguished (VanElzakker et al., 2014).

These two effects on fear – enhanced acquisition and impaired extinction – together result in a lowering of the threshold for fearful reactivity and prolongation of fear memories. In addition to this, PTSD is associated with an increased propensity for fear generalization (VanElzakker *et al.*, 2014), which diminishes the individual's capability to

distinguish between safe and unsafe stimuli and to clearly identify danger (Bonne *et al.*, 2004; Sherin and Nemeroff, 2011). The threatening context thereby expands to the extent that perceived danger becomes both imminent and unpredictable and almost every place is believed to be unsafe. Ultimately there is an overall loss of one's sense of security – 'the world is completely dangerous' (Bonne *et al.*, 2004; Cahill and Foa, 2007; Hembree and Foa, 2010; American Psychiatric Association, 2013).

The combined effect of these neurophysiological changes is an emotional appraisal process that is biased toward the perception of threat rather than safety, producing a response bias of overreaction rather than underreaction (Friedman, 2001). Rather than a normal level of alertness with relaxed attention, individuals with PTSD have an elevated baseline of arousal: the individual continues to function in a 'red alert' status of readiness - hypervigilant, hyperreactive, and primed for another stressful event (Wilson et al., 2001a; Wilson, 2004). Patients display an exaggerated startle response to unexpected stimuli ('jumpiness') and a pronounced reaction to TRCs, are often irritable, and they experience difficulties in sleep and concentration (Bonne et al., 2004; Wilson, 2004; Segman et al., 2007; American Psychiatric Association, 2013).

POSTTRAUMATIC STRESS DISORDER IN ANIMALS

Animal - Experimental. Extensive effort over many decades has been put forth to develop an animal model of PTSD. The specific emotional state that is the primary focus of investigation for many of these proposed models is conditioned fear (Siegmund and Wotjak, 2007) and these studies overlap with, and use the same stressors (e.g., restraint stress, exposure to predators, being held underwater, and foot- and tailshocks [Siegmund and Wotjak, 2006]) as are used in studies on fear conditioning (Southwick et al., 2007). Most animal models of PTSD are based on exposure to stressors that the victim cannot control, that are unpredictable, or are both (Mallonée, 2004). There is substantial agreement that in many of the animal models the physiological and behavioral disturbances following experimental psychological trauma often match the most prominent and cardinal features of PTSD in humans (Foa et al., 1992; Mallonée, 2004; Southwick et al., 2007). Specific psychobehavioral signs produced in these models include traumaassociated contextual fear, increased anxiety-like behaviors, exaggerated startle responses, hyperarousal, avoidance behavior, cognitive impairment, and reduced social interaction (Thoeringer and Wotjak, 2013).

Some of the models include re-exposure to TRCs at a later time, which appears to replicate the events in PTSD in which the person's functional impairments and distress persist as a result of periodical encounters with reminders of the trauma (e.g., a car backfiring, which resembles the sound of gunfire during military combat). For example, in one study with rats (Louvart *et al.*, 2005) an intense and prolonged footshock was followed by three weekly reminders of the event using stimuli present during the event (excluding the UC, i.e., electric shock). The rats demonstrated several long-term alterations: increased anxiety behavior, reduced time spent in an 'aversive-like' context, altered social behavior, and a blunted corticosterone response to stress.

Similarly, recent studies with cows have shown that a simulated wolf encounter in wolf-experienced, but not in wolf-naïve, cows elicited behavioral and physiological changes (Cooke *et al.*, 2013) as well as selected brain-blood biomarkers (brain-derived neurotrophic factor and c-Fos proto-oncogene mRNA regulation) (Cooke *et al.*, 2017) comparable with changes documented in humans and rodent models with stress- and fear-related psychological disorders, including PTSD symptoms (Sherin and Nemeroff, 2011). These findings suggest that exposure to wolves in cows leads to the formulation of fear memories that may be elicited at a later time upon re-encountering the earlier fear-inducing stimulus.

As mentioned above, approximately 15% to 35% of humans exposed to a severe stressor will develop PTSD. Similar information about the course of psychological trauma in animals living natural lives (i.e., outside the laboratory setting) is lacking. However, in a series of laboratory studies Cohen et al. (2006) investigated the prevalence rates of rats displaying an extreme magnitude of behavioral response to a predator stress paradigm. They reported that after exposure to the stressor almost all animals responded 'extremely', but over the next 30 days the incidence of individuals showing extreme behavioral responses dropped to an unvarying 25%, closely conforming to the human data.

Overall, in terms of posttraumatic physiological and behavioral alterations, experimental studies in clinical populations of many human survivors with PTSD are consistent with animal studies (Anda *et al.*, 2006). However, there is, to date, no single accepted

animal model of PTSD; each model has its pros and cons (Whitaker *et al.*, 2014; Richter-Levin *et al.*, 2018). The validity and limitations of existing animal models of PTSD have been recently reviewed (Schöner *et al.*, 2017; Deslauriers *et al.*, 2018; Cabib *et al.*, 2019). Importantly, while animal models have produced neuroendocrine alterations and phenomenology that closely resembles specific aspects of PTSD, none has replicated the human condition in its entirety (Whitaker *et al.*, 2014). This is not surprising, since, as mentioned earlier, many subjective features of PTSD cannot be confirmed with certainty in animals.

Animal – Clinical. The study of posttraumatic psychopathology in animals has been almost exclusively in the laboratory setting. However, there have been a small number of cases of PTSD in a clinical context reported in peer-reviewed and non-reviewed publications.

Peer-reviewed reports

- Yamamoto (2003) reported a 'post-traumatic stress-like syndrome (PTSD)' in a study which surveyed the behavior in 155 dogs after a 2001 earthquake in western Japan. Abnormal behavior was reported in 82 (53%) of the dogs, which included trembling, howling, restlessness, scampering about, or wild excitement. Of the 82 dogs, 15 exhibited tremor, anorexia, intermittent howling, excitement, or repeated diarrhea, which persisted for a variable amount of time from days to 1 year.
- Traumatic stress disorder was reported in an adult female wolf (*Canis lupus*) born in the wild then placed into captivity (Mallonée, 2004). The writer suggested that the wolf's method of capture, which involved being darted twice by helicopter and translocated twice, exposed her to the factors that are important in the etiology of PTSD in humans. He proposed that the wolf displayed symptoms similar to those of humans with PTSD and included generalized fear, avoidance, hypervigilance, arousal, exaggerated startle reactions, and 'looking up' behavior.
- Wild elephants showed signs that Bradshaw et al. (2005) interpreted as resembling PTSD symptoms and meeting the diagnostic criteria for PTSD, such as abnormal startle response, depression, unpredictable asocial behavior, and hyperaggression.

- Bradshaw et al. (2008) reported PTSD in two sanctuary-housed female chimpanzees who had previously sustained prolonged captivity and biomedical experimentation. The animals exhibited a wide array of signs, including intense screaming, self-injurious behavior (SIB), stereotypic rocking, trance-like states, sudden and unpredictable aggression, emotional instability, self-isolation, and hitting oneself continually in the head.
- Ferdowsian *et al.* (2011) reviewed case reports (20 cases in 12 published papers) of sanctuary-housed chimpanzees who were reported to have been subjected to traumatic events, such as maternal separation, social isolation, experimentation, or other similar experiences. Using criteria for PTSD similar to those developed by Scheeringa *et al.* (1995) as alternative criteria for nonverbal infants and children, the authors found that 44% of chimpanzees in sanctuaries fulfilled the diagnostic criteria for PTSD, compared with 0.5% of chimpanzees in the wild.
- Lopresti-Goodman *et al.* (2015) studied 253 chimpanzees formerly used in biomedical research and currently residing at an accredited chimpanzee sanctuary. Based on caregiver reports, 60 (24%) of the animals exhibited at least one symptom of psychological distress, including irritability, social withdrawal, fear of going outside, rocking back and forth while self-clasping, eating and/or smearing of feces, affect dysregulation, anhedonia, dissociative episodes, and SIB. In addition, the authors presented a detailed case study of one chimpanzee who engaged in SIB and met DSM-5 criteria for PTSD.

Without using the term posttraumatic stress, Loeffler et al. (2009) reported on impaired psychological health following prolonged severe stress in bears. The practice of farming bears for bile extraction is legal in China, where bear bile is used in traditional Chinese medicine (despite the fact that it is unnecessary, as more than 50 alternative herbal products with equal or greater medicinal efficacy exist [Liu, 2004]). The Asiatic black bear (*Ursus thibetanus*) comprises most of the estimated 10,000 to 12,000 bears used in these farming operations; some are born in captivity and some are captured from the wild as adults. The bears are confined for their entire lives to very small cages that are only marginally bigger than the bears themselves during which they encounter the following stressors: extreme spatial restrictions, severe restriction of species-typical

behavior, adverse substrate for sleeping and standing, deprivation of social needs, loss of the sense of control, extreme understimulation, and unpleasant interactions with humans (the bile extraction procedure is painful) (see Fig. 14.2a–d).

The study by Loeffler et al. (2009) assessed approximately 250 of the bears that been rescued from bile farms and given refuge at the China Bear Rescue Center (CBRC) operated by the Animals Asia Foundation. On arrival at the CBRC, 95% of the bears exhibited signs of stereotypic behavior, which included head rolling, pacing, rocking, circling, and stepping from side-to-side or back and forth, and bobbing and weaving of the head and body (Fig. 14.2e). Some bears were unusually unresponsive and slept excessively. All but five of the bears demonstrated unusually aggressive behavior, agitation, or nervousness; some of these behaviors resulted in self-injury. Many of the behaviors, such as periodic pacing and head-swaying, persisted for years post-rescue despite intensive rehabilitation efforts.

Nonreviewed reports

- Several anecdotal reports describe signs characteristic of PTSD in canine and feline survivors of Hurricane Katrina (Anon, 2005, 2008; PBS, 2005). Signs reported in the animals were severe personality or temperament changes, new phobias, chronic chewing or paw licking, and depression (Anon, 2008); trembling, hypersalivation, pacing, aggressive behavior, loose stools, vomiting, lack of appetite, elimination in the house, and avoidance of people (Anon, 2005); and indelible fear of storms as well as nervousness, fear, or aggressive behavior in response to TRCs such as heavy winds, rain, or rushing water (PBS, 2005).
- Dodman (2012) described the psychological changes in a dog who was mistakenly shot by a police officer. From that day onward the dog showed hypervigilance, extreme fear when encountering reminders of the event (such as police cars), nocturnal separation anxiety, and presumed nightmares – overall, '[meeting] all the translatable criteria of human PTSD'.
- Garlick and Austen (2014) reported on five kangaroos with a history of exposure to a major stressor at a young age and demonstrating chronic signs deemed to be consistent with symptoms of human PTSD. All of the joeys had been separated from or lost their mother to illness or

other death; findings at the time of rescue included severe malnourishment and fractured bones and extensive wounds due to harassment and attacks by dogs and foxes. The in-care behavior observed included social withdrawal, refusing food, erratic and agitated behavior, destructiveness including SIB, and aggression toward other kangaroos.

Canine PTSD. Most recently, a population of dogs has arisen which has, from a clinical standpoint, provided the most complete knowledge of the animals' psychological make-up pre- and postexposure to extreme stress, and that is military working dogs (MWD) after exposure to combat and violent events in Iraq and Afghanistan. MWDs offer a unique opportunity to study posttraumatic disorders clinically because their histories are well known, allowing researchers to eliminate alternative explanations for posttrauma signs and symptoms and thereby definitively meet the DSM-5 requirement of 'beginning after the traumatic event(s) occurred' for PTSD Criteria B through E (American Psychiatric Association, 2013). This is in contrast to studies of other populations of dogs with suspected psychological trauma - e.g., hoarded dogs (McMillan et al., 2016), former breeding dogs from commercial breeding establishments (McMillan et al., 2011), and abused dogs (McMillan et al., 2015) – for which incomplete histories did not allow potential effects of trauma to be distinguished from other antecedent factors such as inadequate early socialization.

Burghardt (2013) reported findings in 14 MWDs showing extreme psychological changes after exposure to combat in war zones. Clinical signs included hypervigilance and hyperresponsivity to environmental events, behaviors aimed at escaping or avoiding previously positive or neutral environments, failure in the performance of previously mastered critical tasks, and changes in social interaction with their human handler. A breakdown by breed found that Labrador retrievers made up 50% of the case series but only 15% of the MWD population. By task, dogs trained to locate improvised explosive devices made up 60% of the cases but only 20% of the MWD population. Based on an estimate of the number of dogs deployed and at risk, the author suggested an incidence for this disorder of approximately 5% among deployed MWDs.

Little is known about the history of PTS in any nonhuman species, but it is interesting to note that a



Fig. 14.2. (a–d) Bears used for 'bile farming' in Far Eastern countries are confined for prolonged periods in extremely restricted cages. (e) If removed from the bile farm and placed in a sanctuary most will exhibit pronounced signs of psychological disturbances. (Photos courtesy of Animals Asia.)

movie entitled *Courage of Lassie* depicted with considerable accuracy a case of canine PTS resulting from exposure to military combat (Fig. 14.3). Most intriguing is that the movie was released in 1946 –

34 years before the diagnosis of PTSD was formally recognized as a mental disorder in humans, and a full 67 years before the canine form of PTSD appeared in the scientific literature.



Fig. 14.3. In 1946 – decades before PTSD became an official diagnosis – the movie *Courage of Lassie* depicted a case of canine posttraumatic stress resulting from exposure to military combat. (Courtesy of AF archive/Alamy Stock Photo.)

Does PTSD occur in animals?. Can the severe form of PTS in animals be considered the same as the severe form, i.e., PTSD, in humans? Is it correct to say that animals experience 'human-type' PTSD? Some researchers have expressed confidence in the human PTSD being present in nonhumans, but other researchers are less convinced and are careful to describe symptoms with terms like 'analogous' or 'parallel'. Siegmund and Wotjak (2006, p.324) have pointed out that the 'PTSD model' has recently become 'a somewhat fashionable term used in animal studies for almost every stress-induced behavioral alteration. Only a few cases, however, reflect the human disorder closely enough to deserve this term.'

In evaluating for the existence of PTSD in animals, similar limitations in communication (i.e., lack of verbal abilities and language barriers) between very young children and animals makes applying the DSM-5 criteria for young children the most rational for nonhuman species (Ferdowsian *et al.*, 2011, 2012). One important caveat here is that in the young children the trauma is always occurring during the developmental period, which may differ in important ways from trauma in mature animals. Hence, even if young children and animals both fulfill the DSM-5 criteria, the possibility that we may be talking about two different psychological disorders

cannot be ruled out. The implications for this possibility for treatment may be substantial.

In addition to applying the child diagnostic criteria directly to animals, DSM criteria have been construed in ways to construct comparabilities between human and animal symptoms. For example, Foa et al. (1992) discuss an interpretive framework in which a conditioned fear response is a sign that the animal is reprocessing or re-experiencing the US, which would endorse symptom 3 of Criterion B: the child feels and/or acts as if the event were recurring. Similarly, Cabib et al. (2019) wrote that persistent freezing in response to conditioned stimuli is the behavioral phenotype frequently used in rodents to model the 're-experiencing of traumatic memories' by human PTSD patients. Others have taken a more specific, point-by-point comparison. For example, Richter-Levin et al. (2019) suggested that symptoms associated with the criterion of alterations in arousal levels and reactivity are straightforward to recognize in animals, and measurable by the many validated tests for irritability or aggression, hypervigilance, startle reaction, and sleep parameters. In addition, they wrote:

intense or prolonged distress after exposure to traumatic reminders or marked physiologic reactivity after exposure to trauma-related stimuli may be

measured in rodents as part of assessing [adult] criterion B 'Intrusive symptoms'. Likewise, avoidance behavior in face of trauma-related external reminders may be measured for [adult] criterion C 'Avoidance behavior'. [Adult] criterion D, of negative alterations in cognitions and mood, may be assessed by several, well-established tests such as tests of hedonic preference, social preference, and motivation. (p. 1136)

Is it important whether animals experience 'true', that is, human-type, PTSD? We know three things. First, animals experience psychological trauma on a continuum (PTS; Fig. 14.1). Second, making a firm distinction between PTSD and less severe forms of PTS would only matter: (i) if the treatments differed appreciably between the two – and presently in humans, they do not (to be discussed in Section 14.7.1); and (ii) for purposes of health insurance and disability claims. Third, classifying the most severe cases as something special offers no advantage, and in fact may - as mentioned earlier for humans - risk denying adequate care for the individuals who fall below the diagnostic threshold of PTSD but experience significant distress (Cukor et al., 2010).

So, do animals experience PTSD? Based on child criteria for PTSD in DSM-5, a good argument can be made that they do, or at least have the capacity to. But the more important question is, should we make for animals a distinction of PTSD separate from all of the less severe forms of PTS? With current knowledge suggesting that this offers no apparent benefit, and may even risk harm, it is proposed here that the PTS continuum better able to serve nonhuman animals is one which divides PTS into three roughly equal sections – mild, moderate, and severe – with no separate classification for PTSD, as depicted in Fig. 14.4. In such a diagnostic scheme, both humans and animals could be diagnosed with severe PTS, but

only in humans would this include the distinct diagnostic category of PTSD.

It was noted earlier that not all posttraumatic psychopathology is captured within the PTSD diagnosis (van der Kolk et al., 2005). Accordingly, as important as PTSD has become in the field of trauma research, PTSD is only a part of: (i) a continuum of PTS conditions of varying severity and complexity; and (ii) a spectrum of posttraumatic responses. We turn to the latter next. Before beginning this discussion, however, an important point must be made. In humans who have experienced psychological trauma, comorbidity of PTS and mood and anxiety disorders is the rule rather than the exception (Richter-Levin et al., 2018). For example, PTSD and depression frequently coexist in traumatized individuals (Flory and Yehuda, 2015). Accumulating evidence in animal studies has revealed that similar comorbidity also exists in nonhuman species (Whitaker et al., 2014; Richter-Levin et al., 2018). Because of this, it can be difficult in animal models to distinguish PTSD-like behaviors as attributable to PTS versus other psychiatric conditions, in particular depression (Whitaker et al., 2014). Therefore, while the following discussion presents the different posttraumatic disorders as distinct entities, such diagnostic clarity is not to be expected in all animals who have experienced trauma.

14.3.2 Posttraumatic phobias – Specific phobia

In both humans (O'Donnell *et al.*, 2004; Bryant, 2010; American Psychiatric Association, 2013) and animals (Palestrini, 2009; Pageat and Fatjo, 2013; Overall, 2013), individuals can develop specific phobias after a traumatic event. Across species, a specific phobia is a marked and maladaptive fear or anxiety about a specific stimulus or situation that

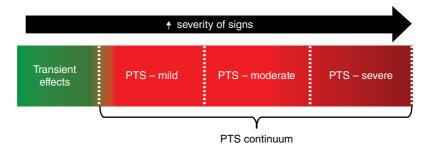


Fig. 14.4. Proposed schematic for posttraumatic stress in animals. PTS, posttraumatic stress.

is out of proportion to the actual danger posed. The fear-inducing stimulus or situation is actively avoided or endured with intense fear or anxiety and the emotional response causes clinically significant distress or impairment in psychosocial functioning and decreased quality of life (American Psychiatric Association, 2013; Landsberg *et al.*, 2013).

Most descriptions of specific phobia regard the exposure to the aversive stimulus or event as sufficient to elicit the psychopathological changes. However, for stress-induced phobias in companion animals, Overall (2013) includes the additional element of uncontrollability of the stimulus in situations that are injurious or potentially injurious. For example, dogs experiencing an inescapable event such as a car accident may become phobic of cars or the restraint system in use when the accident occurred (Overall, 2013).

Whereas not all specific phobias are associated with trauma, those that are may sometimes be difficult to distinguish from other posttraumatic psychopathology. Specific phobia in both humans (Cahill and Foa, 2007) and animals (Landsberg et al., 2013) may exhibit generalization of the specific fear, but some features appear to distinguish posttraumatic generalized fear associated with specific phobia and that with PTS. For example, studies in humans have shown that the fear generalization is greater in the case of PTSD than with specific phobia, causing individuals with PTSD to fear and avoid a wider range of cues than people with phobias, even agoraphobia (Cahill and Foa, 2007). Moreover, individuals with phobia become aroused only when exposed or in anticipation of exposure to the fearful stimulus or situation, whereas individuals with PTSD typically experience a more persistent state of hyperarousal (Friedman, 2006).

14.3.3 Generalized anxiety disorder

Another disorder known in humans (O'Donnell *et al.*, 2004; Bryant, 2010) and animals (Crowell-Davis, 2009; Ferdowsian *et al.*, 2012) to, in some cases, occur subsequently to psychological trauma is GAD. For example, in one human study 4% of individuals were diagnosed with GAD after the Oklahoma City bombing (North *et al.*, 1999); in another study 11% of survivors of traumatic injury developed GAD (Bryant *et al.*, 2010).

In humans, GAD is a disorder consisting of excessive anxiety and worry (apprehensive expectation) about a number of events or activities causing

clinically significant distress or impairment in important areas of functioning (American Psychiatric Association, 2013). In addition, the anxiety and worry is accompanied by a variety of symptoms, including restlessness or feeling keyed up or on edge, being easily fatigued, difficulty concentrating, irritability, muscle tension, and sleep disturbances.

The typical presentation of GAD in companion animals appears as constant or almost constant signs of fear and anxiety, regardless of the context or the stimuli to which the animal is exposed (Crowell-Davis, 2009; Overall, 2013). Signs may become more severe in particular situations but are evident at low levels relatively persistently. Physical and physiological signs primarily involve increased autonomic arousal with dilated pupils and increased heart and respiratory rates (Overall, 2013). Specific behaviors vary among individual animals and can include increased vigilance, pacing, and vocalizing (Crowell-Davis, 2009; Overall, 2013). Comments from the pets' owners often describe the animal as always 'miserable' or 'frightened', or that the pet is 'never happy' (Crowell-Davis, 2009).

In addition to companion animals, GAD has been reported in sanctuary-living chimpanzees with previous histories of experimentation, orphanage, illegal seizure, or violent human conflict (Ferdowsian *et al.*, 2012). Using behaviorally anchored criteria the researchers compared chimpanzees living in wild sites in Africa (n = 196) with those in sanctuaries (n = 168) and found that 18% of the sanctuary chimpanzees met the DSM-IV diagnostic criteria for GAD, compared with 0.5% of those in the wild. The results suggested to the researchers that chimpanzees can exhibit behavioral clusters similar to GAD as a result of potentially traumatic experiences.

14.3.4 Depression and 'learned helplessness'

Affective (mood) disorders are relatively common following exposure to PTEs and, as mentioned earlier, may occur independently of or in conjunction with PTS (O'Donnell et al., 2004; Cohen et al., 2006; Bryant, 2010; American Psychiatric Association, 2013). There is evidence in humans indicating that major depression is the most common form of posttraumatic psychopathology, even more prevalent than PTSD (Rosen et al., 2010a). Data from the studies mentioned above for GAD showed that after the Oklahoma City bombing 22% of people were diagnosed with depression

(North *et al.*, 1999), and among 1084 traumatic injury survivors depression was the most common disorder found, present in 16% of the population (Bryant *et al.*, 2010).

In an experimental setting, stress-induced depression has been one of the most common research paradigms using animal models over the past five decades. Thousands of experiments reported in the literature on what was originally termed 'behavioral despair' involve exposing animals to severe stress until they exhibited signs of anhedonia, social withdrawal, decreases in investigative behaviors and locomotor activity, and learning deficits (Yan et al., 2010) - signs interpreted today as analogous to human depression. Stress-induced behavioral models of depression have used acute, single-exposure stress as well as chronic stress (Mangiavacchi et al., 2001). Much of the work in this field has involved the use of uncontrollable and/or unpredictable stress to induce a state termed 'learned helplessness', which is essentially a 'giving up' of the individual upon learning that their actions are futile in reducing the psychological impact of an aversive stimulus and has been regarded as an analog of human depression (Notari, 2009; see also Chapter 6).

In the review presented earlier describing PTSD symptoms in chimpanzees who had been reportedly subjected to traumatic events (Ferdowsian *et al.*, 2011), the authors also evaluated the prevalence of signs of depression among 20 cases included in 12 published reports. Using criteria for depression similar to those developed by Scheeringa *et al.* (1995) as alternative criteria for nonverbal infants and children, the authors found that 58% of chimpanzees in sanctuaries met the diagnostic criteria, compared with 3% of chimpanzees in the wild.

Clinically, Pageat and Fatjo (2013) described a state of reactive depression – one type in puppies and one type in adult dogs and cats - which occurs after an intensely stressful event such as accidents, violent punishment, painful stimuli, or abandonment. A sign common to both puppy and adult forms is a loss of interest in the environment. The puppy form is associated with a diminishment of normal activities, a generalized state of inhibition and immobility, and drinking less. Dogs and cats experiencing the adult form show decreased appetite and increased sleeping; dogs show increased whining behavior. As described by Pageat and Fatjo, the adult form of reactive depression appears to be comparable to 'adjustment disorder with depressed mood' in humans, which also occurs in response to an identifiable stressor (American Psychiatric Association, 2013). Overall (2013) also describes a similar reactive form of depression in dogs which occurs subsequent to a drastically altered environment over which the patient had no control, such as relinquishment, abandonment, re-homing, or death of a close human or another pet. Signs exhibited in this disorder include withdrawal from social stimuli and activities that were previously engaging and enjoyable, alterations in appetite, and alterations in sleep—wake cycles.

14.3.5 Trauma-related compulsive behaviors (obsessive-compulsive disorder, stereotypies)

Two accounts of compulsive behaviors in animals subsequent to extreme stress have been reported in the literature. Pageat and Fatjo (2013) describe a dissociative syndrome in dogs which may appear spontaneously or in response to a highly stressful event. The disorder is characterized by repetitive behaviors not attributable to underlying medical pathology nor in response to an identifiable stimulus and include snapping at the air, circling, clicking jaws, jumping, and looking upward. In their study of 168 sanctuary-housed chimpanzees with previous histories of experimentation, orphanage, illegal seizure, or violent human conflict, Ferdowsian et al. (2012) applied behaviorally anchored criteria to compare these individuals with 196 chimpanzees living in wild sites in Africa. They found that 19% of chimpanzees in sanctuaries met the criteria for obsessive-compulsive disorder (OCD), compared with 0% of those in the wild. Alternative explanations, however, such as confinement-induced stereotypies, were not considered.

14.4 Psychological Conditions/States that may Resemble and/or Coexist with Psychological Trauma

14.4.1 Inadequate socialization

As mentioned briefly earlier, emotional and behavioral characteristics of animals deprived of adequate early socialization can closely mimic those caused by psychological trauma. Stimuli encountered (in a nonthreatening context) during neonatal cerebral development at a time of greater neuronal plasticity become neurally coded as familiar and 'normal', and fear toward these stimuli is minimized. In this way, the animal is developing the neural substrate

optimally prepared for successfully coping with the stimuli that that animal will be most likely to encounter during its lifetime (Palestrini, 2009). Animals not receiving a broad range of social and environmental experiences during their early development may show substantial fear to other living beings, objects, and situations throughout life (Palestrini, 2009; Landsberg *et al.*, 2013; Overall, 2013). It is possible that abnormally high levels of fear – the predominant emotion of PTS – exhibited by companion animals with an unknown history may be due partly, largely, or solely to inadequate socialization.

This concern is relevant only for animals with incomplete histories, which includes both pretrauma histories for those with known trauma (or PTE exposure) as well as histories in which the existence of trauma itself is not known with certainty. While this problem occurs much more commonly in animals than in humans, there are situations where it is not possible to obtain detailed histories about the precise nature of a child's early experiences (American Psychiatric Association, 2013).

In humans, attachment disorders have been consistently identified in some young children following severe stimulus deprivation in early life. The conditions bearing the closest resemblance to socioenvironmental deprivation in animals are reactive attachment disorder and disinhibited social engagement disorder (American Psychiatric Association, 2013; Humphreys et al., 2017). Both conditions share the common etiology of extreme social neglect in early life, but the former is marked by depressive symptoms and withdrawn behavior, whereas the latter is expressed as disinhibition and externalizing behavior (American Psychiatric Association, 2013). In companion animals, the fearful state resulting from the more extensive deprivation of social and environmental experiences (i.e., collectively termed 'inadequate socialization' in this chapter) is referred to by Overall (2013) as neophobia and by Crowell-Davis (2009) as generalized anxiety disorder.

14.4.2 Stress-induced dishabituation

In the recent literature, some authors (Mills, 2009; Notari, 2009) have discussed a psychological phenomenon in animals which may appear after stress and consist predominately by fear, and could therefore appear to be a posttraumatic psychopathogical disorder. *Stress-induced dishabituation* has been described as what occurs when conditions of chronic stress later in life lead to an emergence of a fear

response to stimuli to which the animal was previously habituated (Mills, 2009; Notari, 2009). Notari (2009) writes that this loss of habituation can be observed in cases such as fear of noises (e.g., fireworks or thunderstorms), but also in cases of habituation to social contacts with humans or other animals and can lead to the onset of avoidance behaviors such as freezing, attempting to escape, or aggressive behavior when the animal previously appeared well habituated or socialized.

14.5 Moderating Factors for Psychological Trauma: Risk and Resilience

Extensive empirical as well as anecdotal evidence has shown that exposure to adversity, while essential for the development of psychological trauma, does not by itself determine which individual will or will not experience posttraumatic distress, nor its severity (Ruscio et al., 2002). As discussed earlier, the human responses to stress and trauma vary widely; under the same stressful circumstances one individual may develop severe PTSD while others may only experience mild psychological symptoms that resolve rapidly (Southwick and Charney, 2012). Animals have shown the same pattern. Experimentally induced trauma in animal subjects, even when the trauma is rigorously standardized, results in substantial individual variation in the animals' responses (Suomi, 2006). Therefore, exposure to extreme adversity appears to be a necessary but not sufficient condition to 'traumatize' an individual (Friedman, 2006; Richter-Levin et al., 2018).

Numerous factors appear to modulate psychological outcomes to stressors, contributing to vulnerability or risk for, or resilience against, the development of psychopathology. Understanding why some individuals develop mental disorders following trauma and others do not has the greatest importance for prevention and treatment. The currently recognized modulating factors include specific characteristics of both the stressor and the experiencer, and although a comprehensive review of all of the factors is beyond the scope of this chapter the following discussion presents those considered to have the greatest impact on outcomes.

14.5.1 Characteristics of the stressor

Traumatic stressors exist on a gradation of severity and there is currently no clear distinction between

traumatic and nontraumatic stressors (Wilson, 2004; Norris and Slone, 2007; Rosen *et al.*, 2010a; Wakefield and Horwitz, 2010) – a fact that is self-evident from the fact that a particular stressor may be traumatic for one individual but not another. In fact, the types of aversive stimuli used in experimental settings to cause psychological trauma in animals are the same stimuli that have been used as standard stressors in stress research for decades. Accordingly, it may not be possible in animals to identify specific stressors, or characteristics of stressors, that have the potential to cause psychological trauma above and beyond 'standard' stress.

However, several stressor-related factors have been found to influence the severity of psychological trauma in both humans and animals. Animal experiments indicate that stressor severity is a major factor: stressors of longer duration and greater intensity lead to stronger avoidance and escape responses, are more difficult to extinguish, promote greater generalization, and are more likely to produce maladaptive responses (Wyler et al., 1971; Brown et al., 1973; Cahill and Foa, 2007). Evidence from both animal and human studies suggest that certain stressors which threaten survival of the organism elicit biological and behavioral reactions that are particularly extreme and persistent (Ronan and Summers, 2008). Work using animal models has also identified the qualitative feature of (un)controllability as a key characteristic of the stressor which determines whether fear sensitization, a major component of psychological trauma, occurs (Maier and Watkins, 1998). As mentioned below, controllability is a characteristic of the experiencer as well as of the stressor.

14.5.2 Characteristics of the experiencer

Factors of the individual that modulate (or are otherwise linked to) the effects of the stressor fall into the general categories of risk or vulnerability factors, which indicate an increased likelihood for pathological outcomes, and protective factors, which indicate a decreased likelihood for such outcomes. The latter is incorporated into the general concept of resilience, which is generally understood as the ability to overcome, successfully adapt to, or bounce back from adversity and trauma (Ong *et al.*, 2006; Southwick and Charney, 2012). Resilience encompasses psychological and biological characteristics intrinsic to an individual that confer protection against

the development of posttraumatic psychopathology after experiencing a severely stressful event or events (Hoge *et al.*, 2007).

Genetics

Accumulating evidence in humans and animals supports the notion that vulnerability and resilience to stress-related psychopathology have a genetic component. Convincing evidence of a genetic contribution to the development of PTSD in humans has come from twin studies, which have shown that genetic influences account for 24% to 72% of the vulnerability to PTSD (Pitman et al., 2012; Cabib et al., 2019). More specifically, Xie et al. (2009) found that a polymorphism of the serotonin transporter gene (5-HTTLPR S-allele) interacted with adult traumatic events and childhood adversity to increase the risk for PTSD. In animals the individual variability in coping and recovering from adverse experiences has been shown in squirrel monkeys to be, at least in part, heritable (Sanchez et al., 2001). Other examples include studies showing that rats which have a genetically determined blunted HPA axis response are predisposed to developing PTSDlike responses to stress exposure (Cohen et al., 2006) and that a genetic predisposition explained phenotypic vulnerability to stress in inbred mouse strains (Cohen et al., 2008).

Early life adversity

A well-documented risk factor for psychopathology in humans and animals is having experienced trauma earlier in life, particularly when exposure to stress occurs during the youngest stages of life (Sanchez et al., 2001; Heim and Nemeroff, 2009; Sherin and Nemeroff, 2011). Current evidence indicates that early life adversity (ELA) - which includes poor maternal care, neglect, abuse, and other highly stressful experiences - has profound and long-lasting effects on the development of neurobiological systems and epigenetic activation, in essence 'programming' a vulnerability to the development of posttraumatic psychopathology in response to stress later in life (Briere and Spinazzola, 2005; Heim and Nemeroff, 2009; Sherin and Nemeroff, 2011; Dietz et al., 2018). The psychopathology may also manifest as mental health problems such as anxiety and depressive mood disorders (Briere and Spinazzola, 2005; Heim and Nemeroff, 2009). In a review of rodent and primate models of early adverse experience, Sanchez *et al.* (2001) showed that early traumatic experiences are associated with long-term alterations in coping style, emotional and behavioral regulation, and neuroendocrine responsiveness to stress, all contributing to later development of psychopathology. Rats exposed to trauma as juveniles were more vulnerable to adverse affects of fear conditioning (Yehuda and LeDoux, 2007) and exhibited more severe PTSD-like behaviors when stressed in adulthood (Imanaka *et al.*, 2006). In all, there is consistent evidence linking ELA to later mental health impairments in humans and animals, and that in animals this is a causal link (Miller *et al.*, 2011).

'Stress inoculation'

Whereas ELA can *increase* risk of psychopathological outcomes when exposed to stress in later life, a process termed 'stress inoculation' produces the opposite effect (i.e., a protective effect). The difference lies in the severity of the initial stress. ELA is considered to be associated with a more intense level of adversity, but early stress that is mild or moderate in intensity can actually promote resilience in the face of future stressful experiences (Lyons and Parker, 2007; Shapero et al., 2015; Santarelli et al., 2017). It is hypothesized that exposure to a challenging but manageable and controllable stressful event enhances emotional processing, cognitive control, curiosity, and neuroendocrine regulation, resulting in enhanced coping efforts in the face of subsequent challenges (Lyons and Parker, 2007). This phenomenon has been well-demonstrated experimentally in animals, in particular, rodents and nonhuman primates. For example, a study with squirrel monkeys demonstrated that moderately stressful early experiences strengthen socioemotional and neuroendocrine resistance to subsequent stressors (Parker et al., 2004).

Sense of control (internal locus of control)

A perception of control over the stressor – a characteristic of the experiencer and having comparable psychological impact as *actual* control (Perlmuter and Monty, 1977) – has been shown in humans and in animals to have protective effects against posttraumatic psychopathology. Conversely, the perception of uncontrollability increases vulnerability to detrimental outcomes. A review of the literature using animal models for PTSD (Foa *et al.*, 1992) showed that all other factors being equal, the less controllable and predictable a stressor is, the more

likely the victim will be to develop PTSD symptoms. The issue of control as it pertains to mental health and well-being is discussed in more depth in Chapter 6.

Social support (social buffering)

There is a large body of literature demonstrating that the presence of a compatible conspecific can buffer stress reactions and protect against posttraumatic psychopathology not only in people, but also in a wide variety of animal species (Hennessy *et al.*, 2009; Rault, 2012). Benefits are derived from social support during as well as after the stressful event. The issue of social support as it pertains to mental health and well-being is discussed in more depth in Chapter 8.

Overlaps in factors associated with risk and resilience

As is the case for many psychological phenomena, certain factors and concepts are not clearly distinguishable. For example, risk and protective factors are often inseparable, as they frequently interact in complex ways (Fairbank et al., 2007; Heim and Nemeroff, 2009). For example, research with children indicates that vulnerability in the genetic domain may be offset by resilience elsewhere, such as with increased social support (Kaufman et al., 2004). In addition, factors associated with the stressor and those with the experiencer may not be distinct from one another. The most evident example here is that the individual's perception and subjective appraisal, and not the stressor, often influences the severity of the stressful event (Foa et al., 1992). As mentioned above, the (un)controllability of the stressor may be a characteristic of the stressor (the stressor either actually is controllable or is not) or of the experiencer (the stressor is *perceived* as controllable or not). A two-axis model can conceptually represent the effect of interacting modifying factors on the degree of psychological harm (Fig. 14.5) (Briere and Spinazzola, 2005).

14.6 Challenges in Distinguishing and Diagnosing PosttraumaticPsychological Disorders in Animals

To a degree, some of the challenges in distinguishing psychological disorders and conditions in animals also plague human psychiatry. However, the challenges appear to be much greater in animals due to

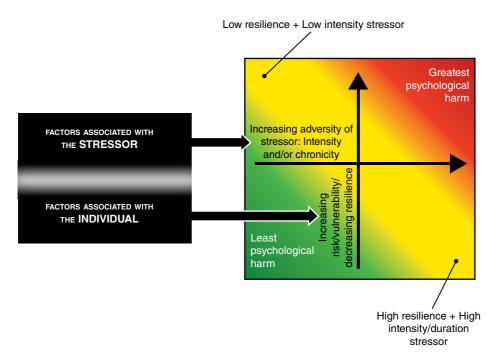


Fig. 14.5. A conceptual representation of the effect of interacting modifying factors on the degree of psychological harm (factors are not quantified to scale of impact; based on Briere and Spinazzola, 2005).

a multitude of factors including language barriers (for the entire population, not only the very young or mentally impaired), the higher incidence of incomplete and unknown histories, and the greater contribution of inadequate socialization. In this way, when trauma is part of the history these three factors can all but erase any lines between PTS, phobia, and GAD in animals.

There are a number of reasons why it is important to distinguish psychopathologic conditions from each other as well as from conditions that may resemble them: (i) accurate assessments inform treatment; (ii) to determine prognosis where euthanasia may be a consideration; (iii) to determine risk factors for the specific disorders; and (iv) to determine the potential of certain environments, e.g., zoos, agriculture, animal shelters, etc., to cause psychological harm – and to monitor success of reforms. Clinical distinctions in animals consist of different types.

14.6.1 Necessary distinctions in diagnosis Distinguishing trauma history from no trauma history

In humans, knowledge of a patient's traumatic history is often relevant to treatment, such as to guide

pharmacotherapeutic decisions (Marshall *et al.*, 1998). Moreover, specific features of the trauma may be important, as the choice of the most appropriate treatment method is a function of variables such as type, duration, and repetition of trauma (Lindy and Wilson, 2001).

For companion animals, the importance of determining a trauma history has not received much attention. Does treatment differ, for example, whether a dog's current fear of humans is a result of trauma or some other cause? This basic question has yet to be answered. One example of trauma information affecting treatment is the dissociative syndrome in dogs described by Pageat and Fatjo (2013). Among 99 dogs, those with the stress-induced form of the disorder, in contrast to those with the disorder not associated with stress, responded better to a specific therapeutic protocol at significantly lower doses and exhibited a longer interval between outbreaks.

In animals, determining a trauma history also involves distinguishing posttraumatic psychopathology from inadequate socialization. Here, too, the question as to whether this distinction influences treatment decisions remains unanswered. A similar issue challenges pediatric psychiatrists, as there appears to be considerable diagnostic overlap

between reactive attachment disorder (found in young children following severe early life stimulus deprivation) and PTSD in infancy and early childhood (Hanson and Spratt, 2000). Symptoms consistent with each disorder may occur when trauma occurs in the context of an infant's primary attachment relationship (e.g., domestic violence, physical abuse, etc.) (Hanson and Spratt, 2000).

Distinguishing among the spectrum of posttraumatic disorders (e.g., PTS, GAD, phobia, depression)

In humans, this distinction equates to making an accurate psychiatric diagnosis and plays a crucial role in treatment decisions (Marshall et al., 1998). One example is that in the treatment of PTSD in people the use of benzodiazepines, which are proven anxiolytic agents, has been shown to be not simply ineffective, but harmful: adverse outcomes include worse overall symptom severity, significantly increased risk of developing PTSD when used after recent trauma, worse psychotherapy outcomes, aggression, and depression (Friedman, 2001; Resick et al., 2007). However, as Rosen et al. (2008) have noted, due to symptom overlap between, as well as comorbidity of, posttraumatic disorders, distinguishing between presentations of phobic reactions, depression, and PTSD can be a challenge to the clinician's diagnostic skills.

Distinguishing PTSD from subthreshold PTSD (distinguishing levels of the PTS continuum)

As discussed in Section 14.3.1, meta-analytical studies have indicated that PTS is a dimensional rather than categorical disorder, which makes it improbable if not impossible to draw any distinct lines within the continuum. However, in considering treatment decisions for humans, several authors (Ruscio et al., 2002; Friedman et al., 2007b; Cukor et al., 2010) have contemplated the need for clearly distinguishing PTSD from less severe forms of PTS. For example, Friedman et al. (2007b, p.544) wrote, 'it would be important to determine whether partial/subsyndromal PTSD responds to treatments shown to be effective for full PTSD, or whether better results might be achieved from different therapeutic approaches'. The first study to report results from a pharmacological intervention for subthreshold PTSD (Naylor et al., 2013) found that paroxetine, FDA-approved for the treatment PTSD,

showed substantial promise for treatment for the less severe forms of PTS. Another study of the treatment of individuals with subthreshold PTSD (Dickstein et al., 2013) determined that cognitive processing therapy is an effective form of treatment among military veterans, and that its effectiveness does not differ between subthreshold and threshold groups. As a whole, although much less attention has been given to the treatment of subthreshold PTSD (Bergman et al., 2015), methods of treatment of 'full' PTSD and subthreshold PTSD have not been shown to differ in any meaningful way. As alluded to earlier, there is currently no evidence to suggest that making a clear distinction of PTSD from less severe forms of PTS would have any benefit for treatment decisions in animals.

14.6.2 Diagnostic methods

The diagnostic criteria contained in the fifth edition of the DSM (American Psychiatric Association, 2013) serve as the current 'gold standard' for a diagnosis of PTSD which, unfortunately for animal applications, heavily rely on patients' subjective reports (Pitman *et al.*, 2012). Research to identify physiological and morphological abnormalities that could statistically discriminate PTSD from non-PTSD control groups have had some success, but no factors yet identified possess the specificity and sensitivity necessary to be regarded as a stand-alone diagnostic test for PTSD (Pitman *et al.*, 2012).

Measures of physiological reactivity have shown considerable promise in the diagnosis of PTSD in humans. Increased heart rate reactivity to loud tones and to trauma-related stimuli has been the most consistently documented effect for PTSD (Southwick et al., 2007). Similarly, an increased startle to sudden, loud tones is a well-replicated psychophysiological marker for PTSD (Segman et al., 2007). Keane et al. (2007) have noted that an advantage of psychophysiological measurements is that the objectivity of the data increases their value for use in individuals impaired in their ability to communicate their subjective states, such as young children and individuals with brain damage. Rosen et al. (2010b) suggested that it is probable that psychophysiological reactivity is the closest approximation currently available for a biological signature for the disorder in people. Similar approaches may be appropriate with animals, in which comparable physiological measurements such as heart rate variability are now used to

assess emotional responding, stress, and welfare (von Borell et al., 2007).

In humans, cortisol concentrations received substantial attention when it was found that many individuals with PTSD had reduced levels (Rosen et al., 2010b). Animal research showed that when nonhuman primates were exposed to variable stress but no overt trauma, baseline cortisol concentrations were low (Marshall et al., 1998). However, the initial enthusiasm in cortisol waned considerably when later human studies showed normal and even increased levels of cortisol in PTSD patients (Rosen et al., 2010b).

14.7 Rehabilitation and Treatment: Healing Psychological Trauma

14.7.1 Treatment principles and goals

Very little information about the clinical treatment of psychological trauma in animals can be found in the veterinary behavior literature. And although it is too early to use specific treatments for human PTSD in animals, many of the general goals and principles of human PTSD treatment have applications for treatment in animals. (The discussion here will focus on PTS – for treatments of other posttraumatic disorders, such as specific phobia, GAD, and depression, the reader is referred to relevant texts, e.g., Landsberg *et al.*, 2013; Overall, 2013.)

The foremost principle guiding therapy is that there are no universally standardized protocols for treatment of PTSD and it is essential to individualize therapy based on the patient's PTSD phenotype (Wilson *et al.*, 2001b). Additional principles include (Herman, 1997; Wilson *et al.*, 2001c):

- Patients must be permitted to progress in processing the trauma at their own pace.
- PTSD symptoms wax and wane over time, and regressions and relapses can be expected.
- Recovery should never be considered complete and final; symptoms are likely to recur under stress.
- The best indices of resolution are the survivor's restored capacity to take pleasure in his/her life and to engage positively in social relationships. The world becomes trustworthy, no longer something to fear.

Specific treatment goals that have relevance in treating animals include (Herman, 1997; Friedman, 2001; Wilson *et al.*, 2001a,b,c; Bryant, 2010):

- Restore the patient's sense of safety (and decrease the sense of vulnerability).
- Restore the patient's sense of control over life events.
- Facilitate the restorations of healthy attachments and relationships.
- Provide social support.
- Identify trigger stimuli for hypervigilance, exaggerated startle response, and conditioned fears associated with the trauma.
- Facilitate normalization toward homeostatic functioning through the reestablishment of the normal (healthy) stress response to the extent possible.
- Facilitate accurate appraisal of stimuli rather than irrational fear or avoidance behaviors.

The two major treatment methods utilized in human PTSD are cognitive-behavioral therapy (CBT) and pharmacotherapy.

Cognitive behavioral therapy

Current clinical practice guidelines established by the International Society of Traumatic Stress Studies identify CBT as the treatment of choice for PTSD (Friedman et al., 2007a). CBT comprises several specific treatment approaches, including prolonged exposure (PE), cognitive therapy, cognitive processing therapy, and stress inoculation therapy (Resick et al., 2007). Among these, exposure therapy has received the most empirical support (Hembree and Foa, 2010). Exposure therapy is conceptually based upon fear extinction, which is impaired in PTSD, and involves fear confrontation through measured exposure to progressively stronger TRCs to create a new association between those cues and safety - all done in a safe and supportive environment (i.e., CS followed by no US) (VanElzakker et al., 2014).

Systematic desensitization (SD), which consists of repeated and brief confrontations with the feared stimuli, was the first exposure procedure used (Wolpe, 1958). However, based on findings showing that long exposures are more effective than short ones, a shift away from SD and toward PE has occurred in recent years (Foa and Meadows, 1998).

Administering cognitive behavior therapy in animal patients requires special considerations due to the obvious limitation of communication integral to talk therapies. Siegmund and Wotjak (2006) agree that the same principles of fear extinction apply to animals. Based on laboratory work, they suggested that aversive memories could be weakened through

repeated nonreinforced presentation of TRCs, during which the animal eventually learns that a particular stimulus no longer predicts the occurrence of an aversive consequence. This concept underlies both PE and desensitization approaches, and although the former has not been clinically adapted to animal patients, desensitization, along with counterconditioning, has shown considerable effectiveness in treating fearful animals in general and traumatized military dogs in particular (see below).

Pharmacotherapy

Several well-controlled studies in humans have determined the selective serotonin reuptake inhibitors (SSRIs) to be the treatment of choice as firstline drugs for treating PTSD (Matar et al., 2006). The FDA has approved two SSRIs, sertraline and paroxetine, for treatment of PTSD (Friedman and Davidson, 2007). Empirical data have demonstrated effectiveness of SSRIs in reducing the three PTSD symptom clusters of intrusion, avoidance, and hyperarousal, and in improving and sustaining quality of life during treatment (Friedman, 2001; Rapaport et al., 2002). However, several meta-analysis studies suggest that the efficacy of such treatments is minor and in some cases equivalent to that of treatment with placebos (Kozarić-Kovačić, 2008; Ragen et al., 2015).

14.7.2 Treatment in animals

In animals, experimental studies have also demonstrated effectiveness of SSRIs to alleviate detrimental effects of stress on the HPA stress response system (Penza et al., 2003). In animal models of PTSD using predator exposure and single prolonged stress, SSRIs reversed PTSD-like symptoms (Yamamoto et al., 2009). However, not all findings have relevant applications to clinical cases of psychological trauma in animals. For example, Matar et al. (2006) found that sertraline reduced anxiety-like responses, avoidant behavior, hyperarousal, and the overall incidence of extreme (PTSD-like) behavioral responses, but only when the drug was administered immediately after stress exposure and by an intraperitoneal route daily for 7 days. Clinically, the presentation of an animal immediately after a PTE would highly improbable, and this type of drug administration regimen would be impractical.

A few reports of treatment of psychological trauma in animals have appeared in the literature. Burghardt's

(2013) work with 14 military working dogs, which he acknowledges is largely anecdotal, describes the first step being relieving the dog from military duty. The dogs are moved to a quieter and less stressful environment, where the dog receives exercise and practices work skills and social interaction with the handler. Some dogs with acute or subacute signs were provided behavioral enrichment along with scheduled task training in a noncombat setting. Acute cases also appeared to respond well to anxiolytic drugs such as alprazolam or buspirone, often combined with a beta-blocker (e.g., propranolol). Dogs exhibiting chronic signs were most often treated with a tricyclic antidepressant (e.g., clomipramine) or SSRI (e.g., fluoxetine), and the treatment may also include a beta-blocker. When practical and safe, desensitization with counterconditioning using TRCs (e.g., gunfire, concussive noise, working locations) showed efficacy in chronic cases.

Progress of the initial treatment plan is evaluated after several weeks and if signs of distress are still evident the dog is returned to the United States. Here, desensitization and counterconditioning is instituted in a nonthreatening environment with some TRCs present. Medications are used when necessary. Other authors (Huntingford, 2013; Overall, 2013) have stressed the value of play therapy, such as having the opportunity to run and chase other dogs, play with people, swim, retrieve, or run an agility course, in facilitating the recovery in dogs with psychological trauma. Overall (2013, p.234) suggests another consideration with regard to treating fears, noting that, 'Protection is undervalued as a treatment strategy'. Recognizing that the cost and effort required to treat some fears may be prohibitive for some pet owners, and that treatments are not always effective, she points out that pet owners who can protect dogs from the objects of their fear might choose protection as a strategy. She stresses, however, that the pet owner must be certain that they can continuously provide the protection for a decade or more.

Outcomes in Burghardt's 14 MWDs showed a variable prognosis. Approximately 50% of dogs treated for 4 months responded well and were able to return to military service. The other 50% did not respond sufficiently to be reexposed to potential triggering stimuli and were either transferred to roles where encountering TRCs would be less likely (such as security or police work in the US) or retired and adopted to private individuals. None of the dogs in the report was euthanized for behavioral or medical problems.

Garlick and Austen's (2014) report of five kangaroos with presumed PTS resulting from early life adversity described a treatment plan consisting a several principles: create a safe environment that builds confidence and minimizes fear from vulnerability and exposure, promote development of social bonds between kangaroos and between kangaroos and human carers, and short-term use of psychotropic medications. Four of the five kangaroos exhibited a favorable outcome.

Lopresti-Goodman *et al.* (2015) stressed a multimodal approach to treatment of chimpanzees diagnosed with PTSD. Key features of therapy include:

- Establish a safe, stable, and predictable environment, including providing places for retreating from other chimpanzees and relaxing.
- Encourage positive relationships between human caregivers and the chimpanzees, allowing a building of the animals' trust in humans.
- Promote social relationships through gradual introductions to other chimpanzees and integrations into a large social group.
- Empower the animals with the ability to make decisions about everyday aspects of their lives, such as allowing them to decide what activities to engage in. This involves creating complex physical environments that are cognitively stimulating and ethologically appropriate, including providing access to large outdoor areas with climbing structures, opportunities to forage for food, and cognitively enriching games, puzzles, and toys.
- Provide adequate veterinary care.
- Use antianxiety and antipsychotic medications as needed for anxiety and SIB.

An important final note on prognosis is that in humans PTSD can be successfully treated and resolved; however, symptoms may recur and even intensify later in response to reminders of the original trauma, ongoing life stressors, or newly experienced traumatic events (Wilson, 2004; American Psychiatric Association, 2013). Accordingly, human patients should not be led to expect that any treatment is absolute or final. Laboratory and clinical data in animals suggest that similar cautionary recommendations would be wise for those caring for animals recovering from psychological trauma.

Note

¹ For the sake of brevity, the term 'socialize' and 'socialization' will refer to experiences with both social and

nonsocial stimuli, and 'inadequate socialization' will be used to denote the more accurate 'deprivation of early socioenvironmental stimulation and experiences'.

14.8 References

- American Psychiatric Association. (2013) *DSM-5*. American Psychiatric Association, Washington, DC, USA.
- Anda, R.F., Felitti, V.J., Bremner, J.D., Walker, J.D., Whitfield, C., et al. (2006) The enduring effects of abuse and related adverse experiences in childhood: A convergence of evidence from neurobiology and epidemiology. European Archives of Psychiatry and Clinical Neurosciences 256, 174–186. http://dx.doi.org/10.1007/s00406-005-0624-4.
- Andreasen, N.C. (2010) Posttraumatic stress disorder: A history and a critique. Annals of the New York Academy of Sciences 1208, 67–71. http://dx.doi. org/10.1111/j.1749-6632.2010.05699.x.
- Anon. (2005) Helping hurricane animals deal with stress. Rally to rescue. *Purina Pro Plan Magazine* 1, 16–19.
- Anon. (2008) A flood of emotion. *Animal Sheltering* Nov/Dec. 51–53.
- Bergman, H.E., Kline, A.C., Feeny, N.C., Zoellner, L.A. (2015) Examining PTSD treatment choice among individuals with subthreshold PTSD. Behaviour Research and Therapy 73, 33–41. http://dx.doi.org/10.1016/j.brat. 2015.07.010.
- Bergman, H.E., Przeworski, A., Feeny, N.C. (2017) Rates of subthreshold PTSD among U.S. military veterans and service members: A literature review. *Military Psychology* 29, 117–127. http://dx.doi.org/10.1037/mil0000154.
- Bonne, O., Grillon, C., Vythilingam, M., Neumeister, A., Charney, D.S. (2004) Adaptive and maladaptive psychobiological responses to severe psychological stress: Implications for the discovery of novel pharmacotherapy. *Neuroscience and Biobehavioral Reviews* 28, 65–94. http://dx.doi.org/10.1016/j. neubiorev.2003.12.001.
- Braastad, B.O. (1998) Effects of prenatal stress on behaviour of offspring of laboratory and farmed mammals. Applied Animal Behaviour Science 61, 159–180. http://dx.doi.org/10.1016/S0168-1591(98)00188-9.
- Bradshaw, G.A., Schore, A.N., Brown, J.L., Poole, J., Moss, C. (2005) Elephant breakdown. *Nature* 433, 807. http://dx.doi.org/10.1038/433807a.
- Bradshaw, G.A., Capaldo, T., Lindner, L., Grow, G. (2008) Building an inner sanctuary: Complex PTSD in chimpanzees. *Journal of Trauma & Dissociation* 9, 9–34. http://dx.doi.org/10.1080/15299730802073619.
- Brancu, M., Mann-Wrobel, M., Beckham, J.C., Wagner, H.R., Elliott, A., et al. (2016) Subthreshold posttraumatic stress disorder: A meta-analytic review of DSM-IV prevalence and a proposed DSM-5 approach to measurement. Psychological Trauma: Theory, Research, Practice, and Policy 8, 222–232. http://dx.doi.org/10.1037/tra0000078.

- Briere, J. and Spinazzola, J. (2005) Phenomenology and psychological assessment of complex posttraumatic states. *Journal of Traumatic Stress* 18, 401–412. http://dx.doi.org/10.1002/jts.20048.
- Brown, G.W., Skair, F., Harris, T.O., Birley, J.L.T. (1973) Life events and psychiatric disorders: Part I. Some methodological issues. *Psychological Medicine* 3, 74–87. http://dx.doi.org/10.1017/S0033291700048492.
- Bryant, R.A. (2010) Treating the full range of posttraumatic reactions. In: Rosen, G.M. and Frueh, B.C. (eds.) *Clinician's Guide to Posttraumatic Stress Disorder.* John Wiley & Sons, Hoboken, NJ, USA, pp. 205–234. http://dx.doi.org/10.1002/9781118269961.ch9.
- Bryant, R.A., Creamer, M., O'Donnell, M., Silove, D., Clark, C.R., et al. (2010) The psychiatric sequelae of traumatic injury. American Journal of Psychiatry 167, 312–320. http://dx.doi.org/10.1176/appi.ajp.2009.09050617.
- Burghardt, W.F. (2013) Preliminary evaluation of case series of military working dogs affected with canine post-traumatic stress disorder (N=14). In: *Proceedings of Veterinary Behavior Symposium*. American College of Veterinary Behaviorists, Chicago, Illinois, USA.
- Cabib, S., Orsini, C., Puglisi, S. A. (2019) Animal models of liability to post-traumatic stress disorder: Going beyond fear memory. *Behavioural Pharmacology* 30(2 and 3 Special Issue), 122–129. http://dx.doi.org/10.1097/FBP.0000000000000475.
- Cahill, S.P. and Foa, E.B. (2007) Psychological theories of PTSD. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 55–77.
- Charney, D.S. (2004) Psychobiological mechanisms of resilience and vulnerability: Implications for the successful adaptation to extreme stress. *American Journal of Psychiatry* 161, 195–216. http://dx.doi.org/10.1176/appi.ajp.161.2.195.
- Cohen, H., Matar, M.A., Richter-Levin, G., Zohar, J. (2006) The contribution of an animal model toward uncovering biological risk factors for PTSD. *Annals of the New York Academy of Sciences* 1071, 335–350. http://dx.doi.org/10.1196/annals.1364.026.
- Cohen, H., Geva, A.B., Matar, M.A., Zohar, J., Kaplan, Z. (2008) Post-traumatic stress behavioural responses in inbred mouse strains: Can genetic predisposition explain phenotypic vulnerability? *International Journal* of *Neuropsychopharmacology* 11, 331–349. http://dx. doi.org/10.1017/S1461145707007912.
- Cooke, R.F., Bohnert, D.W., Reis, M.M., Cappellozza, B.I. (2013) Wolf presence in the ranch of origin: Impacts on temperament and physiological responses of beef cattle following a simulated wolf encounter. *Journal* of Animal Science 91, 5905–5911. http://dx.doi. org/10.2527/jas.2013-6777.
- Cooke, R.F., Mehrkam, L.R., Marques, R.S., Lippolis, K.D., Bohnert, D.W. (2017) Effects of a simulated wolf encounter on brain and blood biomarkers of stressrelated psychological disorders in beef cows with or

- without previous exposure to wolves. *Journal of Animal Science* 95, 1154–1163. http://dx.doi.org/10.2527/ias2016.1250.
- Crowell-Davis, S.L. (2009) Generalized anxiety disorder. Compendium: Continuing Education for Veterinarians 31, 427–430.
- Cukor, J., Wyka, K., Jayasinghe, N., Difede, J. (2010) The nature and course of subthreshold PTSD. *Journal of Anxiety Disorders* 24, 918–923. http://dx.doi.org/10.1016/j.janxdis.2010.06.017.
- Deslauriers, J., Toth, M., Der-Avakian, A., Risbrough, V.B. (2018) Current status of animal models of posttraumatic stress disorder: Behavioral and biological phenotypes, and future challenges in improving translation. Biological Psychiatry 83, 895–907. http://dx.doi.org/10.1016/j.biopsych.2017.11.019.
- Dickstein, B.D., Walter, K.H., Schumm, J.A., Chard, K.M. (2013) Comparing response to cognitive processing therapy in military veterans with subthreshold and threshold posttraumatic stress disorder. *Journal of Traumatic Stress* 26, 703–709. http://dx.doi.org/ 10.1002/jts.21869.
- Dietz, L., Arnold, A.M.K., Goerlich-Jansson, V.C., Vinke, C.M. (2018) The importance of early life experiences for the development of behavioural disorders in domestic dogs. *Behaviour* 155, 83–114. http://dx.doi.org/ 10.1163/1568539X-00003486.
- Dodman, N. (2012) Can dogs suffer from post traumatic stress disorder? Available at: https://www.veterinarypracticenews.com/can-dogs-suffer-from-post-traumatic-stress-disorder (accessed 30 October 2018).
- Fairbank, J.A., Putnam, F.W., Harris, W.W. (2007) The prevalence and impact of child traumatic stress. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) Handbook of PTSD. Guilford Press, New York, USA, pp. 229–251.
- Ferdowsian, H.R., Durham, D.L., Johnson, C.M., Brune, M., Kimwele, C., et al. (2012) Signs of generalized anxiety and compulsive disorders in chimpanzees. Journal of Veterinary Behavior: Clinical Applications and Research 7, 353–361. http://dx.doi.org/10.1016/j. jveb.2012.01.006.
- Ferdowsian, H.R., Durham, D.L., Kimwele, C., Kranendonk, G., Otali, E., et al. (2011) Signs of mood and anxiety disorders in chimpanzees. PLoS ONE 6(6), e19855. http://dx.doi.org/10.1371/journal.pone.0019855.
- Flory, J.D. and Yehuda, R. (2015) Comorbidity between post-traumatic stress disorder and major depressive disorder: Alternative explanations and treatment considerations. *Dialogues in Clinical Neuroscience* 17, 141–150.
- Foa, E.B. and Kozak, M.J. (1986) Emotional processing of fear: Exposure to corrective information. *Psychological Bulletin* 99, 20–35. http://dx.doi.org/10.1037/0033-2909.99.1.20.
- Foa, E.B. and Meadows, E.A. (1998) Psychosocial treatments for posttraumatic stress disorder. In: Yehuda, R.

206 F.D. McMillan

- (ed.) *Psychological Trauma*. American Psychiatric Press, Washington, DC, USA, pp. 179–204.
- Foa, E.B., Zinbarg, R., Rothbaum, B.O. (1992) Uncontrollability and unpredictability in post-traumatic stress disorder: An animal model. *Psychological Bulletin* 112, 218–238. http://dx.doi.org/10.1037/0033-2909.112.2.218.
- Friedman, M.J. (2001) Allostatic versus empirical perspectives on pharmacotherapy for PTSD. In: Wilson, J.P., Friedman, M.J., Lindy, J.D. (eds.) *Treating Psychological Trauma and PTSD*. Guilford Press, New York, USA, pp. 94–124.
- Friedman, M. (2006) Post-traumatic and Acute Stress Disorders. Compact Clinicals, Kansas City, Missouri, USA.
- Friedman, M.J. and Davidson, J.R.T. (2007) Pharmacotherapy for PTSD. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 376–405.
- Friedman, M.J., Resick, P.A., Keane, T.M. (2007a) PTSD: Twenty-five years of progress and challenges. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 3–18.
- Friedman, M.J., Resick, P.A., Keane, T.M. (2007b) Key questions and an agenda for future research. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 540–561.
- Garlick, S. and Austen, R. (2014) Post-traumatic stress disorder in kangaroos. *Proceedings of the Australian Wildlife Rehabilitation Conference*. Hobart, Tasmania, Australia. Available at: https://www.awrc.org.au/uploads/5/8/6/6/5866843/ptsd_in_kangaroos_garlick_and_austen_paper_2014_2.pdf (accessed 10 March 2019).
- Gist, R. and Devilly, G.J. (2010) Early intervention in the aftermath of trauma. In: Rosen, G.M. and Frueh, B.C. (eds.) Clinician's Guide to Posttraumatic Stress Disorder. John Wiley & Sons, Hoboken, NJ, USA, pp. 153–175. http://dx.doi.org/10.1002/9781118269961.ch7.
- Hanson, R.F. and Spratt, E.G. (2000) Reactive attachment disorder: what we know about the disorder and implications for treatment. *Child Maltreatment* 5, 137–145. http://dx.doi.org/10.1177/1077559500005002005.
- Heim, C. and Nemeroff, C.B. (2009) Neurobiology of posttraumatic stress disorder. *CNS Spectrums* 14(1 Suppl 1), 13–24.
- Hembree, E.A. and Foa, E.B. (2010) Cognitive behavioral treatments for PTSD. In: Rosen, G.M. and Frueh, B.C. (eds.) Clinician's Guide to Posttraumatic Stress Disorder. John Wiley & Sons, Hoboken, NJ, USA, pp. 177–203. http://dx.doi.org/10.1002/9781118269961.ch8.
- Hennessy, M.B., Kaiser, S., Sachser, N. (2009) Social buffering of the stress response: Diversity, mechanisms, and functions. Frontiers in Neuroendocrinology 30, 470–482. http://dx.doi.org/10.1016/j. yfrne.2009.06.001.

- Herman, J. (1997) *Trauma and Recovery*. Basic Books, New York, USA.
- Hoge, E.A., Austin, E.D., Pollack, MH. (2007) Resilience: Research evidence for conceptual considerations for posttraumatic stress disorder. *Depression and Anxiety* 24, 139–152. http://dx.doi.org/10.1002/da.20175.
- Humphreys, K.L., Nelson, C.A., Fox, N.A., Zeanah, C.H. (2017) Signs of reactive attachment disorder and disinhibited social engagement disorder at age 12 years: Effects of institutional care history and high-quality foster care. *Development and Psychopathology* 29, 675–684. http://dx.doi.org/10.1017/S0954579417000256.
- Huntingford, J. (2013) Post traumatic stress disorder in dogs. Integrative Veterinary Care Journal. Available at: http://ivcjournal.com/post-traumatic-stress-disorderin-dogs/?hilite=%22Huntingford%22 (accessed 30 October 2018).
- Imanaka, A., Morinobu, S., Toki, S., Yamawaki, S. (2006) Importance of early environment in the development of post-traumatic stress disorder-like behaviors. Behavioural Brain Research 173, 129–137. http:// dx.doi.org/10.1016/j.bbr.2006.06.012.
- Joseph, S. (2011) What Doesn't Kill Us. Basic Books, New York, USA.
- Kaufman. J., Yang, B-Z., Douglas-Palumberi, H., Houshyar, S., Lipschitz, D., et al. (2004) Social supports and serotonin transporter gene moderate depression in maltreated children. Proceedings of the National Academy of Sciences of the United States of America 101, 17316–17321. http://dx.doi.org/10.1073/ pnas.0404376101.
- Keane, T.M., Brief, D.J., Pratt, E.M., Miller, M.W. (2007) Assessment of PTSD and its comorbidities in adults. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) Handbook of PTSD. Guilford Press, New York, USA, pp. 279–305.
- Kozarić-Kovačić, D. (2008) Psychopharmacotherapy of posttraumatic stress disorder. Croatian Medical Journal 49, 459–475. http://dx.doi.org/10.3325/cmj. 2008.4.459.
- Landsberg, G., Hunthausen, W., Ackerman, L. (2013) Behavior Problems of the Dog and Cat, 3rd edn. Saunders. Edinburgh. UK.
- Lang, P.J. (1977) Imagery in therapy: An information processing analysis of fear. *Behavior Therapy* 8, 862–886. http://dx.doi.org/10.1016/S0005-7894(77)80157-3.
- LeDoux, J. (2012) Rethinking the emotional brain. *Neuron* 73, 653–676. http://dx.doi.org/10.1016/j.neuron.2012.02.004.
- Lindy, J.D. and Wilson, J.P. (2001) Respecting the trauma membrane: Above all, do no harm. In: Wilson, J.P., Friedman, M.J., Lindy, J.D. (eds.) *Treating Psychological Trauma and PTSD*. Guilford Press, New York, USA, pp. 432–445.
- Liu, Z. (2004) TCM history shows that bear bile is not a necessary medicine. *Proceedings of the 19th International Congress of Zoology, Symposium: Bear farming*. Beijing, China, pp. 46–48.

- Loeffler, I.K., Robinson, J., Cochrane, G. (2009) Compromised health and welfare of bears farmed for bile in China. *Animal Welfare* 18, 225–235.
- Lopresti-Goodman, S.M., Bezner, J., Ritter, C. (2015) Psychological distress in chimpanzees rescued from laboratories. *Journal of Trauma & Dissociation* 16, 349–366.
- Louvart, H., Maccari, S., Ducrocq, F., Thomas, P., Darnaudéry, M. (2005) Long-term behavioural alterations in female rats after a single intense footshock followed by situational reminders. *Psychoneuroendocrinology* 30, 316–324. http://dx.doi.org/10.1016/j.psyneuen.2004.09.003.
- Lyons, D.M. and Parker, K.J. (2007) Stress inoculationinduced indications of resilience in monkeys. *Journal of Traumatic Stress* 20, 423–433. http://dx.doi.org/10.1002/ jts.20265.
- Maier, S.F. and Watkins, L.R. (1998) Stressor controllability, anxiety, and serotonin. Cognitive Therapy and Research 22, 595–613. http://dx.doi.org/10.1023/A:1018794104325.
- Mallonée, J.S. (2004) Traumatic stress disorder observed in an adult wild captive wolf (*Canis lupus*). *Journal of Applied Animal Welfare Science* 7, 107–126. http://dx.doi.org/10.1207/s15327604jaws0702_3.
- Mangiavacchi, S., Masi, F., Scheggi, S., Leggio, B., De Montis, M.G., et al. (2001) Long-term behavioral and neurochemical effects of chronic stress exposure in rats. Journal of Neurochemistry 79, 1113–1121.
- Marshall, R.D., Davidson, J.R.T., Yehuda, R. (1998) Pharmacotherapy in the treatment of posttraumatic stress disorder and other trauma-related syndromes. In: Yehuda, R. (ed.) *Psychological Trauma*. American Psychiatric Press, Washington, DC, USA, pp. 133–177.
- Matar, M.A., Cohen, H., Kaplan, Z., Zohar, J. (2006) The effect of early poststressor intervention with sertraline on behavioral responses in an animal model of posttraumatic stress disorder. *Neuropsychopharmacology* 31, 2610–2618. http://dx.doi.org/10.1038/sj.npp.1301132.
- McMillan, F.D., Duffy, D.L., Serpell, J.A. (2011) Mental health of dogs formerly used as 'breeding stock' in commercial breeding establishments. *Applied Animal Behaviour Science* 135, 86–94. http://dx.doi.org/ 10.1016/j.applanim.2011.09.006.
- McMillan, F.D., Duffy, D.L., Zawistowski, S.L., Serpell, J.A. (2015) Behavioral and psychological characteristics of canine victims of abuse. *Journal of Applied Animal Welfare Science* 18, 92–111. http://dx.doi.org/10.1080 /10888705.2014.962230
- McMillan, F.D., Vanderstichel, R., Stryhn, H., Yu, J., Serpell, J.A. (2016) Behavioural characteristics of dogs removed from hoarding situations. *Applied Animal Behaviour Science* 178, 69–79. http://dx.doi. org/10.1016/j.applanim.2016.02.006.
- Miller, G.E., Chen, E., Parker, K.J. (2011) Psychological stress in childhood and susceptibility to the chronic diseases of aging: Moving towards a model of behavioral

- and biological mechanisms. *Psychological Bulletin* 137, 959–997. http://dx.doi.org/10.1037/a0024768.
- Mills, D.S. (2009) Training and learning protocols. In: Horwitz, D.F. and Mills, D.S. (eds.) *BSAVA Manual* of Canine and Feline Behavioural Medicine, 2nd edn. British Small Animal Veterinary Association, Gloucester, UK, pp. 49–64. http://dx.doi.org/10.22233/ 9781905319879.5.
- Monson, C.M., Friedman MJ, La Bash HAJ. (2007) A psychological history of PTSD. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 37–52.
- Nayback, A.M. (2009) Posttraumatic stress: A concept analysis. Archives of Psychiatric Nursing 23, 210–219. http://dx.doi.org/10.1016/j.apnu.2008.06.001.
- Naylor, J.C., Dolber, T.R., Strauss, J.L., Kilts, J.D., Strauman, T.J., et al. (2013) A pilot randomized controlled trial with paroxetine for subthreshold PTSD in Operation Enduring Freedom/Operation Iraqi Freedom era veterans. Psychiatry Research 206, 318–320. http://dx.doi.org/10.1016/j.psychres.2012.11.008.
- Norris, F.H. and Slone, L.B. (2007) The epidemiology of trauma and PTSD. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 78–98.
- North, C.S., Nixon, S.J., Shariat, S., Mallonee, S., McMillen, J.C., et al. (1999) Psychiatric disorders among survivors of the Oklahoma City bombing. Journal of the American Medical Association 282, 755–762. http://dx.doi.org/10.1001/jama.282.8.755.
- Notari, L. (2009) Stress in veterinary behavioural medicine. In: Horwitz, D.F. and Mills, D.S. (eds.) *BSAVA Manual of Canine and Feline Behavioural Medicine*, 2nd edn. British Small Animal Veterinary Association, Gloucester, UK, pp. 136–145. http://dx.doi.org/10.22233/9781905319879.13.
- O'Donnell, M.L., Creamer, M., Pattison, P., Atkin, C. (2004) Psychiatric morbidity following injury. *American Journal of Psychiatry* 161, 507–514.
- O'Donnell, M.L., Creamer, M., Cooper, J. Criterion A. (2010) Controversies and clinical implications. In: Rosen, G.M. and Frueh, B.C. (eds.) *Clinician's Guide to Posttraumatic Stress Disorder*. John Wiley & Sons, Hoboken, NJ, USA, pp. 51–75.
- Ong, A.D., Bergeman, C.S., Bisconti, T.L., Wallace, K.A. (2006) Psychological resilience, positive emotions, and successful adaptation to stress in later life. *Journal of Personality and Social Psychology* 91, 730–749. http://dx.doi.org/10.1037/0022-3514.91.4.730.
- Overall, K.O. (2013) Manual of Clinical Behavioral Medicine for Dogs and Cats. Elsevier-Mosby, St. Louis, Missouri, USA.
- Pageat, P. and Fatjo, J. (2013) Terminology, behavioral pathology, and the Pageat (French) approach to canine behavior disorders. In: Landsberg, G., Hunthausen, W., Ackerman, L. (eds.) *Behavior Problems of the Dog and Cat*, 3rd edn. Saunders, Edinburgh, UK, pp. 345–365.

208 F.D. McMillan

- Palestrini, C. (2009) Situational sensitivities. In: Horwitz, D.F. and Mills, D.S. (eds.) BSAVA Manual of Canine and Feline Behavioural Medicine, 2nd edn. British Small Animal Veterinary Association, Gloucester, UK, pp. 169–181. http://dx.doi.org/10.22233/9781905319879.16.
- Panksepp, J. (1998) Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, New York, USA.
- Parker, K.J., Buckmaster, C.L., Schatzberg, A.F., Lyons, D.M. (2004) Prospective investigation of stress inoculation in young monkeys. *Archives of General Psychiatry* 61, 933–941. http://dx.doi.org/10.1001/ archpsyc.61.9.933.
- Parsons, R.G. and Ressler, K.J. (2013) Implications of memory modulation for post-traumatic stress and fear disorders. *Nature Neuroscience* 16, 146. http:// dx.doi.org/10.1038/nn.3296.
- PBS (2005) Katrina's Animal Rescue: Health Effects. Available at: www.pbs.org/wnet/nature/katrinas-animal-rescue-health-effects/2559 (accessed 30 October 2018).
- Penza, K.M., Heim, C., Nemeroff, C.B. (2003) Neurobiological effects of childhood abuse: Implications for the pathophysiology of depression and anxiety. *Archives of Women's Mental Health* 6, 15–22. http:// dx.doi.org/10.1007/s00737-002-0159-x.
- Perlmuter, L.C. and Monty, R.A. (1977) The importance of perceived control: Fact or fantasy? *American Scientist* 65, 759–765.
- Pitman, R.K., Rasmusson, A.M., Koenen, K.C., Shin, L.M., Orr, S.P., et al. (2012) Biological studies of post-traumatic stress disorder. *Nature Reviews* 13, 769–787. http://dx.doi.org/10.1038/nrn3339.
- Quirk, G.J. (2002) Memory for extinction of conditioned fear is long-lasting and persists following spontaneous recovery. *Learning & Memory* 9, 402–407. http:// dx.doi.org/10.1101/lm.49602.
- Ragen, B. J., Seidel, J., Chollak, C., Pietrzak, R. H., & Neumeister, A. (2015). Investigational drugs under development for the treatment of PTSD. Expert Opinion On Investigational Drugs 24, 659–672. http://dx.doi.org/ 10.1517/13543784.2015.1020109.
- Rapaport, M.H., Endicott, J., Clary, C.M. (2002) Posttraumatic stress disorder and quality of life: Results across 64 weeks of sertraline treatment. *Journal of Clinical Psychiatry* 63, 59–65.
- Rault, J.L. (2012) Friends with benefits: Social support and its relevance for farm animal welfare. Applied Animal Behaviour Science 136, 1–14. http://dx.doi. org/10.1016/j.applanim.2011.10.002.
- Ray, S.L. (2008) Evolution of posttraumatic stress disorder and future directions. Archives of Psychiatric Nursing 22, 217–225. http://dx.doi.org/10.1016/j.apnu.2007.08.005.
- Resick, P.A., Monson, C.M., Gutner, C. (2007) Psychosocial treatments for PTSD. In: Friedman, M.J., Keane, T.M.,

- Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 330–358.
- Richter-Levin, G., Stork, O., Schmidt, M.V. (2019)
 Animal models of PTSD: A challenge to be met.
 Molecular Psychiatry 24, 1135–1156. http://dx.doi.
 org/10.1038/s41380-018-0272-5
- Ronan, P. and Summers, C. (2008) Biology, animal models. In: Reyes, G., Elhai, J.D., Ford, J.D. (eds.) Encyclopedia of Psychological Trauma. John Wiley & Sons, Hoboken, New Jersey, USA pp. 80–83.
- Rosen, J.B. and Schulkin, J. (1998) From normal fear to pathological anxiety. *Psychological Review* 105, 325–350. http://dx.doi.org/10.1037/0033-295X.105.2.325.
- Rosen, G.M., Spitzer, R.L., McHugh, P.R. (2008) Problems with the post-traumatic stress disorder diagnosis and its future in DSM-V. *British Journal of Psychiatry* 192, 3–4. http://dx.doi.org/10.1192/bjp.bp.107.043083.
- Rosen, G.M., Frueh, B.C., Elhai, J.D., Grubaugh, A.L., Ford, J.D. (2010a) Posttraumatic stress disorder and general stress studies. In: Rosen, G.M. and Frueh, B.C. (eds.) Clinician's Guide to Posttraumatic Stress Disorder. John Wiley & Sons, Hoboken, NJ, USA, pp. 3–31. http://dx.doi.org/10.1002/9781118269961.ch1.
- Rosen, G.M., Lilienfeld, S.O., Orr, S.P. (2010b) Searching for PTSD's biological signature. In: Rosen, G.M. and Frueh, B.C. (eds.) Clinician's Guide to Posttraumatic Stress Disorder. John Wiley & Sons, Hoboken, NJ, USA, pp. 97–116. http://dx.doi.org/10.1002/9781118269961.ch5.
- Ruscio, A.M., Ruscio, J., Keane, T.M. (2002) The latent structure of posttraumatic stress disorder: A taxometric investigation of reactions to extreme stress. *Journal* of Abnormal Psychology 111, 290–301. http://dx.doi. org/10.1037/0021-843X.111.2.290.
- Sanchez, M.M., Ladd, C.O., Plotsky, P.M. (2001) Early adverse experience as a developmental risk factor for later psychopathology: Evidence from rodent and primate models. *Development and Psychopathology* 13, 419–449. http://dx.doi.org/10.1017/S0954579401003029.
- Santarelli, S., Zimmermann, C., Kalideris, G., Lesuis, S.L., Arloth, J., et al. (2017) An adverse early life environment can enhance stress resilience in adulthood. Psychoneuroendocrinology 78, 213–221. http://dx. doi.org/10.1016/j.psyneuen.2017.01.021.
- Santiago, P.N., Ursano, R.J., Gray, C.L., Pynoos, R.S., Spiegel, D., et al. (2013) A systematic review of PTSD prevalence and trajectories in DSM-5 defined trauma exposed populations: Intentional and non-intentional traumatic events. PLoS ONE 8(4), p.e59236. http:// dx.doi.org/10.1371/journal.pone.0059236.
- Scheeringa, M. (2016) PTSD for Children 6 Years and Younger. Available at: https://www.ptsd.va.gov/professional/treat/specific/ptsd_child_under6.asp (accessed 30 October 2018).
- Scheeringa, M.S., Zeanah, C.H., Drell, M.J., Larrieu, J.A. (1995) Two approaches to the diagnosis of posttraumatic stress disorder in infancy and early childhood.

- Journal of the American Academy of Child and Adolescent Psychiatry 34, 191–200.
- Scheeringa, M.S., Zeanah, C.H., Myers, L., Putnam, F.W. (2003) New findings in alternative criteria for PTSD in preschool children. *Journal of the American Academy of Child and Adolescent Psychiatry* 42, 561–570.
- Schöner, J., Heinz, A., Endres, M., Gertz, K., Kronenberg, G. (2017) Post-traumatic stress disorder and beyond: An overview of rodent stress models. *Journal of Cellular and Molecular Medicine* 21, 2248–2256. http://dx.doi.org/10.1111/jcmm.13161.
- Segman, R., Shalev, A.Y., Gelernter, J. (2007) Geneenvironment interactions: Twin studies and gene research in the context of PTSD. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) *Handbook of PTSD*. Guilford Press, New York, USA, pp. 190–206.
- Shalev, A., Liberzon, I., Marmar, C. (2017) Post-traumatic stress disorder. New England Journal of Medicine 376, 2459–2469. http://dx.doi.org/10.1056/NEJMra 1612499.
- Shapero, B.G., Hamilton, J.L., Stange, J.P., Liu, R.T., Abramson, L.Y., et al. (2015). Moderate childhood stress buffers against depressive response to proximal stressors: a multi-wave prospective study of early adolescents. Journal of Abnormal Child Psychology 43, 1403–1413. http://dx.doi.org/10.1007/s10802-015-0021-z.
- Sherin, J.E. and Nemeroff, C.B. (2011) Post-traumatic stress disorder: The neurobiological impact of psychological trauma. *Dialogues in Clinical Neuroscience* 13, 263–278.
- Siegmund, A. and Wotjak, C.T. (2006) Toward an animal model of posttraumatic stress disorder. *Annals of the New York Academy of Sciences* 1071, 324–334. http://dx.doi.org/10.1196/annals.1364.025.
- Siegmund, A. and Wotjak, C.T. (2007) A mouse model of posttraumatic stress disorder that distinguishes between conditioned and sensitized fear. *Journal of Psychiatric Research* 41, 848–860. http://dx.doi.org/ 10.1016/j.jpsychires.2006.07.017.
- Southwick, S.M. and Charney, D.S. (2012) The science of resilience: implications for the prevention and treatment of depression. *Science* 338, 79–82. http://dx. doi.org/10.1126/science.1222942.
- Southwick, S.M., Davis, L.L., Aikins, D.E., Rasmusson, A., Barron, J., et al. (2007) Neurobiological alterations associated with PTSD. In: Friedman, M.J., Keane, T.M., Resick, P.A. (eds.) Handbook of PTSD. Guilford Press, New York, USA, pp. 166–189.
- Spiers, T. and Harrington, G. (2001) A brief history of trauma. In: Spiers, T. (ed.) *Trauma: The Practitioner's Guide to Counseling*. Taylor & Francis Group, New York, USA, pp. 213–221.
- Suomi, S.J. (2006) Risk, resilience, and gene x environment interactions in rhesus monkeys. *Annals of the New York Academy of Sciences* 1094, 52–62. http://dx.doi.org/10.1196/annals.1376.006.

- Thoeringer, C.K. and Wotjak, C.T. (2013) Evaluating social support-like phenomena in an animal model of posttraumatic stress disorder (PTSD). *Journal of Depression and Anxiety* 3, 143.
- van der Kolk, B.A., Roth, S., Pelcovitz, D., Sunday, S., Spinazzola, J. (2005) Disorders of extreme stress: The empirical foundation of a complex adaptation to trauma. *Journal of Traumatic Stress* 18, 389–399. http://dx.doi.org/10.1002/jts.20047.
- VanElzakker, M.B., Dahlgren, M.K., Davis, F.C., Dubois, S., Shin, L.M. (2014) From Pavlov to PTSD: The extinction of conditioned fear in rodents, humans, and in anxiety disorders. *Neurobiology of Learning and Memory* 113, 3–18. http://dx.doi.org/10.1016/j.nlm.2013.11.014.
- von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., et al. (2007) Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals – A review. Physiology & Behavior 92, 293–316. http:// dx.doi.org/10.1016/j.physbeh.2007.01.007.
- Wakefield, J.C. and Horwitz, A.V. (2010) Normal reactions to adversity or symptoms of disorder? In: Rosen, G.M. and Frueh, B.C. (eds.) Clinician's Guide to Posttraumatic Stress Disorder. John Wiley & Sons, Hoboken, NJ, USA, pp. 33–49. http://dx.doi.org/10.1002/9781118269961.ch2.
- Whitaker, A.M., Gilpin, N.W., Edwards, S. (2014) Animal models of post-traumatic stress disorder and recent neurobiological insights. *Behavioural Pharmacology* 25, 398.
- Wiedenmayer, C.P. (2004) Adaptations or pathologies? Long-term changes in brain and behavior after a single exposure to severe threat. *Neuroscience & Biobehavioral Reviews* 28, 1–12. http://dx.doi. org/10.1016/j.neubiorev.2003.09.005.
- Wilson, J.P. (2004) PTSD and complex PTSD: Symptoms, syndromes, and diagnoses. In: Wilson, J.P. and Keane, T.M. (eds.) Assessing Psychological Trauma and PTSD, 2nd edn. The Guilford Press, New York, USA, pp. 7–44.
- Wilson, J.P., Friedman, M.J., Lindy, J.D. (2001a) Treatment goals for PTSD. In: Wilson, J.P., Friedman, M.J., Lindy, J.D. (eds.) *Treating Psychological Trauma and PTSD*. Guilford Press, New York, USA, pp. 3–27.
- Wilson, J.P., Friedman, M.J., Lindy, J.D. (2001b) A holistic, organismic approach to healing trauma and PTSD. In: Wilson, J.P., Friedman, M.J., Lindy, J.D. (eds.) *Treating Psychological Trauma and PTSD*. Guilford Press, New York, USA, pp. 28–56.
- Wilson, J.P., Friedman, M.J., Lindy, J.D. (2001c) Practical considerations in the treatment of PTSD: Guidelines for practitioners. In: Wilson, J.P., Friedman, M.J., Lindy, J.D. (eds.) *Treating Psychological Trauma and PTSD*. Guilford Press, New York, USA, pp. 409–431.
- Wolpe, J. (1958) *Psychotherapy by Reciprocal Inhibition*. Stanford University Press, Stanford, California, USA.

210 F.D. McMillan

- Wyler, A.R., Masuda, M., Holmes, T.H. (1971) Magnitude of life events and seriousness of illness. *Psychosomatic Medicine* 33, 115–122. http://dx.doi.org/10.1097/00006842-197103000-00003.
- Xie, P., Kranzler, H.R., Poling, J., Stein, M B., Anton, R.F., et al. (2009) Interactive effect of stressful life events and the serotonin transporter 5-HTTLPR genotype on posttraumatic stress disorder diagnosis in 2 independent populations. Archives of General Psychiatry 66, 1201–1209. http://dx.doi. org/10.1001/archgenpsychiatry.2009.153.
- Yamamoto, S., Morinobu, S., Takei, S., Fuchikami, M., Matsuki, A., *et al.* (2009) Single prolonged stress: Toward an animal model of posttraumatic stress

- disorder. *Depression and Anxiety* 26, 1110–1117. http://dx.doi.org/10.1002/da.20629.
- Yamamoto, T. (2003) Unusual behaviour and a posttraumatic stress-like syndrome (PTSD) in dogs after a vigorous earthquake on a seismic scale of 5+. Journal of Veterinary Medicine 56, 535–541.
- Yan, H.C., Cao, X., Das, M., Zhu, X.H., Gao, T.M. (2010) Behavioral animal models of depression. *Neuroscience Bulletin* 26, 327–337. http://dx.doi.org/10.1007/s12264-010-0323-7.
- Yehuda, R. and LeDoux, J. (2007) Response variation following trauma: A translational neuroscience approach to understanding PTSD. *Neuron* 56, 19–32. http://dx. doi.org/10.1016/j.neuron.2007.09.006.

15 Cognitive and Emotional Disorders in the Aging Pet

JACQUELINE WILHELMY AND GARY LANDSBERG

Delaware Valley Veterinary Behavior, Philadelphia, Pennsylvania, USA; Fear Free Research, CanCog Technologies, Fergus, Ontario, Canada

Cognitive decline is a well-recognized group of disorders in domestic dogs. The problem is less common, but of increasing interest, in pet cats. It has been estimated that 45 million dogs around 7 years and older live in the US and Europe; however, this estimate does not include cats. Pet owners and veterinarians may be tempted to dismiss changes in cognition as a normal part of aging in dogs and cats. Pet owners may even fail to recognize clinical signs of what is a treatable disease, and the onus lies on health professionals to proactively inquire about the behavior of aged patients. Extensive research has shown that underlying changes in the brain (some of which are similar to those seen in the brains of aged humans with dementia) can manifest in a list of identifiable clinical signs. Even more importantly, it has been shown that treatments exist which can slow the progression of disease. This can improve quality of life for both pets and owners alike, as well as rescue the human-animal bond from the damage it can otherwise incur.

Cognitive dysfunction syndrome (CDS) is a progressive neurodegenerative disease of aging dogs and cats. Although clinical signs are most commonly reported in pets over 11 years of age, they can appear in animals as young as 6 years (Araujo et al., 2005b; Studzinski et al., 2006; Salvin et al., 2010). The disease manifests in the form of behavioral changes, impaired learning and memory, altered awareness, and confusion. Clinical signs can be categorized as deficits in one of six areas, represented by the acronym DISHAA: disorientation, altered social interactions, sleep-wake disturbances, loss of housetraining and other learned behaviors, increased or decreased activity levels, and increased anxiety or fear (Osella et al., 2007; Rème et al., 2008; Azkona et al., 2009; Rosado et al., 2012; Fast et al., 2013; Madari et al., 2015). Basic functions such as self-hygiene, eating or drinking behavior, and response to stimuli can be compromised or altered (Rofina et al., 2006). In the laboratory (Fig. 15.1), validated neuropsychological tests reveal quantifiable impairment in the learning and memory of affected animals (Milgram et al., 2004; Tapp et al., 2004; Araujo et al., 2012; Pan et al., 2010, 2013).

Outside of the laboratory, CDS is a diagnosis of exclusion. Once suspicion is raised by signalment and clinical signs, it is the veterinarian's job to rule out a number of other physical ailments (not uncommon in an aged population) that mimic the same clinical signs. This job is complicated by the anxiety, fear, and aggression that can also occur or worsen in pets suffering from CDS. This chapter will explore the clinical picture of CDS in dogs and cats, its identification or diagnosis, and available treatment options.

15.1 The Clinical Picture

15.1.1 Characteristics of cognitive dysfunction syndrome

The most common signs of CDS in dogs were found to include increased daytime sleep and night-time restlessness (57%), altered social interactions (51%), disorientation (49%), and anxiety (46%). In mild cases, this study found increased daytime sleep was the most prevalent sign, affecting 70% of dogs (Fast *et al.*, 2013). Another found owners were unlikely to report mild signs of cognitive dysfunction unless specifically asked, but that altered social interactions were most common. Moderately affected dogs were most likely to exhibit sleep—wake disturbances and altered social interactions, with 67% of dogs displaying both signs; in the

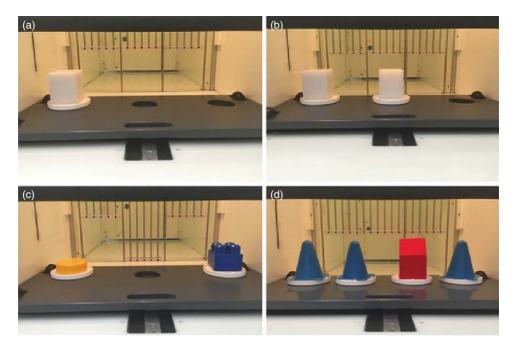


Fig. 15.1. (a) Sample phase of the DNMP task. The dog is required to displace a single block in one of the three positions to obtain a food reward. (b) Choice phase of the DNMP task. Following sample presentation and a predetermined delay, the dog must select the block in the new (nonmatch) position to obtain a food reward. (c) Simple discrimination learning and reversal task. During learning, the dog is required to continually select one of the two objects until learning criteria are reached. Subsequently, the reward contingency is reversed during reversal learning discrimination. (d) Selective attention task. The animal is required to select a single object and not a distractor; however, the number of distractors (i.e., negative stimuli) can vary from 0 to 3 during each trial. (Reprinted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Mad'ari, Norbert Žilka [eds.]; © 2017.)

most severely affected dogs, 67% displayed all four signs (Madari *et al.*, 2015). In cats, affected animals aged 11–14 years were most likely to show altered social interactions, while cats over 15 years of age most commonly displayed aimless activity and vocalization (Gunn-Moore *et al.*, 2007; Landsberg *et al.*, 2010, 2011).

Freedom from fear and distress is crucial for all animals, and safety can be compromised when an animal signals for increased distance using aggression. One study found intermittent manifestations of anxiety to be reported in 61% of dogs with CDS (Rème *et al.*, 2008). Salivary cortisol levels were higher in aged dogs during the Strange Situation Test (Mongillo *et al.*, 2013). Clinically, there is a concern because pets with CDS may experience increased agitation or aggression (Fast *et al.*, 2013), but also because these pets may be the target of aggression by other household pets. Due to decreased awareness (particularly if coupled with

sensory decline or decreased mobility), cognitively impaired dogs or cats can fail to read the social signals of other pets or be perceived as alarming by these housemates due to their atypical behavior.

15.1.2 Prevalence

The reported prevalence of canine CDS in animals over 8 years of age ranges from 14% to over 60% (Neilson *et al.*, 2001; Osella *et al.*, 2007; Azkona *et al.*, 2009; Salvin *et al.*, 2010; Madari *et al.*, 2015). Twenty-eight percent of dogs aged 11–12 years were reported by owners to show impairments in at least two categories of DISHAA, and 10% to show impairments in at least one category. In older dogs, aged 15–16 years, 68% were affected in at least one category, and 36% in two or more (Neilson *et al.*, 2001). Another study found a prevalence of 5% in dogs aged 10–12 years, 23% in dogs aged 12–14 years, and 41% in dogs over 14 years of age (Salvin *et al.*, 2010). Moderate to

marked cognitive dysfunction was reported to occur in 13–16% of dogs aged 8–11 years, and 87–100% of dogs older than 13 years (Katina *et al.*, 2016). When 85 of 300 dogs over 8 years of age were excluded due to medical problems, 159 of the remaining 215 dogs displayed signs of cognitive dysfunction (Madari *et al.*, 2015). Thirty-five percent of cats over 11 years of age were diagnosed with CDS, with 28% of cats 11–15 years and 50% of cats over 15 years affected (Gunn-Moore *et al.*, 2007).

Interestingly, owners' focus does not reflect the above when it comes to seeking veterinary assistance for behavioral concerns. In a group of 270 dogs over 7 years of age presenting for behavior

problems, 32% displayed aggression to family members, 16% aggression to family dogs, 9% barking, 8% separation anxiety, 6% disorientation and aggression toward unfamiliar people, 5% house soiling, 4% destructive and compulsive disorders, and 3% noise fears (Mariotti *et al.*, 2009). Yet in a study of 479 dogs over the age of 8, 14.2% were diagnosed with CDS despite only 13% of these having been previously diagnosed (Salvin *et al.*, 2010). Biannual hospital visits with questionnaire screening for clinical signs of CDS are recommended in pets over age 8 years to provide the earliest possible diagnosis (Landsberg *et al.*, 2010; Salvin *et al.*, 2011; Katina *et al.*, 2016) (Table 15.1).

Table 15.1. Senior canine and feline behavior questionnaire.

SENIOR CANINE BEHAVIOR SCREENING QUESTIONNAIRE

Used with permission of Dr. Gary Landsberg and CanCog Technologies.

Owner:

Pet's Name: Breed:	
Weight:lb / kg BCS (Out of 9)	
Male Neutered: Y N	
Female Spayed: Y N	
INSTRUCTIONS: The purpose of the questionnaire is to identify behavior changes or the onset	
of new behavior problems that have arisen since the age of 8 years using the following key:	
Scoring key (severity): 0 = none (no change) 1 = mild 2 = moderate 3 = severe	
BEHAVIORAL SIGNS	Score
A. Disorientation	
Gets stuck, difficulty getting around objects, goes to hinge side of door	
Stares blankly at walls, floor or into space	
Does not recognize familiar people or pets	
Gets lost in home or yard	
Less reactive to visual (sights) or auditory (sounds) stimuli	
B. Social interactions	
More irritable / fearful / aggressive with visitors, family or other animals	
Decreased interest in approaching, greeting or affection / petting	
C. Sleep-wake cycles	
Pacing / restless / sleeps less / waking at night	
Vocalization at night	
D. House soiling learning and memory	
Less able to learn new tasks or respond to previously learned commands / name / work	
Indoor soiling of urine or stools decreased signaling to go out	
Difficulty getting dog's attention / increased distraction / decreased focus	
E. Activity	
Decrease in exploration or play with toys, family members, other pets	
Increased activity – aimless pacing / wandering	
Repetitive behaviors e.g. circling chewing licking star gazing	
F. Anxiety	
Increased anxiety when separated from owners Mare reactive / faculate viewel (sights) or suditory (sounds) stimuli	
More reactive / fearful to visual (sights) or auditory (sounds) stimuli Increased fear of places / locations e.g. new environments / going outdoors	
increased lear of places / locations e.g. new environments / going outdoors	
Created by Dr. Gary Landsberg CanCog Technologies with support of Nestle Purina PetCare.	

Date:

15.1.3 Progression

Cognitive dysfunction is a progressive disease, and treatment is aimed at slowing progression. In dogs aged at least 11 years, 22% free of clinical signs developed signs within 12-18 months, and 48% of dogs with impairment in one category developed impairment in at least one additional category within this time frame (Bain et al., 2001). In dogs at least 8 years of age, 42% developed clinical signs and 24% progressed from mild to moderate impairment over a 6-month period. Over 1 year, 71.4% of this population developed mild impairment, and 50% progressed in classification from moderate to severe clinical signs (Madari et al., 2015). A third study found that 58% of dogs aged at least 8 years developed borderline CDS over the course of approximately 3 years, and 11% converted from borderline to CDS status (Fast et al., 2013).

15.1.4 Risk factors

Age is, of course, the key risk factor for canine CDS (Neilson *et al.*, 2001; Azkona *et al.*, 2009; Katina *et al.*, 2016). A strong positive correlation (Pearson correlation coefficient r = 0.662, p < 0.0001) has also been found between age and cognitive decline in dogs. Although percentages differ between studies (possibly due to the instruments used), the prevalence of CDS increases gradually with age (Azkona *et al.*, 2009; Salvin *et al.*, 2010).

The impact of body size does not appear to be large, if present at all. Four studies have found no impact of body size on memory or cognitive impairment (Neilson *et al.*, 2001; Salvin *et al.*, 2010; Fast *et al.*, 2013; Katina *et al.*, 2016). CDS was found to be similarly prevalent in small and medium/large dogs aged 8–11 years, but more common in larger breeds aged 11–13 years (55% versus 41%).

A clear influence of sex or castration status has also not been found. Females were suggested as more likely to exhibit CDS (Azkona *et al.*, 2009), but several other studies did not find support for such a difference (Neilson *et al.*, 2001; Yalcin *et al.*, 2010; Salvin *et al.*, 2011; Fast *et al.*, 2013; Katina *et al.*, 2016). CDS was found by two studies to be more prevalent in castrated individuals (Hart, 2001; Azkona *et al.*, 2009). However, two more recent investigations did not identify a difference in prevalence between castrated and intact older dogs (Fast *et al.*, 2013; Katina *et al.*, 2016).

Nutritional support for animals with CDS will be discussed later in this chapter. Risk factors associated with accelerated brain aging and Alzheimer's disease in humans include docosahexaenoic acid deficiency, high homocysteine, low B vitamin levels, high blood pressure, chronic oxidative stress, and chronic low-grade inflammation. Dogs fed low-quality commercial diets or table scraps were significantly more likely to develop CDS than dogs fed commercial diets formulated for age, size, or health (Katina *et al.*, 2016).

Environment may also play a role in the development of neurodegenerative disease. Wild dogs from areas with high air pollution exhibited early occurrence of β-amyloid plaques and elevation of proinflammatory markers. The former changes preceded by several years similar changes in the brains of dogs living in an environment with low air pollution (Calderon-Garciduenas *et al.*, 2008). In 56% of children and 57% of dogs living in an urban area with excessive air pollution, magnetic resonance imaging (MRI) revealed lesions in the prefrontal subcortical white matter (Migliore and Coppede, 2009).

15.2 Evaluation: Identifying Welfare Concerns

15.2.1 Pathophysiology

Changes in the brain range from macroscopic to submicroscopic. MRI scans of dogs with CDS may reveal ventricular enlargement, frontal and temporal lobe atrophy, an increase in lesions in the frontal cortex and caudate nucleus, and a decrease in the diameter of interthalamic adhesions (Tapp et al., 2004, 2006; Hasegawa et al., 2005; Su et al., 2005). Imaging also reveals decreased cerebral regional blood volume in the brains of cognitively impaired dogs, and microhemorrhage and infarcts may contribute to the signs of CDS in dogs and cats. Although changes are not as notable as those seen in dogs, aged cats likewise demonstrate cerebral atrophy, ventricular enlargement, and a widening of sulci (Gunn-Moore et al., 2007; Landsberg et al., 2010; Chambers et al., 2015) (Fig. 15.2).

Microscopically, CDS in dogs is characterized by meningeal calcification, and an overall reduction in neuronal density (Borras *et al.*, 1999; Colle *et al.*, 2000; Tapp *et al.*, 2004; Rofina *et al.*, 2006). As in humans with Alzheimer's disease, cognitively impaired dogs have significantly decreased numbers of noradrenergic neurons in the locus coeruleus (Insua *et al.*, 2010). The dentate gyrus of aged

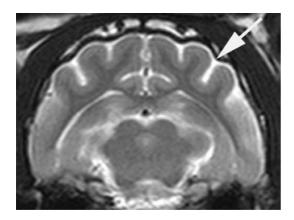


Fig. 15.2. MRI of an aged cat brain showing widening of the sulci (arrow) indicating brain atrophy. (Reprinted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Mad'ari, Norbert Žilka [eds.]; © 2017.)

dogs showed significantly fewer neurons, and decreased numbers of Purkinje cells in the cerebellum were associated with cognitive impairment (Pugliese *et al.*, 2007; Siwak-Tapp *et al.*, 2008). The progression of atrophy is regional, with prefrontal cortical volume decreasing prior to hippocampal volume (Tapp *et al.*, 2004).

Aged cats also display multiple brain changes consistent with neuronal loss. The molecular layer of the cerebellum in 12- to 13-year-old animals shows neuronal loss relative to that of 2- to 3-year-old cats. Decreased neurofilament immunolabeling in older cats also suggests loss of Purkinje cells in the cerebellum (Zhang et al., 2006). Ultrastructural and electrophysiologic experiments in aged cats suggest loss of dendrites in the caudate nucleus, loss of function which may be associated with impaired motor function, and/or habituation to repeated stimuli (Villablanca et al., 1978; Levine et al., 1986, 1987, 1988; Levine, 1988). Hippocampal neuron loss is seen in cats over 14 years (Chambers et al., 2015).

Analogous to changes seen in human Alzheimer's patients, the brains of aged dogs and cats display accumulations of diffuse beta amyloid plaques, as well as perivascular infiltrates (Cummings *et al.*, 1996b; Colle *et al.*, 2000; Tapp *et al.*, 2004; Rofina *et al.*, 2006; Gunn-Moore *et al.*, 2007) (Fig. 15.3). Multiple associations have been found between the amount and location of plaque deposition and the severity of cognitive deficits in dogs (Cummings *et al.*,

1996a,b; Colle *et al.*, 2000; Rofina *et al.*, 2006). Reversal learning deficits indicative of executive dysfunction are associated with amyloid deposits in the prefrontal cortex, and poor size discrimination with deposits in the prefrontal cortex (Cummings *et al.*, 1996a,b; Tapp *et al.*, 2004). Increased soluble Aβ levels in the cerebrospinal fluid (CSF) co-occur with decreased cognitive performance even prior to amyloid deposition (Head *et al.*, 2010; Borghys *et al.*, 2017).

Although the brains of aged cats also show evidence of A\beta plaques, these are more diffuse than those seen in dogs. Prevalence is increased in cats over 10 years of age, which may correlate with increasing cognitive decline (Cummings et al., 1996b; Nakamura et al., 1996; Brellou et al., 2005; Head et al., 2005; Gunn-Moore et al., 2007; Chambers et al., 2015). Tau hyperphosphorylation occurs in both dogs and cats, and has been associated with cognitive decline in dogs (Head et al., 2005; Gunn-Moore et al., 2007; Chambers et al., 2015; Smolek et al., 2016). Like humans with Alzheimer's disease, the hyperphosphorylated tau of cats forms neurofibrillary tangles (Hyman and Trojanowski, 1997; Head et al., 2005; Markesbery, 2010) (Fig. 15.4).

Even at a metabolic level, differences exist between the aging brain and brains of cognitively normal younger animals. Impaired cerebral glucose metabolism results in dogs with severe cognitive dysfunction showing increased CSF levels of pyruvate, lactate, and potassium (Pugliese et al., 2005; Borghys et al., 2017). One potential source of neurodegeneration in aged dogs is an increase in oxidative stress and reduced antioxidant capacity. These are linked to cognitive deficits, and may be due to agerelated mitochondrial dysfunction (Kiatipattanasakul et al., 1997; Papaioannou et al., 2001; Head et al., 2002, 2009; Skoumalova et al., 2003; Rofina et al., 2004, 2006; Hwang et al., 2008; Opii et al., 2008). Muscarinic receptor numbers are reduced in multiple brain regions in aged dogs (Reinikainen et al., 1987, 1990; Araujo et al., 2011b). Impaired cholinergic function may contribute to decreased cognitive and motor function, as well as sleep-wake disturbances (Zhang et al., 2005; Pugliese et al., 2007; Araujo et al., 2011b).

15.2.2 Diagnosis

Definitive diagnosis of cognitive dysfunction can occur only postmortem, with confirmation of representative

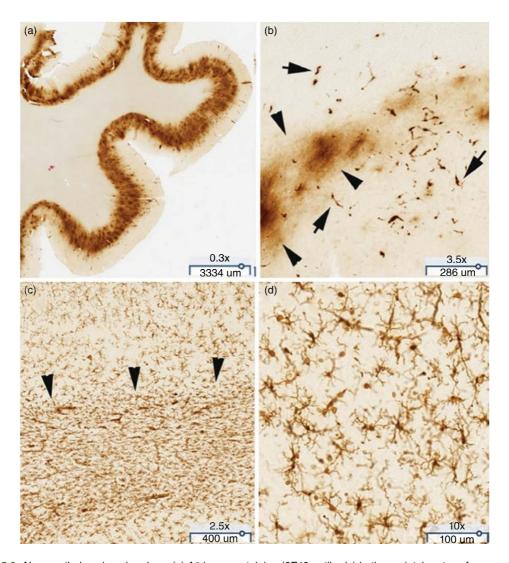


Fig. 15.3. Neuropathology in aging dogs. (a) Aβ immunostaining (6E10 antibody) in the parietal cortex of an aged pet dog (15-year-old Siberian husky) shows extensive plaque deposition affecting deep cortical layers. (b) CAA (6E10 immunostaining – arrows) in the parietal cortex of an aged dog (14-year-old sheltie) shows that vascular pathology can be extensive and tends to occur in clusters. Diffuse plaques are also identified by arrowheads. (c) Low-power photograph showing extensive microglial cell labeling (IBA-1 antibody) in gray matter along with intense labeling in the white matter (area below arrows) of a 15-year-old shih tzu. (d) Higher magnification photograph from (c) showing that individual microglia contain phagocytic vacuoles and have thickened processes suggesting that some have an activated morphology. (Reprinted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Maďari, Norbert Žilka [eds.]; © 2017.)

microscopic changes in the brain. Imaging can suggest disease premortem. Brain atrophy on MRI is compatible with, although not diagnostic for, CDS (Ettinger and Feldman, 2009). Standardized tests for evaluating cognitive function provide an invaluable research tool and questionnaires can be used in

clinical practice to identify affected animals. In all cases, the ruling out of differential diagnoses (both intracranial and extracranial) that mimic the signs of cognitive dysfunction is paramount. In a recent study in which dogs were excluded due to possible medical causes for altered behavior, 15 of 100 dogs

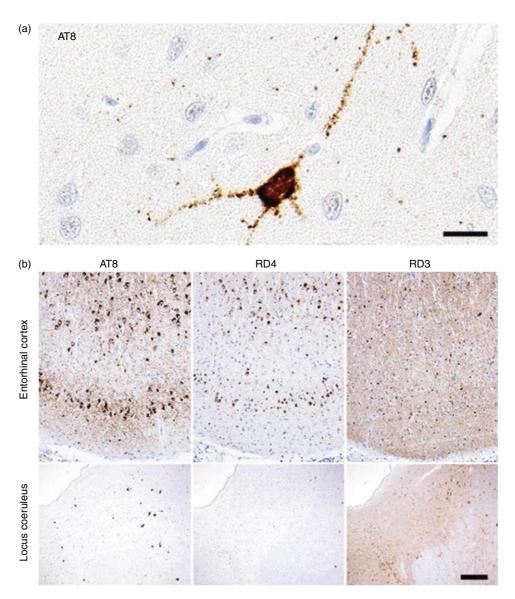


Fig. 15.4. Hyperphosphorylated tau accumulation in the entorhinal cortex and locus coeruleus of cat brains. (a) Immunohistochemistry of the entorhinal cortex of a cat with mild hyperphosphorylated tau accumulation (15-year-old, case no. 13) (AT8). The neuronal soma and dendrites are positively stained for hyperphosphorylated tau. Bar = 20 μm. (b) Immunohistochemistry of the entorhinal cortex and locus coeruleus of a cat with severe hyperphosphorylated tau accumulation (14-year-old, case no. 12) for AT8, 3-repeat tau (RD3), and 4-repeat tau (RD4). AT8-positive aggregates are also positively stained for 3-repeat tau and 4-repeat tau on consecutive sections. Bar = 300 μm. (Reprinted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Mad'ari, Norbert Žilka [eds.]; © 2017.)

were excluded due to baseline laboratory findings alone (Pan et al., 2017).

There is an extensive list of medical rule outs for each category comprising the aforementioned DISHAA group of signs (see Table 15.2). For instance, both acute and chronic pain have been associated with increased irritability, withdrawal, altered activity levels, decreased playfulness, and

Table 15.2. Medical differentials of cognitive dysfunction in dogs and cats.

System	Possible causes	Possible behavioral signs
Sensory	Cataracts/lenticular sclerosis	Fear/anxiety
,	Loss of vision	Disorientation
	Loss of hearing	Decreased response to stimuli
	-	Reduced learning ability
		Aggression
		Avoidance
		Vocalization
Pain/musculoskeletal	Degenerative diseases	Avoidance
	Arthritis	Reduced interest in exercise or play
	Muscular dystrophy	Altered response to stimuli
		Aggression
		Reduced self-hygiene
		Increased vocalization
Cardiovascular	Mitral insufficiency	Disorientation
	Hypertension	Tiredness or reduced interest in play and activity
	Cardiomyopathy	Withdrawal/avoidance
		Irritability
		Fear/anxiety
		Changes in appetite
		Vocalization
Endocrine	Diabetes mellitus	All signs of cognitive dysfunction
	Insulinoma	House soiling/urine marking
	Diabetes insipidus	Appetite – increased/decreased
	Hypothyroidism	Activity – increased/decreased/apathy
	Hyperthyroidism	Irritability
	Hyperadrenocorticism	Aggression
	Hypoadrenocorticism	Changes in sleep-wake cycle
	**	Stereotypic behavior, e.g., licking
		Restlessness, e.g., pacing
		Vocalization
Digestive	Dental diseases	Reduced appetite
	Hepatic diseases	Aggression/irritability
	Infectious/inflammatory	Avoidance/withdrawal
	Constipation	Nighttime waking
	House soiling	Stereotypic behavior, e.g., pacing, licking
	Nutritional imbalances	Coprophagia
	Pain	
Urinary	Renal diseases	House soiling/marking
	Urinary tract infection	Aggression
	Idiopathic cystitis	Withdrawal/avoidance
	Urolithiasis	Pacing
	Urinary incontinence	Sleep-wake changes

Adapted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Mad'ari, Norbert Žilka (eds.); © 2017.

aggression (Camps *et al.*, 2012). Hyperthyroid cats may display sleep–wake disturbances, increased vocalization, aggression (particularly related to food), and repetitive behaviors (Neilson, 2004). Other rule outs may include sensory decline and diseases of the cardiovascular, endocrine, gastrointestinal, or urinary systems. Diseases of the central

and peripheral nervous systems may also directly alter mentation and responsiveness.

Ruling out each differential may require diagnostics beyond basic physical examination and history (see Table 15.3). For instance, any dog or cat with polyuria, polydipsia, periuria, dysuria, or house soiling with inappropriate urination is a candidate

Table 15.3. Medical conditions to rule out.

Condition	Common causes	Testing suggested
Hypoglycemia	Insulinoma (dogs), neoplasia, Addison	Repeated fasting blood glucose, fructosamine
Hyperglycemia	Diabetes mellitus, hyperadrenocorticism	Blood glucose
Hepatic encephalopathy	Congenital portosystemic shunt, chronic hepatopathies and acquired portosystemic shunt	Fasting blood ammonia, dynamic bile acid stimulation test
Hyperthyroidism	Thyroid adenoma (cats)	Total T4
Uremic encephalopathy	Renal insufficiency	Serum urea, creatinine, symmetric dimethylarginine (SDMA) test, urine specific gravity
Hypothyroidism	Lymphoplasmacytic adenitis, idiopathic atrophy (dogs)	Total T4, Thyroid stimulating hormone (TSH)
Hypernatremia	Hyperaldosteronism (cats), adipsia, diabetes insipidus	Serum sodium
Hyponatremia	Hyperadrenocorticism, GI or renal losses, cardiac or hepatic insufficiency	Serum sodium
Hypercalcemia	Paraneoplastic, osteolytic lesions, hyperparathyroidism, renal insufficiency	Ionized calcium
Hypocalcemia	Hypoparathyroidism, nutritional secondary hyperparathyroidism, renal insufficiency	lonized calcium

Adapted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Mad'ari, Norbert Žilka (eds.); © 2017.

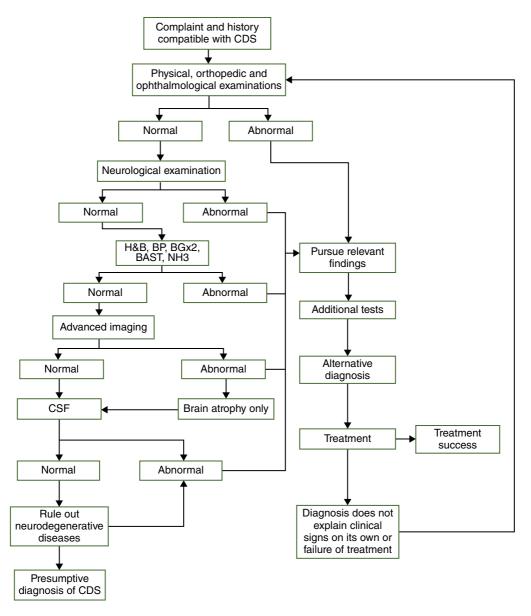
for a complete urinalysis with urine cytology, urine protein:creatinine ratio, and urine culture. MRI should be considered prior to establishing a presumptive diagnosis of CDS, and CSF analysis may also be appropriate. Elevated cell count or protein level suggests an inflammatory process, and cytology may identify infectious agents, viral inclusions, or neoplastic cells (Nelson and Couto, 2014) (Fig. 15.5).

15.2.3 Comorbidity with affective disorders

Of great concern from a welfare perspective is the comorbidity between CDS and a number of affective disorders related to abnormal levels of fear or anxiety. This directly impacts one of the Five Freedoms, namely freedom from fear and distress. Other causes of fear and anxiety are also behavioral rule outs for CDS. Although most behavior problems manifest in younger animals, a change in environment, schedule, or medical status may increase baseline level of stress or anxiety. Aggression may manifest toward a trigger, such as a child or another pet, that was only recently introduced to the family. In other cases, the geriatric dog or cat itself is newly introduced to the household, and may have an unknown history. Changes in schedule or a move to a new environment may cause a relapse or onset of separation-related problems. Noise fear can occur later in life, and continue to worsen over time until it becomes a concern to the owner.

Anxiety is the feeling of unease or apprehension that an undesirable or unsafe situation may occur. It can lead both to increased and decreased activity levels, as well as altered interactions with owners (either due to change in activity level, or to attention-seeking behaviors). Fear and anxiety may also contribute to aggression toward both humans and other pets. Cats may inappropriately eliminate or urine mark as a result of anxiety, and both dogs and cats can lose sphincter control as a result of spiking fear or anxiety (Landsberg *et al.*, 2012).

Chronically anxious pets may exhibit impaired memory, learning ability, or ability to perform previously learned behaviors (Landsberg and Araujo, 2005). Hypervigilant animals may show altered sleep—wake cycles (Ohl *et al.*, 2008), which is a common presenting complaint in cases of CDS (Landsberg *et al.*, 2011, 2013). Repetitive pacing as a displacement behavior caused by anxiety may occur throughout the day but be most noticeable to owners in the evening or at night (Landsberg and Denenberg, 2009; Landsberg *et al.*, 2011).



H&B, hematology and biochemistry; BP, blood pressure; BGx2, blood glucose X 2; BAST', bile acid stimulation test; NH3, ammonia; CSF, cerebrospinal fluid; CDS, cognitive dysfunction syndrome

Fig. 15.5. Algorithm for the diagnosis of canine dysfunction syndrome. (Reprinted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Maďari, Norbert Žilka [eds.]; © 2017.)

A learned component may also exist for some behavior problems. Although not always the inciting cause, attention or food given by the owner may reinforce some behaviors, such as excessive vocalization. Cats and more rarely dogs exhibiting inappropriate elimination may develop a learned substrate or location preference, due to the selfreinforcing nature of voiding bladder or bowels (Pryor *et al.*, 2001). Although punishment may reduce a behavior's frequency, it can increase anxiety and fear, and does not address animal's underlying motivation (Landsberg *et al.*, 2011).

Finally, even geriatric pets require the freedom to express normal behavior. Owners may believe that senior pets do not need stimulation, do not respond to training, or need to be left alone to rest due to physical disease. Although exercise and lifestyle adjustments may be necessary, enrichment is still beneficial and even needed for older pets. Repetitive, destructive, or attention-seeking behaviors may stem from lack of stimulation or boredom. Enrichment and the opportunity to practice species-specific behaviors should be provided to pets of all ages.

15.3 Treatment: Addressing Welfare Concerns

15.3.1 Enrichment

When used in combination with medical and nutritional therapies (discussed below), physical exercise and mental enrichment have been shown to slow the progression of cognitive impairment (Milgram et al., 2004; Head, 2007; Head et al., 2009). Aged dogs trained to run on a treadmill for 10 minutes daily showed acutely improved performance on both a concurrent discrimination task and a novel object location task (Snigdha et al., 2014). When this exercise regimen was continued, dogs showed improved performance on an object location memory task. In humans, exercise is known to benefit brain function, and has been shown to delay the onset of cognitive decline associated with Alzheimer's disease. This may be due to increased growth of neurons and blood vessels, as well as improvement in this organ's ability to cope with oxidative stress (Radak et al., 2007). Enrichment in aged dogs protected against neuronal loss in the hippocampus (Siwak-Tapp et al., 2008).

As previously discussed, such exercise and enrichment must allow for limits of age and disease in some older patients. However, both dogs and cats should have the opportunity to perform species-specific behaviors, such as scratching, perching, and hunting behaviors in cats and chewing in dogs. Senior pets in particular should be provided with the opportunity to retreat to a quiet location protected from the chaos of children, visitors, and other pets. Desired resources such as resting spots

or litter boxes should be available in this location. Additional enrichment can take the form of operantly conditioned behaviors (ranging from simple tricks to sports such as nose work), play, time on walks spent exploring novel environments, and food toys or puzzles. Although novelty can be a source of enrichment, moderation is suggested. Aged dogs and cats, perhaps especially those with cognitive or sensory deficits, may be less anxious if their routine and environment is kept structured and predictable.

15.3.2 Nutraceuticals

A number of supplements have been demonstrated to benefit patients with cognitive dysfunction. Senilife® (Ceva Animal Health) contains phosphatidylserine, a cell membrane component postulated to aid in neuronal signal transduction and cholinergic transmission (Tsakiris and Deconstantinos, 1985; Osella *et al.*, 2007). It additionally contains vitamin B6 (pyridoxine), which may exert a neuroprotective effect (Dakshinamurti *et al.*, 2003). This supplement is approved in both dogs and cats, and has been shown to improve cognition both in clinical studies and a laboratory model in dogs (Osella *et al.*, 2007; Araujo *et al.*, 2008).

Aktivait® (VetPlus Ltd.), another supplement containing phosphatidylserine, has been shown to significantly improve social interactions, disorientation, and house soiling in dogs with CDS (Heath *et al.*, 2007). Cholodin®-Fel (MVP Labs) is a supplement for senior cats that contains phosphatidylserine and pyridoxine. In a preliminary study, 9 of 21 aged cats treated with this supplement showed lessened confusion and improved appetite (Messonier, 2001).

Novifit® (Virbac Animal Health) contains S-adenosylmethionine, which may help maintain cell membrane fluidity and receptor function, regulate neurotransmitter levels, and decrease oxidative stress (Rème et al., 2008; Araujo et al., 2012). A placebocontrolled trial found clinical improvement in cognitively impaired dogs (Rème et al., 2008), and aged beagle dogs showed a trend toward improved reversal learning. Aged cats with milder clinical signs also showed fewer reversal learning errors consistent with improved executive function (Araujo et al., 2012).

NeutricksTM (Neutricks LLC) contains apoaequorin, a calcium-buffering protein found in jellyfish that may be neuroprotective. In one laboratory trial, apoaequorin-treated dogs demonstrated improved performance relative to controls on discrimination

learning and attention tasks, although not a spatial memory task. In another study, apoaequorin was found to be superior to selegiline in the treatment of cognitive dysfunction in dogs (Milgram *et al.*, 2015). Although this product is available for cats, no evidence-based studies are available.

15.3.3 Prescription diets

The goal of nutritional therapies for cognitive decline is to reduce oxidative stress, correct metabolic changes associated with impaired cognition, and improve mitochondrial function and neuronal signaling (Head et al., 2002, 2009; Milgram et al., 2004; Araujo et al., 2005b; Kidd, 2005; Sullivan and Brown, 2005; Scarmeas et al., 2006; Gunn-Moore et al., 2007; Head, 2007; Siwak-Tapp et al., 2008; Joseph et al., 2009; Landsberg et al., 2010; Pan et al., 2010, 2013, 2017; Pop et al., 2010; Pan, 2011; Dowling and Head, 2012; Fahnestock et al., 2012). As previously mentioned, dogs fed commercial diets specific to size, breed, age, or health status carried a lower risk for CDS than dogs fed low-quality commercial diets or leftovers (Katina et al., 2016). More specific diet-related brain effects were observed in other studies. For example, aging dogs fed diets rich in antioxidants showed improved mitochondrial function (Head et al., 2009) and improved cognition, as well as reduced oxidative damage and AB pathology (Dowling and Head, 2012).

Multiple diets specifically formulated for dogs and cats with cognitive dysfunction have been studied. Prescription Diet b/d Canine (Hill's Pet Nutrition) is supplemented with fatty acids, antioxidants (vitamins C and E, beta-carotene, selenium, flavonoids, carotenoids), and DL-alpha-lipoic acid and L-carnitine. A 3-year longitudinal study of 48 beagle dogs aged 8 to 12 years found improvement in a landmark task within 2 weeks, subsequent improvement in oddity discrimination, and maintenance of reversal learning. The greatest benefit occurred in dogs receiving both the diet and added behavioral enrichment (Milgram et al., 2004; Araujo et al., 2005b; Head, 2007; Head et al., 2009; Dowling and Head, 2012; Fahnestock et al., 2012). These dogs showed decreased oxidative damage, as well as increased brain-derived neurotrophic factor and neuronal health (Milgram et al., 2004; Head, 2007; Head et al., 2009; Pop et al., 2010; Dowling and Head, 2012; Fahnestock et al., 2012). Young dogs fed the diet showed no cognitive changes (Scarmeas et al., 2006).

Purina ProPlan Bright Mind or Optiage (Nestle Purina Research) is a diet supplemented with medium-chain triglycerides (MCT). Dogs at even 6 years of age show significantly reduced cerebral glucose metabolism compared with dogs at 1 year of age, and MCTs provide ketone bodies as an alternative energy source for aging neurons (London et al., 1983). Compared with controls, dogs fed a diet supplemented with 5.5% MCT over 8 months showed significantly better performance in landmark one and landmark two discriminations, an egocentric learning and egocentric reversal task, and a variable oddity task (Pan et al., 2010; Pan, 2011). Treated dogs demonstrated elevated levels of the ketone body β-hydroxybutyrate (Sullivan and Brown, 2005; Taha et al., 2009). A double-blinded placebo-controlled clinical trial of ProPlan Veterinary Diets Neurocare in dogs with CDS found significant improvement in all categories of DISHAA signs over a 3-month period. This diet is supplemented with 6.5% MCT and a brain protection blend containing B vitamins and antioxidants, among other components (Pan et al., 2017).

15.3.4 Prescription pharmacotherapy (Table 15.4)

In North America, selegiline hydrochloride (Anipryl®, Zoetis Animal Health) is the only pharmaceutical that is approved for use in dogs suffering from CDS. Selegiline is a selective irreversible inhibitor of monoamine oxidase B (MAOB), although its mechanism of action in dogs is not entirely clear. Concurrent use with other MAO inhibitors or serotonergic drugs is contraindicated. Administration results in a number of effects in the central nervous system: enhanced dopaminergic and catecholaminergic function in the cortex and hippocampus, increased release and reduced reuptake of norepinephrine, increased free radical scavenging enzymes, and neuroprotective effects. Its metabolites L-amphetamine and L-methamphetamine can enhance cognitive function and improve behavior (Milgram et al., 1993, 1995; Ruehl et al., 1996).

When given in laboratory dogs at a dose of 0.5–1 mg/kg in the morning, selegiline resulted in reduced clinical signs of CDS and improved working memory. Although improvement was seen at 2 weeks in some dogs, others took up to 2 months to respond (Ruehl *et al.*, 1995; Head *et al.*, 1996; Campbell *et al.*, 2001). Although selegiline's use in cats is extra-label, improvement in disorientation, vocalization, and decreased

Table 15.4. Drug doses for adjunctive therapy of clinical signs

Drug	Dog dose	Cat dose
Lorazepam	0.025–0.1 mg/kg sid to prn	0.125-0.25 mg/cat sid-bid
Oxazepam	0.2-1.0 mg/kg sid-bid	0.2-0.5 mg/kg sid-bid
Fluoxetine	1.0-2.0 mg/kg sid	0.5–1.5 mg/kg sid
Sertraline	1-5 mg/kg sid or divided bid	0.5–1.5 mg/kg sid
Clonidine	0.01-0.05 mg/kg bid or prn	5–10 μg/kg bid–tid
Dexmedetomidine oromucosal gel	125 μg/m²	
Propranolol	0.5–2.0 mg/kg bid or prn	
Buspirone	0.5–2.0 mg/kg bid–tid	0.5–1 mg/kg bid
Trazodone	2-5 mg/kg (to 12 mg/kg) prn to tid	25-50 mg/cat sid-bid
Gabapentin	10-30 mg/kg bid-tid	5-20 mg/kg sid-tid
Selegiline	0.5-1 mg/kg sid in am	0.5-1 mg/kg sid in am

sid, once daily; bid, twice daily; tid, three times daily; prn, when needed; am, morning.

Adapted by permission from Springer Nature: Springer; Canine and Feline Dementia: Molecular Basis, Diagnostics and Therapy by Gary Landsberg, Aladár Mad'ari, Norbert Žilka (eds.); © 2017.

affection have been reported in cats at a dose of 0.5–1 mg/kg in the morning (Landsberg, 2006; Gunn-Moore *et al.*, 2007; Landsberg *et al.*, 2010; Overall, 2010). A small study found no evidence of toxicity at a dose of up to 10 mg/kg (Ruehl *et al.*, 1996).

In some countries in Europe and in Australia, propentofylline (Vivitonin®, Karsivan Vet®, MSD Animal Health) is also licensed at a dose of 5 mg/kg twice daily for use in dogs showing mental dullness, lethargy, and tiredness in the absence of any other identifiable cause. Propentofylline is a xanthine derivative that may increase oxygenation in the brain and periphery, by means of improving microcirculation and inhibiting thrombus formation (Parkinson *et al.*, 1994). However, aged beagle dogs treated with propentofylline in a laboratory trial showed no change in behavioral activity (Siwak *et al.*, 2000). There are anecdotal reports of efficacy at a dose of 12.5 mg per cat twice daily (Gunn-Moore *et al.*, 2007; Landsberg *et al.*, 2010; Overall 2010).

Also licensed for use in some European countries, nicergoline is an alpha 1 and 2 adrenergic agonist recommended for use at a dose of 0.5 mg/kg once daily. Nicergoline may enhance cerebral circulation and neuronal transmission, as well as exerting a neuroprotective effect (Penaliggon et al., 1997; Siwak et al., 2000). Anticholinergic drugs may accelerate cognitive decline, and avoidance in aged pets is suggested (Araujo et al., 2005a, 2011a,b; Cai et al., 2013; Gray et al., 2015; Cross et al., 2016). Drugs that enhance cholinergic transmission, such as donepezil and phenserine, might theoretically improve clinical signs in CDS patients (Araujo et al., 2005a).

15.3.5 Symptom-based anxiolysis

As previously discussed, dogs and cats suffering from cognitive dysfunction may experience an increase in anxiety. This can result in sleep—wake disturbances, cause or exacerbate agitation or aggression, and generally compromise the welfare of both patient and owner. Therefore, symptomatic treatment for night waking and anxiety is often productive. Clomipramine, amitriptyline, and paroxetine should be avoided, as anticholinergic drugs are contraindicated. Fluoxetine, sertraline, or buspirone can be considered (Araujo *et al.*, 2005a, 2011a,b; Zhang *et al.*, 2005; Pugliese *et al.*, 2007). Trazodone can also be considered, either alone or in combination with an SSRI or buspirone. Serotonergic drugs should not be used concurrently with selegiline.

Benzodiazepines do carry the risk of exacerbating cognitive deficits, as well as causing sedation or ataxia. However, they can provide anxiolysis, and importantly mitigate nighttime waking. Lacking active intermediate metabolites, lorazepam or oxazepam might be preferred. Adjunctive use of propranolol, clonidine, or oromucosal dexmedetomidine may inhibit release or block the effects of noradrenaline, exerting anxiolytic effects. Gabapentin may reduce reactivity, as well as provide analgesia in a painful senior pet (Landsberg et al., 2011). Although not directly beneficial in slowing the progression of CDS in the manner of those listed above, other natural products can be used to directly treat anxiety: pheromones (Adaptil, Feliway), L-theanine, alpha-casozepine, L-tryptophan, or Phellodendron and Magnolia extracts.

15.4 Concluding Remarks

Almost every veterinarian has likely heard a client relate, 'Well, my dog or cat's behavior has changed, but I think he or she is just getting old.' Although age is not a disease, diseases associated with aging can affect the central nervous system as well as other systems of the body. Behavior change can be a manifestation of disease both centrally and peripherally, and it is the job of the veterinarian to tease out contributing causes. A majority of dogs and cats reaching a certain age will experience changes in behavior: disorientation, altered social interactions, sleep-wake disturbances, loss of housetraining and other learned behaviors, increased or decreased activity levels, and increased anxiety or fear. These changes can be associated with accumulations of diffuse beta amyloid plaques, as well as distinctive macro- and microscopic degeneration, within the brain. Cognitive dysfunction is not a curable disease, but its progression can be slowed through use of enrichment, diet change and nutraceuticals, and medication. Associated increases in fear, anxiety, and aggression can also be treated symptomatically to improve quality of life in affected pets.

15.5 References

- Araujo, J.A., Studzinski, C.M., Milgram, N.W. (2005a) Further evidence for the cholinergic hypothesis of aging and dementia from the canine model of aging. *Progress in Neuro-Psychopharmacology and Biological Psychiatry* 29, 411–422. http://dx.doi.org/10.1016/j.pnpbp.2004.12.008.
- Araujo, J. A., Studzinski, C. M., Head, E., Cotman, C. W., Milgram, N. W. (2005b) Assessment of nutritional interventions for modification of age-associated cognitive decline using a canine model of human aging. *Age* 27, 27–37.
- Araujo, J.A., de Rivera, C., Milgram, N.W. (2008) Visual attention is decreased in aged dogs. *Alzheimer's Dementia* 4, T205–T206. http://dx.doi.org/10.1016/j.jalz.2008.05.586.
- Araujo, J.A., Greig, N.H., Ingram, D.K., Sandin, J., de Rivera, C., et al. (2011a) Cholinesterase inhibitors improve both memory and complex learning in aged beagle dogs. *Journal of Alzheimer's Disease* 26, 143–155. http://dx.doi.org/10.3233/JAD-2011-110005.
- Araujo, J.A., Nobrega, J.N., Raymond, R., Milgram, N.W. (2011b) Aged dogs demonstrate both increased sensitivity to scopolamine impairment and decreased muscarinic receptor density. *Pharmacology Biochemistry and Behavior* 98, 203–209. http://dx.doi.org/10.1016/j.pbb.2011.01.005.

- Araujo, J.A., Faubert, M.L., Brooks, M.L., Landsberg, G.M., Lobprise, H. (2012) NOVIFIT® (NoviSAMe®) Tablets improve executive function in aged dogs and cats: Implications for treatment of cognitive dysfunction syndrome. *International Journal of Applied Research in Veterinary Medicine* 10, 90–98.
- Azkona, G., Garcia-Belenguer, S., Chacón, G., Rosado, B., León, M., et al. (2009) Prevalence and risk factors of behavioural changes associated with age-related cognitive impairment in geriatric dogs. *Journal of Small Animal Practice* 50, 87–91. http://dx.doi.org/10.1111/j.1748-5827.2008.00718.x.
- Bain, M.J., Hart, B.L., Cliff, K.D., Ruehl, W.W. (2001) Predicting behavioral changes associated with agerelated cognitive impairment in dogs. *Journal of the American Veterinary Medical Association* 218, 1792–1795. http://dx.doi.org/10.2460/javma.2001. 218.1792.
- Borghys, H., Van Broeck, B., Dhuyvetter, D., Jacobs, T., de Waepenaert, K., et al. (2017) Young to middle-aged dogs with high amyloid-β levels in cerebrospinal fluid are impaired on learning in standard cognition tests. *Journal of Alzheimer's Disease* 56, 763–774. http://dx.doi.org/10.3233/JAD-160434.
- Borras, D., Ferrer, I., Pumarola, M. (1999) Age-related changes in the brain of the dog. *Veterinary Pathology* 36, 202–211. http://dx.doi.org/10.1354/vp.36-3-202.
- Brellou, G., Vlemmas, I., Lekkas, S., Papaioannou, N. (2005) Immunohistochemical investigation of amyloid ß-protein (Aß) in the brain of aged cats. *Journal of Histology & Histopathology* 20, 725–731.
- Cai, X., Campbell, N., Khan, B., Callahan, C., Boustani, M. (2013) Long-term anticholinergic use and the aging brain. *Alzheimer's Dementia* 9, 377–385. http://dx.doi.org/10.1016/j.jalz.2012.02.005.
- Calderon-Garciduenas, L., Mora-Tiscareno, A., Ontiveros, E., Gomez-Garza, G., Barragan-Mejia, G., et al. (2008) Air pollution, cognitive deficits and brain abnormalities: A pilot study with children and dogs. Brain and Cognition 68, 117–127. http://dx.doi.org/10.1016/j.bandc.2008.04.008.
- Campbell, S., Trettien, A., Kozan, B. (2001) A noncomparative open-label study evaluating the effect of selegiline hydrochloride in a clinical setting. *Veterinary Therapeutics* 2, 24–39.
- Camps, T., Amat, M., Mariotti, V.M., Brech, S.L., Manteca, X. (2012) Pain-related aggression in dogs: 12 clinical cases. *Journal of Veterinary Behavior:* Clinical Applications and Research 7, 99–102. http:// dx.doi.org/10.1016/j.jveb.2011.08.002.
- Chambers, J.K., Tokuda, T., Uchida, K., Ishii, R., Tatebe, H., et al. (2015) The domestic cat as a natural animal model of Alzheimer's disease. Acta Neuropathologica Communications 3, 78. DOI: 10.1186/s40478-015-0258-3
- Colle, M.A., Hauw, J.J., Crespeau, F., Uchihara, T., Akiyama, H., et al. (2000) Vascular and parenchymal

- Aβ deposition in the aging dog: Correlation with behavior. *Neurobiology of Aging* 21, 695–704. http://dx.doi.org/10.1016/S0197-4580(00)00113-5.
- Cross, A.J., George, J., Woodward, M.C., Ames, D., Brodaty, H., et al. (2016) Potentially inappropriate medications and anticholinergic burden in older people attending memory clinics in Australia. *Drugs and Aging* 33, 37–44. http://dx.doi.org/10.1007/s40266-015-0332-3.
- Cummings, B.J., Head, E., Afagh, A.J., Milgram, N.W., Cotman, C.W. (1996a) β-amyloid accumulation correlates with cognitive dysfunction in the aged canine. Neurobiology of Learning and Memory 66, 11–23. http://dx.doi.org/10.1006/nlme.1996.0039.
- Cummings, B.J., Satou, T., Head, E., Milgram, N.W., Cole, G.M., et al. (1996b) Diffuse plaques contain C-terminal Aß42 and not Aß40: Evidence from cats and dogs. Neurobiology of Aging 17, 653–659. http://dx.doi.org/10.1016/S0197-4580(96)00062-0.
- Dakshinamurti, K., Sharma, S.K., Geiger, J.D. (2003) Neuroprotective actions of pyridoxine. *Biochimica et Biophysica Acta (BBA) – Proteins and Proteomics* 1647, 225–229.
- Dowling, A.L.S. and Head, E. (2012) Antioxidants in canine model of human aging. *Biochimica et Biophysica Acta (BBA) Molecular Basis of Disease* 1882, 685–689.
- Ettinger, S.J. and Feldman, E.C. (2009) *Textbook of Veterinary Internal Medicine*, 7th edn. Saunders, St. Louis, Missouri, USA.
- Fahnestock, M., Marchese, M., Head, E., Pop, V., Michalski, B., et al. (2012) BDNF increases with behavioral enrichment and an antioxidant diet in the aged dog. *Neurobiology of Aging* 33, 546–554. http://dx. doi.org/10.1016/j.neurobiolaging.2010.03.019.
- Fast, R., Schütt, T., Toft, N., Møller, A., Berendt, M. (2013) An observational study with long-term followup of canine cognitive dysfunction: Clinical characteristics, survival and risk factors. *Journal of Veterinary Internal Medicine* 27, 822–829. http://dx.doi. org/10.1111/jvim.12109.
- Gray, S.L., Anderson, M.L., Dublin, S., Hanlon, J.T., Hubbard, R., et al. (2015) Cumulative use of strong anticholinergics and incident dementia: A prospective cohort study. JAMA Internal Medicine 175, 401–407. http://dx.doi.org/10.1001/jamainternmed.2014.7663.
- Gunn-Moore, D., Moffat, K., Christie, L.A., Head, E. (2007) Cognitive dysfunction and the neurobiology of ageing in cats. *Journal of Small Animal Practice* 48, 546–553. http://dx.doi.org/10.1111/j.1748-5827.2007.00386.x.
- Hart, B.L. (2001) Effect of gonadectomy on subsequent development of age-related cognitive impairment in dogs. *Journal of the American Veterinary Medical* Association 219, 51–56. http://dx.doi.org/10.2460/ javma.2001.219.51.
- Hasegawa, D., Yayoshi, N., Fujita, Y., Fujita, M., Orima, H. (2005) Measurement of interthalamic adhesion

- thickness as a criteria for brain atrophy in dogs with and without cognitive dysfunction (dementia). *Veterinary Radiology & Ultrasound* 46, 452–457. http://dx.doi.org/10.1111/j.1740-8261.2005.00083.x.
- Head, E. (2007) Combining an antioxidant-fortified diet with behavioral enrichment leads to cognitive improvement and reduced brain pathology in aging canines. *Annals of the New York Academy of Sciences* 1114, 398–406. http://dx.doi.org/10.1196/annals.1396.004.
- Head, E., Hartley, J., Kameka, A.M., Mehta, R., Ivy, G.O., et al. (1996) The effects of L-deprenyl on spatial short term memory in young and aged dogs. Progress in Neuro-Psychopharmacology and Biological Psychiatry 20, 515–530. http://dx.doi.org/10.1016/0278-5846(96) 00014-0.
- Head, E., Liu, J., Hagen, T.M., Muggenburg, B.A., Milgram, N.W., et al. (2002) Oxidative damage increases with age in a canine model of human brain aging. Journal of Neurochemistry 82, 375–381. http://dx.doi.org/10.1046/j.1471-4159.2002.00969.x.
- Head, E., Moffat, K., Das, P., Sarsoza, F., Poon, W.W., et al. (2005) β-Amyloid deposition and tau phosphorylation in clinically characterized aged cats. Neurobiology of Aging 26, 749–763. http://dx.doi. org/10.1016/j.neurobiolaging.2004.06.015.
- Head, E., Nukala, V.N., Fenoglio, K.A., Muggenburg, BA., Cotman, C.W., et al. (2009) Effects of age, dietary, and behavioral enrichment on brain mitochondria in a canine model of human aging. Experimental Neurology 220, 171–176. http://dx.doi.org/10.1016/j. expneurol.2009.08.014.
- Head, E., Pop, V., Sarsoza, F., Kayed, R., Beckett, T.L., et al. (2010) Amyloid-β peptide and oligomers in the brain and cerebrospinal fluid of aged canines. *Journal* of Alzheimer's Disease 20, 637–646. http://dx.doi. org/10.3233/JAD-2010-1397.
- Heath, S.E., Barabas, S., Craze, P.G. (2007) Nutritional supplementation in cases of canine cognitive dysfunction—a clinical trial. *Applied Animal Behaviour Science* 105, 284–296. http://dx.doi.org/10.1016/j. applanim.2006.11.008.
- Hwang, I.K., Yoon, Y.S., Yoo, K.Y., Li, H., Choi, J.H., et al. (2008) Differences in lipid peroxidation and Cu, Zn-superoxide dismutase in the hippocampal CA1 region between adult and aged dogs. *Journal of Veterinary Medical Science* 70, 273–277. http://dx.doi.org/10.1292/jyms.70.273.
- Hyman, B.T. and Trojanowski, J.Q. (1997) Consensus recommendations for the postmortem diagnosis of Alzheimer disease from the National Institute on Aging and the Reagan Institute Working Group on diagnostic criteria for the neuropathological assessment of Alzheimer disease. *Journal of Neuropathology & Experimental Neurology* 56, 1095–1097. http://dx.doi.org/10.1097/00005072-199710000-00002.
- Insua, D., Suárez, M.L., Santamarina, G., Sarasa, M., Pesini, P. (2010) Dogs with canine counterpart of

- Alzheimer's disease lose noradrenergic neurons. *Neurobiology of Aging* 31, 625–635. http://dx.doi.org/10.1016/j.neurobiologing.2008.05.014.
- Joseph, J.A., Shukitt-Hale, B., Willis, L.M. (2009) Grape juice, berries, and walnuts affect brain aging and behavior. *Journal of Nutrition* 139, 1813–1817. http:// dx.doi.org/10.3945/jn.109.108266.
- Katina, S., Farbakova, J., Madari, A., Novak, M., Zilka, N. (2016) Risk factors for canine cognitive dysfunction syndrome in Slovakia. Acta Veterinaria Scandinavica 58, 17.
- Kiatipattanasakul, W., Nakamura, S.I., Kuroki, K., Nakayama, H. (1997) Immunohistochemical detection of anti-oxidative stress enzymes in the dog brain. *Neuropathology* 17, 307–312. http://dx.doi.org/10. 1111/j.1440-1789.1997.tb00058.x.
- Kidd, P.M. (2005) Neurodegeneration from mitochondrial insufficiency: Nutrients, stem cells, growth factors, and prospects for brain rebuilding using integrative management. Alternative Medicine Review 10, 268.
- Landsberg, G. (2006) Therapeutic options for cognitive decline in senior pets. *Journal of the American Animal Hospital Association* 42, 407–413. http://dx. doi.org/10.5326/0420407.
- Landsberg, G. and Araujo, J.A. (2005) Behavior problems in geriatric pets. Veterinary Clinics: Small Animal Practice 35, 675–698.
- Landsberg, G. and Denenberg, S. (2009) Behaviour problems in the senior pet. In: Horwitz, D., Mills, D.S. (eds.) *BSAVA Manual of Canine and Feline Behavioural Medicine*, 2nd edn. BSAVA, Gloucester, UK, pp. 127–135. http://dx.doi.org/10.22233/9781905319879.12.
- Landsberg, G.M., Denenberg, S., Araujo, J.A. (2010) Cognitive dysfunction in cats: A syndrome we used to dismiss as 'old age'. *Journal of Feline Medicine & Surgery* 12, 837–848. http://dx.doi.org/10.1016/j. jfms.2010.09.004.
- Landsberg, G.M., DePorter, T., Araujo, J.A. (2011) Clinical signs and management of anxiety, sleeplessness, and cognitive dysfunction in the senior pet. Veterinary Clinics: Small Animal Practice 41, 565–590.
- Landsberg, G.M., Nichol, J., Araujo, J.A. (2012) Cognitive dysfunction syndrome a disease of canine and feline brain aging. Veterinary Clinics: Small Animal Practice 42, 749–768.
- Landsberg, G.M., Hunthausen, W., Ackerman, L.A.
 (2013) The effect of aging on behavior in senior pets.
 In: Landsberg, G.M., Hunthausen, W., Ackerman,
 L.A. (eds.) Behavior Problems of the Dog and Cat,
 3rd edn. Saunders, Edinburgh, UK. pp. 211–235.
- Levine, M.S. (1988) Neurophysiological and morphological alterations in caudate neurons in aged cats. Annals of the New York Academy of Sciences 515, 314–328. http://dx.doi.org/10.1111/j.1749-6632.1988. tb33002.x.

- Levine, M.S., Adinolfi, A.M., Fisher, R.S., Hull, C.D., Buchwald, N.A., et al. (1986) Quantitative morphology of medium-sized caudate spiny neurons in aged cats. Neurobiology of Aging 7, 277–286. http://dx. doi.org/10.1016/0197-4580(86)90008-4.
- Levine, M.S., Lloyd, R.L., Fisher, R.S., Hull, C.D., Buchwald, N.A. (1987) Sensory, motor and cognitive alterations in aged cats. *Neurobiology of Aging* 8, 253–263. http://dx.doi.org/10.1016/0197-4580(87) 90010-8.
- Levine, M.S., Adinolfi, A.M., Fisher, R.S., Hull, C.D., Guthrie, D., et al. (1988) Ultrastructural alterations in caudate nucleus in aged cats. *Brain Research* 440, 267–279. http://dx.doi.org/10.1016/0006-8993(88) 90995-X.
- London, E.D., Ohata, M., Takei, H., French, A.W., Rapoport, S.I. (1983) Regional cerebral metabolic rate for glucose in beagle dogs of different ages. *Neurobiology of Aging* 4, 121–126. http://dx.doi. org/10.1016/0197-4580(83)90035-0.
- Madari, A., Farbakova, J., Katina, S., Smolek, T., Novak, P., et al. (2015) Assessment of severity and progression of canine cognitive dysfunction syndrome using the Canine Dementia Scale (CADES). Applied Animal Behaviour Science 171, 138–145. http://dx.doi.org/10.1016/j.applanim.2015.08.034.
- Mariotti, V.M., Landucci, M., Lippi, I., Amat, M., Manteca, X., Guidi, G. (2009) Epidemiological study of behavioural disorders in elderly dogs. Abstract. In: Heath, S. (ed.) Proceedings of the Seventh International Meeting of Veterinary Behaviour Medicine. Edinburgh, UK, pp. 241–245.
- Markesbery, W.R. (2010) Neuropathologic alterations in mild cognitive impairment: A review. *Journal of Alzheimer's Disease* 19, 221–228. http://dx.doi. org/10.3233/JAD-2010-1220.
- Messonier, S.P. (2001) The Natural Health Bible for Dogs and Cats. Three Rivers Press, New York,
- Migliore, L. and Coppede, F. (2009) Environmental-induced oxidative stress in neurodegenerative disorders and aging. *Mutation Research Genetic Toxicology* and *Environmental Mutagenesis* 674, 73–84. http://dx.doi.org/10.1016/j.mrgentox.2008.09.013.
- Milgram, N.W., Ivy, G.O., Head, E., Murphy, M.P., Wu, P.H., et al. (1993) The effect of I-deprenyl on behavior, cognitive function, and biogenic amines in the dog. Neurochemical Research 18, 1211–1219. http://dx.doi.org/10.1007/BF00975038.
- Milgram, N.W., Ivy, G.O., Murphy, M.P., Head, E., Wu, P.H., et al. (1995) Effects of chronic oral administration of L-deprenyl in the dog. Pharmacology Biochemistry & Behavior 51, 421–428. http://dx.doi. org/10.1016/0091-3057(94)00417-H.
- Milgram, N.W., Head, E., Zicker, S.C., Ikeda-Douglas, C., Murphey, H., et al. (2004) Long term treatment

- with antioxidants and a program of behavioural enrichment reduces age-dependent impairment in discrimination and reversal learning in beagle dogs. *Experimental Gerontology* 39, 753–765. http://dx.doi.org/10.1016/j.exger.2004.01.007.
- Milgram, N.W., Landsberg, G., Merrick, D., Underwood, M.Y. (2015) A novel mechanism for cognitive enhancement in aged dogs with the use of a calciumbuffering protein. *Journal of Veterinary Behavior:* Clinical Applications and Research 10, 217–222. http://dx.doi.org/10.1016/j.jveb.2015.02.003.
- Mongillo, P., Pitteri, E., Carnier, P., Gabai, G., Adamelli, S., et al. (2013) Does the attachment system towards owners change in aged dogs? *Physiology & Behavior* 120, 64–69. http://dx.doi.org/10.1016/j.physbeh.2013. 07.011.
- Nakamura, S.I., Nakayama, H., Kiatipattanasakul, W., Uetsuka, K., Uchida, K., et al. (1996) Senile plaques in very aged cats. Acta Neuropathologica 91, 437– 439. http://dx.doi.org/10.1007/s004010050448.
- Neilson, J.C. (2004) Feline house soiling: Elimination and marking behaviors. *Clinical Techniques in Small Animal Practice* 19, 216–224. http://dx.doi.org/10.1053/j.ctsap.2004.10.003.
- Neilson, J.C., Hart, B.L., Cliff, K.D., Ruehl, W.W. (2001) Prevalence of behavioral changes associated with agerelated cognitive impairment in dogs. *Journal of the American Veterinary Medical Association* 218, 1787– 1791. http://dx.doi.org/10.2460/javma.2001.218.1787.
- Nelson, R.W. and Couto, C.G. (2014) Small Animal Internal Medicine, 5th edn. Mosby, St. Louis, Missouri, USA.
- Ohl, F., Arndt, S.S., van der Staay, F.J. (2008) Pathological anxiety in animals. *The Veterinary Journal* 175, 18–26. http://dx.doi.org/10.1016/j.tvjl.2006.12.013.
- Opii, W.O., Joshi, G., Head, E., Milgram, N.W., Muggenburg, B.A., et al. (2008) Proteomic identification of brain proteins in the canine model of human aging following a long-term treatment with antioxidants and a program of behavioral enrichment: Relevance to Alzheimer's disease. Neurobiology of Aging 29, 51–70. http://dx.doi.org/10.1016/j.neurobiolaging.2006.09.012
- Osella, M.C., Re, G., Odore, R., Girardi, C., Badino, P., et al. (2007) Canine cognitive dysfunction syndrome: Prevalence, clinical signs and treatment with a neuroprotective nutraceutical. Applied Animal Behaviour Science 105, 297–310. http://dx.doi.org/10.1016/j.applanim.2006.11.007.
- Overall, K.L. (2010) Assessing brain aging in cats. Available at: http://veterinarynews.dvm360.com/assessing-brain-aging-cats (accessed 8 November 2018).
- Pan, Y. (2011) Enhancing brain functions in senior dogs: A new nutritional approach. *Topics in Companion Animal Medicine* 26, 10–16. http://dx.doi.org/10.1053/j.tcam.2011.01.002.

- Pan, Y., Larson, B., Araujo, J.A., Lau, W., De Rivera, C., et al. (2010) Dietary supplementation with medium-chain TAG has long-lasting cognition-enhancing effects in aged dogs. *British Journal of Nutrition* 103, 1746–1754. http://dx.doi.org/10.1017/S0007114510000097.
- Pan, Y., Araujo, J.A., Burrows, J., de Rivera, C., Gore, A., et al. (2013) Cognitive enhancement in middle-aged and old cats with dietary supplementation with a nutrient blend containing fish oil, B vitamins, antioxidants and arginine. British Journal of Nutrition 110, 40–49. http://dx.doi.org/10.1017/S0007114512004771.
- Pan, Y., Landsberg, G., Mougeot, I., Kelly, S., Xu, H., Bhatnagar, S., et al. (2017) Efficacy of a therapeutic diet on dogs with clinical signs of cognitive dysfunction syndrome (CDS); a double blinded placebo controlled study. In: Proceedings of the American College of Veterinary Internal Medicine Forum. ACVIM, Washington DC.
- Papaioannou, N., Tooten, P.C., van Ederen, A.M., Bohl, J.R., Rofina, J., et al. (2001) Immunohistochemical investigation of the brain of aged dogs. I. Detection of neurofibrillary tangles and of 4-hydroxynonenal protein, an oxidative damage product, in senile plaques. Amyloid 8, 11–21. http://dx.doi.org/10.3109/13506120108993810.
- Parkinson, F.E., Rudolphi, K.A., Fredholm, B.B. (1994) Propentofylline: A nucleoside transport inhibitor with neuroprotective effects in cerebral ischemia. *General Pharmacology: The Vascular System* 25, 1053–1058.
- Penaliggon, J., Mills, D.S., Heath, S.E., Harrington, L.J. (1997). The use of nicergoline in the reversal of behavioural changes due to ageing in dogs: A multicentre clinical field trial. In: *Proceedings of the First International Conference on Veterinary Behavioural Medicine*. UFAW, Birmingham, UK, pp. 37–41.
- Pop, V., Head, E., Hill, M.A., Gillen, D., Berchtold, N.C., et al. (2010) Synergistic effects of long-term antioxidant diet and behavioral enrichment on β-amyloid load and non-amyloidogenic processing in aged canines. Journal of Neuroscience 30, 9831–9839. http://dx.doi.org/10.1523/JNEUROSCI.6194-09.2010.
- Pryor, P.A., Hart, B.L., Bain, M.J., Cliff, K.D. (2001) Causes of urine marking in cats and effects of environmental management on frequency of marking. *Journal of the American Veterinary Medical Association* 219, 1709–1713. http://dx.doi.org/10.2460/javma. 2001.219.1709.
- Pugliese, M., Carrasco, J.L., Andrade, C., Mas, E., Mascort, J., et al. (2005) Severe cognitive impairment correlates with higher cerebrospinal fluid levels of lactate and pyruvate in a canine model of senile dementia. Progress in Neuro-Psychopharmacology and Biological Psychiatry 29, 603–610. http://dx.doi. org/10.1016/j.pnpbp.2005.01.017.
- Pugliese, M., Gangitano, C., Ceccariglia, S., Carrasco, J.L., Del Fà, A., et al. (2007) Canine

- cognitive dysfunction and the cerebellum: Acetylcholinesterase reduction, neuronal and glial changes. *Brain Research* 1139, 85–94. http://dx.doi.org/10.1016/j.brainres.2006.12.090.
- Radak, Z., Kumagai, S., Taylor, A.W., Naito, H., Goto, S. (2007) Effects of exercise on brain function: role of free radicals. *Applied Physiology*, *Nutrition*, and *Metabolism* 32, 942–946. http://dx.doi.org/10. 1139/H07-081.
- Reinikainen, K.J., Riekkinen, P.J., Halonen, T., Laakso, M. (1987) Decreased muscarinic receptor binding in cerebral cortex and hippocampus in Alzheimer's disease. *Life Sciences* 41, 453–461. http://dx.doi.org/10.1016/0024-3205(87)90221-9.
- Reinikainen, K.J., Soininen, H., Riekkinen, P.J. (1990) Neurotransmitter changes in Alzheimer's disease: Implications to diagnostics and therapy. *Journal of Neuroscience Research* 27, 576–586. http://dx.doi.org/10.1002/jnr.490270419.
- Rème, C.A., Dramard, V., Kern, L., Hofmans, J., Halsberghe, C., et al. (2008) Effect of S-adenosylmethionine tablets on the reduction of age-related mental decline in dogs: A double-blind placebo-controlled trial. Veterinary Therapeutics 9, 69–82.
- Rofina, J.E., Singh, K., Skoumalova-Vesela, A., van Ederen, A.M., van Asten, A.J., et al. (2004) Histochemical accumulation of oxidative damage products is associated with Alzheimer-like pathology in the canine. *Amyloid* 11, 90–100. http://dx.doi.org/10.1080/13506120412331285779.
- Rofina, J.E., van Ederen, A.M., Touissaint, M.J.M., Secreve, M., Van Der Spek, A., et al. (2006) Cognitive disturbances in old dogs suffering from the canine counterpart of Alzheimer's disease. Brain Research 1069, 216–226. http://dx.doi.org/10.1016/j.brainres. 2005.11.021.
- Rosado, B., Gonzalez-Martinez, A., Pesini, P., García-Belenguer, S., Palacio, J., et al. (2012) Effect of age and severity of cognitive dysfunction on spontaneous activity in pet dogs. Part 1 Locomotor and exploratory behavior. *The Veterinary Journal* 194, 189–195. http://dx.doi.org/10.1016/j.tvjl.2012.03.025.
- Ruehl, W.W., Bruyette, D.S., DePaoli, A., Cotman, C.W., Head, E., et al. (1995) Canine cognitive dysfunction as a model for human age-related cognitive decline, dementia and Alzheimer's disease: Clinical presentation, cognitive testing, pathology and response to 1-deprenyl therapy. Progress in Brain Research 106, 217–225. http://dx.doi.org/10.1016/S0079-6123(08) 61218-2.
- Ruehl, W.W., Neilson, J., Hart, B., Head, E., Bruyette, D.S., et al. (1996) Therapeutic actions of I-deprenyl in dogs: A model of human brain aging. In: Goldstein, D. (ed.) Catecholamines: Bridging Basic Science with Clinical Medicine, Progress in Brain Research. Vol. 106. Elsevier Press, New York, USA, pp. 217–225.

- Salvin, H.E., McGreevy, P.D., Sachdev, P.S., Valenzuela, M.J. (2010) Under diagnosis of canine cognitive dysfunction; a cross-sectional survey of older companion dogs. *The Veterinary Journal* 184, 277–281. http://dx. doi.org/10.1016/j.tvjl.2009.11.007.
- Salvin, H., McGreevy, P.D., Sachdev, P.S., Valenzuela, M.J. (2011) Growing old gracefully – Behavioral changes associated with successful aging in the dog, Canis familiaris. Journal of Veterinary Behavior: Clinical Applications and Research 6, 313–320. http://dx.doi.org/10.1016/j.jveb.2011.04.004.
- Scarmeas, N., Stern, Y., Tang, M.X., Mayeux, R., Luchsinger, J.A. (2006) Mediterranean diet and risk for Alzheimer's disease. *Annals of Neurology* 59, 912–921. http://dx.doi.org/10.1002/ana.20854.
- Siwak, C.T., Gruet, P., Woehrlé, F., Muggenburg, B.A., Murphey, H.L., et al. (2000) Comparison of the effects of adrafinil, propentofylline, and nicergoline on behavior in aged dogs. American Journal of Veterinary Research 61, 1410–1414. http://dx.doi. org/10.2460/ajvr.2000.61.1410.
- Siwak-Tapp, C.T., Head, E., Muggenburg, B.A., Milgram, N.W., Cotman, C.W. (2008) Region specific neuron loss in the aged canine hippocampus is reduced by enrichment. *Neurobiology of Aging* 29, 39–50. http:// dx.doi.org/10.1016/j.neurobiolaging.2006.09.018.
- Skoumalova, A., Rofina, J., Schwippelova, Z., Gruys, E., Wilhelm, J. (2003) The role of free radicals in canine counterpart of senile dementia of the Alzheimer type. *Experimental Gerontology* 38, 711–719. http://dx.doi. org/10.1016/S0531-5565(03)00071-8.
- Smolek, T., Madari, A., Farbakova, J., Kandrac, O., Jadhav, S., et al. (2016) Tau hyperphosphorylation in synaptosomes and neuroinflammation are associated with canine cognitive impairment. *Journal of Comparative Neurology* 524; 874–895.
- Snigdha, S., de Rivera, C., Milgram, N.W., Cotman. C. (2014) Exercise enhances memory consolidation in the aging brain. Frontiers in Aging Neuroscience 6, 3. http://dx.doi.org/10.3389/fnagi.2014.00003.
- Studzinski, C.M., Christie, L.A., Araujo, J.A., Burnham, W.M., Head, E., et al. (2006) Visuospatial function in the beagle dog: An early marker of cognitive decline in a model of human aging and dementia. Neurobiology of Learning and Memory 86, 197–204. http://dx.doi.org/10.1016/j.nlm.2006.02.005.
- Su, M.Y., Tapp, P.D., Vu, L., Chen, Y.F., Chu, Y., et al. (2005) A longitudinal study of brain morphometrics using serial magnetic resonance imaging analysis in a canine model of aging. Progress in Neuro-Psychopharmacology and Biological Psychiatry 29, 389–397. http://dx.doi. org/10.1016/j.pnpbp.2004.12.005.
- Sullivan, P.G. and Brown, M.R. (2005) Mitochondrial aging and dysfunction in Alzheimer's disease. Progress in Neuro-Psychopharmacology and Biological Psychiatry 29, 407–410. http://dx.doi.org/10.1016/j.pnpbp. 2004.12.007.

- Taha, A.Y., Henderson, S.T., Burnham, W.M. (2009) Dietary enrichment with medium chain triglycerides (AC-1203) elevates polyunsaturated fatty acids in the parietal cortex of aged dogs: Implications for treating age-related cognitive decline. *Neurochemical Research* 34, 1619–1625. http://dx.doi.org/10.1007/ s11064-009-9952-5.
- Tapp, P.D., Siwak, C.T., Gao, F.Q., Chiou, J.Y., Black, S.E., et al. (2004) Frontal lobe volume, function, and beta-amyloid pathology in a canine model of aging. *Journal of Neuroscience* 24, 8205–8213. http:// dx.doi.org/10.1523/JNEUROSCI.1339-04.2004.
- Tapp, P.D., Head, K., Head, E., Milgram, N.W., Muggenburg, B.A., et al. (2006) Application of an automated voxel-based morphometry technique to assess regional gray and white matter brain atrophy in a canine model of aging. NeuroImage 29, 234–244. http://dx.doi.org/10.1016/j.neuroimage.2005.07.043.
- Tsakiris, S. and Deliconstantinos, G. (1985)
 Phosphatidylserine and calmodulin effects on Ca
 2+-stimulated ATPase activity of dog brain synaptosomal plasma membranes. *International Journal*

- of Biochemistry 17, 1117–1119. http://dx.doi.org/ 10.1016/0020-711X(85)90045-X.
- Villablanca, J.R., Olmstead, C.E., de Andres, I. (1978) Effects of caudate nuclei or frontal cortical ablations in kittens: responsiveness to auditory stimuli and comparisons with adult-operated littermates. *Experimental Neurology* 61, 635–649. http://dx.doi.org/10.1016/ 0014-4886(78)90029-8.
- Yalcin, E., Kasap, S., Demir, G. (2010) Prevalence of behavioral changes associated with age-related cognitive impairment in geriatric dogs, Bursa, Turkey. *Journal of Animal and Veterinary Advances* 9, 1828–1832.
- Zhang, C., Hua, T., Zhu, Z., Luo, X. (2006) Age-related changes of structures in cerebellar cortex of cat. *Journal of Biosciences* 31, 55–60. http://dx.doi.org/10.1016/j.brainres.2005.06.008.
- Zhang, J.H., Sampogna, S., Morales, F.R., Chase, M.H. (2005) Age-related changes in cholinergic neurons in the laterodorsal and the pedunculo-pontine tegmental nuclei of cats: A combined light and electron microscopic study. *Brain Research* 1052, 47–55.

16 Mental Health Issues in Farm Animals: A Music Mixing Board Model of Behavioral Characteristics Using the Panksepp Emotional System

TEMPLE GRANDIN

Department of Animal Science, Colorado State University, Ft. Collins, Colorado, USA

16.1 Introduction

At the time of my contribution to the first edition of this book in 2005 my research group had conducted some of the early research that showed that cattle temperament had an effect on weight gain. Beef cattle that struggled or moved more while loosely held in a squeeze chute (chute test) had lower weight gains (Voisinet et al., 1997). Other studies have replicated this result in cattle and pigs (Benhajali et al., 2010; Holl et al., 2010). Studies using another type of temperament testing, termed exit speed scoring, found that beef cattle that run out of a squeeze chute quickly have lower weight gain, poorer reproductive performance, and higher physiological measures of stress (Burrows and Dillon, 1997; Vetters et al., 2013; Kasimanickam et al., 2014).

The above studies served as motivation for the US beef cattle industry to include both chute scoring and exit scoring in their criteria for selecting breeding animals. Twenty years later, I have observed that this has resulted in improved mental well-being in herds of beef cattle: the animals are much less reactive and calmer when they are handled. In the United States, today's extensively raised beef cattle are very different – in emotionality and temperament – than the beef cattle that were raised before chute scoring and exit speed scoring became a regular industry practice.

16.2 When Fearfulness is Reduced, Other Personality Traits Become Evident

Twenty years of temperament selection has reduced fearfulness in beef cattle. This may be similar to the reduction in fearfulness in domestic dogs. Zapata et al. (2016) found genetic variations that reduce fear that may have contributed to dog domestication. Recent studies are showing that temperament or personality in farm animals cannot be completely explained by determining an animal's overall fear level. For example, whereas the exit speed test would measure fear, the chute test measures fear combined with another trait (Bruno et al., 2016). In addition, Brazilian researchers evaluated the influence of different genes while using an electronic chute test to measure struggling while held in a squeeze chute (dos Santos et al., 2017). They concluded that temperament is a complex trait that incorporates a variety of different behavioral phenotypes. I hypothesize that standard industry temperament tests mainly measure fear, but in some cases they may also be measuring other emotional traits such as aggression or separation distress (Grandin and Deesing, 2014), which likely differ from fear.

16.3 Panksepp Emotional System

After reading many papers in the farm animal, pet and wildlife literature I came to the conclusion that the Panksepp (1998, 2011; Montag and Panksepp, 2017) basic emotional systems would be the best way to explain many conflicting results in scientific studies of farm animal temperament. Different researchers use different terms and the trait of fearfulness is often confused with other behavioral traits. What follows is an outline of the Panksepp emotional system – with my added explanations – which may provide a good framework for animal personality traits.

- Fear Motivates animals to escape danger. This
 trait was measured in early cattle temperament
 studies with chute score and exit speed tests.
 Twenty years of temperament selection on cattle
 raised on extensive US rangeland appears to have
 had a substantial effect in lessening this trait.
- Ragelanger Motivates aggression, e.g., fighting off a predator or a mother animal defending her infant (Panksepp, 1971).
- *Panic* Separation distress; motivates agitated behavior or vocalizations when a mother is separated from her infant or a single animal is separated from its herd mates. Some temperament tests, such as flight zone tests and open field tests, may also measure this trait (Grandin and Deesing, 2014).
- Seek Motivates exploration, boldness and novelty seeking. Measured with an open field test, approach a novel object test or GPS tracking of cattle on pasture.
- Lust Motivates mating behavior.
- CareInurture Motivates mother-young nurturing behavior such as licking, adult animals grooming each other, or animals approaching people for stroking.
- *Play* All young animals engage in this; it is the physical social engagement system.

Panksepp (2011) and a review by Morris et al. (2011) have explained the brain systems that underlie these seven emotional systems. While many of these older studies were done with invasive procedures that would never be approved today due to animal welfare concerns, the findings of those studies are still valid today. One of the advantages of using an electrode penetrating the brain to study emotional circuits is that it can definitively determine which node on a network activates an entire network, something functional magnetic resonance imaging (fMRI) cannot do. The early studies with electrical stimulation clearly show that subcortical brain structures activate the emotional networks.

Social behavior has a strong emotional basis, with some animals being more social than others. For example, chimpanzees and lions are more social whereas orangutans, panthers and tigers are more solitary. Some recent research has indicated that social behaviors of solitary-living and nonmonogamous mammals, which do not form strong social bonds, resemble behaviors in humans with autism, a neurodevelopmental disorder connected with impairment in social interactions and communication

(Reser, 2014; Persson et al. 2016). For example, Reser (2014) reports that solitary mammals exhibit certain biomarkers that are characteristic of autism, such as reduced oxytocin and vasopressin signaling during social interactions as well as reduced hypothalamic-pituitary-adrenal activity when they are separated or isolated from other animals. Another study by Persson et al. (2016) found common genes for social contact in dogs and in humans with autism spectrum disorder. I hypothesize that the solitary animals have lower levels of Panksepp's Nurture and Panic (separation distress) traits. Within the nurture system there are subsystems for different aspects of nurturing behavior, each of which may also be affected by genetics. The nurture system appears to underlie parenting behavior, and a study by Bendesky et al. (2017) identified four parenting behaviors in mice: pup retrieval, huddling, licking the pups, and nest building.

16.4 Music Mixing Board of the Seven Panksepp Emotional Traits

A music mixing board consists of separate volume control for many different soundtracks. Now imagine that each emotional trait has a separate sliding volume control knob. Each of the seven Panksepp emotional traits can be viewed as a separate channel on a music mixing board, where the 'volume' or intensity of each trait is determined by an interaction of inherited genetic factors, learning from previous experience and direct effects of experiences on nervous system reactivity (Fig. 16.1). An example of a



Fig. 16.1. Different emotional traits can be viewed as separate channels on a music mixing board, where the 'volume' or intensity of each trait is determined by an interaction of a variety of factors. (Image used under license from Shutterstock.com.)

Z32 T. Grandin

genetic influence would be temperament in cattle (Voisinet et al., 1997). An example of a learned influence would be the benefits of low-stress cattle handling (Ligon, 2015). The probable effects of these two influences are either an inherited or learned reduction in fear. Neonatal handling experiments reviewed by Raineki et al. (2014) show that handling may have direct effects on the development of the nervous system by either deregulating or downregulating different emotional traits. Recent work by Montag et al. (2017) supports the idea that the primary emotional systems may work as a continuum with variable strengths, providing support for the music mixing board as a model.

Recent studies in beef cattle that have been selected for ease of handling clearly show that cattle behavioral traits, like temperament and personality mentioned earlier, cannot be fully explained by fear levels. Wesley et al. (2012) recently demonstrated that when cattle were handled and restrained their cortisol levels were very low – between 5.5 ng/ml and 8.8 ng/ml. In contrast, older studies of beef cattle handling (reviewed by Grandin, 1997) found much higher levels of cortisol during restraint - ranging from 20 ng/ml to 60 ng/ml. This difference is likely due to the herd of the more recent study having been selected for calmness by using standard industry temperament tests. In an even more recent study, Reeves and Derner (2015) found that in cattle raised extensively on rangeland flight speed score had no effect on average daily gain – seeming to confirm the reduced fear over the past two decades of culling the most fearful animals. Reeves and Derner (2015) concluded that ranchers on extensive rangeland can now be less selective on temperament. Scoring beef cattle for temperament is now a common industry practice (Northcutt and Bowman, 2010).

Ranchers who operate in areas with lots of predators have used a simple but effective set of criteria for selecting range cows.

- 1. Wean a live calf every year. One requirement for this is the cow being able to defend her calf from predators.
- 2. Breed back quickly.
- **3.** Cows that attack people are culled. It is likely that genetic traits that are associated with attacking people are different than the traits that motivate the cow to fight a predator.

At the Lasater Ranch in Colorado, they used similar criteria with one added test: replacement heifers had to be willing to approach people and eat treats

off the end of a stick. This resulted in a herd that would approach people and would seek out stroking (Grandin and Deesing, 2014). Using the Panksepp model, I hypothesize that they had selected for an increase of the Nurture and Seek traits.

Wesley et al. (2012) and Goodman et al. (2016) divided cattle into two behavior groups by using GPS tracking devices to monitor grazing behavior (see Table 16.1). I hypothesize that on the Seek trait the go getters are high and the laid-back cattle are low. A study with wild boars (Vetter et al., 2016) shows how differences in these personality traits may have a positive effect on the number of young raised to full independence. Mothers that had a greater exploratory drive (Seek) had more juvenile mortality when food was abundant, but not when food availability was reduced. It is likely that when food is scarce, greater exploratory behavior may help prevent starvation. However, when food is abundant, greater exploratory behavior may increase exposure to predators.

16.5 The Fear Factor

Veterinarians, animal scientists, and industry people often use the vague word 'stress' but the word 'fear' is often avoided. In the 10 years that has elapsed since the first edition of this text was published the word fear is more widely accepted, yet there remains some resistance to its use. The steer in a slaughter plant that refuses to move forward when it sees a shiny reflection is likely experiencing the emotion of fear. Numerous studies by Paul Hemsworth and his colleagues have shown that pigs and dairy cattle that fear people are less productive (Hemsworth and Coleman, 1998; Rushen

Table 16.1. Division of cattle into two behavior groups.

Go getters	Laid back
Cortisol 8.8 ng/ml during handling	Cortisol 5.5 ng/ml
Eats fast	Eats slowly
Spends less time at water	Spends more time loafing at the water point
Larger pasture foraging area	Smaller pasture foraging area
Less concentrated search pattern	More concentrated search pattern
Gains more weight Heavier weaning weights	Gains less weight Lighter weaning weights

Based on Wesley et al. (2012) and Goodman et al. (2016).

and dePassille, 2015). Pigs and cattle that have been treated in an aversive manner, such as being slapped or shocked, will have lower productivity (Hemsworth and Barnett, 1991). Dairy cows that had been treated harshly also had larger flight zones and lower milk production (Breuer *et al.*, 2000; Hemsworth *et al.*, 2002). A newer study showed that animals will be more productive if they are cared for by stock people who have a positive attitude toward them (Kauppinen *et al.*, 2012).

Reducing an animal's fearfulness during handling and transport is an easy thing to do and requires no expensive equipment. During a 40-year career as a designer of livestock handling equipment, I have observed that people are often much more willing to make an expensive investment in equipment rather than learning behaviorally based, low-stress animal handling methods. Cattle handling has improved greatly in recent years (Woiwode et al., 2016) but there are still some people who continue to yell at animals and frequently use electric prods. Why do they continue to do this? Both research and practical experience shows that it costs money. It is difficult for some people to comprehend that what the animal experiences is important. I have observed that highly verbal people who have poor visual skills are often the ones who have the most difficulty understanding how an animal may think or feel. Since animals do not have verbal language, it is hard for these people to imagine that the animal feels fear in a manner comparable to humans (this concept is discussed in greater detail in Grandin and Johnson [2005]). However, research shows very clearly that the brain circuits that control fear are very similar in people and animals (LeDoux, 1996; Rogan and LeDoux, 1996). In some of his later papers, LeDoux questions animal emotions and calls them 'survival circuits', based on the hypothesis that verbal language is required to fully experience emotions (LeDoux and Brown, 2017). I disagree with this hypothesis and reasoning.

16.6 Fear Circuits in the Brain

Fear is a primary emotion in all animals and promotes survival by motivating animals to avoid predators and other threatening circumstances in the wild (Boissy, 1995; LeDoux, 1996; Boissy and Lee, 2014). All mammals and birds can be conditioned to fear things that are perceived as dangerous. The amygdala is the location of the central fear system involved in both fear behavior and learning to fear certain

things or people (Davis, 1992). In humans, electrical stimulation of the amygdala elicits feelings of fear (Gloor et al., 1981). Stimulating the amygdala in the animal brain elicits nervous system responses similar to fear responses in humans (Redgate and Fahringer, 1973). Conversely, destroying the amygdala will block both unconditioned (unlearned) and conditioned (learned) fear responses (LeDoux, 1996; Rogan and LeDoux, 1996). Lesioning of the amygdala also had a taming effect on wild rats (Kemble et al., 1984). An example of an unlearned fear response would be a horse being spooked at the sound of a firecracker. A learned fear response has occurred if the horse refuses to enter the place where the firecracker went off. Fear learning takes place in a subcortical pathway; extinguishing a learned fear response is difficult because it requires the animal to suppress the fear memory via an active learning process. A single, very frightening or painful event can produce a strong learned fear response (see also Chapter 14, this volume), but eliminating this fear response is much more difficult (LeDoux, 1996). Accordingly, animals may develop fear memories that are difficult to eliminate.

The most recent research shows that the amygdala has separate circuits for a freezing fear response and an active flight response (Fadok *et al.*, 2017). In some situations, a freezing response may be more adaptive than a flight response. There may also be genetic differences in how fearful cattle react. The author has observed that *Bos indicus* cattle are more likely to become tonic and immobile when restrained and certain genetic lines of Saler cattle have such an active response they may injure themselves when they are restrained.

16.7 Good First Experiences are Important

First experiences with new things make major and lasting impressions on animals, and it is important that an animal's first experience with such things as a new corral, trailer, or restraining chute be pleasant in nature. My observations on cattle ranches have shown that to prevent cattle and sheep from becoming averse to and fearful of a new squeeze chute or corral system, painful or frightening procedures that cause visible signs of agitation should be avoided the first time the animals enter the facility (Grandin, 1997, 1998; Grandin and Shivley, 2015). In addition, practical experience has shown that if a horse has a frightening or painful experience the

Z34 T. Grandin

first time it goes into a trailer, teaching the animal to get in a trailer may be difficult. This happens because the horse has developed a fear memory.

When an animal is first brought into a new farm or laboratory, its first experiences should be made pleasant by feeding it and giving it time to settle down. Nonslip flooring is essential because slipping and falling in the new facility may create a fear memory. Locking head stanchions are often used for dairy cows because they make it easy to restrain the animals for vaccinations or artificial insemination. I have observed that they also work well for Angus beef cows on grass-fed beef farms in Ireland. To create a positive association with the stanchions, the animals are fed in the stanchions for 2 weeks before experiencing having their heads locked in. Separating the calves for vaccinations is then easy when the mothers are eating in the stanchions; the calves are vaccinated and returned before the cows realize they are gone.

16.8 Sensory Basis and Specificity of Fear Memories in Animals

Because I think in pictures rather than language, my autism allows me to closely relate to how an animal may think or feel (Grandin, 1995, 1997; Grandin and Johnson, 2005). Many practical experiences with animals indicate that fear memories are stored as pictures or sounds. Fear memories are often very specific. I observed a horse that was afraid of black cowboy hats because it had been abused by a person wearing such a hat (Grandin and Johnson, 2005), whereas white cowboy hats and baseball caps had no effect on this horse. The black hat was most threatening when it was on a person's head and somewhat less threatening when it was on the ground. At a zoo, an elephant with a fear of bearded men became aggressive toward a new keeper who had a beard. The new keeper was accepted after he shaved off the beard.

Research published since the first edition continues to substantiate this specificity of animal learning. To horses, umbrellas and flapping tarps look totally different, and if a horse is carefully habituated to a suddenly opening umbrella this does not transfer to a flapping tarp (Leiner and Fendt, 2011). I have observed that cattle differentiate between a person on a horse and a person walking on the ground. Cattle that have been handled exclusively by people on horseback may panic if they are suddenly confronted with a person on the ground. It is

important to train cattle that both people walking on the ground and people on horses are safe. Because cattle are visual thinkers, people on horses and people on the ground are perceived as different things.

The human voice can be a very specific stimulus for animals, and animals have the ability to distinguish between the voices of individual people. Animals that had been darted by the zoo veterinarian were able to recognize his voice, and they would run and hide. The opposite emotional effect has been seen by ranchers, who report that fearful cattle will often quiet down when they hear the voice of a familiar person who is associated with previous positive experiences. The auditory memories of animals are hyperspecific.

Research on animal perception indicates that cattle are able to differentiate between 'good' and 'bad' people. Animals have a tendency to associate bad experiences with prominent visual features on people such as beards (mentioned above) or lab coats, or they may associate a scary or painful experience with a specific place. For instance, pigs and cattle can recognize a person by the color of their clothing (Koba and Tanida, 1999; Rybarczyk et al., 2003) and can also learn that some places are safe and others are scary and bad. Cattle can learn that a certain person is scary or dangerous in a specific context (Rushen and dePassille, 2015). For example, the animal may see the person as bad only when that person is in the milking parlor because he gave injections there. Cooke et al. (2009) found that beef cattle that became acclimated to people being close to them while feeding did not display a reduction in agitated responses to handling in the corrals.

It is also possible for an animal to associate a painful or scary experience with a prominent feature in the environment. In one case, a young stallion fell down and was whipped during his first attempt to mount a dummy for semen collection. He developed a fear of overhead garage doors because he had been looking at one when he fell. A future collection was done easily when it was done outdoors away from buildings and garage doors. Unfortunately, a fear of something as common and unavoidable as garage doors can create problems when a horse is ridden.

Sometimes, problems with bucking or rearing in horses can be stopped by changing the type of bridle or saddle because the horse has a fear memory associated with the feeling of certain equipment. A different bridle or saddle feels different. In this

case, the fear memory may be a 'touch' picture. For example, a horse that was abused with a jointed snaffle bit may tolerate a hackamore or a standard one-piece western bit. One horse had a sound fear memory because it had a bad experience with a canvas tarp; horse blankets that sounded like a tarp were scary, but a wool blanket that made little sound was well tolerated.

Animal fears may be very specific, but they also can generalize. One common generalization is that men are a threat to be avoided and women are safe. Fear of a man in blue coveralls can generalize to other people wearing blue coveralls. I was once asked how a fear memory can be a specific visual image if it can spread and generalize. I observed an example of both generalization and specificity in a dog named Red Dog. This dog developed a fear of hot air balloons after one flew over the house and its burner roared. Red Dog's fear then spread to round plastic balls on electric lines. A few months later when she was riding in a car, she became afraid of the round rear end of a tanker truck and a round streetlight. I was puzzled why other round objects such as traffic lights and round globe lights on a building were tolerated. I finally figured out that the dog had made a very specific generalization. Round objects with the sky as a background had become feared because the original hot air balloon was a round object against the sky. The globe lights on the building had a brown brick background, and the traffic lights were mounted on a black metal rectangle; therefore, they were not round objects with a sky background.

16.9 Handling Training

Training animals to handling procedures and using feed rewards can greatly reduce agitation and make animal handling easier (Hutson, 1985). When an animal becomes accustomed to a procedure, fear will be reduced. Pigs will become easier to handle and transport if they become accustomed to people walking through their pens (Grandin, 1993). In my work, I have found that getting pigs accustomed to people walking among them makes it possible to greatly reduce electric prod use, which is highly detrimental to pig welfare (Benjamin et al., 2001) (Fig. 16.2). Pigs that have been walked in the aisles during finishing are easier to handle (Geverink et al., 1998; Goumon et al., 2013). Moving pigs a month prior to slaughter improved their willingness to move (Abbott et al., 1997).

Australian researchers have found that walking quietly among calves produced calmer adult cows (Binstead, 1977; Fordyce, 1987; Fordyce *et al.*, 1988). During the training, the animals were walked through the corrals and chutes and taught to follow a lead horseman. Becker and Lobato (1997) also found that handling zebu cross calves produced calmer adults. Recent studies also show the benefits



Fig. 16.2. When pigs are exposed to nonthreatening people they become accustomed to human presence, offering desired behavior with less use of aversive stimuli such as electric prods.

236 T. Grandin

of acclimating young heifers by moving them through the races, which produced calmer adults and improved conception rates after artificial insemination (Cooke et al., 2012). Kicking and stepping behavior in dairy buffaloes was reduced by acclimating the animals to the milking parlor (Polikarpus et al., 2014). Acclimating heifers 10 days before calving to moving through the milking room produced animals that would stand more calmly during milking (Kutzer et al., 2015).

Adult animals can be trained to move through chutes and to voluntarily enter a restrainer device for blood tests or injections; training an animal to cooperate reduces both physiological and behavioral indicators of stress (Grandin, 1989a). Bongo antelope that had been trained to voluntarily enter a box for medical procedures had significantly lower levels of blood parameters commonly associated with stress – cortisol and glucose – than did untrained antelope that had been immobilized with a dart (Phillips *et al.*, 1998). Westerath *et al.* (2014) found that providing a calf access to a preferred special feed or being brushed by people was a positive experience. Then when given a choice, the calves preferred brushing compared to entering an empty pen.

16.10 The Paradox of Novelty

Animals often become highly fearful when something new is suddenly introduced but that same object may be attractive if the animal is allowed to voluntarily approach it. For example, cattle will run away from a flag that is suddenly waved at them but will approach it and investigate the same flag if it is put out in a pasture. New things can be both scary and attractive (Grandin and Deesing, 2014). To prevent a fear of new things, handlers should gradually expose animals in a positive and nonthreatening way to many different people and vehicles. This will help prevent panic when the animals are taken to new places. Working with sheep, Reid and Mills (1962) were the first researchers to suggest that animals could become accustomed to variations in their routine. Producers have observed that playing a radio in the barn will help produce pigs that are less likely to startle at every small sound. Providing pigs in a barren environment with objects to chew and manipulate produced calmer animals that were less easily startled (Grandin, 1989b). It is best to have a variety of music and talk. However, it is important to not subject the animal to noise overload.

16.11 The Need for Novelty

Many farm animals are reared in environments where little stimulation and novelty exist. As mentioned previously, novelty is feared when it is suddenly introduced, but animals will actively seek new things to investigate and manipulate. Varied environmental stimulation is beneficial to nervous system development. Walsh and Cummins (1975), Melzack and Burns (1965), and Schultz (1965) all concluded that when the variety of stimuli is reduced, the nervous system becomes sensitized and sensory thresholds become lower. This would explain why pigs reared on a concrete floor would startle more easily than pigs reared on straw. Melzack and Burns (1965) learned years ago that rearing puppies in barren kennels produced dogs that still showed signs of hyperexcitability in their adulthoods. The changes in the nervous system remained permanent even after the dogs had been returned to a farm family environment. In my doctoral research, I found that pigs reared in barren pens were more excitable and had abnormal dendritic growth of neurons in the brain as compared to pigs reared on straw with a variety of objects to manipulate (Grandin, 1989b) (Fig. 16.3). Pigs in the barren pens spent significantly more time rubbing their noses on the floor and on each other as compared to pigs in the straw pens. This excessive rubbing resulted in an abnormal growth of extra dendrites on the neurons of the somatosensory cortex. I had to use video cameras to observe the abnormal nosing activity, as most of the behavior occurred at night when no one was present to observe. When people entered the room, the pigs housed in the barren pens became hyperexcited.

The pigs in the barren pens were both highly fearful and high in novelty seeking as compared to my straw-bedded pigs. During the first few days of pen washing, the pigs in the barren pens were afraid of the hose. After a few days they changed from being fearful to hyperactively seeking novelty. They would continuously bite at the water and the hose. When I cleaned feeders, the barren-environment pigs repeatedly bit my hands, whereas the strawbedded pigs could be easily moved away. They were not attracted to chewing on hands because they had straw to chew on. These pigs were also the first pigs to start jumping in fear when they heard a plane fly over the building.

Regrettably, I saw that my attitude toward the two groups of pigs differed even though they were littermate pairs. While I enjoyed working with the calm,





Fig. 16.3. Pigs reared in pens with straw bedding with a variety of manipulable objects were less excitable and had better brain development than pigs raised in barren pens (Grandin, 1989b). (Images used under license from Shutterstock.com.)

straw-bedded pigs, I disliked working with the barrenenvironment pigs that constantly bit at the hose and at my hands. I now know that the latter pigs were starving for stimulation.

16.12 Intensive vs Intensive Environment

The animal best suited for an intensive confined environment may not be the best animal for an extensive environment. This principle applies to both domestic and wild animals. The laid-back cows that were described previously would probably do well in a feedlot, but they do less well in a more challenging environment where they have to work hard to find food. A study of parrots showed that wild caught parrots are less likely to be killed by predators or recaught after release back into the wild than captive bred parrots (Cabezas et al., 2013). On the other hand, captive bred parrots would be better able to tolerate a captive environment because the highest fear birds have probably already died from stress. Studies of deer show that the type of natural environment that the animal is living in has an effect on the behavioral traits that influence survival of their offspring (Monestier et al., 2015). I hypothesize that the high-fear mother knows how to hide in an environment that provides cover for hiding. On the open grassland, a mother who has a higher Seek trait obtains more to eat to nourish her fawn.

16.13 Concluding Remarks

The Jaak Panksepp seven emotional traits of Fear, Rage, Panic (separation distress), Seek, Lust, Nurture/ care and Play form the basis of animal personality. The strength or weakness of each trait can be influenced by a combination of inherited factors, learning or direct environmental effects, or nervous system reactivity. A music mixing board with separate volume controls for each Panksepp emotional trait provides an easy-to-understand framework for individual differences in behavior.

6.14 References

Abbott, T.A., Hunter, E.J., Guise, J.H., Penny, R.H.C. (1997) The effect of experience of handling on pig's willingness to move. *Applied Animal Behaviour Science* 54, 371–375. http://dx.doi.org/10.1016/S0168-1591(97)00045-2.

Becker, B.G., Lobato, J.F.P. (1997) Effect of gentle handling on the reactivity of the zebu cross calves to humans. Applied Animal Behaviour Science 53, 219–224. http://dx.doi.org/10.1016/S0168-1591(96)01091-X.

Bendesky, A., Mikwon, Y., Lassance, J.M., Lewarch, C.L., Yao, S., et al. (2017) The genetic basis of parental care in monogamous mice. *Nature* 544, 434–439. http://dx.doi.org/10.1038/nature22074.

Benhajali, N., Bovin, X., Sapa, J., Pellegrin, P., Boulesteix, P. et al. (2010) Assessment of different on-farm measures of beef cattle temperament for genetic evaluation. Journal of Animal Science 88, 3529–3537. http://dx.doi.org/10.2527/jas.2010-3132.

Benjamin, M.F., Gonyou, H.W., Ivers, D.L., Richard, L.F., Jones, D.J., et al. (2001) Effect of handling method on the incidence of stress response in market swine in a model system. Journal of Animal Science 79 (Suppl. 1), 279 (Abstract).

Binstead, M. (1977) Handling cattle. *Queensland Agricultural Journal* 103, 293–295.

Boissy, A. (1995) Fear and fearfulness in animals. Quarterly Review of Biology 70, 165–191. http://dx.doi.org/10.1086/418981.

Z38 T. Grandin

- Boissy, A. and Lee, C. (2014) How assessing relationships between emotions and cognition can improve animal welfare. Revue scientifique et technique (International Office of Epizootics) 33, 103–110.
- Breuer, K., Hemsworth, P.H., Barnett, J.L., Matthews, L.R., Coleman, G.J. (2000) Behavioral response to humans and productivity of commercial dairy cows. *Applied Animal Behaviour Science* 66, 273–288. http://dx.doi.org/10.1016/S0168-1591(99)00097-0.
- Bruno, K.A., Vanzant, E.S., Vanzant, K.A. Meleod, K.R. (2016) Relationships of a novel object chute score and exit velocity with growth performance of receiving cattle. *Journal of Animal Science* 94, 4819–4831. http://dx.doi.org/10.2527/jas.2016-0438.
- Burrows, H.M. and Dillon, R.D. (1997) Relationships between temperament and growth in feedlot and commercial carcass traits of *Bos indicus* crossbreds. *Australian Journal of Experimental Agriculture* 37, 407–411.
- Cabezas, S., Carrette, M., Teila, J.P., Marchant, T.A. Bortolotti, G.R. (2013) Differences in acute stress responses between wild caught and captive-bred birds: A physiological mechanism contributing to current avian invasions? *Biological Invasions* 15, 521–527. http://dx. doi.org/10.1007/s10530-012-0304-z.
- Cooke, R.F., Arthington, D., Austin, B.R., Yellich, J.V. (2009) Effects of acclimation to handling on performance, reproductive and physiological responses of Brahman crossbred heifers. *Journal of Animal Science* 87, 3403– 3412. http://dx.doi.org/10.2527/jas.2009-2021.
- Cooke, R.F., Ohmart, D.W., Cappellozza, B.J., Mueller, C.J. DelCurto, T. (2012) Effects of temperament and acclimation to handling on reproductive performance of *Bos taurus* beef females. *Journal of Animal Science* 90, 3547–3555. http://dx.doi.org/10.2527/jas.2011-4768.
- Davis, M. (1992) The role of the amygdala in fear and anxiety. *Annual Review of Neuroscience* 15, 353–375. http://dx.doi.org/10.1146/annurev.ne.15.030192.002033.
- dos Santos, F.C., Peixoto, G.C.D., Fonseca, P.A.S., Pires, M.F.A., Cruz, R.V.V., et al. (2017) Identification of candidate genes for reactivity in Guzerat (Bos indicus) Cattle: A genome-wide association study. PloS One 12(1), e0169163. http://dx.doi.org/10.1371/journal.pone.0169163.
- Fadok, J. P., Krabbe, S., Markovic, M., Courtin, J., Xu, C., et al. (2017) A competitive inhibitory circuit for selection of active and passive fear responses. *Nature* 542, 96–99. http://dx.doi.org/10.1038/nature21047.
- Fordyce, G. (1987) Weaner training. *Queensland Agricultural Journal* 6, 323–324.
- Fordyce, G., Dodt, R.M., Wythes, J.R. (1988) Cattle temperaments in extensive herds in northern Queensland. Australian Journal of Experimental Agriculture 28, 683–688. http://dx.doi.org/10.1071/EA9880689.
- Geverink, N.A., Kappers, A. Van deBurgwal, E., Lambooij, E., Blokhuis, H. J., et al. (1998) Effects of regular moving and handling on the behavioral and physiological

- responses of pigs to pre-slaughter treatment and consequences for meat quality. *Journal of Animal Science* 76, 2080–2085. http://dx.doi.org/10.2527/1998.7682080x.
- Gloor, P., Oliver, A., Quesney, L.F. (1981) The role of the amygdala in the expression of psychic phenomenon in temporal lobe seizures. In: Ben Avi, Y. (ed.) *The Amygdaloid Complex*. Elsevier, New York, USA, pp. 489–507.
- Goodman, L.E., Cibils, A.F., Wesley, R.L., Mulliniks, J.T., Petersen, M.K., et al. (2016) Temperament affects rangeland use patterns and reproduction performance of beef cows. Rangelands 38, 292–296. http://dx.doi. org/10.1016/j.rala.2016.07.002.
- Gouman, S., Bergeron, R., Faucitano, L., Crowe, T., Connor, M.L, et al. (2013) Effect of previous ramp exposure and regular handling on heart rate, ease of handling, and behaviour in near market weight pigs during simulated loading. Canadian Journal of Animal Science 93, 461–470.
- Grandin, T. (1989a) Voluntary acceptance of restraint by sheep. *Applied Animal Behavior Science* 23, 257–261. http://dx.doi.org/10.1016/0168-1591(89)90116-0.
- Grandin, T. (1989b) Effect of rearing environment and environmental enrichment on behavior and neutral development of young pigs. Doctoral dissertation. University of Illinois, Urbana-Champaign, Illinois, USA.
- Grandin, T. (1993) Behavioral agitation during handling of cattle is persistent over time. *Applied Animal Behaviour Science* 36, 1–9. http://dx.doi.org/10.1016/0168-1591(93)90094-6.
- Grandin, T. (1995) *Thinking in Pictures*. Vintage Press (Random House), New York, USA.
- Grandin, T. (1997) Assessment of stress during handling and transport. *Journal of Animal Science* 74, 249–257.
- Grandin, T. (1998) Handling methods and facilities to reduce stress on cattle. Veterinary Clinics of North America, Food Animal Practice 14, 325–341. http:// dx.doi.org/10.1016/S0749-0720(15)30257-7.
- Grandin, T. and Deesing, M.J. (2014) *Genetics and the Behavior of Domestic Animals*. Academic Press, Elsevier, Amsterdam.
- Grandin, T. and Johnson, C. (2005) *Animals in Translation*. Simon and Schuster. New York. USA.
- Grandin, T. and Shivley, C. (2015) How farm animals react and perceive stressful situations such as handling restraint and transport. *Animals* 5, 1233–1251. http://dx.doi.org/10.3390/ani5040409.
- Hemsworth, P.H. and Barnett, J.L. (1991) The effects of aversively handling pigs either individually or in groups on their behaviour growth and corticosteroids. *Applied Animal Behavior Science* 30, 61–72. http://dx.doi.org/10.1016/0168-1591(91)90085-C.
- Hemsworth, P.H. and Coleman, G.J. (1998) Human Livestock Interactions. CAB International, Wallingford. UK.
- Hemsworth, P.H., Coleman, G.J., Barnett, J.L. Borg, S., Dowling, S. (2002) The effects of cognitive behavioral

- intervention on the attitude and behavior of stock persons and the behavior and productivity of commercial dairy cows. *Journal of Animal Science* 80, 68–78. http://dx.doi.org/10.2527/2002.80168x.
- Holl, J.W., Rohrer, G.A., Brown-Brandi, T.M. (2010) Estimates of genetic parameters among scale activity scores in growth and fitness in pigs. *Journal of Animal Science* 35, 1011–1013.
- Hutson, G.D. (1985) The influence of barley food rewards on sheep movement through a handling system. Applied Animal Behavior Science 14, 263–275. http:// dx.doi.org/10.1016/0168-1591(85)90007-3.
- Kasimanickam, R., Asay, M., Schroeder, S., Kasimanickam, V., Gay, J. M., et al. (2014) Calm temperament improves reproductive performance of beef cows. Reproduction in Domestic Animals 49, 1063–1067. http://dx.doi.org/ 10.1111/rda.12436.
- Kauppinen, T., Vesala, K.M., Valros, A. (2012) Farmer attitudes towards improvement of animal welfare is correlated with piglet production. *Livestock Science* 143, 142–150. http://dx.doi.org/10.1016/j.livsci.2011.09.011.
- Kemble, E.D., Blanchard, D.C., Takushi, R. (1984) Taming of wild rats following medical amygdaloid lesions. *Physiology and Behavior* 32, 131–134. http://dx.doi. org/10.1016/0031-9384(84)90084-2.
- Koba, Y. and Tanida, H. (1999) How do miniature pigs discriminate between people? The effect of exchanging ever between a non-handler and their familiar handler on discrimination. Applied Animal Behavior Science 61, 239–252. http://dx.doi.org/10.1016/ S0168-1591(98)00192-0.
- Kutzer, T., Stellar, M., Gygax, L., Wischsler, B. (2015) Habituation of dairy heifers to milking routine: Effects on human avoidance distance, behaviour and cardiac activity during milking. *Journal of Dairy Science* 98, 5241–5251. http://dx.doi.org/10.3168/jds.2014-8773.
- LeDoux, J.E. (1996) *The Emotional Brain*. Simon and Schuster, New York, USA.
- LeDoux, J.E. and Brown, R. (2017) A higher-order theory of emotional consciousness. *Proceedings of the National Academy of Sciences* 114, 2431–2433. http://dx.doi.org/10.1073/pnas.1619316114.
- Leiner, L. and Fendt, M. (2011) Behavioral fear and heart rate responses in horses after exposure to novel objects effects of habituation. *Applied Animal Behavior Science* 131, 104–109. http://dx.doi.org/10.1016/j.applanim.2011.02.004.
- Ligon, J.M. (2015) The effects of low stress cattle handling and weaning training on postweaning weight gain and calf activity. Doctoral dissertation. Virginia Tech, Blacksburg, Virginia, USA.
- Melzack, R. and Burns, S.K. (1965) Neurophysiological effects of early sensory restriction. *Experimental Neurology* 13, 163–175. http://dx.doi.org/10.1016/ 0014-4886(65)90106-8.
- Monestier, C., Morellet, N., Gaillard, J.M., Cargnelutti, B., Vanpe, C. (2015) Is a proactive mum a good mum? A

- mother's coping style influences early fawn survival in roe deer. *Behavioral Ecology* 26, 1395–1403. http://dx.doi.org/10.1093/beheco/arv087.
- Montag, C. and Panksepp, J. (2017) Primary emotional systems and personality: An evolutionary perspective. Frontiers in Psychology 8, 464. http://dx.doi. org/10.3389/fpsyg.2017.00464.
- Montag, C., Widenhorn-Müller, K., Panksepp, J., Kiefer, M. (2017) Individual differences in Affective Neuroscience Personality Scale (ANPS) primary emotional traits and depressive tendencies. *Comprehensive Psychiatry* 73, 136–142. http://dx.doi.org/10.1016/j. comppsych.2016.11.007.
- Morris, C.L., Grandin, T., Irlbeck, N.A. (2011) Companion Animals Symposium: Environmental enrichment for companion, exotic, and laboratory animals. *Journal* of Animal Science 89, 4227–4238. http://dx.doi. org/10.2527/jas.2010-3722.
- Northcutt, S. and Bowman, B. (2010). By the numbers: Docility genetic evaluation research. *Angus Journal* 2010, A1.
- Panksepp, J. (1971) Aggression elicited by electrical stimulation of the hypothalamus in albino rats. *Physiology and Behavior* 6, 321–329. http://dx.doi.org/10.1016/0031-9384(71)90163-6.
- Panksepp, J. (1998) Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, Oxford, UK.
- Panksepp, J. (2011) The basic emotional circuits of mammalian brains: Do animals have emotional lives? Neuroscience and Biobehavioral Reviews 35, 1791–1804. http://dx.doi.org/10.1016/j.neubiorev. 2011.08.003.
- Persson, M. E., Wright, D., Roth, L. S., Batakis, P., Jensen, P. (2016) Genomic regions associated with interspecies communication in dogs contain genes related to human social disorders. *Scientific Reports* 6, 33439. http://dx.doi.org/10.1038/srep33439.
- Phillips, M., Grandin, T., Graffam, W., Irlbeck, N.A., Cambre, R.C. (1998) Crate conditioning of bongo (*Tragelaphus eurycerus*) for veterinary and husbandry procedures at the Denver Zoological Gardens. *Zoo Biology* 17, 25–32.
- Polikarpus, A., Napolitano, F., DeRose, C. (2014) Effect of pre-partum habituation to milking routine on the behavior and lactation of buffalo heifers. *Applied Animal Behaviour Science* 161, 1–6. http://dx.doi.org/10.1016/j.applanim.2014.10.003.
- Rainecki, C., Lucion, A.B., Weinberg, J. (2014) Neonatal handling: An overview of positive and negative effects. *Developmental Psychobiology* 56, 1613–1625.
- Redgate, E.S. and Fahringer, E.E. (1973) A comparison of pituitary adrenal activity elicited by electrical stimulation of preoptic amygdaloid and hypothalamic sites in the rat brain. *Neuroendocrinology* 12, 334–343. http://dx.doi.org/10.1159/000122182.

Z40 T. Grandin

- Reeves, J.L. and Derner, J.D. (2015) Temperament does not affect steer weight gains on extensively managed semiarid rangeland. *Rangelands* 37, 186–190. http:// dx.doi.org/10.1016/j.rala.2015.07.004.
- Reid, R.L. and Mills, S.C. (1962) Studies on the carbohydrate metabolism of sheep. XIV. The adrenal response to psychological stress. *Australian Journal of Agricultural Research* 13, 282–294. http://dx.doi.org/10.1071/AR9620296.
- Reser, J.E. (2014) Solitary animals provide an animal model for autism spectrum disorders. *Journal of Comparative Psychology* 128, 99–113. http://dx.doi.org/10.1037/ a0034519.
- Rogan, M.T. and LeDoux, J.E. (1996) Emotion: Systems, cells and synaptic plasticity. Cell 85, 469–475. http://dx.doi.org/10.1016/S0092-8674(00)81247-7.
- Rushen, J. and dePassille,A.M. (2015) The importance of stockmanship and its benefits to animals. In: Grandin, T. (ed.) *Improving Animal Welfare: A Practical Approach*. CAB International, Wallingford, UK, pp. 125–138. http://dx.doi.org/10.1079/9781780644677.0125.
- Rybarczyk, P., Rushen, J., dePassille, A.M. (2003) Recognition of people by dairy calves using color of clothing. *Applied Animal Behaviour Science* 81, 307–319. http://dx.doi.org/10.1016/S0168-1591(02)00273-3.
- Schultz, D. (1965) Sensory Restriction. Academic Press, New York, USA.
- Vetter, S.G., Brandstatter, C., Macheiner, M., Suchentrunk, F., Gerritsmann, H., et al. (2016) Shy is sometimes better: Personality and juvenile body mass affect adult reproductive success in wild boars, Sus scrofa. Animal

- Behavior 115, 193–205. http://dx.doi.org/10.1016/j.anbehav.2016.03.026.
- Vetters, M.D.D., Engle, T.E., Ahola, J.K., Grandin, T. (2013) Comparison of flight speed and exit score as measurements of temperament in beef cattle. *Journal* of Animal Science 91, 374–381.
- Voisinet, B.D., Grandin, T., Tatum, J.D., O'Connor, S.F., Struthers, J.J. (1997) Feedlot cattle with calm temperaments have higher average daily gains than cattle with excitable temperaments. *Journal of Animal Science* 75, 892–896. http://dx.doi.org/10.2527/1997.754892x.
- Walsh, R.N. and Cummins, R.A. (1975) Mechanisms mediating the production of environmentally induced brain changes. *Psychological Bulletin* 82, 986–100. http://dx.doi.org/10.1037/0033-2909.82.6.986.
- Wesley, R.L., Cibils, A.F., Mulliniks, J.T., Pollak, E.R. Petersen, M.K. (2012) An assessment of behavioral syndrome in rangeland raised beef cattle. *Applied Animal Behaviour Science* 139, 3–4. http://dx.doi. org/10.1016/j.applanim.2012.04.005.
- Westerath, H.S., Gygax, L., Hillman, E. (2014) Are special feed and being brushed judged as positive by calves? *Applied Animal Behavior Science* 156, 12–21. http://dx.doi.org/10.1016/j.applanim.2014.04.003.
- Woiwode, R., Grandin, T., Kirch, B., Paterson, J. (2016) Compliance of large feedyards in the northern high plains with the Beef Quality Assurance Feedyard Assessment. *The Professional Animal Scientist* 32, 750–757. http://dx.doi.org/10.15232/pas.2015-01472.
- Zapata, I., Serpell, J.A., Alvarez, C.E. (2016) Genetic mapping of canine fear and aggression. *BMC Genomics* 17, 572. http://dx.doi.org/10.1186/s12864-016-2936-3.

17 Mental Health Issues in the Horse

DANIEL S. MILLS, CLAIRE RICCI-BONOT, AND SOPHIE S. HALL

Animal Behaviour Cognition and Welfare Group, School of Life Sciences, University of Lincoln, Lincoln, UK

17.1 Introduction

Equids fit a unique niche in their relationship with humans. In many contexts they are working animals kept for their utility and managed outside the immediate domestic environment; in this situation the mental health challenges facing them may be similar to those facing many farmed or production animals. But in other contexts, they are close companions with a strong emotional bond extended from their carers; in this situation the mental health challenges facing them may be similar to those facing companion animals. In either context, expectations of their role and potential are critical. Thus the World Health Organization's (2014) definition of mental health as 'a state of well-being in which every individual realizes his or her own potential, can cope with the normal stresses of life, can work productively and fruitfully, and is able to make a contribution to her or his community' (emphasis added) is very easily transposed to the horse, with some clarification of some of the more anthropocentric features of the WHO definition. Accordingly, we suggest that, for the horse, mental health can be defined as 'a state of well-being in which a horse can live in a way that does not compromise its potential performance, is able to cope with the inevitable stressors of its management and work so that it can fulfil an appropriate role; and for a horse involved in human-based activities this should be extended to include the ability to willingly participate in goal-based activities'. From this definition, we can identify several potential areas of physical and psychological threat to their mental health, namely:

• Living conditions which may compromise their potential performance. This includes not only housing that might induce chronic frustration (discussed further in Section 17.4.1), but also

- the mental strain induced by struggling to breathe effectively in an aerial environment heavily contaminated with allergens and fungal spores (Mills and Clarke, 2007) or compromised performance arising from poor rider-horse communication (McGreevy et al., 2009).
- Circumstances that unnecessarily reduce their coping capacity, such as certain restrictions to autonomy, including the deprivation of appropriate ad lib forage (Sykes et al., 2015) and the imposition of meal-feeding practices (discussed in Section 17.1.1).
- Inappropriate expectations of the role or performance capacity of the individual, including a failure to recognize the effect of chronic pain (Lesimple et al., 2013) or to match a horse to its capability as well as problems arising from poor knowledge and/or anthropomorphization of the needs of the horse.
- Training or activities that can undermine willing participations, such as the use of compulsion in the form of restrictive riding gear (von Borstel et al., 2009) or punishment (Waran et al., 2007). From the rider's perspective rollkur (hyperflexion of the neck), has been associated with potential benefits, including improving horse's strength and responsiveness to the rider (van Oldruitenborgh-Oosterbaan et al., 2006). However, it is also associated with greater displays of conflict behaviors (e.g., tail swishing, changes in gait) and fear responses (von Borstel et al., 2009; Kienapfel et al., 2014), suggesting that both the training styles used within different disciplines as well as the demands of the discipline itself need to be considered.

However, it should be noted that the proposed definition also recognizes that there may be inevitable stressors, and so appropriate preventive measures

may be as much about building the capacity of horses to cope with what is necessary as about avoidance of certain unnecessary activities. Central to this is a solid scientific understanding of not only what horses are capable of, but also their limitations; even when they may be able to cope, the effort required may come at some mental health cost. We therefore begin this chapter by considering the issues of coping and adaptation in relation to the cost they may impose, before reviewing specific types of challenges that should be of concern and how they might be addressed. We draw on the available scientific literature, but in places this may be lacking. In these cases we try to guide the reader on the basis of logical argument built on a compassionate interest in horses, giving them the benefit of the doubt when logic may indicate there are grounds for concern, rather than arguing, as some do, that the absence of scientific evidence means that all positions have equal merit or that the majority/ popular view is necessarily the best view. Both of the latter positions have historically resulted in considerable suffering for horses.

17.1.1 Coping in the domestic environment and mental health

Coping implies that an animal is able to make the necessary changes in order to adapt and if a horse cannot cope, then it is clear that there is a problem. However, simply being seen to cope is not sufficient for good welfare or mental health. The effort required to adapt comes at a cost, and if this cannot be sustained then there is cause for concern as not only may the animal be unable to cope in the longer term, but the anticipated cost of trying to cope may compromise its mental health. This is because it is not just the nature of the challenge but also the individual's evaluation of its ability to cope with that challenge (secondary appraisal, sensu Lazarus [1966]) which is an important component of the resulting emotional response (Folkman, 1984). The concept of secondary appraisal was originally developed within human psychology, but this does not make its consideration in other animals anthropomorphic since it is a general biological process that may exist at different psychological levels depending on the cognitive capacity of the species or individual concerned. Primary appraisal involves assessment of the type of challenge faced by an individual, while secondary appraisal involves evaluating what the individual can potentially do in order to adapt to this challenge and the extent to which it evaluates that this will succeed. An inability to identify an appropriate response to the challenge or a prediction that the effort needed is beyond the capacity of the individual in either the short term (e.g., response of excessive magnitude required, or response not possible due to current environmental constraints) or longer term (e.g., response required for longer than the animal predicts it can sustain) is likely to result in mental health problems. Inspired by Fraser *et al.* (1997), we elaborate three different types of circumstance that may lead to mental health issues in horses; namely:

- 1. Evolutionarily natural challenges: The nature (if not the specific form) of these stressors aligns closely with the type of challenges that have shaped the species-typical behavior of the horse, and so the responses that follow retain a clear functional purpose. For example, being able to respond appropriately to the posturing of another that results in individual herd rank and helps to reduce the longer-term risk of harm from antagonistic interactions over limited resources. Included in this class of challenges are circumstances that may be unique to the domestic situation, but which have the general emotional qualities of natural processes that can be deployed to facilitate coping (e.g., habituation to traffic).
- 2. Unmet evolutionary expectations: There are some physiological and behavioral tendencies that have arisen through evolution, which are no longer advantageous in the domestic environment. The brain is geared toward making decisions about how to divide the available time between competing activities to survive and maximize fitness. However, in the domestic setting the opportunity for these activities often occupies only a proportion of the time available, meaning the animal is faced with the problem of how to fill the available time. The default state, if the animal is safe and secure in its basic biological needs, is to explore and learn about the physical and social environment, and so opportunities to engage in these activities are important and an enriched environment is not a luxury but an essential prerequisite for good mental health (Meagher et al., 2017). We suggest that a range of problems, including 'box-walking' can arise from this tendency for natural inquisitiveness combined with a restricted environment.
- 3. Novel domestic challenges: These are specific challenges that are unique to how domestic horses have been kept and for which there has been no

selective pressure for adaptation. For example, horses have evolved to trickle feed on forage to obtain their nutritional requirements, but in the stabled environment the nutrient needs may be met with concentrates and without the need for grazing/foraging behaviors. However, the individual may still be motivated to perform associated actions. For example, horses may be intrinsically motivated to perform grazing/foraging behaviors which if not met may result in problems including the discomfort associated with gastric ulceration (since acid production in the stomach is not largely regulated by food intake, as it is in humans [Alexander, 1966]), or other problems associated with prolonged failure of the normal negative feedback associated with achievement of the goal of a behavior. This includes specifically preventing them from interacting with other horses that they can see by confining them to individual housing in the form of stalls, or making them work in an outline/posture/way that they may not be physically mature enough to sustain. In these circumstances the individual must use its evolutionary rules of thumb to try to solve the problem, but may not be successful and consistent failure can be expected to result in problems with mental well-being.

17.1.2 Maladaptive versus malfunctional responses

Before elucidating these further in the second part of this chapter, we believe it is important to make an important distinction between the terms 'maladaptive' and 'malfunctional', which may be used in relation to coping strategies as it has important implications for both mental health and the nature of any additional interventions aimed at helping the animal. If a strategy is invoked on the basis of evolutionary rules of thumb then it is a functional strategy, but if it does not result in the animal coping well it has not fulfilled its adaptive role and so may be considered maladaptive (Mills, 2003). From a welfare and mental health perspective it can be expected that the animal will continue to perceive a need to try to adapt and so both mental health and welfare may be compromised. Accordingly, medication used in this context should not be seen as 'correcting' a mental pathology. The challenge faced by the animal still exists, and so the possibility that the intervention has simply suppressed the signs of failure to cope (e.g., through the nonspecific

suppression of physiological arousal) also needs to be considered. Only if psychological arousal is reduced so the animal is no longer aware of the challenge will it improve welfare, but its effects on mental health still remain questionable, as the animal has not improved its intrinsic ability to cope with the situation. In a natural setting, animals typically have a lot of autonomy, whereas this is often reduced in captivity as boundaries are imposed by the animal's keepers. Evolution has resulted largely in the development of strategies to deal with immediate rather than prolonged threats to well-being. Therefore, it is not surprising that another common type of threat to horse mental health comes not from the quality of the challenge, but rather its prolonged nature. This can result in organizational changes in brain micro-architecture (such as changes in neuronal sensitivity) which in the natural setting may be adaptive but are not helpful in the domestic setting. Again, we would argue that these are functional changes and not pathological.

In a limited number of contexts, such as in dementia-related conditions, coping fails because the strategy is not following the evolutionary rules of thumb, due to an organic lesion limiting normal regulatory processes (e.g., loss of neuronal function). In this situation the system may be considered both malfunctional and maladaptive. Treatments which restore both normal function and facilitate coping will improve both welfare and mental health. Accordingly, in contrast to the medical perspective of human psychiatry, we argue that few of the mental health issues affecting horses should be thought of as diseases or disorders. This difference in perspective should not be used to imply that they are any less important, only that the role of medicine (or veterinary medicine) is perhaps somewhat different to how it may sometimes be portrayed.

An example outside of mental health may help to illustrate this subtle but important difference between maladaptive versus malfunctioning processes. If a horse develops diarrhea because the gut is hyperperistaltic and reduces the normal transit time in order to eject an irritant, then the gut is still operating in a functional way, even if the horse becomes dehydrated for a while as a result. The gut is not diseased as such. However, if the lining of the gut is so damaged that it is unable to absorb water and diarrhea results, then this has arisen as a result of a malfunction of the gut. In both cases the horse has the signs of diarrhea, but in only one is there a pathology of the gut. The same can be said of mental states.

17.2 Evolutionarily Natural Challenges Impacting on Mental Health

17.2.1 Fears, frustrations, and anxieties

Fears are natural responses to perceived threats, whereas anxieties are anticipations of potential danger and thus involve a greater degree of uncertainty (Forkman et al., 2007). The natural adaptive response to a fear-eliciting stimulus is for the individual to protect itself, preferably by taking flight (for which the horse is well adapted) but also through self-defense if flight is not possible and the threat comes from a social source. A horse may also freeze in fear, especially if there is no clear escape from the situation. This may help to avoid attention from a threat like a predator and conserve resources until escape becomes either necessary or possible or the event passes. By contrast, when anxious the horse can be expected to engage in responses directed toward gathering more information in order to reduce the uncertainty of the situation. This often takes the form of behavioral inhibition (not to be confused with the complete immobility of fear) where the eyes, ears, and nose are used to discover more about the situation. Thus, the horse may snort, flick its ears, or move its head around to focus on various aspects of the environment.

The term anxiety is also popularly used to describe another situation that may arise in captivity, i.e., when an animal is uncertain about what it should do about a situation. However, this is related to motivational conflict and has a less reliable association with fear. Three forms of motivational conflict are generally recognized:

- Approach–avoidance conflict when an animal is uncertain about the potential risks associated with approaching something that is of interest. Horses are naturally quite cautious when approaching new stimuli, even if benign. The consequences will determine the outcome, and the use of punishment at this time will likely have the opposite to the desired effect as a negative association is then established.
- Avoidance–avoidance conflict when an individual can only escape from one threat by facing another threat. For example, when a horse is anxious about going forward but its rider tries to coerce it to move on, or if the use of aids is inconsistent so the horse cannot predict what is required to avoid the application of an aversive. In this situation, the relationship with the rider

- may be critical in order to assure that the horse has a secure base to provide support. An association between the rider and punishment is largely incompatible with this, and we discuss the issue of social support in more detail in Section 17.4.3.
- Approach—approach conflict when the individual is uncertain which stimulus of interest it should approach first. The risks to mental health from this situation are less than the first two described here which involve trying to avoid one or more aversives and so this is another reason why positive rather than negative reinforcement should be used in training. It is worth noting that the former approach is associated with fewer behavioral problems and enhanced ridden performance (Warren-Smith et al., 2007).

In these conflict situations, the animal typically engages in ambivalent behavior rather than behavioral inhibition (possibly alongside increased sensory activity). We suggest that other displacement behaviors may also occur at this time. These take the form of simple acts which may appear functionally unrelated to resolving the problem, but their expression may be important as they may serve to reduce the arousal arising from the failure to consummate the goal of the conflicting behaviors (Scopa et al., 2018). In the horse, common displacement behaviors seen in such situations include foot stamping, tail swishing, headshaking, the sudden 'snatching' of grass, and possibly flehmen (lip curling) (Górecka-Bruzda et al., 2015). Any of these conflicts may be misunderstood and misrepresented by horse-people as 'stubbornness' on the part of the horse and used to justify the use of physical punishments which can turn a minor conflict into an active avoidance (e.g., in the form of shying), which may result in a vicious cycle of handler punishment and more major mental health issues as the supportive bond with its primary carer breaks down. Through classical conditioning this may even result in problems with tacking up, as these are predictable preludes to the problems that occur under saddle. Thus, poor rider understanding of natural horse behavior and the inappropriate use of aversives are major sources of equine mental health concern. Therefore, riders should be educated that although undesirable from a riding perspective such behaviors may ultimately have a positive effect on the horse's performance and displays of these behaviors should not be punished.

Different species are thought to have inherent predispositions to the type of stimuli that they find aversive (unconditioned fears), and horses are naturally neophobic (Leiner and Fendt, 2011). This may include some of the stimulus properties associated with predation or harm, such as sudden changes in movement around the horse or, given that its primary defense mechanism is based on flight, any circumstance that potentially limits this or the ability to detect such circumstances. Accordingly, horses may naturally avoid confined or dark spaces (especially if moving from a brightly lit area) or any action that may restrict their locomotion (foot or more general body restraint). Experience can shape anxiety and fear responses in both a positive and negative way. If an anxious horse is punished for hesitation when anxious, such as when loading into a trailer (a stimulus set that horses can be expected to naturally avoid - see Fig. 17.1), this will exacerbate the mental challenge. Likewise, fear may develop to novel or even benign stimuli through an association with punishment or pain (conditioned fears), including handlers who become frequently associated with the use of aversives. By the same measure, many simple fears can be resolved by associating them with positive experiences. In this regard, giving the horse time to resolve any conflict is as important as ensuring that there is a clear reward available for responding as we wish. These counterconditioning exercises are typically combined with desensitization, in which the fear evoking stimulus is presented according to an intensity gradient which seeks to avoid an intense avoidance response (Gough, 1997).

As a herd animal, social transmission of fear reactions may be expected to occur between individuals (Nicol, 1995), and so fear responses may arise within an individual even if it perceives no direct threat. However, the tendency for such emotional contagion may also be used to good effect to help reduce fear responses, with younger animals exhibiting a reduced response to a potentially anxiogenic stimulus in the presence of less reactive older ones (Rørvang and Christensen, 2018).

Rewards or relative rewards may also be used to help motivational conflicts by ensuring that there is a clearly preferable response. In the case of avoidance avoidance conflict, there may need to be a focus on reducing the perceived aversiveness of one of the options outside of the problem situation, so that conflict does not arise in the future.

Aspects relating to rider positioning/style include the use of the bit, rein tension, and consistency. Misuse of the bit has been associated with behavioral signs of discomfort as well as physical damage

(Cook, 2003). When pressure from a bit, applied through rein tension, is not appropriately released or 'softened', horses often display conflict behaviors, fear, and general body tension (Visser et al., 2009; Christensen et al., 2011), which they learn to avoid rather than habituate to. Horses are usually trained to associate changes in pressure with a behavioral response (e.g., increase pressure on the mouth to slow, increased pressure on their sides to move forward), removing the pressure (e.g., releasing rein contact) acts as a reinforcer, increasing the likelihood the response will occur again (McGreevy, 2007). If the pressure is not consistently reduced sometimes the horse will not be reinforced for displaying the riderdesired behavior, resulting in confusion for the horse, which may lead to unwanted 'evasive' behaviors.

Further misuse of the bit is seen in the delivery of inconsistent communication between the rider's hand and leg, i.e., kicking and pulling, or 'crank and yank' as it is referred to. This conflicting signal is seen in riders across the disciplines (McLean, 2003), and again is likely to result in a confused horse which shows evasive, fearful, or 'learned helplessness' type behaviors.

In the wild state it would be unusual for fear-, anxiety-, and frustration-related problems not to be resolved relatively quickly by these actions, but that does not mean that they are not of concern. As mentioned previously, if the stimuli are particularly intense, frequent, or enduring they may threaten the animal's mental health even if the immediate situation is resolved, as the animal may adapt by being more vigilant of danger. This then may take its toll over time as resources are diverted from other activities to maintain a heightened state of arousal (Forkman et al., 2007; Leiner and Fendt, 2011). If, however, the responses do not result in successful adaptation in terms of eliminating the stressor, then there may be other, less natural, consequences; these are considered in the section on novel domestic challenges (Section 17.4), since this is not the natural outcome.

17.2.2 Separation anxiety

Separation anxiety is the normal response of a dependant to prolonged separation from its carer (attachment figure) (Bowlby, 1973). While it can result in fear, anxiety, and frustration as the individual seeks to reinstate contact with its carer, its particular relationship with an attachment figure and dependent neurophysiological associations with opiate systems make it a special case for consideration



Fig. 17.1. A typical horse box with common features that horses may find aversive. First, the horse has to step up onto the ramp, which may be an action naturally avoided. Second, the ramp is at an angle and so the lower joints of the limb may need to hyperextend, which may be uncomfortable. The black surface will also naturally be avoided as may be a surface associated with vibrations underfoot. It must also be recognized that the horse box is a very novel looking and potentially smelling, enclosed environment associated with isolation in a dead-end space, all of which are features that horses will naturally avoid; this is further exacerbated by high contrast features making the transition from inside to outside very strong. Finally, the surface may also be slippery and not provide a solid grip. Failure to appreciate and address effectively how these features affect a horse can lead an owner to use punishment on the horse who hesitates or refuses to enter, which will add a further learned negative association to the box, resulting in horses who are traumatized at the prospect of loading or traveling.

(Panksepp, 1998). From a veterinary behavioral perspective, true separation anxiety is not just frustration or anxiety at being alone, but rather a specific aversion to the absence or loss of the attachment

figure which results in a panic-like response (from an evolutionary perspective the loss of one's mother is a life or death situation for a mammalian infant). Horses are a highly social species, i.e., show great mutual dependency, and we speculate, on the basis of clinical behavioral observations, that this probably means that similar bonds may have the potential to form with both humans who take on a care-giving role as well as members of the same species. Although there is a lack of academic research on this emotional process in horses, it has been noted anecdotally that it may be more common when the relationship with the handler is inconsistent, such as when intermittent punishment is used in training (McLean and McLean, 2008). This is in agreement with the human literature indicating that attachment problems arise as a result of a dysfunctional style of attachment rather than through over-attachment, which is commonly spoken about in relation to other species.

17.2.3 Pain

Although a review of chronic pain is outside the scope of this chapter, it is important to appreciate that it is both common in horses (Landman et al., 2004; Fonseca et al., 2006) and often goes unrecognized by owners (Lesimple et al., 2013). As with humans, chronic pain, and especially back pain, is often associated with a range of mental health issues including depression (Fureix et al., 2012) and increased aggressivity including toward humans (Fureix et al., 2010), as well as more subtle signs such as reduced attention to the environment (Rochais et al., 2016). If these problems remain unrecognized, it may result in inappropriate behavior by the owner toward the horse, as they may misrepresent these changes as stubbornness and resistance to perform the desired work. The use of punishment in an attempt to correct the perceived 'problem' can result in further mental health issues, associated with anxiety, etc., as described above. Behavioral indicators of chronic pain may not be very reliable, but increasing attention is being paid to the potential value of distinctive facial expressions (Dalla Costa et al., 2014; De Grauw and Van Loon, 2016).

17.3 Unmet Evolutionary Expectations Impacting on Mental Health

There are several potential challenges arising from the evolutionary mismatch between the biases created in the equine brain to aid survival in their natural habitat and the domestic environment of many horses (genome lag; Fraser *et al.*, 1997). These typically arise from the well-intentioned and appropriate care provided by owners to ensure their basic needs are met.

17.3.1 Boredom

Boredom may be defined as a negative affective state associated with the interpretation of one's environment as lacking interest, because it is highly predictable and controllable (Fureix and Meagher, 2015; Burn, 2017). It does not necessarily imply that there is a lack of stimulation, but that the stimulation which is available is perceived as irrelevant (Burn, 2017); in particular, the lack of unexpected positive reinforcement may be a cause for concern.

In the absence of varied stimulation, we suggest that animals may engage in exploratory tasks that may be problematic, such as wood chewing and walking around their restricted enclosure. With repetition, the changes that occur with complex movement become more predictable and so the behavior may become simpler in its form (Fentress and Gadbois, 2001), a process that appears to be facilitated by dopaminergic activity in striatal structures within the brain (Cools, 1992). This may lead to repetitive simplified behaviors such as box-walking, wood chewing, and possibly some other behaviors in the horse, which are often (and we suggest erroneously) referred to as compulsive disorders or stereotypies. Unlike these disorders, however, these repetitive behaviors are not associated with either a specific anxiety or frustration (see Section 17.4 for a discussion of these issues). This hypothesis deserves empirical evaluation, and it would be predicted that individuals expressing this form of repetitive behavior problem would not only live in an unstimulating environment, but also show increased apathy at other times, compared to the increased arousal associated with specific frustrations (discussed in the next section).

Owners often misunderstand the reason for repetitive behaviors and blame the horse, as is implied in the commonly used term 'vice' to describe them. This may then be used to justify attempts at resolution based either on suppression or punishment (Hothersall and Casey, 2012) (e.g., muzzles, or the use of shock collars [Houpt, 2018]), which may have their own mental health implications. However, these problems should be alleviated by simple environmental enrichment, which may take the form of a more visually complex physical environment (Cooper et al., 2000) or increased social contact (Yarnell et al., 2015). For example, increased paddock size has been shown to reduce the amount of time spent standing passively as well as increase foraging activity (Jørgensen and Bøe, 2007), and a diet of varied forage may in itself be enriching (Goodwin et al., 2002; Thorne et al., 2005). The role of stable toys is less straightforward, as while they may increase the diversity of activity, their effects may be varied if careful consideration is not given to what the goal of the enrichment is (Jørgensen et al., 2011). In this way, they may also introduce specific frustrations that increase problem behavior in a proportion of individuals (Henderson and Waran, 2001).

17.4 Novel Domestic Challenges Impacting on Mental Health

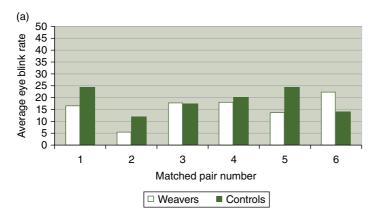
Whereas in the previous section we considered problems that may arise in the domestic situation as a result of evolutionary tendencies not being fulfilled, there are some specific novel challenges associated with the domestic environment for which it should not be expected that horses have evolved adaptive coping strategies. As a result, the horse's behaviors may appear 'stupid' or 'stubborn' to those who do not appreciate that they are governed by the evolutionary rules of thumb that evolved in their wild ancestors, since there has not been selection in captivity for adaptation to these traits. Of particular note here are the consequences of insoluble problems for the horse, inconsistent communication by the rider toward the horse, and the absence of social support often found in the domestic environment.

17.4.1 Insoluble tasks

Insoluble tasks faced by the horse, in which it is the sole agent involved (i.e., those not involving humans or other horses), are quite common. For example, the horse kept in a stable, where it can see other horses but not interact with them, will likely be motivated to try to approach them, but it cannot do so due to the stable door. The horse's brain is not geared to simply accept this situation and so this can lead to chronic frustration of locomotion directed toward exiting the stable, and it is believed that this can lead to the repetitive behavior commonly referred to as weaving (Mills, 2005). Horses are commonly relieved of this frustration on an occasional basis by being turned out, and this might explain why the problem is easily resolved by enrichment, which may simply distract the horse from the specific frustration, such as the provision of a stable mirror (McAfee et al., 2002; Mills and Davenport, 2002), or, at least in the short term, a simple poster of another horse (Mills and Riezebos, 2005). While these represent acute recurring frustrations, not all domestic frustrations are like this; some appear to be more persistent, for example, crib-biting. Cribbiting is associated with changes in dopaminergic sensitivity (McBride and Hemmings, 2005; Wickens and Heleski, 2010) which are not apparent in weaving horses. Blinking may be used as a simple behavioral correlate of dopaminergic activity (Lethbridge et al., 2007). Interestingly, an extension of the latter study demonstrated that, when compared to carefully matched controls, horses who weave were found not to differ significantly in their blink rate whereas horses who crib-bite blink significantly more frequently (Fig. 17.2). This would suggest that the repetitive behavior associated with cribbing, but not weaving, is more like the stereotypies described in human mental health conditions such as schizophrenia, hyperactivity disorder, and autism, as well as stereotypies induced with dopaminergic agents in the laboratory (Jongkees and Colzato, 2016). The exact etiology of this change remains uncertain, but frustration of a high level of forage-based feeding is a consistent finding (Wickens and Heleski, 2010), suggesting that the change may occur as a result of the persistent failure to meet some physiological need associated with trickle feeding in the horse.

17.4.2 Unresolved conflicts associated with equitation

Some insoluble conflicts for the domestic horse arise as a result of inconsistent communication between riders and their horses and inappropriate training methods. As a consequence, the environment may become unpredictable at this time and the horse may lose the normal level of control over its environment that it might expect (McLean and McGreevy, 2010) with no clear way to avoid punishment. This is the contingency required for the development of learned helplessness/depression-like conditions (Overmier and Seligman, 1967). Such behavior was first documented in horses in the 1980s (Ödberg, 1987) and has received some attention since (Hall et al., 2008; Fureix et al., 2015; McLean and Christensen, 2017). Alternatively, seemingly undesirable behaviors, which may be seen as expressions of noncompliance by the rider, such as bucking, shying, and issues with tacking up, may be expressed as the horse tries to avoid the context leading to the uncontrollable punishment. There is also some evidence to suggest that the type of work the horse undertakes may also affect its mental health. Disciplines which



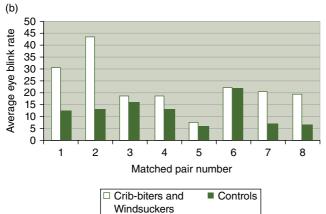


Fig. 17.2. Average blink rates of size-matched horses in similar lighting conditions. (a) Weavers and their controls show no significant difference (p = 0.33); (b) crib-biters blink significantly more often than their controls (p = 0.02). This difference remains even when the two pairs with most extreme difference (1 and 2) are removed.

require high amounts of rider control and obedience (e.g., classical equitation, eventing, or dressage) are associated with a greater risk of problematic behaviors (including repetitive behaviors) than horses ridden western style (Normando *et al.*, 2011) or other disciplines in which the rider has looser contact through the bit with the horse's mouth (McGreevy *et al.*, 1995; Hausberger *et al.*, 2009).

Whereas depression in humans is assessed through clinical enquiry, often supplemented by psychometric assessment, assessing depression in horses is subject to greater methodological challenges. Nonetheless, identifying proxies of this mental health issue is important. States involving profound inactivity and low responsiveness to external stimuli (i.e., appearing withdrawn) have been linked to depressive states in horses (Swann, 2006; Burn *et al.*, 2010; Fureix *et al.*, 2012). Horses that have been identified as having impaired welfare and being in pain often show reduced responsiveness to the environment (Pritchard *et al.*, 2005; Hausberger *et al.*, 2016; Burn, 2017).

Such 'withdrawn' states are commonly defined through a stationary, atypical, flat-necked posture, wide open and unblinking eyes, fixed gaze, and backward-pointing ears (Fureix et al., 2012). As well as low behavioral reactivity to stimuli, depressive-like states in horses have also been associated with differences in attention and its adaptation. Nonwithdrawn horses show greater reactions to novel auditory stimuli, and these reactions are displayed for a longer period of time than is seen in withdrawn horses, who show less reaction. With repeated exposure, nonwithdrawn horses showed reduced attention to the stimuli (e.g., less time spent orientated toward the speaker), whereas withdrawn horses showed consistent behavior over time (Rochais et al., 2016). Additionally, depressed horses may show altered eating habits and preferences. Horses that displayed depressive symptoms have been reported as showing reduced food consumption and reduced latency to consume food (Fureix et al., 2015), as well as anhedonia (a loss of pleasure), as assessed

through reduced consumption of sucrose, compared to horses that displayed nonwithdrawn behaviors (Fureix et al., 2015). Failure to recognize these behaviors as being potential indicators of impaired mental health is likely to further exacerbate the problem. For some owners, 'withdrawn' behaviors may be desirable, making the horse easier to handle and seemingly more compliant with the demands of their environment; for others, however, the horse may be seen as stubborn as performance expectations are not met. Either way, this is a cause for concern, especially if this state is misinterpreted as a positive psychological state, such as feeling calm and content. Important ancillary signs that may help to differentiate this are wider signs of anxiety (Fureix et al., 2012) and reduced attentional processing (Rochais et al., 2016), which may be most apparent from poor learning and performance (Hall et al., 2008). It is therefore important that owners are educated on behaviors indicative of depressive-like symptoms in horses.

Adaptive behavior and reduced stress in the face of challenges requires an ability to make advantageous decisions by predicting the likelihood of future success based upon previous experience. The inability to predict results in increases in arousal and is distressing (Weiss, 1972; Shihata et al., 2016) even if it does not lead to learned helplessness. Within the human health literature intolerance of uncertainty has been related to psychopathologies, particularly obsessive-compulsive disorders (OCD) (Laposa et al., 2015) and generalized anxiety disorder (GAD) (Norton et al., 2005). Inconsistency may result in the expectation that uncertainty, ambiguity, newness, and change are potentially dangerous (Grenier et al., 2005; Buhr and Dugas, 2009). Horses normally use the riders' actions rather than their words to predict what is required, and so signaling consistency including the use of aids, such as the leg and seat, is paramount. Sometimes signals are conflicting, e.g., the rider urges the horse forward with the leg but keeps restraining it through the mouth bit (McGreevy and McLean, 2005); at other times signals and aids may be simply applied unsystematically (Hockenhull and Creighton, 2013). In either case the consequence is a loss of control to which the horse is unable to adapt. It is natural for a horse to resist such confusion and frustration, but this may be seen as disobedience and result in inappropriate punishment or more technical solutions which are likely to exacerbate the situation if the fundamental signaling consistency issue is not addressed. In this regard it is interesting to note that Hockenhull and Creighton (2012) found that ridden horse behavior problems were more likely when more technical aids were used, although the causal nature of the relationship cannot be established.

17.4.3 Lack of social support

Social support offers physical and psychological protection when faced with stressful events and is associated with feelings of subjective well-being and thriving; its absence, in contrast, is associated with specific mental health problems (see Chapter 8, this volume). Two models are predominantly used to explain the concept of social support. The first model describes the effect of social support, which provides beneficial effects to the recipient regardless of whether the individual is under stress or not. The second model describes the phenomenon in relation to social buffering, which can be defined as the ability of social partners to modulate or downregulate the impact of stressors on the health of the recipient (Nakamura et al., 2016; reviewed by Cohen and Wills, 1985; Kikusui et al., 2006; Hennessy et al., 2009; Rault, 2012). For a highly social species such as the horse, it is likely that social support is critical for normal healthy mental functioning, due to the evolutionary pressure not to become an isolated individual who would be easy prey. Humans and nonhuman animals that have social support from conspecifics during stressful events show reduced stress reactions to a range of challenges that horses might face in captivity (Gust et al., 1996; Ruis et al., 1999). To date, most research on the stress associated with social isolation has focused largely on the specific context of social separation (discussed above), with relatively little attention given to the wider importance of social support to animal welfare. In many parts of the world, horses are kept in social isolation, deprived of the benefits of conspecific or heterospecific social contact, with an increase in the risk of a range of health and behavior problems believed to be the consequence (Pierard et al., 2019). Even worse perhaps, as mentioned in the previous section, the social contact that many horses receive may be primarily with an inconsistent human, which may exacerbate the situation.

17.4.4 Cognitive dysfunction and associated problems

Finally, it is worth noting that in many industrialized nations, the horse population is, like the human one, an aging one, with an increased potential for dementia-like problems. While Alzheimer-like conditions have been identified in other companion species such as the dog (Azkona et al., 2009) and cat (Gunn-Moore et al., 2007), less attention has been paid to the horse. Our own work suggests that older horses may show some of the learning deficits commonly seen in dogs with this condition (Milgram et al., 1994), but whether or not there is a similar pathological correlate is unknown. Nonetheless, older horses are also prone to Cushing's disease (McCue, 2002) and the increased cortisol production associated with this condition, like Alzheimer disease, is likely to increase the risk of anxiety related problems, which are of concern. There is therefore not only a need to monitor the physical health of older horses and address related issues, but also to give careful consideration to their secondary psychological effects.

17.5 Concluding Remarks

When it comes to their mental health, it is clear that the horse occupies a unique position among domestic species, as they may face potential suffering from issues relating to close association with often wellmeaning individuals who fail to take into account the horse's perspective on things, as well as from the stresses associated with expectations of performance. In modern equitation many individuals want rapid results, despite the implications this might have for the horse; however, to obtain a safe and ethically correct training environment, the mental state of the horse should be taken into consideration (Hendriksen et al., 2011). Not only rider impatience, but also rider inconsistency is a particular problem (Hemsworth et al., 2015) and it would surely be advantageous if riders learned more about horse ethology and communicating with their horse through training them from the ground, while also learning some equitation skills, such as balance and seat, leg, and hand independence on horse simulators. In this way they might reduce the risk of sending confusing signals to the horse. Furthermore, the increasing use of automated equipment and software to track the rider's position and body movements, as well as rein tension (McGreevy, 2007), means it is now possible to provide feedback to riders on the clarity of their signaling and appropriate use of pressure-release. Horses are not deliberately disobedient or stubborn, and it is essential that riders reappraise this perspective on a

horse's behavior and come to more fully appreciate the world from a horse's perspective. In this way, the unique partnership between humans and horses can be enjoyed and the mental well-being of both enhanced as a result.

17.6 References

- Alexander, F. (1966) A study of parotid salivation in the horse. The Journal of Physiology 184, 646–656. http:// dx.doi.org/10.1113/jphysiol.1966.sp007937.
- Azkona, G., Garcia-Belenguer, S., Chacón, G., Rosado, B., León, M., et al. (2009) Prevalence and risk factors of behavioural changes associated with age-related cognitive impairment in geriatric dogs. Journal of Small Animal Practice 50, 87–91. http://dx.doi. org/10.1111/j.1748-5827.2008.00718.x.
- Bowlby, J. (1973) Attachment and Loss (Vol. II). Separation, Anxiety, and Anger. Basic Books, New York, USA.
- Buhr, K. and Dugas, M.J. (2009) The role of fear of anxiety and intolerance of uncertainty in worry: An experimental manipulation. *Behaviour Research and Therapy* 47, 215–223. http://dx.doi.org/10.1016/j.brat.2008.12.004.
- Burn, C.C. (2017) Bestial boredom: A biological perspective on animal boredom and suggestions for its scientific investigation. *Animal Behaviour* 130, 141–151. http://dx.doi.org/10.1016/j.anbehav.2017.06.006.
- Burn, C.C., Dennison, T.L., Whay, H.R. (2010) Relationships between behaviour and health in working horses, donkeys, and mules in developing countries. *Applied Animal Behaviour Science* 126, 109–118. http://dx.doi. org/10.1016/j.applanim.2010.06.007.
- Christensen, J.W., Zharkikh, T.L., Antoine, A., Malmkvist, J. (2011) Rein tension acceptance in young horses in a voluntary test situation. *Equine Veterinary Journal* 43, 223–228. http://dx.doi.org/10.1111/j.2042-3306.2010.00151.x.
- Cohen, S. and Wills, T.A. (1985) Stress, social support, and the buffering hypothesis. *Psychological Bulletin* 98, 310–357. http://dx.doi.org/10.1037/0033-2909.98.2.310.
- Cook, W.R. (2003) Bit-induced pain: A cause of fear, flight, fight and facial neuralgia in the horse. *Pferdeheilkunde* 19, 75–82
- Cools, A.R. (1992) Striatal structures, dopamine and the mobility gradient model. *Behavioral and Brain Sciences* 15, 271–272. http://dx.doi.org/10.1017/ S0140525X0006859X.
- Cooper, J.J., McDonald, L. Mills, D.S. (2000) The effect of increasing horizons on stereotypic weaving: Implications for the social housing of stabled horses. Applied Animal Behaviour Science 69, 67–83. http://dx.doi.org/10.1016/S0168-1591(00)00115-5.
- Dalla Costa, E., Minero, M., Lebelt, D., Stucke, D., Canali, E., et al. (2014) Development of the Horse Grimace Scale (HGS) as a pain assessment tool in horses undergoing

- routine castration. *PLoS One* 9(3), e92281. http://dx.doi.org/10.1371/journal.pone.0092281.
- De Grauw, J.C. and Van Loon, J.P.A.M. (2016) Systematic pain assessment in horses. *The Veterinary Journal* 209, 14–22. http://dx.doi.org/10.1016/j.tvjl.2015.07.030.
- Fentress, J.C. and Gadbois, S. (2001) The development of action sequences. In: Blass, E.M. (ed.) Developmental Psychobiology, Vol 13: The Handbook of Neurobiology Series. Springer, Boston, Massachusetts, USA, pp. 393– 431. http://dx.doi.org/10.1007/978-1-4615-1209-7_11.
- Folkman, S. (1984) Personal control and stress and coping processes: A theoretical analysis. *Journal of Personality and Social Psychology* 46, 839. http://dx.doi.org/10.1037/0022-3514.46.4.839.
- Fonseca, B.P.A., Alves, A.L.G., Nicoletti, J.L.M., Thomassian, A., Hussni, C.A., et al. (2006) Thermography and ultrasonography in back pain diagnosis of equine athletes. *Journal of Equine Veterinary Science* 26, 507–516. http://dx.doi.org/10.1016/j.jevs.2006.09.007.
- Forkman, B., Boissy, A., Meunier-Salaün, M.-C., Canali, E., Jones, R.B. (2007) A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiology* & *Behavior* 92, 340–374. http://dx.doi.org/10.1016/j. physbeh.2007.03.016.
- Fraser, D., Weary, D.M., Pajor, E.A., Milligan, B.N. (1997) A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare* 6, 187–205.
- Fureix, C. and Meagher, R.K. (2015) What can inactivity (in its various forms) reveal about affective states in nonhuman animals? A review. Applied Animal Behaviour Science 171, 8–24. http://dx.doi.org/10.1016/j. applanim.2015.08.036.
- Fureix, C., Menguy, H., Hausberger, M. (2010) Partners with bad temper: Reject or cure? A study of chronic pain and aggression in horses. *PloS One* 5(8), e12434. http://dx.doi.org/10.1371/journal.pone.0012434.
- Fureix, C., Jego, P., Henry, S., Lansade, L., Hausberger, M. (2012) Towards an ethological animal model of depression? A study on horses. *PloS One* 7(6), e39280. http://dx.doi.org/10.1371/journal.pone.0039280.
- Fureix, C., Beaulieu, C., Argaud, S., Rochais, C., Quinton, M., et al. (2015) Investigating anhedonia in a nonconventional species: Do some riding horses Equus caballus display symptoms of depression? Applied Animal Behaviour Science 162, 26–36. http://dx.doi. org/10.1016/j.applanim.2014.11.007.
- Goodwin, D., Davidson, H.P.B., Harris, P. (2002) Foraging enrichment for stabled horses: Effects on behaviour and selection. *Equine Veterinary Journal* 34, 686–691.
- Górecka-Bruzda, A., Kosińska, I., Jaworski, Z., Jezierski, T., Murphy, J. (2015) Conflict behavior in elite show jumping and dressage horses. *Journal of Veterinary Behavior* 10, 137–146. http://dx.doi.org/10.1016/j. jveb.2014.10.004.
- Gough, M.R. (1997) Clipping horses. Equine Veterinary Education 9, 161–165. http://dx.doi.org/10.1111/ j.2042-3292.1997.tb01297.x.

- Grenier, S., Barrette, A.M., Ladouceur, R. (2005) Intolerance of uncertainty and intolerance of ambiguity: Similarities and differences. *Personality and Individual Differences* 39, 593–600. http://dx.doi.org/10.1016/j.paid.2005.02.014.
- Gunn-Moore, D., Moffat, K., Christie, L.A., Head, E. (2007) Cognitive dysfunction and the neurobiology of ageing in cats. *Journal of Small Animal Practice* 48, 546–553. http://dx.doi.org/10.1111/j.1748-5827.2007.00386.x.
- Gust, D., Gordon, T., Brodie, A., McClure, H. (1996) Effects of companions in modulating stress associated with new group formation in juvenile rhesus macaques. *Physiology & Behavior* 59, 941–945. http://dx.doi. org/10.1016/0031-9384(95)02164-7.
- Hall, C., Goodwin, D., Heleski, C., Randle, H., Waran, N. (2008) Is there evidence of learned helplessness in horses? *Journal of Applied Animal Welfare Science* 11, 249–266. http://dx.doi.org/10.1080/10888700802101130.
- Hausberger, M., Gautier, E., Biquand, V., Lunel, C., Jego, P. (2009) Could work be a source of behavioural disorders? A study in horses. *PloS One* 4(10), e7625. http://dx.doi.org/10.1371/journal.pone.0007625.
- Hausberger, M., Fureix, C., Lesimple, C. (2016) Detecting horses' sickness: In search of visible signs. Applied Animal Behaviour Science 175, 41–49. http://dx.doi.org/10.1016/j.applanim.2015.09.005.
- Hemsworth, L.M., Jongman, E., Coleman, G.J. (2015) Recreational horse welfare: The relationships between recreational horse owner attributes and recreational horse welfare. *Applied Animal Behaviour Science* 165, 1–6. http://dx.doi.org/10.1016/j.applanim.2014.11.019.
- Henderson, J.V. and Waran, N.K. (2001) Reducing equine stereotypies using an Equiball™. *Animal Welfare* 10, 73–80.
- Hendriksen, P., Elmgreen, K., Ladewig, J. (2011) Trailer-loading of horses: Is there a difference between positive and negative reinforcement concerning effectiveness and stress-related signs? *Journal of Veterinary Behavior* 6, 261–266. http://dx.doi.org/10.1016/j.jveb.2011.02.007.
- Hennessy, M.B., Kaiser, S., Sachser, N. (2009) Social buffering of the stress response: Diversity, mechanisms, and functions. *Frontiers in Neuroendocrinology* 30, 470–482. http://dx.doi.org/10.1016/j.yfrne.2009.06.001.
- Hockenhull, J. and Creighton, E. (2012) Equipment and training risk factors associated with ridden behaviour problems in UK leisure horses. *Applied Animal Behaviour Science* 137, 36–42. http://dx.doi.org/10.1016/j.applanim.2012.01.007.
- Hockenhull, J. and Creighton, E. (2013) Training horses: Positive reinforcement, positive punishment, and ridden behavior problems. *Journal of Veterinary Behavior* 8, 245–252. http://dx.doi.org/10.1016/j.jveb.2012.06.002.
- Hothersall, B. and Casey, R. (2012) Undesired behaviour in horses: A review of their development, prevention, management and association with welfare.

- Equine Veterinary Education 24, 479–485. http://dx.doi.org/10.1111/j.2042-3292.2011.00296.x.
- Houpt, K.A. (2018) Domestic Animal Behavior for Veterinarians and Animal Scientists. John Wiley & Sons, Hoboken, New Jersey, USA.
- Jongkees, B.J. and Colzato, L.S. (2016) Spontaneous eye blink rate as predictor of dopamine-related cognitive function A review. *Neuroscience & Biobehavioral Reviews* 71, 58–82. http://dx.doi.org/10.1016/j.neubiorev.2016.08.020.
- Jørgensen, G.H.M. and Bøe, K.E. (2007) A note on the effect of daily exercise and paddock size on the behavior of domestic horses (*Equus caballus*). *Applied Animal Behaviour Science* 107, 166–173. http://dx.doi. org/10.1016/j.applanim.2006.09.025.
- Jørgensen, G.H.M., Liestøl, S.H.O., Bøe, K.E. (2011) Effects of enrichment items on activity and social interactions in domestic horses (*Equus caballus*). *Applied Animal Behaviour Science* 129, 100–110. http://dx.doi.org/10.1016/j.applanim.2010.11.004.
- Kienapfel, K., Link, Y., Borstel, U.K.V. (2014) Prevalence of different head-neck positions in horses shown at dressage competitions and their relation to conflict behaviour and performance marks. *PloS One* 9(8), e103140. http://dx.doi.org/10.1371/journal.pone.0103140.
- Kikusui, T., Winslow, J.T., Mori, Y. (2006) Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society of London Series B. Biological Sciences* 361, 2215–2228.
- Landman, M.A.A., de Blaauw, J.A., van Weeren, P.R., Hofland, L.J. (2004) Field study of the prevalence of lameness in horses with back problems. *Veterinary Record* 155, 165–168. http://dx.doi.org/10.1136/ vr.155.6.165.
- Laposa, J.M., Collimore, K.C., Hawley, L.L., Rector, N.A. (2015) Distress tolerance in OCD and anxiety disorders, and its relationship with anxiety sensitivity and intolerance of uncertainty. *Journal of Anxiety Disorders* 33, 8–14. http://dx.doi.org/10.1016/j. janxdis.2015.04.003.
- Lazarus, R.S. (1966) Coping and the Process of Secondary Appraisal: Degree of Threat and Factors in the Stimulus Configuration. Psychological Stress and the Coping Process. McGraw-Hill Book Company, New York, USA.
- Leiner, L. and Fendt, M. (2011) Behavioural fear and heart rate responses of horses after exposure to novel objects: Effects of habituation. *Applied Animal Behaviour Science* 131, 104–109. http://dx.doi.org/10.1016/j.applanim.2011.02.004.
- Lesimple, C., Fureix, C., Biquand, V., Hausberger, M. (2013) Comparison of clinical examinations of back disorders and humans' evaluation of back pain in riding school horses. *BMC Veterinary Research* 9, 209. http://dx.doi.org/10.1186/1746-6148-9-209.
- Lethbridge, E., Pollux, P., Mills, D. (2007) Behavioural correlates of stereotypic behaviour in horses: A pilot

- study. In: Landsberg, G., Mattiello, S., Mills, D. (eds.) *Proceedings of the 6th International Veterinary Behaviour Meeting & European College of Veterinary Behavioural Medicine*. Companion Animals European Society of Veterinary Clinical Ethology, Riccione, Italy, pp. 72–73.
- McAfee, L.M., Mills, D.S., Cooper, J.J. (2002) The use of mirrors for the control of stereotypic weaving behaviour in the stabled horse. *Applied Animal Behaviour Science* 78, 159–173. http://dx.doi.org/10.1016/ S0168-1591(02)00086-2.
- McBride, S.D. and Hemmings, A. (2005) Altered mesoaccumbens and nigro-striatal dopamine physiology is associated with stereotypy development in a nonrodent species. *Behavioural Brain Research* 159, 113–118. http://dx.doi.org/10.1016/j.bbr.2004.10.014.
- McCue, P.M. (2002) Equine Cushing's disease. The Veterinary Clinics of North America: Equine Practice 18, 533–543.
- McGreevy, P.D. (2007) The advent of equitation science. The Veterinary Journal 174, 492–500. http://dx.doi.org/10.1016/j.tvjl.2006.09.008.
- McGreevy, P.D. and McLean, A. (2005) Behavioural problems with the ridden horse. In: Mills D.S., McDonnell S.M. (eds.) *The Domestic Horse*. Cambridge University Press, Cambridge, UK, pp. 196–211.
- McGreevy, P.D., French, N.P., Nicol, C.J. (1995) The prevalence of abnormal behaviours in dressage, eventing and endurance horses in relation to stabling. *The Veterinary Record* 137, 36–37. http://dx.doi.org/10.1136/vr.137.2.36.
- McGreevy, P.D., Oddie, C., Burton, F.L., McLean, A.N. (2009) The horse–human dyad: Can we align horse training and handling activities with the equid social ethogram? *The Veterinary Journal* 181, 12–18. http://dx.doi.org/10.1016/j.tvjl.2009.03.005.
- McLean, A.N. (2003) *The Truth About Horses*. Penguin, Victoria, Australia.
- McLean, A.N. and Christensen, J.W. (2017) The application of learning theory in horse training. *Applied Animal Behaviour Science* 190, 18–27. http://dx.doi.org/10.1016/j.applanim.2017.02.020.
- McLean, A.N. and McGreevy, P.D. (2010) Horse-training techniques that may defy the principles of learning theory and compromise welfare. *Journal of Veterinary Behavior* 5, 187–195. http://dx.doi.org/10.1016/j.jveb.2010.04.002.
- McLean, M. and McLean, A. (2008) Academic Horse Training: Equitation Science in Practice. Australian Equine Behaviour Centre, Victoria, Australia.
- Meagher, R.K., Campbell, D.L.M., Mason, G.J. (2017) Boredom-like states in mink and their behavioural correlates: A replica to study. *Applied Animal Behaviour Science* 197, 112–119. http://dx.doi.org/10.1016/j. applanim.2017.08.001.
- Milgram, N.W., Head, E., Weiner, E., Thomas, E. (1994) Cognitive functions and aging in the dog: Acquisition of

- nonspatial visual tasks. *Behavioral Neuroscience* 108, 57. http://dx.doi.org/10.1037/0735-7044.108.1.57.
- Mills, D.S. (2003) Medical paradigms for the study of problem behaviour: A critical review. Applied Animal Behaviour Science 81, 265–277. http://dx.doi. org/10.1016/S0168-1591(02)00286-1.
- Mills, D.S. (2005) Repetitive movement problems in the horse. In: Mills, D.S. and McDonnell, S.M. (eds.) The Domestic Horse: The Origins, Development and Management of its Behaviour. Cambridge University Press, Cambridge, UK, pp. 212–227.
- Mills, D.S. and Clarke, A. (2007) Housing, management and welfare. In: Waran, N. (ed.) *The Welfare of Horses*. Springer, Dordrecht, The Netherlands, pp. 77–97.
- Mills, D.S. and Davenport, K. (2002) The effect of a neighbouring conspecific versus the use of a mirror for the control of stereotypic weaving behaviour in the stabled horse. *Animal Science* 74, 95–101.
- Mills, D.S. and Riezebos, M. (2005) The role of the image of a conspecific in the regulation of stereotypic head movements in the horse. Applied Animal Behaviour Science 91, 155–165. http://dx.doi.org/10.1016/j. applanim.2004.08.027.
- Nakamura, K., Ishii, A., Kiyokawa, Y., Takeuchi, Y., Mori, Y. (2016). The strain of an accompanying conspecific affects the efficacy of social buffering in male rats. Hormones and Behavior 82, 72–77. http://dx.doi.org/10.1016/j.yhbeh.2016.05.003.
- Nicol, C.J. (1995) The social transmission of information and behaviour. Applied Animal Behaviour Science 44, 79–98. http://dx.doi.org/10.1016/0168-1591(95)00607-T.
- Normando, S., Meers, L., Samuels, W.E., Faustini, M., Ödberg, F.O. (2011) Variables affecting the prevalence of behavioural problems in horses. Can riding style and other management factors be significant? Applied Animal Behaviour Science 133, 186–198. http://dx.doi.org/10.1016/j.applanim.2011.06.012.
- Norton, P.J., Sexton, K.A., Walker, J.R., Ron Norton, G. (2005) Hierarchical model of vulnerabilities for anxiety: Replication and extension with a clinical sample. Cognitive Behaviour Therapy 34, 50–63. http://dx.doi. org/10.1080/16506070410005401.
- Ödberg, F.O. (1987) Chronic stress in riding horses. *Equine Veterinary Journal* 19, 268–269. http://dx.doi.org/10.1111/j.2042-3306.1987.tb01402.x.
- Overmier, J.B. and Seligman, M.E. (1967) Effects of inescapable shock upon subsequent escape and avoidance responding. *Journal of Comparative and Physiological Psychology* 63: 28. http://dx.doi.org/10.1037/h0024166.
- Panksepp, J. (1998) Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, New York, USA.
- Pierard, M., McGreevy, P., Geers, R. (2019) Effect of density and relative aggressiveness on agonistic and affiliative interactions in a newly formed group of horses. *Journal of Veterinary Behavior* 29, 61–69.

- Pritchard, J.C., Lindberg, A.C., Main, D.C.J., Whay, H.R. (2005) Assessment of the welfare of working horses, mules and donkeys, using health and behaviour parameters. *Preventive Veterinary Medicine* 69, 265–283. http://dx.doi.org/10.1016/j.prevetmed.2005.02.002.
- Rault, J. (2012) Friends with benefits: Social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science* 136, 1–14. http://dx.doi. org/10.1016/j.applanim.2011.10.002.
- Rochais, C., Fureix, C., Lesimple, C., Hausberger, M. (2016) Lower attention to daily environment: A novel cue for detecting chronic horses' back pain? *Scientific Reports* 6, 20117. http://dx.doi.org/10.1038/srep20117.
- Rørvang, M.V. and Christensen, J.W. (2018) Attenuation of fear through social transmission in groups of same and differently aged horse. *Applied Animal Behaviour Science* 209, 41–46. http://dx.doi.org/10.1016/j. applanim.2018.10.003.
- Ruis, M.A., te Brake, J.H., Buwalda, B., De Boer, S.F., Meerlo, P., et al. (1999). Housing familiar male wildtype rats together reduces the long-term adverse behavioural and physiological effects of social defeat. Psychoneuroendocrinology 24, 285–300. http://dx. doi.org/10.1016/S0306-4530(98)00050-X.
- Scopa, C., Palagi, E., Sighieri, C., Baragli, P. (2018) Physiological outcomes of calming behaviors support the resilience hypothesis in horses. *Scientific Reports* 8, 17501. http://dx.doi.org/10.1038/s41598-018-35561-7.
- Shihata, S., McEvoy, P.M., Mullan, B.A., Carleton, R.N. (2016) Intolerance of uncertainty in emotional disorders: What uncertainties remain? *Journal of Anxiety Disorders* 41, 115–124. http://dx.doi.org/10.1016/j. janxdis.2016.05.001.
- Swann, W.J. (2006) Improving the welfare of working equine animals in developing countries. Applied Animal Behaviour Science 100, 148–151. http:// dx.doi.org/10.1016/j.applanim.2006.04.001.
- Sykes, B.W., Hewetson, M., Hepburn, R.J., Luthersson, N., Tamzali, Y. (2015) European College of Equine Internal Medicine Consensus Statement – Equine gastric ulcer syndrome in adult horses. *Journal of Veterinary Internal Medicine* 29, 1288–1299. http://dx.doi.org/10.1111/ jvim.13578.
- Thorne, J.B., Goodwin, D., Kennedy, M.J., Davidson, H.P.B., Harris, P. (2005) Foraging enrichment for individually housed horses: Practicality and effects on behaviour. Applied Animal Behaviour Science 94, 149–164. http://dx.doi.org/10.1016/j.applanim.2005.02.002.
- van Oldruitenborgh-Oosterbaan, M.S., Blok, M.B., Begeman, L., Kamphuis, M.C.D., Lameris, M.C., et al. (2006) Workload and stress in horses: Comparison in horses ridden deep and round ('rollkur') with a draw rein and horses ridden in a natural frame with only light rein contact. *Tijdschr Diergeneeskd* 131, 114–119.
- Visser, E.K., VanDierendonck, M., Ellis, A.D., Rijksen, C., Van Reenen, C.G. (2009) A comparison of sympathetic

- and conventional training methods on responses to initial horse training. *The Veterinary Journal* 181, 48–52. http://dx.doi.org/10.1016/j.tvjl.2009.03.009.
- von Borstel, U.U., Duncan, I.J.H., Shoveller, A.K., Merkies, K., Keeling, L.J., et al. (2009) Impact of riding in a coercively obtained Rollkur posture on welfare and fear of performance horses. Applied Animal Behaviour Science 116, 228–236. http://dx.doi. org/10.1016/j.applanim.2008.10.001.
- Waran, N., McGreevy, P., Casey, R.A. (2007) Training methods and horse welfare. In: Waran, N. (ed.) *The Welfare of Horses*. Springer, Dordrecht, The Netherlands, pp. 151–180.
- Warren-Smith, A.K., Curtis, R.A., Greetham, L., McGreevy, P.D. (2007) Rein contact between horse and handler during specific equitation movements.

- Applied Animal Behaviour Science 108, 157–169. http://dx.doi.org/10.1016/j.applanim.2006.11.017.
- Weiss, J.M. (1972) Psychological factors in stress and disease. *Scientific American* 226, 104–113. http://dx.doi.org/10.1038/scientificamerican0672-104.
- Wickens, C.L. and Heleski, C.R. (2010) Crib-biting behavior in horses: A review. Applied Animal Behaviour Science 128, 1–9. http://dx.doi.org/10.1016/j.applanim.2010.07.002.
- World Health Organization. (2014) Mental health. Available at: https://www.who.int/features/factfiles/mental_health/ en/ (accessed 21 January 2019).
- Yarnell, K., Hall, C., Royle, C., Walker, S.L. (2015) Domesticated horses differ in their behavioural and physiological responses to isolated and group housing. *Physiology & Behavior* 143, 51–57. http://dx.doi. org/10.1016/j.physbeh.2015.02.040.

18 Mental Health Issues in Shelter Animals

VICTORIA CUSSEN AND PAMELA J. REID

Anti-Cruelty Behavior Team, American Society for the Prevention of Cruelty to Animals, New York, USA

18.1 Background

The realities of animal sheltering have changed drastically over recent decades. Over six million animals are estimated to be held in shelters every year in the United States (American Society for the Prevention of Cruelty to Animals, 2017a, 2018). However, the percentage of the pet population that is free roaming has decreased dramatically, and intake rates have also decreased in some areas of the country (Scarlett, 2013).

A major focus of animal sheltering is reducing the number of animals entering shelters and increasing the proportion of shelter animals that leave alive every year. In this respect, efforts have been impressively successful, with live release rates as high as 96% in some states (Shelter Animals Count, 2016); however, this is highly variable across the country and difficult to quantify accurately (see Scarlett, 2013 for an in-depth consideration of shelter reporting). Transportation of animals from shelters with lower live release rates to other shelters with higher live release rates, or to rescue groups, has increased as differences in excess shelter capacity, driven by intake and release rates, have emerged (Scarlett, 2013).

At the same time, length of stay (LOS) – how long the animal spends in the facility from intake to release – appears to be increasing. Twenty years ago, a national survey indicated dogs spent an average of 9.5 days in the shelter (Wenstrup and Dowidchuk, 1999 as cited in Gunter *et al.*, 2016). A more recent study reported a median LOS of 14 days, with a range from 1 to 71 days (Protopopova *et al.*, 2014). An animal's LOS is influenced by many factors (Marston and Bennett, 2003), from shelter location (Kay *et al.*, 2018) and behavior (Protopopova *et al.*, 2014), to visitor biases (Brown *et al.*, 2013; Gunter *et al.*, 2016; Protopopova and Wynne, 2016).

However, the overall shelter population picture is obscured because reporting is far from evenly distributed either within or between organizations (Scarlett, 2013). Furthermore, commonly reported metrics logically focus on intake and live release rates and do not include LOS (Shelter Animals Count, 2004). Adding overall duration in shelters or rescues for dogs that are transferred from one to the other, or for animals adopted and then returned, further complicates the picture.

Shelter policies vary and some hold animals for much longer than others. For example, a study of two shelters reported an average LOS of 42 days for adult dogs, with five individuals held for over a year (Brown *et al.*, 2013). Italy introduced national legislation forbidding the euthanasia of medically and behaviorally sound stray dogs, which has created 'chronic overpopulation' and welfare concerns in shelters due to life-long holds for the dogs (Cafazzo *et al.*, 2014). Animal sanctuaries are, by definition, intended to hold unplaceable animals for the remainder of their lives (Best Friends Animal Society, 2019).

Other long-term hold situations stem from legal proceedings, such as animal cruelty prosecutions. In the US, animals seized in cruelty cases are evidence in the criminal case and remain the property of the defendant unless there is a voluntarily relinquishment or a court-ordered forfeiture. Until those issues are resolved, the seized animals cannot be adopted and options for humane euthanasia are severely limited (Lockwood, 2006). Due to judicial backlog, laws that do not provide for prompt adjudication of ownership, and/or vigorous litigation caused by defendants, cases can sometimes take years.

The welfare of dogs in shelter has been studied since the 1990s (Beerda et al., 1997, 1998). LOS has important implications for physical health (University of Wisconsin Shelter Medicine, 2015) and also for mental well-being (McMillan, 2013). The effects of chronic stress are cumulative (Mills et al., 2014), meaning welfare impacts are compounded over the duration of an animal's shelter stay. This can result in a vicious feedback loop where LOS erodes an animal's welfare, leading to the development of behaviors that make them less adoptable, which increases their LOS, and on and on (McMillan, 2013). These cumulative welfare deficits can have long-lasting impacts on the animals. This chapter will focus on the mental well-being of dogs in shelters, especially with regard to long LOS.

18.2 Relinquishment Reasons with Mental Well-being Implications

The accepted wisdom is that behavior problems are major drivers for relinquishment of pets to shelters (Segurson *et al.*, 2005). This area has received much attention from welfare organizations and applied scientists. In a recent scoping review, Coe and colleagues (2014) identified almost 200 primary articles, reviews, and commentaries on relinquishment – almost all aimed at clarifying why animals are relinquished to shelters.

From the perspective of mental well-being, understanding why animals end up in the shelter environment may tell us what to expect of them while there. Because of differences in population demographics, source, record-keeping in shelters (Scarlett, 2013), and study design and conclusions in research articles (Lambert *et al.*, 2015), knowledge of psychological problems that cause the animal to be relinquished to the shelter is lacking.

Aggressive behavior was cited in 58% of reviewed publications, with moving house and owner's personal issues cited as the two major nonbehavioral reasons (54% and 50% of publications, respectively; Coe *et al.*, 2014). Caution should be used, however, before assuming dogs end up in the shelter because of pre-existing problematic behaviors that resulted in their relinquishment. In a later meta-analysis from the same institution (Lambert *et al.*, 2015), a large degree of variability was reported across studies, with, for example, moving reported two times as frequently as behavior problems in some studies and the reverse (i.e., behavior two times as frequently as moving) in others.

Further complicating the picture is that the behavioral background of most of the shelter population is unknown at the time of intake. Reasons for this include owners' reluctance to honestly report certain types of behavior problems (Segurson *et al.*, 2005), and a large subset of animals entering the shelter as either strays (Gunter *et al.*, 2018) or cruelty/neglect victims (Reid and Collins, 2015). Regardless of behavior on intake, animals in shelters *do* have behavior problems, and those problems can have direct impacts on mental well-being by increasing the animal's LOS, rendering them less able to cope with the shelter environment during their stay, or both (McMillan, 2013).

Shelter staff report that aggression is the most pressing behavior concern in shelters (Reid and Collins, 2015). Aggressive behavior is undesirable from the perspectives of staff safety and ultimate disposition (the latter because aggressive animals are more likely to be euthanized), but it is not necessarily directly troublesome from a mental well-being perspective. Aggression can be a normal behavior that may be driven by multiple underlying motivational states (Lindsay, 2005). Offensive aggression may not be mediated by a negatively valanced affective state – but if the behavior causes the dog to be more isolated or restricted while in the shelter it could indirectly result in psychological suffering.

Defensive, or fear-based aggression, also has implications for mental well-being, because it is indicative of a negative internal state – i.e., the animal is afraid and attempting to defend itself from perceived threats. The brain circuitry necessary for fear and panic is found across all mammals and animals will work to avoid fear-invoking situations or stimuli (Panksepp, 2011). Fear, either in conjunction with aggression or on its own, is a normal emotion – but one with a negative valence. In dogs, chronic states of fear cause psychological suffering, increase risk for certain diseases, and decrease life span (Dreschel, 2010).

Fear of strangers is a commonly reported behavior cited by owners relinquishing their animals (Segurson et al., 2005). Fear across multiple contexts is prevalent in animals that did not receive appropriate opportunities for social interactions in early life (McMillan, 2013). Because of inappropriate housing and/or aversive early life experiences, fear can also be experienced to such a degree that the animal cannot function in the normal day-to-day life of a companion animal (Miller et al., 2018). Approximately one-third of 3,000 dogs seized from cruelty cases exhibited

extreme, debilitating fear (Cussen and Reid, unpublished data). While extreme fear necessitates specialist behavior interventions such as is provided at the American Society for the Prevention of Cruelty to Animals' (ASPCA) Behavioral Rehabilitation Center (Miller *et al.*, 2018), even mild to moderate fear is also psychologically detrimental and, sadly, likely more widespread across shelter populations.

18.3 Shelter Environment Aspects with Mental Well-being Implications

While fear may not be the direct cause of relinquishment, it is likely experienced by a significant proportion of the shelter population. Reid and Collins (2015) called fear 'the most insidious behavior concern among shelter dogs'. They explained that fearful dogs may be quiet and withdrawn (Reid and Collins, 2015) and may still be viewed as easily adoptable by shelter staff. This could result in a situation where fearful dogs essentially 'suffer in silence' during their shelter stay.

Classic fear behaviors include panting, pacing, and trembling (Overall et al., 2001). Freezing and hiding behaviors are also associated with fear and are shown in response to threatening stimuli such as predators (Fureix and Meagher, 2015). More subtle indicators include tongue flicks, looking away, and a slightly lowered head or body carriage (Horwitz and Mills, 2009). These behaviors are frequently displayed by dogs in the shelter environment, but not all volunteers or staff may pick up on them (Flint et al., 2017). It is important that all staff and volunteers are trained in body language for the species they are working with in the shelter. Even those staff not working directly with animals benefit from such training, because it allows them to adjust their own behavior based on the animal's behavioral indicators of emotional discomfort before the situation becomes overwhelming to the animal. For example, a facility's staff moving equipment past a row of kennels could notice stress indicators and slow down to reduce noise and minimize stress.

Shelter programs dedicated to the behavioral well-being of their animals are an important and necessary resource to address psychological suffering in fearful and other psychologically distressed animals (Reid *et al.*, 2004; see also Chapter 24). But there are simple interventions any staff or volunteers can do, such as the ASPCA's 'Drive by Treats' protocol where all people offer or drop treats into

kennels as they walk past to create positive associations with activity outside the kennel (see Reid and Collins, 2015).

It is important for shelters to include psychological suffering and behavioral interventions in calculations of capacity for care. One recent example of time allocation at a facility indicated the required staff hours for minimum standards of care (based on a 15-minute-per-animal-per-day minimum standard) was between two to four times less than what the population size warranted and led to periods where staff time averaged 2.5 minutes per animal per day (Koret Shelter Medicine Program, 2019). This is clearly inadequate to provide for anything but the most basic physical needs of the animal and cannot provide for their psychological well-being. Fearful animals will be especially impacted by a lack of human attention, given the generally stressful nature of the shelter environment, which will be briefly summarized next.

18.3.1 Shelter environment and 'overall' welfare

While sheltering has advanced significantly in recent decades (Scarlett, 2013), it still holds true that dogs in shelters endure spatial and social restrictions because of practical realities of housing large numbers of animals. There is widespread concurrence across sheltering professionals and shelter-based researchers that the shelter environment is not designed to provide for the mental well-being of animals long term (Fig. 18.1).



Fig. 18.1. Stressors in the shelter environment include loud noises, unfamiliar smells, and spatial and social restrictions. Shelter stressors challenge the mental wellbeing of dogs.

Captivity is known to expose animals, including domesticated species, to a wide array of stressors, including loud noises, smells, restricted movement, forced proximity to humans and conspecifics coupled with the inability to interact directly, and others (Morgan and Tromborg, 2007). Most research has concerned the effect of the shelter environment or management on animals' behavior and overall welfare. The general approach is to compare some type of management change - e.g., space allowance, single or group housing, human interaction – and see how it impacts animals' behavior (Taylor and Mills, 2007a). Beerda and colleagues (1997, 1998, 1999a,b) did a series of seminal studies in the late 1990s that established references for physical and physiological manifestations of 'stress' in dogs. The measures are still commonly used in shelter-based research but typically not in a way that allows interpretation of results (see Hennessy, 2013 for a review of the difficulties). For example, the finding of a null effect on cortisol is ambiguous: was the animal unresponsive (and therefore not stressed) or was the hypothalamic-pituitary-adrenal axis hyporesponsive due to chronic stress (Hennessy, 2013)?

Results to date for behavioral, physiological, and immunological outcomes of shelter-based research are variable and, at times, contradictory (Part et al., 2014; Protopopova, 2016). Multiple reviews have been written on the subject, and readers are referred to them for more information (Taylor and Mills, 2007a). The equivocal results on shelter animal behavior likely result in part from looking for effects at the group, rather than the individual, level (Taylor and Mills, 2007a). Additionally, multicenter studies would be a welcome addition to the literature, as researchers using this approach found that the random variability between facilities explained more of the variation in the data than any of the wide range of management factors under study (Kiddie and Collins, 2014). This is not surprising, given the typically small sample sizes and/ or restricted number of observation points in shelter research. From a practical perspective, shelter managers should be cautious about adopting widespread management changes based on one or two studies or successes at other shelter facilities.

That said, the preponderance of evidence supports some aspects of the environment as being important to an animal's welfare. As noted in the introduction, the current leaders in shelter medicine agree the LOS is the largest risk factor for illness in shelter animals (Koret Shelter Medicine Program,

2019). Long LOSs are known to cause withinindividual changes in behavior that may be indicative of negative affective states, such as spending more time at the back of the kennel (Wells *et al.*, 2002a). In the authors' experience, the same is true for psychological suffering – the longer animals spend in the shelter the more likely they will display behavior that is indicative of poor mental well-being.

Restricted movement of mammals is known to be a powerful stressor and is linked with stereotypical or repetitive behaviors across a wide range of species (Mason, 2010). Studies on exercise in kennel-housed dogs do not consistently find that exercise per se is enriching (Jongman et al., 2018), but conclusive evidence is limited because exercise is usually confounded with increased space, social enrichment, and other factors (Cafazzo et al., 2014). The effect of exercise on shelter dog behavior is usually framed within the paradigm of increasing adoptability (by promoting behavior desired by humans). Because of that perspective, research focuses on short-term changes in behaviors related to kennel presence - as opposed to determining if exercise can improve the mental well-being of the animal directly (Protopopova et al., 2018). The authors are not aware of any investigations where shelter animals were given access to treadmills or other similar devices that would allow for increased exercise while holding other variables constant. This could be a promising area for future shelter-based research, as exercise is known to reduce stress in dogs generally (Horwitz and Mills, 2009) and allowing individuals to self-regulate could promote mental and physical health (see Section 18.4).

Noise is another known stressor in the shelter environment. It interferes with dogs' ability to rest and sleep (Fullagar et al., 2015), elicits a physiological stress response (Beerda et al., 1998, 1999b), and is related to poor postoperative recovery rates in human medical patients (Hekman et al., 2014; Fullagar et al., 2015). Dogs in shelters are frequently exposed to noise levels over 100 dB (Coppola et al., 2006a) and persistent exposure over 3 months led to hearing loss in shelter dogs (Scheifele et al., 2012). Design of shelters should incorporate noise dampening elements into the construction plans (Coppola et al., 2006a). Most shelters do not have the luxury of creating new facilities, and so pragmatic approaches are needed. Since much of the noise is created by the barking of the dogs themselves, decreasing arousal is a high priority in shelters.

Limiting visitor access during the day can significantly lower noise levels and promote resting behavior in shelter dogs (Hewison *et al.*, 2014), and many shelters now use 'quiet times' where all staff and volunteers have to be off the floor for a period during the day. These strategies could also be leveraged to decrease frustration and increase predictability, which would be beneficial for the mental well-being of shelter dogs (see Section 18.3.2). However, human interaction also has benefits, so balancing restful periods against social enrichment is important.

Providing social enrichment through human interaction consistently changes behavior and physiological indicators of stress in dogs in shelter (see Pullen et al., 2012 for an overview) (Fig. 18.2). Even opportunities for passive proximity to humans outside the home kennel decreased vocalizations and panting – compared to control dogs that were removed from their kennels but did not have human interaction – as much as petting or playing with the dog during the session (Shiverdecker et al., 2013). Relatively short sessions can be as effective as interactions twice as long (Willen et al., 2017). Dogs seem to prefer to interact with familiar people (Pullen et al., 2012) but also appear to benefit from contact with unfamiliar people (Coppola et al., 2006b).

There is some evidence that the beneficial effects of human interaction are short-lived (Willen *et al.*, 2017) and influenced by the dog's history (Pullen *et al.*, 2012). Because length of interactions vary between studies there is no rule of thumb for how best to set up human interaction. Maximizing time spent with the dog may increase welfare and provides an



Fig. 18.2. Social enrichment through human and/or conspecific interaction are well-established ways to reduce dogs' stress during a shelter stay.

opportunity to gather information about that animal's temperament (Coppola et al., 2006b). Care should be taken to avoid one-size-fits-all mandates for interactions because individual differences in personality and life history can affect whether dogs actually enjoy, and therefore benefit from, interacting with humans. Much of the human-interaction work is framed in an adoptability paradigm (see Pullen et al., 2012), so the long-term effects are largely unknown. One study found that areas of the dog's brain associated with reward were activated by smelling the scent of a familiar - but not an unfamiliar – human (Berns et al., 2015). Many shelters use olfactory enrichment already (Miller and Zawistowski, 2013). Incorporating scents specific to humans familiar to the dog may be a novel way to extend the benefit of social enrichment after the dog returns to the kennel, but this has yet to be

Social enrichment through interaction with conspecifics is another powerful way to offset the stress of the shelter environment. Providing dogs opportunities for social interaction with conspecifics through pair housing is known to reduce stress (Grigg et al., 2017). Dogs can be separated for feeding or enrichment if there are concerns about aggression, but aggression occurs at very low levels and is typically agonistic as opposed to actual fighting (Taylor and Mills, 2007a). Precautions against disease transmission should be included in social enrichment protocols (Miller and Zawistowski, 2015). Another way to provide social enrichment is playgroups. Playgroups are used by shelters to teach dogs appropriate social skills and promote positive mental health (American Society for the Prevention of Cruelty to Animals, 2017b). Depending on resources and shelter population, playgroups vary in their complexity (e.g., dyads versus group play) and formality (e.g., volunteer versus behavior staff, information collected during playgroup). The unifying idea is that interacting with other dogs is a powerful method for reducing the effects of shelter stress (Sadler, 2018). Anecdotal reports support the benefits of using playgroups (Dogs Playing for Life, 2018), but the effects on in-kennel behavior outside the play yard are yet to be systematically studied. Play has been extensively studied in a range of animals as a potential indicator, or even cause, of both positive emotions and welfare (for a review, see Held and Spinka, 2011). In general, play behavior decreases as welfare decreases, but some forms of play are known to increase during periods of stress

(Held and Spinka, 2011). For example, in both humans and animals, increases in solitary play (parallel play or object-directed), as opposed to interactive play, may indicate stress and negative mental well-being (Ahloy-Dallaire et al., 2018). Propensity for play in dogs is known to vary with breed (Svartberg, 2006; Asp et al., 2015) and temperament (Starling et al., 2013). Play in dogs is generally thought to increase social cohesion but it is also heterogeneous - i.e., forms include solitary, intraspecific, and interspecific – and types of play are mediated by different factors (reviewed by Sommerville et al., 2017). For example, intraspecific play may be more competitive than interspecific play (Bradshaw et al., 2015). These points have practical implications, inasmuch as absolute recommendations for amounts of play in shelter, or viewing all play as good play, are likely misleading. Here again, documenting baseline and withinindividual changes in behavior is necessary to track how well animals are coping with the shelter environment. Collecting and pooling such information across shelters could be a powerful way to identify risk factors for a variety of states associated with negative mental well-being (e.g., hyperarousal or anhedonia, see Section 18.4).

Importantly, the subjective experience of the shelter environment is influenced by the animal's previous experience. Hubrecht and colleagues (1992) found that dogs were less negatively impacted by individual housing in a kennel if they had experienced adverse social or thermal conditions in their housing prior to indoor kenneling. After entering a shelter, behavioral indicators of habituation increased over the first 10 days (increased self-care, decreased panting and paw lifting) but a physiological stress indicator (cortisol to creatinine ratio) of owner-surrendered dogs increased over time, whereas strays showed the reverse (Hiby *et al.*, 2006).

The physiological results may be explained by differences in adversity prior to intake: strays may be exposed to more physical stressors, but the physiological indicators did not relate to 'stress' behaviors within individuals (Hiby *et al.*, 2006). Similarly, a within-subjects design study found that prior habituation to the kennel in a home environment significantly lowered the magnitude of the dogs' stress response when they entered a training kennel compared to the control group dogs. Further, those dogs with no prior experience failed to adapt to the kennel environment, even after 3 months (Rooney *et al.*, 2007).

While at the time of intake owner-surrendered dogs did not differ significantly from strays when comparing hair cortisol levels (a measure of longterm cortisol release), they did not show a physiological response to human interaction, whereas stray dogs showed an acute decrease in cortisol (Willen et al., 2017). That may be counterintuitive, but dogs in shelters have been shown to form attachments more quickly than pet dogs (Thielke and Udell, 2018) and to seek proximity to humans, especially familiar humans, more than laboratory-reared dogs (Pullen et al., 2012). Owner-surrendered dogs may be more distressed due to the loss of a stable attachment figure (Tuber et al., 1999). So, perception of and response to various environmental aspects likely differ between dogs with varied histories and or personalities (see Section 18.4).

18.3.2 Ontogeny in a shelter environment

A special note is warranted on pregnant bitches and puppies whelped in animal shelters. Regardless of LOS, puppies born in a shelter environment are indirectly impacted by their mother's prenatal and postnatal stress and are directly exposed to a stressful environment during an important developmental period. Therefore, the impacts are outsized in relation to the LOS and could potentially impact the puppies' mental well-being for their entire lives (Fig. 18.3).

The importance of early postnatal development periods is well known (summarized by Scott and Fuller, 1965). There are breed-specific differences in ontogenic timing (e.g., of fear, see Morrow *et al.*, 2015). Puppies need to experience some degree of novelty so that, as adults, they can cope with the



Fig. 18.3. Puppies born in a shelter environment are exposed to a stressful environment during an important developmental period. These stressors could potentially impact the puppies' mental well-being for their entire lives.

everyday things experienced by pet dogs (Estep, 1991). Controlled and gradual exposure during early development is important for reducing fear and anxiety in dogs (Rooney *et al.*, 2016). Environments that fail to meet puppies' developmental needs can cause a range of behavior problems including fear, reactivity, impulse control deficits, and anxiety (Hammerle *et al.*, 2015). The negative impacts are especially pronounced when dogs endure inappropriate conditions from a young age (McMillan *et al.*, 2016).

Although direct comparisons cannot be made between shelters and commercial breeders or hoarding cases, puppies in shelters face many of the same challenges, such as prenatal maternal stress, restricted exposure to environmental and/or social stimuli, and maternal separation (reviewed by McMillan, 2017). Hetts and colleagues (2005) recommended developing proactive behavioral health programs with criteria that reflect mental health (see also Chapter 10). Howell and Bennett (2011) specifically addressed possible approaches to ensuring the behavioral health of puppies raised in shelters. Ensuring the appropriate behavioral development of those puppies could potentially stave off development of behaviors that would cause them to be returned to shelters later in their life. This represents an opportunity to protect mental well-being twice in an animal's life by using interventions that occur at a single point of development.

18.4 Psychological Environment

While much shelter-based research has examined aspects of the animal's physical and social environment there is little in the way of addressing what Taylor and Mills (2007a) call the 'psychological environment'. This aspect is arguably of the most importance for the subjective experience of the animal, because it involves agency and choice (Meehan and Mench, 2007). Agency – or lack thereof – may be the most directly relevant aspect of the shelter environment as concerns mental well-being (see Chapter 6 for more on personal control in animals). A sustained absence of control, in conjunction with forced proximity to unpredictably available rewards or aversive stimuli, can lead to extreme frustration or apathy (Brando and Buchanan-Smith, 2018).

18.4.1 Hyperarousal and frustration

As discussed above, shelters are loud, with much of the noise coming from the dogs themselves. Sounds associated with food preparation and people walking past the kennel fronts tend to trigger high arousal behaviors such as barking, spinning, and wall bouncing in kenneled dogs (Wells and Hepper, 2000; Denham *et al.*, 2014). Hyperarousal is a common complaint in the shelter and several studies have looked at training low-arousal behaviors such as sitting, eye contact, and not barking in kennel to increase adoptability (see Reid and Collins, 2015 for an overview of this research) (Fig. 18.4).

High arousal behavior is likely maintained, at least partially, by a conditioned emotional response to the appearance of people and high-value reinforcers such as time outside of the kennel, human interaction, or food delivery (Protopopova *et al.*, 2018). To a point, increasing anticipatory behaviors can indicate a positive subjective state, because the animal has an expectancy of obtaining an impending reward and is not suffering from anhedonia (Spruijt *et al.*, 2001; van der Harst and Spruijt, 2007). Above



Fig. 18.4. Hyperarousal, sensitization to reward, and frustration may all be related to a restricted environment and are all indicators of poor mental well-being.

a certain point, however, excess anticipatory behavior may appear almost manic, and may indicate a sensitization to reward (Bassett and Buchanan-Smith, 2007). Reward sensitization can occur when the environment offers so few rewards that *any* reward becomes highly salient and the animal is neurologically primed to have a large emotional response to it (Spruijt *et al.*, 2001; Cabib, 2006). The *degree* of the anticipatory response could be a potential metric of affective state in shelter dogs (van der Harst and Spruijt, 2007). This is an area that remains unexplored and is likely linked to individual personality or coping style.

Dogs in shelters repeatedly see and hear other dogs and humans, with no means to interact with them, which can lead to frustration (Taylor and Mills, 2007a). All mammals, and possibly all vertebrates, are thought to share several 'core' emotional systems, including seeking, rage, joy, and others (Panksepp, 2005). The 'seeking' system supports the expression of goal-directed behaviors such as foraging. Animals in shelters may be motivated to engage in appetitive behavior, such as seeking social interaction, but due to the physical restrictions of the kennel environment they may be unable to reach the consummatory phase of behavior, e.g., interaction with a person or a conspecific. The core emotional systems in the brain are interconnected by inhibitory and excitatory synapses. Repeated frustration of goal-directed behavior causes excitation of the 'rage' system, which is associated with aggressive behavior in animals (Panksepp, 1998). Whether or not this mechanism underpins the development of barrier aggression or reactivity in shelter dogs is not known. However, frustration and conflict are two known risk factors for repetitive behaviors in companion animals (Luescher, 2009).

Stereotypical behavior is a subset of repetitive behavior. Repetition is necessary, but not sufficient, to classify a behavior as stereotypical. A dog that spins two or three times in response to environmental triggers and/or anticipation (Denham *et al.*, 2014) is different from an animal that paces invariantly in the absence of environmental triggers (see Mason, 2010). In practice, however, shelter-based research tends to conflate the two, making study comparisons and interpretation of results difficult (Protopopova, 2016). Physical or chemical prevention of repetitive/stereotypical behavior is not advised, because it is likely *some* of these behaviors serve as a coping mechanism to help the animal deal with a suboptimal environment (Mason and

Latham, 2004). However, behavioral indicators of chronic stress in shelter animals are still unsettled (Hewson *et al.*, 2007). This is in part because of the loose definitions mentioned above, but it is also likely because there are multiple mechanisms underpinning stereotypies (Mason and Latham, 2004). Altering known risk factors, including the animal's physical, auditory, and/or social environment (see Mason and Rushen, 2008 for a complete overview), should be the first step in addressing these behaviors in the shelter.

18.4.2 Anhedonia and helplessness

The flipside to reward sensitization is the loss of neurological or behavioral responsiveness to environmental rewards. This phenomenon is called 'anhedonia', or a loss of enjoyment in previously enjoyed activities or rewards, and has been used in animal models of human depression (Fig. 18.5). Outside of the laboratory, however, anhedonia can be difficult to distinguish from relaxed resting if relying only on behavioral measures (Mason and Latham, 2004). For example, dogs suffering from a depressive-like state probably spend the majority of their time lying at the back of their kennel, much the same as would a dog that has adjusted to the shelter environment and is lying down to relax (Wells *et al.*, 2002a; Mason and Latham, 2004).



Fig. 18.5. A loss of interest in previously pleasurable activities, known as 'anhedonia', is a characteristic of human depression and is used in animal models of depression. It may co-occur with learned helplessness – where an animal learns their actions do not influence outcomes in their environment and cease trying. Distinguishing negatively valanced passivity from resting requires monitoring changes in behavior over time and may include a subjective assessment.

So how can these states be distinguished? One approach is to use subjective assessments such as the Qualitative Behavioral Assessment (QBA; Wemelsfelder, 2005). Here, multiple observers watch the same short video clip and freely describe the animal, statistical methods are then used to compile and extract results. QBA generally finds high agreement between people with varying levels of familiarity and expertise for a given species and has been validated in a variety of species (Wemelsfelder, 2005).

The rationale behind QBA is that animals manifest their internal subjective states through qualitative changes to their behavior – e.g., not *if* they sit but *how* they are sitting – what Wemelsfelder and colleagues called the 'whole animal' approach (Wemelsfelder *et al.*, 2001). QBA was developed for farm animals but has since been applied to assessing emotional expressions in dogs (Walker *et al.*, 2010). More recently, QBA was compared to behavioral and physiological indicators of welfare between dogs in the home and both short- and long-term shelter environments (Walker *et al.*, 2016). The need for complicated statistical analyses likely limits widespread use of QBA in shelters.

Another 'direct report' method of assessing animals' affective states is using operant paradigms that assess cognitive function. Changes in cognitive function called cognitive biases (e.g., attention bias; see Cussen and Mench, 2014) can be caused by acute or chronic stress. The most common paradigm measures judgment biases, to see if an animal is 'optimistic' or 'pessimistic' about the outcome of an ambiguous situation (Paul et al., 2005; see also Chapter 23). Cognitive biases shed light on the animal's internal emotional state, which is of great importance to psychological well-being. For example, dogs diagnosed with separation anxiety, which is acutely stressful during the owner's absence, were also found to have a more negative expectation in the owner's presence compared to control dogs (Mendl et al., 2010). A later study replicated this finding and extended it by showing treatment with a selective serotonin reuptake inhibitor (fluoxetine) abolished the negative judgment bias as compared to nonanxious controls (Karagiannis et al., 2015). Cognitive bias paradigms require training the animals on the operant discrimination task and must be carefully controlled to allow interpretation of results. For those reasons, they may be useful in shelter-based research, but are limited in their usefulness as dayto-day quality of life (QOL) assessments.

A more familiar but less well validated approach is to simply use a rating scale to make some sort of qualitative assessment of how shelter animals appear to be doing as regards measures thought to be related to QOL (McMillan, 2000; Belshaw et al., 2015). The acceptability of this type of proxy report for animals' emotional experiences is debated (McMillan, 2007; Taylor and Mills, 2007b) but it could be combined with quantitative behavior measures to help interpret what the animal is experiencing (Hewson et al., 2007). If shelters decide to use a subjective-scale assessment, care must be taken to control for: (i) transient, nonrepresentative, behavior associated with a particular context; and/ or (ii) differences in interpretation of behaviors within a context. For point (i), a dog with overall poor QOL may show some interest on walks but show such signs as listlessness, social withdrawal, and disengagement with enrichments the majority of the time. Multiple people rating an animal increases the likelihood that an accurate description of their typical behavior will emerge. For point (ii), standardizing the information used when making the assessment can highlight differences in how people 'see' and interpret the same behavior. Information can be standardized by using, for example, a video clip á la QBA. Whatever approach is used, being aware of how the chosen method may impact QOL assessment results is important to allow for the best decision making possible.

As discussed above, the inability to access desired stimuli can lead to frustration, reward sensitization, and possibly to the development of stereotypies. Similarly, the inability to escape aversive stimuli can have a devastating effect on psychological wellbeing. Dogs that could perform a behavior to avoid an aversive event (shock) learned to do so, whereas those whose behavior did not impact exposure could not learn to do so later - even when avoidance was possible - a phenomenon called 'learned helplessness' (Seligman and Maier, 1967). Further, dogs that were able to turn off an electric shock showed a significantly lower increase in cortisol compared to dogs that had no control over a shock of the same intensity (Dess et al., 1983). Importantly, the behavioral impacts of learned helplessness were long-lasting (Seligman and Groves, 1970).

Dogs in shelters often cannot retreat from aversive physical and/or social stimuli and this is likely a major in-shelter stressor (Blackwell *et al.*, 2010). Providing crates in kennels affords dogs a place to retreat (Miller and Zawistowski, 2013) but should

be balanced against the ability to monitor their health and allow viewing by potential adopters. In addition, because individual dogs vary in their response to a range of situations, opportunities to avoid aversive stimuli should be built into those situations to prevent forced exposure. An example of this is the playgroup activities conducted by the ASPCA Anti-Cruelty Behavior Team. The playvards have 'stash pens' that are used as airlocks to bring dogs in and out of the yard, and for safely holding dogs in the event of a fight. Anecdotally, some dogs will 'self-stash' - i.e., they walk over to and stand in front of a stash pen door until they are let out of the yard. In some cases, they will come back into the yard after a self-imposed time-out, in others they will orient toward the exit of the stash pen until they are returned to their kennel. Other dogs, however, are not so clear in their exit-directed behavior. In those cases, relatively more subtle signs of stress such as hugging the perimeter of the yard, panting, and sniffing need to be attended to by shelter staff.

This example is used to illustrate a larger point that involves giving the animals agency wherever possible. We may think, based on our experience or applied research, that something should be positive or rewarding and therefore incorporate it into our shelter operations (e.g., playgroups, one-on-one time), this is not always the case. For example, one study found an increased activation of the sympathetic nervous system, a physiological stress response, in response to human interaction (Bergamasco et al., 2010). The valence of different experiences is no doubt variable, either between individuals or within individuals across days. Accordingly, providing opportunities for control also applies to putatively 'positive' situations, such as human or conspecific interaction. It is very important that all staff are trained in basic body language of the species they work with, and that they are encouraged to assess the animal in front of them. Standard operating procedures for the time per day a dog is played, trained, walked, etc., need to build in enough flexibility that animals can 'opt out' of a nonrequired situation.

The takeaway is that chronic environmental stress profoundly impacts animals and can cause changes to the structure and function of animals' brains (Cabib, 2006). Behaviorally, this manifests in many ways, including as an increasing responsivity to pleasurable stimuli (reward sensitization) or the *converse*, a decrease in responsivity to pleasurable stimuli (anhedonia). These opposing neural

changes likely underpin hyperarousal and helplessness in shelter animals, but this has not been studied to date. An important component of these opposing processes is change over time. As discussed above, LOS in the shelter is known to impact animals' behavior (Wells *et al.*, 2002a), underscoring the importance of longitudinal monitoring of within-individual changes in the shelter to assess the welfare of an individual animal.

For example, if a QOL instrument included activity without respect to baseline behavior on intake, it would not be possible to determine if increasing activity indicated an uptick in arousal and possible sensitization - and was therefore an indicator of chronic stress for an initially 'normal' dog - or if it reflected increasing engagement with the environment and decreasing apathy - and was therefore an indicator of positive mental well-being for an initially 'shut-down' dog. Therefore, routine assessments are necessary to track changes in an individual's behavior, if any. Similarly, if at the population level a new intervention was trialed at a shelter (e.g., increased exercise opportunities) and half the dogs decreased in-kennel activity and half increased in-kennel activity, then lacking knowledge of preintervention behavior the results may be uninterpretable as it is entirely possible that all of the animals had their welfare improved, or, conversely, compromised.

Are there predictors that indicate which direction of behavioral change is positive or negative for an animal? Could these be assessed at intake, and animals assigned to a particular behavioral subpopulation? These questions are critical for monitoring the psychological well-being of the shelter population, but currently remain largely unexplored.

18.5 Personality, Coping Styles, and Individual Differences

How animals respond to stress is mediated by multiple factors including genetics and previous experience (Southwick and Charney, 2012). Two concepts related to individual differences in animal behavior are coping styles and personality, terms often used interchangeably although they differ in important ways, including assessments and predictions (Zidar *et al.*, 2017). Both the related concepts seek to explain variability between animals of the same species in their behavioral responses to a given situation or stimulus.

Animals vary in both *how* they respond to stress (coping style) and the *amount* they respond (stress

reactivity or emotionality) (Koolhaas and van Reenen, 2016). Coping styles emphasize the relationship between observed behavioral tendency and the physiological mechanisms that underpin the behavior; the two commonly used classifications are 'proactive' and 'reactive' coping styles (Koolhaas et al., 1999). Proactive individuals are less behaviorally flexible, more impulsive, and more easily frustrated than reactive individuals, which renders them less able to deal with changing environments (Coppens et al. 2010).

There are some indications dogs have stable coping styles, but this area has yet to be fully explored. Denham et al. (2014) found categorical differences in the strength of kenneled dogs' physiological response (i.e., stress reactivity) to a stress challenge test. Importantly, dogs in the 'high' group showed significantly more repetitive behaviors than other dogs – and they were the *only* individuals to show repetitive behaviors in the absence of environmental triggers such as food preparation or humans walking in front of their kennels (Denham et al., 2014). Other authors have loosely referenced coping strategies (Rooney et al., 2007; Blackwell et al., 2010), but coping styles per se have not been systematically studied in dogs. An exception is a study with Austrian police dogs during a simulated social stress test (Horváth et al., 2007). Those authors speculated a 'proactive' coping style may be related to aggressiveness while a 'reactive' coping style may be related to fearfulness (Horváth et al., 2007).

Coping style research is concerned with the mechanisms causing differences in behavior and the fitness advantages conferred by different coping styles in different environments (Coppens et al., 2010). Comparative personality is also interested in individual differences but differs conceptually from coping styles (Gosling and Vazire, 2002). Both coping styles and personality are directly relevant to shelters because they have implications for resiliency to stress and disease susceptibility (Cavigelli, 2005; Capitanio, 2008; Koolhaas, 2008; Koolhaas et al., 2010). For example, a recent shelter-based research study found a link between coping styles in stray dogs and disease development in the shelter (Corsetti et al., 2018).

Personality research in nonhuman animal species has a long history (reviewed by Gosling and John 1999; Gosling, 2001). Recent years have seen a large expansion of research focused specifically on dog personality (Gosling *et al.*, 2003; reviewed by Jones and Gosling, 2005). This includes the familiar

Canine Behavioural Assessment and Research Questionnaire (C-BARQ) (Hsu and Serpell, 2003; Segurson *et al.*, 2005) and the less ubiquitous but extensively validated Dog Personality Questionnaire (Jones, 2008). Much interest in dog personality is driven by the need to predict suitability of guide dogs and military working dogs. Because of this, most dog personality research has not used shelter dogs, but at the same time shelter-based personality assessments are generally better validated than others in the literature (Jones, 2008).

Subjective rating scales used to assess personality can be reliable within and between raters (Cussen and Mench, 2014), but they are sensitive to the familiarity of the rater with the animal (Gosling, 1998). Reliably classifying personality requires aggregate observation (Epstein, 1979). Behavior assessments typically measure individual trait(s) - e.g., 'fear' or 'aggression' - as opposed to overall personality. This approach can decrease the predictive value (Reid et al., 2004). Not surprisingly, longitudinal behavior assessments based on observations over a month's time were better able to explain variability within and between dogs in a shelter than were stand-alone behavior assessments (Goold and Newberry, 2017). However, current shelter behavior assessments are generally not repeated and instead provide a snapshot of behavior at the time of the test. As a result of all of these factors, shelter-based assessments at present tend to be not terribly predictive of future behavior (Shabelansky et al., 2015) but there are exceptions (Reid and Collins, 2012).

The need for familiarity limits the usefulness of personality ratings as a means of quickly classifying animals as they enter the shelter – although they are likely useful for animals with longer stays. Developing easy-to-administer and predictive tests may benefit from the large literature on coping styles, where simple assessments (e.g., a back restrain test) are predictive of future behavior (Bolhuis et al., 2004). Shelter dogs in Italy were assigned to 'shy' or 'bold' coping styles using relatively simple novel object, T-maze, and novel environment assessments. A blood sample was taken on admission and 30 days later. Dogs classified as 'bold' were reported to be less susceptible to disease compared to dogs classified as 'shy' on intake (Corsetti et al., 2018). An approach where simple, validated assessments are used to classify coping style on intake would allow dogs to be assigned to a category of psychological management - e.g., high or low novelty, housing in quiet or active areas of the shelter, etc. - to best prevent mental suffering and

behavioral deterioration during their time in the shelter. This could be coupled with longitudinal, aggregate personality assessments that may enable more accurate predictions of future behaviors following placement.

18.6 Recommendations

18.6.1 Agency, or, 'behavioral engineering' revisited

Environmental enrichment has been extensively studied in farm, zoo, and shelter animals (Mench, 1998; Young, 2003; Miller and Zawistowski, 2013). Wells (2004) provides the most recent review of in-shelter enrichment, but the authors are aware that a new review article on shelter enrichment covering the intervening years of research since that report is forthcoming. Such a review is a welcome and needed addition to the literature – because given the changes in shelter realities, we need a reconsidering of what we know about animals in shelters.

Early zoo-based enrichment work was designed to increase animals' degree of control without reference to naturalness, an approach dubbed 'behavioral engineering' (Markowitz, 1982). The purpose was to provide opportunities for animals to act on and alter outcomes in their environments; 'unnatural' manipulanda were used out of expediency to retrofit barren zoo enclosures (Markowitz, 1982). This approach addressed the overarching biological imperative to act on a responsive environment. One example was essentially a primate vending machine where plastic tokens could be exchanged for food. Individuals varied in how much they hoarded the tokens, when and how they traded them in, the strategies they used to take others' food, and tactics used to avoid theft (Markowitz and Aday, 1998). On its face this promoted unnatural behavior (i.e., using tokens in a vending machine) but it also facilitated choices about feeding patterns, environmental appraisal, effort exerted, and the like.

The term 'behavioral engineering' gave way to 'behavioral enrichment' and then to 'environmental enrichment'. Along the way, more emphasis was placed on 'naturalizing' time budgets and housing environments (Fraser, 2009). It is not clear what time budget standard to compare shelter dog activity against (Taylor and Mills, 2007a). For example, pet dogs are often left home alone for extended periods of time, so it is unclear if promoting an (in) activity pattern that mirrors that of pet dogs is

advisable (Owczarczak-Garstecka and Burman, 2016). Naturalizing time budgets has led to a focus on terminal behaviors as opposed to the psychological imperatives – e.g., agency, problem solving – underpinning the behaviors (Meehan and Mench, 2007). For example, feeding enrichments are often provided without consideration of promoting food acquisition behavior, so consumption of a desired food item is elicited but the cognitive or physical challenges associated with foraging are not.

Food enrichments in animal shelters are given to promote quiet time or relaxed chewing/licking in dogs with the goal of decreasing arousal levels and barking (Schipper et al., 2008) (Fig. 18.6). How 'enriching' the items are to the animals, i.e., their biological relevance and their influence on satiating underlying motivations (Newberry, 1995), is rarely assessed in shelter programs due to time constraints. Feeding enrichment is generally given in addition to the daily ration and is therefore essentially a treat rather than a mechanism to increase agency (see Meehan and Mench, 2007). The only choice the animal has is to eat the treat or not – as opposed to choosing how much of their nutrition they will work for, when they will work for it, and what they will do to acquire it. Many dogs deteriorate in shelters despite the provisioning of 'enrichment' of some sort.

An alternative approach may be to feed the animals' daily ration in a way such that they must act



Fig. 18.6. Environmental enrichments, such as this frozen Kong® stuffed with peanut butter, often promote terminal behaviors such as licking, chewing, and eating. Developing enrichments that also increase an animal's ability to control their environment may help to prevent frustration or helplessness; this is a promising area for future research.

on the environment to obtain it and can decide how or when to do so. The tendency of animals to work to obtain food even when the same type of food is freely available is called 'contrafreeloading' (Jensen, 1963), and is well documented across a wide range of vertebrate species (Inglis et al., 1997). Contrafreeloading appears strongly related to food acquisition (i.e., appetitive foraging behavior) – for example, animals will also work for access to water but show less of a preference for doing so - and preference for contrafreeloading is stronger when the value of the food reinforcer is higher (Osborne, 1977). Research on contrafreeloading is sparse for canids (e.g., contrafreeloading enrichment in the maned wolf; da Silva Vasconcellos et al., 2012), so it is possible they would fail to problem solve or prefer freely available food. Concerns about caloric intake can be addressed in a manner similar to Markowitz (1982), where any food left unforaged at the end of the day was provided freely to the animal. That approach accounts for individuals that are unwilling or unable to work for food and allows staff to monitor food intake. This approach holds potential as an easy way to increase agency in the shelter environment.

Providing response-dependent enrichments reduced agonistic and aggressive behaviors in both primates and marine mammals, and they were still used by the animals over periods of months or years (Markowitz, 1982). Dogs are known to habituate to enrichment objects over time (Taylor and Mills, 2007a). To avoid this, shelter-based enrichment programs rotate enrichment items and modalities to sustain interest (Miller and Zawistowski, 2013), but the long-term effect of such programs on within-individual changes in behavior has yet to be rigorously examined.

While typically tied to foraging, increased choice and agency can be created by allowing the animals to manipulate their micro-environment in some way. Markowitz (1982) empowered captive animals to control the light and music in their enclosure. Training a dog to operate an on-off switch is a trivial task that could be applied to a speaker in the kennel. They could then select whether, for example, to listen to classical music, white noise, some other type of music, or nothing. Given that dogs habituate quickly to auditory enrichment (Bowman *et al.*, 2015) and genre of music is known to influence its efficacy (Wells *et al.*, 2002b; Bowman *et al.*, 2017), providing choice may maximize the impact of auditory enrichment by allowing individuals to select

the music they hear. Similarly, in a yoked-control study, marmosets given supplemental light alone showed significant improvements in behavioral indicators of well-being, but supplemental light given in conjunction with the ability to control it was significantly better (Buchanan-Smith and Badihi, 2012). So, not only what resources are provided to captive animals, but also *how* they are provided is important. Allowing control over any element in the environment could be beneficial, which provides shelters with limited numbers of resources another avenue of promoting mental well-being. Shelter staff are nothing if not inventive, and many other possibilities would likely present themselves once people began to look for opportunities to allow animals to make choices in their day-to-day life.

18.6.2 Predictability

Predictability is another important aspect of the psychological environment (see Chapter 6). For a given reinforcer, animals prefer a signaled (i.e., predictable) reinforcer more than the same reinforcer given to them without a signal, and they show conditioned place preferences for areas associated with predictable reinforcement compared to areas associated with unpredictable reinforcement (Osborne, 1977). Neurophysiological studies on the neural basis of anticipation show that after an association is learned, neural activity shifts backward in time such that cells associated with the reinforcer begin to fire in response to the conditioned stimulus, i.e., before the reinforcer is presented. So, animals are rewarded more quickly when an associated cue precedes the reward.

Conversely, rodent models of predictability found that predictable aversive stimuli reduced the animals' physiological stress response compared to the same but unpredicted stimulus (e.g., footshock in rodents; Gliner, 1972). Dess and colleagues (1983) reported a somewhat different relationship between predictability and stress in dogs: no difference was found in physiological responsiveness to an unpredictable versus predictable aversive stimuli. But, importantly, when tested later in a novel environment, dogs with a history of unpredictable shock were sensitized to an aversive stimulus in the novel environment, resulting in significantly larger cortisol responses (Dess et al., 1983). Therefore, it seems clear that predictability ameliorates the physiological response to unpleasant experiences on some timescale.

An environment that provides animals the opportunity to both predict future events and control them when they occur is important for mental wellbeing. This can be challenging in animal shelters but need not be impossible. Simple predictive cues preceding normal operations, especially for temporally variable events such as opportunities for social interaction, walks, and other activities, could have a profound impact on shelter animals. Logically, predictive cues could increase arousal through anticipation of access to reinforcers, but they should also decrease arousal at other times when opportunities for reward are not signaled. Currently, animals make associations between humans or facility noises and rewards (Denham et al., 2014; Protopopova et al., 2018), but as predictive cues they have a high rate of nonreinforcement; for example, human presence may have nothing to do with a specific dog or activity at that specific time. Learning theory suggests variable schedules of reinforcement maintain responding in the absence of reward through the gambling effect (Reid, 1996). Encouraging associations with cues only present during the target activity (e.g., feeding, walk time) may, then, reduce overall arousal and frustration in shelter animals. At present, this has yet to be evaluated in shelters.

18.7 Concluding Remarks

Animal shelters are tasked with providing care for large numbers of animals. The psychological environment is a critical component of that care. Individual differences in such factors as experiences, genetics, and personality result in animals that are more or less able to cope with the shelter environment. Animals' behavior, their response to stress, and their mental well-being are inherently individualistic.

Assessing within-individual or within-categorical (e.g., coping style) changes in behavior over time are necessary – both to provide for the welfare of individual animals and to assess the efficacy of shelter-based behavioral interventions. An infinite number of operational procedures in shelters are not possible, nor are they necessary to ensure mental well-being. Behavioral observations on intake or shortly thereafter could be used to assign individual animals to one of a finite number of psychological risk groups, e.g., resilient, fearful, high arousal, etc. Specific management protocols based on risk category could then streamline the use of shelter resources and decrease behavioral deterioration of animals

with longer LOSs. This approach would also allow for more refined intervention impact assessments, because population-level assessments can miss meaningful differences in behavioral responses between risk categories.

Overarching components of psychological wellbeing, namely control and predictability, can be built into existing operations. This allows shelters to provide for the mental well-being of animals in their care while continuing their important work.

18.8 References

- Ahloy-Dallaire, J., Espinosa, J., Mason, G. (2018) Play and optimal welfare: Does play indicate the presence of positive affective states? *Behavioural Processes* 156, 3–15. http://dx.doi.org/10.1016/j.beproc. 2017.11.011.
- American Society for the Prevention of Cruelty to Animals. (2017a) ASPCA Releases new data showing remarkable progress for homeless dogs & cats. Available at: https://www.aspca.org/about-us/press-releases/aspca-releases-new-data-showing-remarkable-progress-homeless-dogs-cats (accessed 24 March 2019).
- American Society for the Prevention of Cruelty to Animals. (2017b) APSCA and the Petco Foundation Partner to grant \$1.5 million to dogs playing for life to expand life-saving playgroups nationwide. Available at: https://www.aspca.org/about-us/press-releases/aspca-and-petco-foundation-partner-grant-15-million-dogs-playing-life-expand (accessed 20 February 2019).
- American Society for the Prevention of Cruelty to Animals. (2018) Pet statistics. Available at: https://www.aspca.org/animal-homelessness/shelter-intake-and-surrender/pet-statistics (accessed 20 December 2018).
- Asp, H.E., Fikse, W.F., Nilsson, K., Strandberg, E. (2015) Breed differences in everyday behaviour of dogs. Applied Animal Behaviour Science 169, 69–77.
- Bassett, L. and Buchanan-Smith, H.M. (2007) Effects of predictability on the welfare of captive animals. Applied Animal Behaviour Science 102, 223–245. http://dx.doi.org/10.1016/j.applanim.2006.05.029.
- Beerda, B., Schilder, M.B., van Hooff, J.A., de Vries, H.W. (1997) Manifestations of chronic and acute stress in dogs. *Applied Animal Behaviour Science* 52, 307–319. http://dx.doi.org/10.1016/S0168-1591(96)01131-8.
- Beerda, B., Schilder, M.B., van Hooff, J.A., de Vries, H.W., Mol, J.A. (1998) Behavioural, saliva cortisol and heart rate responses to different types of stimuli in dogs. *Applied Animal Behaviour Science* 58, 365–381. http:// dx.doi.org/10.1016/S0168-1591(97)00145-7.
- Beerda, B., Schilder, M.B., van Hooff, J.A., De Vries, H.W., Mol, J.A. (1999a) Chronic stress in dogs subjected to social and spatial restriction. I. Behavioral responses.

- Physiology & Behavior 66, 233–242. http://dx.doi.org/10.1016/S0031-9384(98)00289-3.
- Beerda, B., Schilder, M.B., Bernadina, W., van Hooff, J.A., De Vries, H.W., et al. (1999b) Chronic stress in dogs subjected to social and spatial restriction. II. Hormonal and immunological responses. *Physiology* & *Behavior* 66, 243–254. http://dx.doi.org/10.1016/ S0031-9384(98)00290-X.
- Belshaw, Z., Asher, L., Harvey, N.D., Dean, R.S. (2015) Quality of life assessment in domestic dogs: An evidence-based rapid review. *The Veterinary Journal* 206, 203–212. http://dx.doi.org/10.1016/j. tvjl.2015.07.016.
- Bergamasco, L., Osella, M.C., Savarino, P., Larosa, G., Ozella, L., et al. (2010). Heart rate variability and saliva cortisol assessment in shelter dog: Human–animal interaction effects. Applied Animal Behaviour Science 125, 56–68. http://dx.doi.org/10.1016/j.applanim.2010.03.002.
- Berns, G.S., Brooks, A.M., Spivak, M. (2015) Scent of the familiar: An fMRI study of canine brain responses to familiar and unfamiliar human and dog odors. Behavioural Processes 110, 37–46. http://dx.doi. org/10.1016/j.beproc.2014.02.011.
- Best Friends Animal Society. (2019) The Sanctuary. Available at: https://bestfriends.org/sanctuary/explore-sanctuary (accessed 10 February 2019).
- Blackwell, E.J., Bodnariu, A., Tyson, J., Bradshaw, J.W.S., Casey, R.A. (2010) Rapid shaping of behaviour associated with high urinary cortisol in domestic dogs. *Applied Animal Behaviour Science* 124, 113–120. http://dx.doi.org/10.1016/j.applanim. 2010.02.011.
- Bolhuis, J.E., Schouten, W.G., de Leeuw, J.A., Schrama, J.W., Wiegant, V.M. (2004) Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behavioural Brain Research* 152, 351–360. http://dx.doi.org/10.1016/j.bbr.2003.10.024.
- Bowman, A., Scottish SPCA, Dowell, F.J., Evans, N.P. (2015) 'Four Seasons' in an animal rescue centre: Classical music reduces environmental stress in kennelled dogs. *Physiology & Behavior* 143, 70–82. http://dx.doi.org/10.1016/j.physbeh.2015.02.035.
- Bowman, A., Scottish SPCA, Dowell, F.J., Evans, N.P. (2017) The effect of different genres of music on the stress levels of kennelled dogs. *Physiology & Behavior* 171, 207–215. http://dx.doi.org/10.1016/j.physbeh.2017.01.024.
- Bradshaw, J.W., Pullen, A.J., Rooney, N.J. (2015). Why do adult dogs 'play'? *Behavioural Processes* 110, 82–87. http://dx.doi.org/10.1016/j.beproc.2014.09.023.
- Brando, S. and Buchanan-Smith, H.M. (2018) The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes* 156, 83–95. http://dx.doi.org/10.1016/j.beproc.2017.09.010.
- Brown, W.P., Davidson, J.P., Zuefle, M.E. (2013) Effects of phenotypic characteristics on the length of stay of

- dogs at two no kill animal shelters. *Journal of Applied Animal Welfare Science* 16, 2–18. http://dx.doi.org/10.1080/10888705.2013.740967.
- Buchanan-Smith, H.M. and Badihi, I. (2012) The psychology of control: Effects of control over supplementary light on welfare of marmosets. *Applied Animal Behaviour Science* 137, 166–174. http://dx.doi.org/10.1016/j.applanim.2011.07.002.
- Cabib S. (2006) The neurophysiology of stereotypy II: The role of stress. In: Mason, G. and Rushen, J. (eds.) Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare, 2nd edn. CAB International, Wallingford, UK, pp. 227–255.
- Cafazzo, S., Maragliano, L., Bonanni, R., Scholl, F., Guarducci, M., et al. (2014) Behavioural and physiological indicators of shelter dogs' welfare: Reflections on the no-kill policy on free-ranging dogs in Italy revisited on the basis of 15 years of implementation. *Physiology* & Behavior 133, 223–229. http://dx.doi.org/10.1016/j. physbeh.2014.05.046.
- Capitanio, J.P. (2008) Personality and disease. *Brain, Behavior, and Immunity* 22, 647–650. http://dx.doi.org/10.1016/j.bbi.2008.02.002.
- Cavigelli, S.A. (2005) Animal personality and health. *Behaviour* 142, 1229–1250. http://dx.doi.org/10.1163/156853905774539355.
- Coe, J.B., Young, I., Lambert, K., Dysart, L., Nogueira Borden, L., et al. (2014) A scoping review of published research on the relinquishment of companion animals. *Journal of Applied Animal Welfare Science* 17, 253–273. http://dx.doi.org/10.1080/10888705.2014.899910.
- Coppens, C.M., de Boer, S.F., Koolhaas, J.M. (2010) Coping styles and behavioural flexibility: Towards underlying mechanisms. *Philosophical Transactions* of the Royal Society B: Biological Sciences 365, 4021–4028. http://dx.doi.org/10.1098/rstb.2010.0217.
- Coppola, C.L., Enns, R.M., Grandin, T. (2006a) Noise in the animal shelter environment: Building design and the effects of daily noise exposure. *Journal of Applied Animal Welfare Science* 9, 1–7. http://dx.doi.org/10.1207/s15327604jaws0901_1.
- Coppola, C.L., Grandin, T., Enns, R.M. (2006b) Human interaction and cortisol: Can human contact reduce stress for shelter dogs? *Physiology & Behavior* 87, 537– 541. http://dx.doi.org/10.1016/j.physbeh.2005.12.001.
- Corsetti, S., Borruso, S., Di Traglia, M., Lai, O., Alfieri, L., et al. (2018) Bold personality makes domestic dogs entering a shelter less vulnerable to diseases. *PloS ONE* 13(3), e0193794. http://dx.doi.org/10.1371/journal.pone.0193794.
- Cussen, V.A. and Mench, J.A. (2014) Personality predicts cognitive bias in captive psittacines, *Amazona amazonica*. *Animal Behaviour* 89, 123–130. http://dx.doi. org/10.1016/j.anbehav.2013.12.022.
- da Silva Vasconcellos, A., Adania, C.H., Ades, C. (2012) Contrafreeloading in maned wolves: Implications for their management and welfare. Applied Animal

- Behaviour Science 140, 85–91. http://dx.doi.org/10.1016/j.applanim.2012.04.012.
- Denham, H.D., Bradshaw, J.W., Rooney, N.J. (2014) Repetitive behaviour in kennelled domestic dog: Stereotypical or not? *Physiology & Behavior* 128, 288–294. http://dx.doi.org/10.1016/j.physbeh.2014.01.007.
- Dess, N.K., Linwick, D., Patterson, J., Overmier, J.B., Levine, S. (1983) Immediate and proactive effects of controllability and predictability on plasma cortisol responses to shocks in dogs. *Behavioral Neuro-science* 97, 1005–1016. http://dx.doi.org/10.1037/ 0735-7044.97.6.1005.
- Dogs Playing for Life. (2018) Impact report. Available at: https://drive.google.com/file/d/1pTWmwy_zejBZGGpa-VOmSp-0-52HDrWZT/view (accessed 20 January 2019).
- Dreschel, N.A. (2010) The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science* 125, 157–162. http://dx.doi.org/10.1016/j.applanim.2010.04.003.
- Epstein, S. (1979) The stability of behavior: I. On predicting most of the people much of the time. *Journal of Personality and Social Psychology* 37, 1097–1126. http://dx.doi.org/10.1037/0022-3514.37.7.1097.
- Estep, D.Q. (1991) The ontogeny of behavior. In: Voith, V.L. and Borchelt, P.L. (eds.) Readings in Companion Animal Behavior. Veterinary Learning Systems, Trenton, New Jersey, USA, pp 19–31.
- Flint, H.E., Coe, J.B., Serpell, J.A., Pearl, D.L., Niel, L. (2017) Risk factors associated with stranger-directed aggression in domestic dogs. *Applied Animal Behaviour Science* 197, 45–54. http://dx.doi.org/10.1016/j.applanim.2017.08.007.
- Fraser, D. (2009) Assessing animal welfare: Different philosophies, different scientific approaches. *Zoo Biology* 28, 507–518.
- Fullagar, B., Boysen, S.R., Toy, M., Makwana, C., Pang, D.S.J. (2015) Sound pressure levels in 2 veterinary intensive care units. *Journal of Veterinary Internal Medicine* 29, 1013–1021. http://dx.doi.org/10.1111/ jvim.13574.
- Fureix, C. and Meagher, R.K. (2015) What can inactivity (in its various forms) reveal about affective states in non-human animals? A review. Applied Animal Behaviour Science 171, 8–24. http://dx.doi.org/10.1016/ j.applanim.2015.08.036.
- Gliner, J.A. (1972) Predictable vs. unpredictable shock: Preference behavior and stomach ulceration. *Physiology & Behavior* 9, 693–698. http://dx.doi.org/10.1016/0031-9384(72)90036-4.
- Goold, C. and Newberry, R.C. (2017) Modelling personality, plasticity and predictability in shelter dogs. *Royal Society Open Science* 4, 170618. http://dx.doi.org/10.1098/rsos.170618.
- Gosling, S.D. (1998) Personality dimensions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology* 112, 107–118. http://dx.doi.org/10.1037/0735-7036.112.2.107.

- Gosling, S.D. (2001) From mice to men: What can we learn about personality from animal research? *Psychological Bulletin* 127, 45–86. http://dx.doi.org/10.1037/0033-2909.127.1.45.
- Gosling, S.D. and John, O.P. (1999) Personality dimensions in nonhuman animals: A cross-species review. Current Directions in Psychological Science 8, 69–75. http://dx.doi.org/10.1111/1467-8721.00017.
- Gosling, S.D. and Vazire, S. (2002) Are we barking up the right tree? Evaluating a comparative approach to personality. *Journal of Research in Personality* 36, 607–614. http://dx.doi.org/10.1016/S0092-6566(02)00511-1.
- Gosling, S.D., Kwan, V.S., John, O.P. (2003) A dog's got personality: A cross-species comparative approach to personality judgments in dogs and humans. *Journal of Personality and Social Psychology* 85, 1161–1169. http://dx.doi.org/10.1037/0022-3514.85.6.1161.
- Grigg, E.K., Nibblett, B.M., Robinson, J.Q., Smits, J.E. (2017) Evaluating pair versus solitary housing in kennelled domestic dogs (*Canis familiaris*) using behaviour and hair cortisol: A pilot study. *Veterinary Record Open* 4(1), e000193. http://dx.doi.org/10.1136/vetreco-2016-000193.
- Gunter, L.M., Barber, R.T., Wynne, C.D. (2016) What's in a name? Effect of breed perceptions & labeling on attractiveness, adoptions & length of stay for pit-bulltype dogs. *PloS ONE* 11(3), e0146857. http://dx.doi. org/10.1371/journal.pone.0146857.
- Gunter, L.M., Barber, R.T., Wynne, C.D. (2018) A canine identity crisis: Genetic breed heritage testing of shelter dogs. *PloS ONE* 13(8), e0202633. http://dx.doi. org/10.1371/journal.pone.0202633.
- Hammerle, M., Horst, C., Levine, E., Overall, K., Radosta, L., et al. (2015) 2015 AAHA canine and feline behavior management guidelines. *Journal of the American Animal Hospital Association* 51, 205–221. http://dx. doi.org/10.5326/JAAHA-MS-6527.
- Hekman, J., Karas, A., Sharp, C. (2014) Psychogenic stress in hospitalized dogs: Cross species comparisons, implications for health care, and the challenges of evaluation. *Animals* 4, 331–347. http://dx.doi. org/10.3390/ani4020331.
- Held, S.D. and Špinka, M. (2011) Animal play and animal welfare. *Animal Behaviour* 81, 891–899. http://dx.doi.org/10.1016/j.anbehav.2011.01.007.
- Hennessy, M.B. (2013) Using hypothalamic–pituitary–adrenal measures for assessing and reducing the stress of dogs in shelters: A review. *Applied Animal Behaviour Science* 149, 1–12. http://dx.doi.org/10.1016/j.applanim.2013.09.004.
- Hetts, S., Estep, D., Marder, A.R. (2005) Psychological well-being in animals. In: McMillan, F. (ed.) *Mental Health and Well-Being in Animals*. Blackwell Publishing, Ames, Iowa, USA, pp. 211–220. http://dx.doi.org/10.1002/9780470384947.ch15.
- Hewison, L.F., Wright, H.F., Zulch, H.E., Ellis, S.L. (2014) Short term consequences of preventing visitor access to kennels

- on noise and the behaviour and physiology of dogs housed in a rescue shelter. *Physiology & Behavior* 133, 1–7. http://dx.doi.org/10.1016/j.physbeh.2014.04.045.
- Hewson, C.J., Hiby, E.F., Bradshaw, J.W.S. (2007) Assessing quality of life in companion and kennelled dogs: A critical review. *Animal Welfare* 16, 89–95.
- Hiby, E.F., Rooney, N.J., Bradshaw, J.W. (2006) Behavioural and physiological responses of dogs entering re-homing kennels. *Physiology & Behavior* 89, 385–391. http:// dx.doi.org/10.1016/j.physbeh.2006.07.012.
- Horváth, Z., Igyártó, B.Z., Magyar, A., Miklósi, Á. (2007) Three different coping styles in police dogs exposed to a short-term challenge. *Hormones and Behavior* 52, 621–630. http://dx.doi.org/10.1016/j. yhbeh.2007.08.001.
- Horwitz, D.F. and Mills, D.S. (2009) BSAVA Manual of Canine and Feline Behavioural Medicine, 2nd edn. British Small Animal Veterinary Association, Gloucester. UK.
- Howell, T.J. and Bennett, P.C. (2011) Puppy power! Using social cognition research tasks to improve socialization practices for domestic dogs (*Canis familiaris*). *Journal of Veterinary Behavior* 6, 195–204. http:// dx.doi.org/10.1016/j.jveb.2011.01.004.
- Hsu, Y. and Serpell, J.A. (2003) Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. *Journal of the American Veterinary Medical Association* 223, 1293–1300. http://dx.doi.org/10.2460/javma.2003.223.1293.
- Hubrecht, R.C., Serpell, J.A., Poole, T.B. (1992) Correlates of pen size and housing conditions on the behaviour of kennelled dogs. *Applied Animal Behaviour Science* 34, 365–383. http://dx.doi. org/10.1016/S0168-1591(05)80096-6.
- Inglis, I.R., Forkman, B., Lazarus, J. (1997) Free food or earned food? A review and fuzzy model of contrafreeloading. *Animal Behaviour* 53, 1171–1191. http:// dx.doi.org/10.1006/anbe.1996.0320.
- Jensen, G.D. (1963) Preference for bar pressing over 'freeloading' as a function of number of rewarded presses. *Journal of Experimental Psychology* 65, 451–454. http://dx.doi.org/10.1037/h0049174.
- Jones, A.C. (2008) Development and validation of a dog personality questionnaire. PhD thesis. University of Texas, Austin, Texas, USA.
- Jones, A.C. and Gosling, S.D. (2005) Temperament and personality in dogs (*Canis familiaris*): A review and evaluation of past research. *Applied Animal Behaviour Science* 95, 1–53. http://dx.doi.org/10.1016/j.applanim.2005.04.008.
- Jongman, E.C., Butler, K.L., Hemsworth, P.H. (2018) The effects of kennel size and exercise on the behaviour and stress physiology of individually-housed greyhounds. *Applied Animal Behaviour Science* 199, 29–34. http://dx.doi.org/10.1016/j.applanim.2017.11.002.
- Karagiannis, C.I., Burman, O.H., Mills, D.S. (2015) Dogs with separation-related problems show a 'less

- pessimistic' cognitive bias during treatment with fluoxetine (Reconcile[™]) and a behaviour modification plan. *BMC Veterinary Research* 11, 80. http://dx.doi.org/10.1186/s12917-015-0373-1.
- Kay, A., Coe, J.B., Young, I., Pearl, D. (2018) Factors influencing time to adoption for dogs in a provincial shelter system in Canada. *Journal of Applied Animal Welfare Science* 21, 375–388. http://dx.doi.org/10.1080/10888705.2018.1436917.
- Kiddie, J.L. and Collins, L.M. (2014) Development and validation of a quality of life assessment tool for use in kennelled dogs (*Canis familiaris*). Applied Animal Behaviour Science 158, 57–68.
- Koolhaas, J.M. (2008) Coping style and immunity in animals: Making sense of individual variation. *Brain, Behavior, and Immunity* 22, 662–667. http://dx.doi.org/10.1016/j.bbi.2007.11.006.
- Koolhaas, J.M. and van Reenen, C.G. (2016) Animal behavior and well-being symposium: Interaction between coping style/personality, stress, and welfare: Relevance for domestic farm animals. *Journal of Animal Science* 94, 2284–2296. http://dx.doi.org/10.2527/jas.2015-0125.
- Koolhaas, J.M., Korte, S.M., De Boer, S.F., van Der Vegt, B.J., van Reenen, C.G., et al. (1999). Coping styles in animals: Current status in behavior and stressphysiology. Neuroscience & Biobehavioral Reviews 23, 925–935. http://dx.doi.org/10.1016/S0149-7634(99)00026-3.
- Koolhaas, J.M., De Boer, S.F., Coppens, C.M., Buwalda, B. (2010) Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology* 31, 307–321. http://dx.doi.org/10.1016/j.yfrne.2010.04.001.
- Koret Shelter Medicine Program. (2019) Calculating Shelter capacity. Available at: https://www.shelter-medicine.com/library/resources/?utf8=%E2%9C%9-3&site=sheltermedicine&search%5Bslug%5D=calculating-shelter-capacity (accessed 20 February 2019).
- Lambert, K., Coe, J., Niel, L., Dewey, C., Sargeant, J.M. (2015) A systematic review and meta-analysis of the proportion of dogs surrendered for dog-related and owner-related reasons. *Preventive Veterinary Medicine* 118, 148–160. http://dx.doi.org/10.1016/j. prevetmed.2014.11.002.
- Lindsay, S.R. (2005) Handbook of Applied Dog Behavior and Training. Blackwell Publishing: Ames, Iowa, USA. http://dx.doi.org/10.1002/9780470344514.
- Lockwood, R. (2006). Animal Cruelty Prosecution: Opportunities for Early Response to Crime and Interpersonal Violence. American Prosecutors Research Institute, Alexandria, Virginia, USA.
- Luescher, A.U. (2009) Repetitive and compulsive behaviour in dogs and cats. In: Horwitz, D.F. and Mills, D.S. (eds.) *BSAVA Manual of Canine and Feline Behavioural Medicine*, 2nd edn. British Small Animal Veterinary Association, Gloucester, UK, pp. 236–244. http://dx.doi.org/10.22233/9781905319879.20.

- Markowitz, H. (1982) Behavioral Engineering in the Zoo. van Nostrand Reinhold, New York, USA.
- Markowitz, H. and Aday, C. (1998) Power for captive animals: Contingencies and nature. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (eds.) Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press, Washington, DC, USA, pp. 47–58.
- Marston, L.C. and Bennett, P.C. (2003) Reforging the bond – Towards successful canine adoption. *Applied Animal Behaviour Science* 83, 227–245. http://dx.doi. org/10.1016/S0168-1591(03)00135-7.
- Mason, G.J. (2010) Species differences in responses to captivity: Stress, welfare and the comparative method. *Trends in Ecology & Evolution* 25, 713–721. http:// dx.doi.org/10.1016/j.tree.2010.08.011.
- Mason, G.J. and Latham, N. (2004) Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare* 13, 57–69.
- Mason, G. and Rushen, J. (2008) Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare, 2nd edn. CAB International, Wallingford, UK.
- McMillan, F.D. (2000) Quality of life in animals. *Journal of the American Veterinary Medical Association* 216, 1904–1910. http://dx.doi.org/10.2460/javma.2000.216.1904.
- McMillan, F.D. (2007) Predicting quality of life outcomes as a guide for decision-making: The challenge of hitting a moving target. *Animal Welfare* 16, 135–142.
- McMillan, F.D. (2013) Quality of life, stress, and emotional pain in shelter animals. In: Miller, L. and Zawistowski, S. (eds.) *Shelter Medicine for Veterinarians and Staff*, 2nd edn. Wiley-Blackwell, Ames, Iowa, USA, pp. 83–92.
- McMillan, F.D. (2017) Behavioral and psychological outcomes for dogs sold as puppies through pet stores and/or born in commercial breeding establishments: Current knowledge and putative causes. *Journal of Veterinary Behavior* 19, 14–26. http://dx.doi.org/10.1016/j.jveb.2017.01.001.
- McMillan, F.D., Vanderstichel, R., Stryhn, H., Yu, J., Serpell, J.A. (2016) Behavioural characteristics of dogs removed from hoarding situations. *Applied Animal Behaviour Science* 178, 69–79. http://dx.doi. org/10.1016/j.applanim.2016.02.006.
- Meehan, C.L. and Mench, J.A. (2007) The challenge of challenge: Can problem solving opportunities enhance animal welfare? Applied Animal Behaviour Science 102, 246–261. http://dx.doi.org/10.1016/j. applanim.2006.05.031.
- Mench, J.A. (1998) Environmental enrichment and the importance of exploratory behavior. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (eds.) Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution Press, Washington, DC, USA, pp. 30–46.
- Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., et al. (2010). Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. Current

- Biology 20, R839–R840. http://dx.doi.org/10.1016/j.cub.2010.08.030.
- Miller, K. and Zawistowski, S. (2013) Behavioral enrichment. In: Miller, L. and Zawistowski, S. (eds.) Shelter Medicine for Veterinarians and Staff, 2nd edn. Wiley-Blackwell, Ames, Iowa, USA, pp. 541–557.
- Miller, L. and Zawistowski, S. (2015) Housing, husbandry, and behavior of dogs in animal shelters. In: Weiss, E., Mohan-Gibbons, H., Zawistowski, S. (eds.) Animal Behavior for Shelter Veterinarians and Staff. Wiley Blackwell, Ames, Iowa, USA, pp. 145–159. http:// dx.doi.org/10.1002/9781119421313.ch7.
- Miller, K., Cussen, V.A., Collins, K., Reid, P. (2018) Optimizing treatment outcomes for extremely fearful dogs at the ASPCA Behavioral Rehabilitation Center. Proceedings of the 55th Annual Conference of the Animal Behavior Society. Milwaukee, Wisconsin, USA.
- Mills, D., Karagiannis, C., Zulch, H. (2014) Stress Its effects on health and behavior: A guide for practitioners. Veterinary Clinics: Small Animal Practice 44, 525–541.
- Morgan, K.N. and Tromborg, C.T. (2007) Sources of stress in captivity. Applied Animal Behaviour Science 102, 262–302. http://dx.doi.org/10.1016/j. applanim.2006.05.032.
- Morrow, M., Ottobre, J., Ottobre, A., Neville, P., St-Pierre, N., et al. (2015) Breed-dependent differences in the onset of fear-related avoidance behavior in puppies. Journal of Veterinary Behavior 10, 286–294. http://dx.doi.org/10.1016/j.jveb.2015.03.002.
- Newberry, R.C. (1995) Environmental enrichment: Increasing the biological relevance of captive environments. Applied Animal Behaviour Science 44, 229– 243. http://dx.doi.org/10.1016/0168-1591(95)00616-Z.
- Osborne, S.R. (1977) The free food (contrafreeloading) phenomenon: A review and analysis. *Animal Learning & Behavior* 5, 221–235. http://dx.doi.org/10.3758/BF03209232.
- Overall, K.L., Dunham, A.E., Frank, D. (2001) Frequency of nonspecific clinical signs in dogs with separation anxiety, thunderstorm phobia, and noise phobia, alone or in combination. *Journal of the American Veterinary Medical Association* 219, 467–473. http:// dx.doi.org/10.2460/javma.2001.219.467.
- Owczarczak-Garstecka, S.C. and Burman, O.H. (2016) Can sleep and resting behaviours be used as indicators of welfare in shelter dogs (*Canis lupus familiaris*)? *PloS ONE* 11(10), e0163620. http://dx.doi.org/10.1371/journal.pone.0163620.
- Panksepp, J. (1998) Affective Neuroscience: The Foundations of Human and Animal Emotion. Oxford University Press, New York, USA.
- Panksepp, J. (2005) Affective consciousness: Core emotional feelings in animals and humans. Consciousness and Cognition 14, 30–80. http://dx.doi.org/10.1016/j.concog.2004.10.004.
- Panksepp, J. (2011) The basic emotional circuits of mammalian brains: Do animals have affective lives?

- Neuroscience & Biobehavioral Reviews 35, 1791–1804. http://dx.doi.org/10.1016/j.neubiorev.2011.08.003.
- Part, C.E., Kiddie, J.L., Hayes, W.A., Mills, D.S., Neville, R.F., et al. (2014) Physiological, physical and behavioural changes in dogs (*Canis familiaris*) when kennelled: Testing the validity of stress parameters. *Physiology & Behavior* 133, 260–271. http://dx.doi.org/10.1016/j.physbeh.2014.05.018.
- Paul, E.S., Harding, E.J., Mendl, M. (2005) Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience & Biobehavioral Reviews* 29, 469–491. http://dx.doi.org/10.1016/j. neubiorev.2005.01.002.
- Protopopova, A. (2016) Effects of sheltering on physiology, immune function, behavior, and the welfare of dogs. *Physiology & Behavior* 159, 95–103. http://dx.doi.org/10.1016/j.physbeh.2016.03.020.
- Protopopova, A. and Wynne, C.D. (2016) Judging a dog by its cover: Morphology but not training influences visitor behavior toward kenneled dogs at animal shelters. Anthrozoös 29, 469–487. http://dx.doi.org/10.1080/08 927936.2016.1181381.
- Protopopova, A., Mehrkam, L.R., Boggess, M.M., Wynne, C.D.L. (2014) In-kennel behavior predicts length of stay in shelter dogs. *PloS one* 9(12), e114319. http://dx.doi.org/10.1371/journal.pone.0114319.
- Protopopova, A., Hauser, H., Goldman, K.J., Wynne, C.D. (2018) The effects of exercise and calm interactions on in-kennel behavior of shelter dogs. *Behavioural Processes* 146, 54–60. http://dx.doi.org/10.1016/j.beproc.2017.11.013.
- Pullen, A.J., Merrill, R.J., Bradshaw, J.W. (2012) The effect of familiarity on behaviour of kennel housed dogs during interactions with humans. *Applied Animal Behaviour Science* 137, 66–73. http://dx.doi. org/10.1016/j.applanim.2011.12.009.
- Reid, P. (1996) EXCEL-erated Learning: Explaining in Plain English How Dogs Learn and How Best To Teach Them. James and Kenneth Publishers, Berkeley, California, USA.
- Reid, P. and Collins, K. (2012) Assessing conspecific aggression in fighting dogs. Proceedings of the ACVB/AVSAB Veterinary Behavior Symposium. San Diego, California, USA.
- Reid, P.J. and Collins, K. (2015) Training and behavior modification for the shelter. In: Weiss, E., Mohan-Gibbons, H., Zawistowski, S. (eds.) *Animal Behavior* for Shelter Veterinarians and Staff. Wiley Blackwell, Ames, Iowa, USA, pp. 172–187. http://dx.doi. org/10.1002/9781119421313.ch9.
- Reid, P., Goldman, J., Zawistowski, S. (2004) Animal shelter behavior programs. In: Miller, L. and Zawistowski, S. (eds.) Shelter Medicine for Veterinarians and Staff. Blackwell Publishing, Ames, Iowa, pp. 317–331.
- Rooney, N.J., Gaines, S.A., Bradshaw, J.W. (2007) Behavioural and glucocorticoid responses of dogs (*Canis familiaris*) to kennelling: Investigating

- mitigation of stress by prior habituation. *Physiology* & *Behavior* 92, 847–854. http://dx.doi.org/10.1016/j.physbeh.2007.06.011.
- Rooney, N.J., Clark, C.C., Casey, R.A. (2016) Minimizing fear and anxiety in working dogs: A review. *Journal of Veterinary Behavior* 16, 53–64. http://dx.doi.org/10.1016/j.jveb.2016.11.001.
- Sadler A. (2018) Every day, Every dog Let them play! The impact of play groups. Available at: https://www.maddiesfund.org/let-them-play-the-impact-of-play-groups.htm (accessed 20 February 2019).
- Scarlett, J. (2013) Population statistics. In: Miller, L. and Zawistowski, S. (eds.) Shelter Medicine for Veterinarians and Staff, 2nd edn. Wiley-Blackwell, Ames, Iowa, USA, pp. 13–20.
- Scheifele, P., Martin, D., Clark, J.G., Kemper, D., Wells, J. (2012) Effect of kennel noise on hearing in dogs. *American Journal of Veterinary Research* 73, 482–489. http://dx.doi.org/10.2460/ajvr.73.4.482.
- Schipper, L.L., Vinke, C.M., Schilder, M.B., Spruijt, B.M. (2008) The effect of feeding enrichment toys on the behaviour of kennelled dogs (*Canis familiaris*). *Applied Animal Behaviour Science* 114, 182–195. http://dx.doi. org/10.1016/j.applanim.2008.01.001.
- Scott, J.P. and Fuller, J.L. (1965) *Genetics and the Social Behavior of the Dog*. The University of Chicago Press, Chicago, Illinois, USA.
- Segurson, S.A., Serpell, J.A., Hart, B.L. (2005) Evaluation of a behavioral assessment questionnaire for use in the characterization of behavioral problems of dogs relinquished to animal shelters. *Journal of the American Veterinary Medical Association* 227, 1755–1761. http://dx.doi.org/10.2460/javma.2005.227.1755.
- Seligman, M.E.P. and Groves, D.P. (1970) Nontransient learned helplessness. *Psychonomic Science* 19, 191–192.
- Seligman, M.E. and Maier, S.F. (1967) Failure to escape traumatic shock. *Journal of Experimental Psychology* 74, 1–9. http://dx.doi.org/10.1037/h0024514.
- Shabelansky, A., Dowling-Guyer, S., Quist, H., D'Arpino, S.S., McCobb, E. (2015) Consistency of shelter dogs' behavior toward a fake versus real stimulus dog during a behavior evaluation. *Applied Animal Behaviour Science* 163, 158–166. http://dx.doi.org/10.1016/j. applanim.2014.12.001.
- Shelter Animals Count (2004) The Asilomar Accords. Available at: https://www.shelteranimalscount.org/docs/default-source/DataResources/2004aaccords5.pdf?sfvrsn=31c1ff76_0 (accessed 20 February 2019).
- Shelter Animals Count. (2016) 2016 Animal sheltering statistics. Available at: https://shelteranimalscount.org/docs/default-source/DataResources/2016animalshelteringstatistics.pdf?sfvrsn=12 (accessed 20 February 2019).
- Shiverdecker, M.D., Schiml, P.A., Hennessy, M.B. (2013) Human interaction moderates plasma cortisol

- and behavioral responses of dogs to shelter housing. *Physiology & Behavior* 109, 75–79. http://dx.doi.org/10.1016/j.physbeh.2012.12.002.
- Sommerville, R., O'Connor, E.A., Asher, L. (2017) Why do dogs play? Function and welfare implications of play in the domestic dog. *Applied Animal Behaviour Science* 197, 1–8. http://dx.doi.org/10.1016/j.applanim.2017.09.007.
- Southwick, S.M. and Charney, D.S. (2012) The science of resilience: Implications for the prevention and treatment of depression. *Science* 338, 79–82. http://dx. doi.org/10.1126/science.1222942.
- Spruijt, B.M., van den Bos, R., Pijlman, F.T. (2001) A concept of welfare based on reward evaluating mechanisms in the brain: Anticipatory behaviour as an indicator for the state of reward systems. *Applied Animal Behaviour Science* 72, 145–171. http://dx.doi.org/10.1016/S0168-1591(00)00204-5.
- Starling, M.J., Branson, N., Thomson, P.C., McGreevy, P.D. (2013) 'Boldness' in the domestic dog differs among breeds and breed groups. *Behavioural Processes* 97, 53–62. http://dx.doi.org/10.1016/j.beproc.2013.04.008.
- Svartberg, K. (2006) Breed-typical behaviour in dogs historical remnants or recent constructs? Applied Animal Behaviour Science 96, 293–313. http://dx.doi. org/10.1016/j.applanim.2005.06.014.
- Taylor, K.D. and Mills, D.S. (2007a) The effect of the kennel environment on canine welfare: A critical review of experimental studies. *Animal Welfare* 16, 435–447.
- Taylor, K.D. and Mills, D.S. (2007b) Is quality of life a useful concept for companion animals? *Animal Welfare* 16, 55–65.
- Thielke, A.L. and Udell, M. (2018) Evaluating attachment styles in shelter, foster & pet dogs: Implications for welfare and separation anxiety. *Proceedings of the 55th Annual Conference of the Animal Behavior Society*. Milwaukee, Wisconsin, USA.
- Tuber, D.S., Miller, D.D., Caris, K.A., Halter, R., Linden, F., et al. (1999) Dogs in animal shelters: Problems, suggestions, and needed expertise. Psychological Science 10. 379–386.
- University of Wisconsin Shelter Medicine (2015) Length of stay (LOS). Available at: www.uwsheltermedicine. com/library/resources/length-of-stay-los (accessed 20 February 2019).
- van der Harst, J.E. and Spruijt, B.M. (2007) Tools to measure and improve animal welfare: Reward-related behaviour. *Animal Welfare* 16, 67–73.
- Walker, J., Dale, A., Waran, N., Clarke, N., Farnworth, M., et al. (2010) The assessment of emotional expression

- in dogs using a Free Choice Profiling methodology. *Animal Welfare* 19, 75–84.
- Walker, J.K., Dale, A.R., D'Eath, R.B., Wemelsfelder, F. (2016) Qualitative Behaviour Assessment of dogs in the shelter and home environment and relationship with quantitative behaviour assessment and physiological responses. *Applied Animal Behaviour Science* 184, 97–108. http://dx.doi.org/10.1016/j.applanim.2016.08.012.
- Wells, D.L. (2004) A review of environmental enrichment for kennelled dogs, *Canis familiaris*. *Applied Animal Behaviour Science* 85, 307–317. http://dx.doi.org/10.1016/j.applanim.2003.11.005.
- Wells, D.L. and Hepper, P.G. (2000) The influence of environmental change on the behaviour of sheltered dogs. Applied Animal Behaviour Science 68, 151–162. http://dx.doi.org/10.1016/S0168-1591(00)00100-3.
- Wells, D.L., Graham, L., Hepper, P.G. (2002a) The influence of length of time in a rescue shelter on the behaviour of kennelled dogs. *Animal Welfare* 11, 317–325.
- Wells, D.L., Graham, L., Hepper, P.G. (2002b) The influence of auditory stimulation on the behaviour of dogs housed in a rescue shelter. *Animal Welfare* 11, 385–393.
- Wemelsfelder, F. (2005) Animal boredom: Understanding the tedium of confined lives. In: McMillan, F. (ed.) Mental Health and Well-Being in Animals. Blackwell Publishing, Ames, Iowa, USA, pp. 79–91.
- Wemelsfelder, F., Hunter, T.E., Mendl, M.T., Lawrence, A.B. (2001) Assessing the 'whole animal': A free choice profiling approach. *Animal Behaviour* 62, 209–220. http://dx.doi.org/10.1006/anbe.2001.1741.
- Wenstrup, J. and Dowidchuk, A. (1999) Pet overpopulation: Data and measurement issues in shelters. *Journal of Applied Animal Welfare Science* 2, 303–319. http://dx.doi.org/10.1207/s15327604jaws0204_5.
- Willen, R.M., Mutwill, A., MacDonald, L.J., Schiml, P.A., Hennessy, M.B. (2017) Factors determining the effects of human interaction on the cortisol levels of shelter dogs. *Applied Animal Behaviour Science* 186, 41–48. http://dx.doi.org/10.1016/j.applanim.2016.11.002.
- Young, R.J. (2003) Environmental Enrichment for Captive Animals. Blackwell Science, Inc. Malden, Massachusetts, USA. http://dx.doi.org/10.1002/9780470751046.
- Zidar, J., Balogh, A., Favati, A., Jensen, P., Leimar, O., et al. (2017) A comparison of animal personality and coping styles in the red junglefowl. *Animal Behaviour* 130, 209–220. http://dx.doi.org/10.1016/j.anbehav.2017.06.024.

19 The Mental Health of Laboratory Animals

CARINE ELKHORAIBI, AMY ROBINSON-JUNKER, GINA ALVINO, AND LARRY CARBONE

Institutional Animal Care and Use Program, University of California, San Francisco, California, USA; Laboratory Animal Resource Center, University of California, San Francisco, California, USA; Institutional Animal Care and Use Program, University of California, San Francisco, California, USA; Institutional Animal Care and Use Program, University of California, San Francisco, California, USA

19.1 Introduction

Mouse, monkey, zebrafish, pig: what makes an animal a *laboratory animal* is not species, but the setting in which the animal lives, and the uses to which the animal is put. Animals in medical research are subject to a range of diseases, pains, and stresses that scientists induce so that they can model similar states in humans.

In this chapter we focus mainly on animals in medical research, though their use in laboratories is broader than that. Most laboratory animals are kept in confinement for all or most of their lives. Their housing varies, from groups of nearly identical mice in rooms housing thousands of animals, to singly caged monkeys or pigs, to large outdoor corrals for primates or hoofstock. Many, especially the smaller species such as rats, mice, and zebrafish, may be seen only a few minutes a day by their human caregivers. Many research projects include intensive handling and restraint to administer test substances or to collect tissues and data.

The laboratory can entail occasional conflict between animal welfare and human priorities. What is best for the animals might require added human labor or increased expense. For example, animals on farms, in zoos, or in laboratories may be housed in small easy-to-clean cages, prioritizing cost and efficiency over what may be truly best for the animals.

In the laboratory, while finances constrain some welfare advances, the most important conflict can be between the animals' welfare and the need for high-quality, reliable scientific data from the experiments. A serious challenge to animal welfare is that scientists may avoid various treatments and refinements that could improve animals' mental lives for fear that they will weaken the quality of their science, whether by introducing excess variability in their study populations or in other ways changing the animals' bodies and behaviors and how they perform as experimental subjects.

The simplest animal experimental design tests a hypothesis by comparing two groups of animals. To test the hypothesis that drug A can be effective against bone cancer, the scientists may implant bone cancer cells to two groups of mice, give the experimental group the drug and the controls a placebo, and then measure outcomes such as tumor size, the speed of metastasis to the lungs, the signs of bone cancer pain, or the degree of tumor regression. Similarly, a scientist might explore whether a particular gene affects brain development or function, whether the microorganisms in the gut affect diabetes, or whether the animals' housing temperature affects immune function. In these simplest paradigms, researchers want the groups to differ in a single way - the drug, the gene, the microbiome, the housing temperature - while all other factors remain constant. If mice who receive drug A have statistically lower rates of bone cancer metastasis. the scientists will be able to credit this difference exclusively to the drug if they believe they have held constant the housing, food, handling, lighting, social interactions, various forms of stress, other drugs animals receive, and various enrichments and novelty in their environments. In most cases, scientists will want low variability within each of the two groups, so that differences between the experimental and control groups stand out clearly. It is that search for low within-group variability that drives scientists' concern about adding any possible complicating or confounding factors, including welfare enhancements of various sorts, to the experiments. This drives scientists' concern for tight control over every aspect of animal housing and *care*, as well as experimental manipulations and animal *use*.

19.2 Regulatory and Historical Context

In the US, two main federal laws cover laboratory animal care and use. The Animal Welfare Act (AWA), first passed in 1966, limits its coverage to warm-blooded animals, with the curious exclusion of laboratory bred mice and rats, which comprise the vast majority of laboratory mammals.

The Health Research Extension Act of 1985 is the AWA's companion law. It requires National Institutes of Health oversight of all vertebrate animals in research, based on compliance with the *Guide for the Care and Use of Laboratory Animals* (the *Guide*), though only if the work is funded by federal research grants (Institute for Laboratory Animal Research, 2011). Animals these laws do not cover, such as mice in private industry or in undergraduate classrooms, may be covered by state or local laws or voluntary accreditation. Or, their care may have no external oversight at all.

Russell and Burch (1959) developed a widely used framework for improving laboratory animal welfare. They described a system for categorizing the sources of pain, distress, and suffering. Suffering can be the result of how scientists house and care for research animals, a result of how they use them in experiments, or both. Animal suffering in laboratories can be either *direct* or *contingent*. Animals experience direct suffering when their suffering is the subject of study. For instance, a researcher investigating the neurobiology of pain may need to first induce pain; prevention or alleviation of that pain would invalidate the study. Contingent suffering is a side effect of the animal's environment or experimental use, such as pain after a surgical procedure.

Along with a framework for identifying causes of suffering, Russell and Burch also proposed their framework for reducing suffering: the 'Three Rs' of replacement, reduction, and refinement alternatives. *Replacement* refers to replacing sentient animals with nonsentient cells, computer simulations, even human clinical data. *Reduction* comprises the various ways an experiment might use fewer animals. *Refinement* is the suite of activities that can improve humane treatment when animals must be used. Most of our coverage in this chapter pertains to various refinements of animal housing and animal use.

Suffering is not purely pain or exclusively physical. Regulations have increasingly and incrementally focused explicit attention on the mental health of laboratory animals, but this was not always the case. The US Drug Administration (USDA) once feared that *anxiety* was a 'psychiatric term that is only applicable to humans', while distress is 'more descriptive of the physical visible state of the animal' (Carbone, 2004, p. 209). Then Congress amended the AWA in 1985 with a provision for environments that enhance the psychological well-being of zoo and laboratory animals, though only for nonhuman primates (NHPs).

The *Guide* has also expanded its focus on the mental health and well-being of animals in laboratories through its eight editions. It now sets some general standards for behavioral management and for enrichment, including a default expectation that social animals should be housed with compatible conspecifics (Institute for Laboratory Animal Research, 2011). For the most part, welfare standards in the *Guide* and the AWA are quite general and leave to individual research institutions, working with their institutional animal care and use committee (IACUC) and their veterinarians, the development of their own specific policies and procedures.

19.3 Animal Welfare and Animal Research Data: How One Influences the Other

At first this seems paradoxical: most biomedical animal research requires healthy, normal, comfortable, unstressed animals. The researcher wants her animal groups to differ solely by whether they are receiving the placebo or the test cancer drug. She wants them to be eating normally, not stressed by rough handling or painful injections. Their cage should be comfortable, not too cold or hot or stuffy or brightly lit. If they live in groups, the groups should be compatible, with no fear of bullying, no fighting, and no painful infected fight wounds. If the drug makes the animals too sick or in too much pain

278 C. Elkhoraibi et al.

to eat, it introduces unwanted variability in nutritional status. If cancer rates then differ, is this credited to the drug or to nutritional factors? Have animal lives been wasted on an inconclusive experiment?

Russell and Burch used the term *psychosomiasis* to describe the very real interaction between physical and mental health, a mind-body interaction that informs this chapter (though modern writers avoid this term and its modern connotations; see also Chapter 4, this volume). Significant mental and emotional stressors can lead not just to distress and poor mental well-being in animals, but also to physical consequences. Severe stress may lead to illness, which may in turn add to the animals' mental suffering. Stress may also have less dramatic effects on the animal's body, altering immune function, for example, but not to the degree that the animal actually feels ill.

Knowledgeable animal researchers understand that changes in an animal's emotional or affective state can affect how the animal's body functions, even if they do not know the specific physical effects of specific changes in animals' mental state. Scientists evaluate any suggestions laboratory animal professionals or IACUCs make to improve the animals' welfare through the lens of their concern over outcomes in physical function and the quality of their data.

While some welfare improvements raise concerns about the quality and variability of the effects on data, animal welfare improvements may instead lead to better science. For example, the less stressed the animal is, the more normal many aspects of the animal's biology and the more reliable studies of that animal may be. Unfortunately, there are times when welfare improvements can work against the goals of the experiment. For example, mice on a lung cancer study might feel more comfortable with supplemental oxygen therapy, but if that changes how the cancer cells respond to drugs, the small improvement in animal welfare may render the experiment useless.

Regulations recognize that refinements such as pain medicines and tranquilizers might have a negative impact on data. The AWA requires annual reports of animal use, with a special focus on animals who experience significant unalleviated pain or distress, when scientists are concerned that use of anesthetics, analgesics, or tranquilizers would adversely affect research procedures, outcomes, or data interpretation. Missing from regulations and guidelines is a clear discussion of how unalleviated pain and distress can also affect data outcomes. Pain and stress can affect immune function, social

interaction, cancer biology, food consumption, sleep, and other functions, all of which can affect research data. As scientists and IACUCs review whether pain medications and other refinements might disrupt data outcomes, they need to also consider the effects of unalleviated distress and pain.

There are but a small number of model-specific side-by-side comparisons of data outcomes when welfare enhancements are used (e.g., pain medications, stable compatible group housing, enrichments) compared to when they are not. These would be the gold standard to help scientists make determinations and they may sometimes show that welfare refinements affect data in some cases but not in others. When they do, the size of the effect is important; a significant improvement in animal well-being that only minimally affects data outcomes might be worth adopting.

Scientists frequently report quite limited details about the housing, pain management, enrichment, or other refinements in their animals' lives, making it difficult to establish a standard practice in their field (Würbel, 2007a; Carbone and Austin, 2016). For example, a scientist who believes her peers are not treating pain in a cancer study will believe she cannot use pain medications herself, fearing that pain medications will invalidate her data or make it unpublishable. In reality, it may be the case that her peers simply omit such details from their papers, believing them to be tangential to the data they are presenting. Fuller reporting of animal welfare measures as part of scientists' Materials and Methods sections of their publication has the potential to both universalize a standard of care for animals, and potentially could improve better research reproducibility (Kilkenny et al., 2010).

As with pain, so is the case with other refinements. Scientists may fear that environmental enrichments such as large complex cages, dietary novelty, social interactions, and opportunities to explore will introduce too much variability in their study populations and will skew their experimental data. And, in truth, animals in such environments may develop differently and behave differently from animals in barren solitary cages. Scientists must consider whether such effects would invalidate their studies, have no strong effect, or possibly improve them (Würbel, 2007b; Li et al., 2013). Scientists must remember that for many welldesigned and well-controlled experiments, differing data outcomes are not necessarily 'truer'; scientists who worry that environmental enrichment, pain medications, or other refinements 'affect' animal data may be overlooking the effects of isolation, boredom, pain, lack of thermoregulatory options, and lack of control over one's life.

19.4 Stress, Distress, and Laboratory Animals

Stress is a generalized response to events, environments, and bodily processes that have the potential to change an animal's health, safety, or physiological equilibrium (homeostasis). Animals respond to stressors behaviorally, physiologically, or with a combination of the two. Stress is a welfare matter when it rises in severity and/or duration to the level of true emotional distress. Stress can also affect research outcomes, as stressed animals may have profound differences in their biology compared to nonstressed animals. Researchers should bear in mind that even small stressors can affect biology, including behavior, immune function, and metabolism. Minimizing stressors and timing research procedures around stressful events may lead to better data outcomes.

Some stressors pose minimal risk to animals' well-being and short-term transient stress is inevitable. Even something as seemingly minor as a cage change can induce changes in behavior and activate the classic 'stress response' via the hypothalamic-pituitary-adrenal (HPA) axis. However, animals can cope behaviorally if they are able to explore the environment, mark it as they deem necessary, and build their nests. Animals may respond to cold stress behaviorally by building a nest, huddling with other animals, and fluffing up their fur or feathers. Physiologically, they may shiver or activate their brown fat and generate body heat. Thus, behavior and physiology combine to bring the animal to thermal homeostasis.

However, stressors can lead to emotional distress in animals if the stressors exceed the animals' ability to adjust and cope, and the animal laboratory potentially poses many limitations on animals' ability to cope. If a cage contains insufficient nesting material, a mouse cannot build a nest for his security, territory, and thermoregulatory needs. Genetically manipulated mice may lack the physical, physiological, or behavioral capacities to cope with some stressors; for example, piloerection is not a physical option for a nude mouse in a cold cage with no fur to fluff up for insulation.

Confronted by multiple serious stressors, animals will prioritize their coping mechanisms and preserve some functions at the expense of others, partitioning their finite physiological resources. Though first described as the 'fight-or-flight response', this prioritization of functions is not restricted to confrontations with predators or with bellicose cage mates. If mice in a cold environment with insufficient nesting material shunt their resources toward thermoregulation, this could suppress their immune function and cancer protections. This may decrease their value in some cancer studies as well as decreasing their well-being.

Scientists need to be aware of these stressors, remove the ones they can, limit their duration, and provide the animals with biologically relevant resources to help them cope. A researcher may also choose to accept the effects of stressors and fold that information into their study, which can most easily be accomplished by incorporating them into the experimental design (Richter *et al.*, 2009). This has the added advantage that the investigator need not specifically identify all stressors, but, rather, strive to ensure that they impact all study animals equally. These methods of design may include statistical blocking factors, Latin square designs, housing treatment, and control animals in the same cages, and balancing for housing location.

19.5 Opportunities and Considerations for the Improvement of Well-Being in Laboratory Animals

With these general principles in mind, we next focus on some specific welfare challenges, chosen because of how common they are, how serious they are, or both. This is by no means an exhaustive list of all well-being challenges and opportunities in the laboratory. The 'Five Freedoms' that the United Kingdom's Brambell Report (Brambell, 1965) listed for farm animals in the 1960s also serves as a useful organizing framework for laboratory animals:

- 1. Freedom from hunger or thirst.
- 2. Freedom from discomfort.
- 3. Freedom from pain, injury, or disease.
- 4. Freedom to express [most] normal behavior by providing sufficient space, proper facilities, and company of the animal's own kind.
- 5. Freedom from fear and distress.

As mentioned earlier, most research animals are caged or confined in some way. Important considerations of their confined environment include temperature, light, complexity of the cage, noise,

280 C. Elkhoraibi et al.

food, and water. The social environment must meet the species' and individuals' needs for access to compatible animals but also provide protection from incompatible animals. Many animals want a place to escape and hide from potential predators and aggressors and a way to safely watch, smell, and listen to the world around them.

Beyond review of their housing, we must consider some aspects of the experiments the animals undergo. Pain, contingent or direct, is a crucial factor for laboratory animal well-being. Many welfare concerns straddle the categories of animal housing (or *care*) and research manipulations (or *use*). Human caregivers and researchers are an important part of an animal's world, both for their daily lives and for how people handle them for experiments. Often, research requirements, such as a need to easily restrain animals for examinations, drug administrations, or sample collections, drive particular choices to house animals in smaller cages or in solitary housing.

Researchers have an ethical and regulatory obligation to seek ways to minimize animal suffering. We recommend a birth-to-death inventory checklist of all of the welfare points of concern during an animal's life in the laboratory, along with all the refinements, analgesics, early euthanasia endpoints, and strategies appropriate for each one. The range of welfare challenges in the animal laboratory require that scientists customize these checklists for their own research program. Table 19.1 illustrates some representative birth-to-death welfare inventories for some common animal research models.

For most of this discussion, we focus primarily on mice and monkeys. Monkeys present challenges due to their size, social complexity, and cognitive emotional sophistication, as well as the public concerns for the ethical use of primates in research. Mice are numerically the most important research mammals, are used in a wide array of research programs, and their biology is well-characterized on many welfare-relevant factors. Laboratory mice also face welfare challenges in their wide range of genetically encoded deficits and diseases. Whether through selective breeding of animals with spontaneous mutations or through genetic engineering, mice may be genetically prone to conditions like high anxiety, decreased tolerance to pain, or susceptibility to a wide range of immunologic, neoplastic, neurologic, respiratory, and other diseases. They are harbingers of emerging welfare challenges for other species, too; as new technologies make genetic manipulation of other species easier, we can look ahead to primates in laboratories with genetic predisposition to depression, autism, and other diseases; to ferrets with debilitating cystic fibrosis; and to other genetically modified animals developed to model human diseases.

19.5.1 The physical environment

A modern mouse vivarium is a highly efficient operation with numerous challenges to animal well-being. Vivarium design reflects several factors, including cost and labor efficiencies, as well as the drive to eliminate infectious diseases from the mouse colony, and to prevent their mouse-to-mouse spread should they occur. The increasingly standard mouse cage is a sterilized plastic box with sterilized food, water, and bedding, as well as HEPA-filtered sterile air supply. Its size conforms to minimum recommendations in the *Guide* without 'wasting' space to oversized cages. For monkeys or other larger animals, the plastic may instead be metal and standards of sterility lower, but their cages similarly present challenges.

The physical environment includes the cage, tank or pen, food, water, air, light, sounds, smells, and items in the enclosure, such as bedding, perches, shelter, and nest boxes. All can affect animal well-being and all can affect animals' biology as research subjects. Here we discuss air temperature, noise, and light to illustrate the range of concerns for well-being and research that the physical environment presents.

Temperature

Homeothermic animals have a thermoneutral zone (TNZ), the range of temperatures in which they can maintain their body temperature without having to increase their metabolism. Just as humans put on a sweater or crawl under a blanket, a mouse in a cool environment below his TNZ will ruffle his fur and build a nest or huddle with cage mates. Their discomfort at cooler temperatures motivates them to perform these behaviors; conditions that thwart these behaviors, such as housing mice in a cool ambient temperature without mates or nesting material, will decrease their well-being. Especially in under-resourced cages, solitary mice with their high surface-to-volume ratio are expending a great deal of energy on maintaining their body temperature. When mice are not cold challenged, they may

Table 19.1. Birth-to-death welfare inventory for three exemplar experiments, highlighting potential welfare points of concerns with alternatives to consider.

Model	Welfare points of concern	Possible alternatives for improved welfare
Cancer studies in rodents	Genotyping – tissue	Saliva or hair as DNA source
	collection	Analgesics for tail or toe clipping
	Surgery to place tumor	Subcutaneous injection of tumor cells
	cells	Analgesia for surgeries
	Large tumors that interfere	Earlier euthanasia endpoints
	with mobility	Place tumors where they will not interfere with animals' movement
	Ulcerated tumors –	Earlier euthanasia endpoints
	infections	Topical treatments; analgesics
	Chemotherapy drugs –	Nursing care, with soft palatable food and fluid sources
	pain, nausea	Monitoring for earlier endpoints
	Lung metastasis – dyspnea	Oxygen-enriched cages
		Euthanize all of cohort when the first animal presents with dyspnea
		Set endpoints based on noninvasive imaging rather than clinical presentation
	Bone metastasis – pain,	Analgesics
	mobility	Easy access to food and water
	Euthanasia – handling/ restraint and dyspnea	Avoid carbon dioxide and injectable drugs as euthanasia agents
Capture-and-release	Capture distress	Minimize time in captivity
field studies: small mammals	•	Minimize handling
	Invasive marking methods	Dyes for short-term marking
	(e.g., toe amputation) Effects of ID methods on fitness	Analgesics for physical methods
	Anesthesia in field	Short-acting/reversible anesthetics
		Confine animals until recovered enough for safe climbing, swimming, etc.
	Hypothermia/hyperthermia	Provide sufficient nesting material and food/fluid in traps
	in live traps	Frequent trap checks
Neurologic	Food, water restriction as	Rewards that are sweeter, more nutritious, or higher
recording from single brain cells: rodents or	behavioral motivators	valence than plain water
		Acclimation to the restriction regimen
	Rigid restraint during	Flexible tethers for cables
nonhuman	recording	Implanted telemetry
primates	Surgery to place brain	Anesthesia/analgesia
	implants for neural recording	Nonacrylic implant fixation (e.g., titanium implants and screws)
	Social isolation, single housing	Social housing for implanted animals

breed better and also have more normal immune function and physiology (Gaskill *et al.*, 2013a,b; Kokolus *et al.*, 2013).

Just as cold mice may be welfare-challenged and be biologically abnormal as experimental subjects, a cage can also be too warm for mouse health and comfort. Laboratory mice live in the same ambient temperature throughout their active and resting periods, though their temperature preferences may vary throughout the day. However, mouse cages are usually not large enough to allow for warmer and cooler areas where the animals can choose to spend time through their day's cycle. Behavioral thermoregulation is more feasible for warming an animal in a cold cage than cooling an animal in warm cage. For these various reasons, the *Guide* and

others recommend slightly cooler ambient temperatures, which best fit mice during their nocturnal active period, with sufficient resources (like nesting material) for the animals' freedom to alleviate temperature discomfort.

Noise and vibration

Noise and vibration are abundant in animal facilities, though humans do not always perceive them. Hearing ranges in animals are highly species dependent: while Japanese macaques hear more or less what humans do, mice likely cannot hear us speaking, and we certainly hear very few of their vocalizations (Heffner and Heffner, 2007). Sensitivity to vibration also varies with species, with rodents thought to be some of the most sensitive. Fish also respond to vibration.

Rodents communicate at least partially in ultrasound at frequencies too high for humans to detect unaided. There may be distressing levels of ultrasound and lower frequency noises in the laboratory environment that are audible to the animals but inaudible to humans, who therefore may be unaware of their presence (Reynolds et al., 2010). Animals chronically exposed to ultrasound may develop physiological and behavioral changes, including seizures and auditory damage (Sales et al., 1988). Loud, unpredictable noises can startle and stress animals. Common procedures, such as cleaning hard steel or plastic cages, and common equipment, such as the blowers in ventilated racks of mouse cages, can produce distressing levels of noise and vibrations which affect the animals' well-being and biological functions. Periodic audits of excessive noise and vibration, especially those humans cannot hear, are necessary and require specialized equipment.

Light

Light's impact on animal health and well-being can come from intensity or from photoperiod. Light can also affect how animals serve as research subjects.

Bright lights are aversive to many species, and rodents will work to avoid brightly lit chambers (Barker *et al.*, 2010). However, some species, such as caged primates, may benefit from brighter lighting than humans or rodents would prefer. Albino rodents are susceptible to retinal damage from lights that humans perceive as normal intensity (Bellhorn, 1980). This may affect their behavior as

experimental subjects; they could score poorly on maze tasks that rely on following visual cues, not because they are losing cognitive function but because they cannot see the visual cues. Decreased vision is not necessarily a welfare problem for these animals, however, as they are living in small, predictable predator-free environments and relying as much on hearing and olfaction as they do on sight.

Photoperiod is also quite important for animal health, well-being, and normal biology. Various studies have demonstrated that disruption of diurnal cycles can lead to altered metabolism, behavior, reproduction, and other effects in animals (Karatsoreos *et al.*, 2011; Walton *et al.*, 2011).

As with noise, human caregivers may not notice perturbations of room lighting without a specific effort to look for them. Light meters can reveal light intensity, and their use should include a check of the light levels on the top shelves, just below the ceiling lights. Timers can maintain a standard 12:12 hour light:dark cycle in a room, but staff need to explicitly check periodically that the lights are, in fact, going off at night. Graduate students can be semi-nocturnal and may want to turn on lights for experiments during what should be the animals' dark phase, with significant effects on the animals' circadian rhythms. Dim, red lights can improve on this, but do not entirely eliminate stimulation of the rodent retina and ganglia (Hattar *et al.*, 2002).

19.5.2 The social environment

Following publication of the Brambell Report, the UK Government's Farm Animal Welfare Council called for, 'Freedom to express (most) normal behaviour by providing ... company of the animal's own kind.' The *Guide* recommends, 'Social animals should be housed in stable pairs or groups of compatible individuals unless they must be housed alone for experimental reasons or because of social incompatibility.' Social housing is the first item in the USDA's suggestions for meeting the AWA's requirements for the psychological well-being of NHPs. Social housing in compatible groups is the default expectation for housing laboratory animals.

Despite the regulatory presumption for compatible social housing, many laboratory animals do in fact live alone in their cages. Others, though this is often not obvious on a quick walk through the animal facility, live in an incompatible group.

Under natural conditions, animal packs, troops, herds, harems, and warrens cover enough territory

that individual adult animals are neither totally solitary nor side-by-side 24 hours a day. Most laboratory animals live indoors in cages that are too small for them to shift their proximity to others throughout the day, making it impossible for them to choose close contact and affiliation some of the time and avoid agonistic conflict at others.

Common laboratory species – rodents, primates, dogs, cats, pigs, rabbits – range in how social they are under natural conditions. Within a species, an individual's interest in social contact with conspecifics may reflect that individual's history, age, and sex, and also depend on various features of the physical environment as well as who the candidate conspecifics for sociality are.

Given the range of species, we focus here on mice and monkeys to explore the challenge of deciding what is best for them in the caged environment. We review common reasons scientists might prefer singly caged animals. Economics and efficiency do play a role, leading institutions to choose smaller, simpler, easily cleaned cages while simultaneously keeping costs down by housing multiple animals per cage.

Mice and rats live in dynamic shifting groups and their social preferences depend in part on how they were reared and what resources their environment offers (Olsson and Westlund, 2007). Caged rodents often seek social interaction; for example, female rats show greater motivation for access to conspecifics than for any other resource (Patterson-Kane *et al.*, 2002) and male mice show a preference for sleeping in close proximity to a familiar male (Van Loo *et al.*, 2003). Teasing out the main motivator can be difficult – do they want warmth? companionship? – and that information can help tailor environments to best suit animal needs and preferences.

Depriving rodents of desired social contact can decrease their well-being (see Chapter 8, this volume). Social isolation can be a stressor, resulting in increased corticosterone and neurobehavioral alterations (Olsson and Westlund, 2007). Social isolation during development is linked to increased anxiety-like behaviors, increased fear behavior, and reduced social contact later in life (Lukkes *et al.*, 2009; Ros-Simo and Valverde, 2012). Solitary animals in a multi-animal room are not truly solitary if they can hear, smell, and see their conspecifics. In the vivarium, however, individually ventilated cages block most of this cage-to-cage social communication.

Aggression is common in rodents under common conditions, with mice usually more aggressive than rats, males more aggressive than females, and

additional differences related to strain and to an individual's history (Berdoy, 2003; Olsson and Westlund, 2007). Wild mice live in territories inhabited by only one adult male, several females, and their offspring, therefore male mice do not naturally share territories and resident males are highly intolerant of intruders (Kappel et al., 2017) and can be 'despotic territory-holders' (Latham and Mason, 2004). It is not possible at this point to firmly conclude if male mice have a better quality of life when housed alone (with added nesting material for thermoregulation) or in a same-sex group, as it is highly context-dependent and varies depending on strain, age, social status, and husbandry practices (Kappel et al., 2017). Subordinate animals and high-ranking individuals experience life in an enclosed space differently, and where dominant individuals might prefer a group setting in which they rule the hierarchy, subordinate animals might actually fare better in a solitary cage.

Thus, rodents choose to be together (sometimes), are stressed by solitary confinement (sometimes), and may fight when they are together (sometimes). If co-housing is on balance the better option for animal welfare, and coincidentally, for economic efficiency, the challenge then is finding ways to maximize success in co-housing. Strategies include finding optimal group sizes for the strain and sex (three per cage is a common recommendation), maintaining stable groups, and transferring enough scent-marked bedding at cage change so that pheromones associated with a stable hierarchy continue (Van Loo *et al.*, 2003; Olsson and Westlund, 2007).

Macaques, such as rhesus monkeys, are the most numerous NHPs in laboratories. They live in large male–female groups with hierarchies, which are more easily accommodated in large corrals (common at the large primate centers) than in smaller cages. Socially housed macaques display more affiliative interactions, more play and locomotor behaviors, and fewer abnormal, stereotypic, and self-injurious behaviors than singly housed monkeys (Baker *et al.*, 2012; Hannibal *et al.*, 2016). In a restricted environment, enforced co-housing can lead not just to distress but to outright fighting, and even in corral housing animals may lose fingers and tails to aggressors.

As with mice, if monkey housing cannot accommodate a large male-female group with its shifting dynamics, affiliative moves, and defense retreats,

C. Elkhoraibi et al.

strategies are needed to house smaller numbers, typically just pairs, compatibly. A common strategy for establishing compatible macaque pairs requires extended familiarization of the animals to allow them to establish a dominance relationship, progressing from visual-only contact to limited touch via a 'grooming bar' panel of slats between two cages, to supervised full contact. In a small laboratory the available choices of potential social partners will be limited (Baker et al., 2014). If full-time unsupervised co-housing is not successful, singly caged animals in a room will still have visual and auditory social contact, establishing a stable hierarchy without ever actually touching each other. Caregivers can supplement this with grooming bar 'protected contact' (Baker et al., 2014; Hannibal et al., 2016).

No social housing program can succeed if it undermines the needs of the research project. Given the complexity of socially housing mice and monkeys, and the violent consequences of doing it wrong, researchers have several reasons to prefer singly caging their animals. They may fear that increasing social interaction will introduce greater variability in their research subjects, especially if an unstable hierarchy creates added stress to subordinate animals. They may believe that single caging better standardizes their subjects' biology. Research animals may have assorted 'implants' and foreign bodies (attachments to the skull that allow for brain recording, sutures from a recent surgery, etc.) and researchers need to keep these items undisturbed by cage mates. Group-caged animals in infectious disease research could crosstransmit infections in an uncontrolled way. Group-caged animals often live in an unstable, shifting social milieu, as a group of five mice goes down to four and three and two as animals are removed for analysis. This shifting social environment can be both a welfare and a researchconsistency concern.

Along with the welfare obligation to give animals the freedom to express normal social behavior, scientists should realize that the stress of social isolation also may impact data outcomes. They should work with their veterinarian, IACUC, and behavior specialists to plan the best course for the particular experiment, and then publish social milieu as a relevant factor just as they do their animals' genetics, the pH of reagents, research manipulations, and other salient components of their Materials and Methods.

19.5.3 Human–animal interactions in the laboratory

Laboratory animals cannot avoid contact with people, including both their daily caregivers and the researchers performing experiments. Whether these interactions increase or decrease an animal's welfare varies with the species, the animal's history of human interaction, and whatever it is the person is doing and how they are doing it.

Thoroughly domestic species such as dogs, cats, and pigs may find human contact comforting, assuming they were socialized correctly at an earlier date. Mice, rats, and monkeys frequently find humans threatening, though they can be tamed and acclimated to human contact. Whereas dogs or pigs may readily learn in the laboratory to follow their human caregiver, present a limb for blood collection, or climb on the scale for their weekly weigh-in, most mice, rats, and monkeys do not interact this way. They may be caught and lifted for a cage change, restrained for an injection, and, in the case of primates, may be sedated even for simple procedures such as blood collection or physical examination.

Forced restraint and handling can scare and stress animals. Some methods are better than others. A busy caregiver will not train all his mice to jump into his hand for cage changing, but he can use gentler methods for picking them up than by the tail, which causes anxiety (Gouveia and Hurst, 2013). Scooping or cupping the animals into the hand or coaxing them into a small tube to lift them results in more voluntary interactions and less stress (Hurst and West, 2010). Rats habituate to human handling and respond well to tickling, a human–animal interaction that caregivers may enjoy as well, thereby decreasing stress for both human and animal (LaFollette *et al.*, 2017).

Gentle handling and close contact may be dangerous for highly immune-compromised animals or for animals infected for microbiology studies. Risks of human-animal and animal-human cross-infection may require a more hands-off approach. Macaque monkeys are large and aggressive, and are natural carriers of viruses that can infect people. Direct contact is dangerous, so people may use various squeeze-back cages to restrain animals to inject a sedative, or fit them with collars and train them to cooperate with a restraint pole hooked to the collar. Positive reinforcement training can replace coercion with cooperation. As in zoos, monkeys in laboratories

will also learn to approach people to present a limb for blood collection or for injection (Perlman *et al.*, 2012; Kemp *et al.*, 2017; see Fig. 19.1).

Animals are not capable of true informed consent as human research volunteers must be. They may understand what injections are as a momentary procedure, but not the reason they are being injected. True informed consent would require knowledge of the present procedure and its longterm consequences. Positive reinforcement training can lead to the animals' cooperation with the short-term procedure. Going beyond this training, at least in the case of Great Apes, scientists can strive to obtain assent from chimps or other apes (Institute of Medicine and National Research Council, 2011; Fenton, 2014). Assent means allowing the animals to choose to do what they have been trained to do, or to terminate an interactionin-progress (i.e., to *dissent*).

19.5.4 Pain and laboratory animals

Pain is a physical and emotional state that profoundly affects animals' mental health and well-being. The physical aspects of pain, or *nociception*, are a welfare concern when they lead to emotional distress in animals.

Not all nociception is severe enough to cause suffering, and humans and animals may willingly submit to pain in pursuit of some valued goal. On the other hand, nociceptive input (e.g., electric shocks) may end, but the suffering may continue as animals remember the pain or anticipate its return.

Pain is more of a concern with animal *use* in experiments than in animal care and housing. While scientists may induce pain in order to study it, more commonly pain is a contingent side effect of other research programs. Surgery is a common cause of acute pain in laboratory animals, while advanced cancers, some inflammatory conditions, some toxicity testing, and many other models can cause chronic animal pain.

Current regulations and guidelines consider pain, along with distress, as the focus of concern, and set a threshold – 'more than minor or momentary' – above which a scientist must pay special attention to the effects of what she is doing to animals. At this point she must consult a veterinarian on pain management and consider alternative methods and refinements to reduce the pain. Of course, lesser pains can also matter to the animals, and though below the level of regulatory concern, scientists can brainstorm ways to avoid causing even small pains.



Fig. 19.1. A cynomolgus macaque (*Macaca fascicularis*) trained through positive reinforcement to present a limb for injections and for blood collection. (Photo credit: Melanie Graham, used with permission.)

286 C. Elkhoraibi et al.

For example, rather than a test drug being administered by daily injections, it may be formulated into an oral version and mixed into the animal's diet.

Pain diagnosis is challenging in all animals, including those in the laboratory. The animals cannot tell us in language we understand precisely how they are feeling, nor is there one single simple physical or behavioral test of pain. People need to know the nonverbal signs of pain to watch for. Decreases in normal behaviors (e.g., grooming, feeding, nest-building, social interaction) and increases in abnormal behaviors (e.g., twitching, grimacing, hiding) may indicate pain; however, these signs may not be evident in all situations involving pain. A particular challenge is that so many near-identical small animals typically receive only a few minutes of human observation per day, often at the wrong time of day, and thus subtle signs of mild-to-moderate pain are easily missed. Good pain management relies on good pain diagnosis, and good pain diagnosis is a vexing challenge.

Armed with good knowledge of the model and its pain potential, scientists should consider ways to: (i) prevent the pain; (ii) treat the pain; and, finally, to (iii) terminate the pain. Prevention includes efforts to find alternative, less invasive methods. Veterinarians can advise on analgesic drugs and nursing care to treat animals' pain. Every research protocol must include humane or intervention endpoints, which will ensure that the study is ended (typically through euthanasia) when animal suffering reaches pre-defined criteria such as weight loss, decreased mobility, or other disease-specific signs of advanced pain or illness.

As noted above, IACUCs have the authority to approve studies in which scientists plan to withhold pain medications for painful conditions. Pain, and the analgesic drugs used to treat it, both can have powerful effects on the animals' biology and can influence research outcomes. Pain and pain medications can affect immune function, food consumption, sleep patterns, and a host of bodily functions, and scientists and IACUCs must consider both before too readily approving projects with significant unalleviated pain (National Research Council, 2009; Carbone, 2011; Carbone and Austin, 2016).

19.5.5 Environmental enrichment

Following decades of efforts to improve the lives of captive animals, the AWA gave the term 'environmental enrichment' (EE) its legal status in 1985, though only for NHPs. The AWA amendment stated

that zoos and laboratories must have a 'plan for environment enhancement adequate to promote the psychological well-being of nonhuman primates' (Carbone, 2004, p.36). The plan must address the social environment, but also EE, adding 'means of expressing noninjurious species-typical activities' to the animals' enclosures (Carbone, 2004, p.228). Welfare scientists study enrichment strategies not just for primates but also for other species (see Hubrecht, 1993; Newberry, 1995; Olsson and Dahlborn, 2002; Würbel and Garner, 2007; Baumans *et al.*, 2010; Collymore *et al.*, 2015; Coleman and Novak, 2017).

The term *environmental enrichment* has different meanings in different contexts, thus leading to its inconsistent use in the scientific and welfare literature (Newberry, 1995). Scientists may study EE and nonenriched environments to model human developmental neurology. Those studies give the animals cognitive, motor, and sensory stimulation at levels that greatly exceed standard housing, but also exceed the degree of EE used in vivaria as an animal welfare tool (see van Praag *et al.*, 2000; Alwis and Rajan, 2014).

Enrichment is a problematic word to the extent that it implies going beyond some sort of default standard in which an animal lives alone in a barren cage. It can sound like it is an optional 'extra' for the animals' housing, when in fact the bare 'standard' cage is actually 'controlled deprivation' and should not at all be standard or default (Burghardt, 1996). The term can also challenge IACUCs, when neurobiologists read the literature on EE as a research variable that affects neural development and fear that anything beyond a bare solitary cage is enrichment that will skew their experimental outcomes (see Baumans et al., 2010; Toth et al., 2011; André et al., 2018; Bailoo et al., 2018). Clear definitions can lead the way to a compromise situation in which animals are neither over-stimulated nor living in impoverished environments.

In addition, modern EE goes beyond simply placing a toy or a novel food in the cage on the hunch that animals might like it. Effective EE must be biologically relevant. EE improves animals' well-being by allowing them the opportunity to perform natural behaviors and to have enhanced control over their environment as a way to better cope with the stresses of captivity and confinement (Mason *et al.*, 2007; see also Chapter 6, this volume).

Würbel and Garner (2007) devised a three-level classification scheme for EE including 'pseudo-enrichments', 'conditionally beneficial enrichments',

and 'beneficial enrichments'. This classification scheme covers biological relevance, welfare benefits, detriments, and consequences. For example, marbles in the mouse cage are a 'pseudo-enrichment' that animals interact with, not for play, but to remove them to the extent possible by burying. Shelters are conditionally beneficial; in cases where shelters elicit aggression they can be detrimental. Nesting material tends to provide high EE value with little downside to the animals.

EE is biologically relevant when it meets important needs or desires of the animals, a determination that requires rigorous examination. Nesting material allows a natural behavior that gives mice a place to hide and helps them stay comfortably warm (Gaskill *et al.*, 2013a,b). Predictions of a particular enrichment's value require testing and continuing refinement. When are shelters valuable, versus a cause of aggression? How can social enrichment meet animals' needs without promoting fighting and social stress? Are puzzle feeders a useful way to simulate foraging behavior, or are they too frustrating, too boringly simple to solve, or a place for monkeys to entrap their fingers?

Even when demonstrated to be biologically relevant, EE strategies may present some challenges. Nesting material may clog drains. Devices cost money, take time to maintain, take up space in the enclosure, must be safe if eaten, and must be monkey-proof to avoid injuries. An effective EE program must consider both animal and human needs, and strike a balance between them.

19.6 Concluding Remarks

Efforts to maintain mental health and well-being in animals face challenges common to other settings: the available space, resources, and human knowledge to develop the best possible outcomes for the situation. Beyond that, scientists should know that enriched, physically and mentally healthy animals are biologically different from isolated, stressed, painful animals, and experimental data will differ when studying healthy versus stressed subjects. Scientists may successfully justify restricting their animals' welfare in various ways for some compelling experiments, but that does not mean that animals sitting alone in a barren cage, or animals without effective pain medications, are necessarily the 'truer' model of whatever human condition scientists are studying. Responsible stewardship of laboratory animals requires an informed inventory of welfare challenges for every study and every situation, and careful review of refinements and alternatives before any decision to proceed with an option that compromises welfare.

19.7 Acknowledgment

Our thanks to David Takacs for helpful critical feedback on this chapter.

19.8 References

- Alwis, D.S. and Rajan, R. (2014) Environmental enrichment and the sensory brain: The role of enrichment in remediating brain injury. Frontiers in Systems Neuroscience 8, 156. doi:10.3389/fnsys.2014.00156.
- André, V., Gau, C., Scheideler, A., Aguilar-Pimentel, J.A., Amarie, O.V., et al. (2018) Laboratory mouse housing conditions can be improved using common environmental enrichment without compromising data. PLoS Biol 16(4): e2005019. doi:10.1371/journal. pbio.2005019
- Bailoo, J.D., Murphy, E., Boada-Saña, M., Varholick, J.A., Hintze, S., et al. (2018) Effects of cage enrichment on behavior, welfare and outcome variability in female mice. Frontiers in Behavioral Neuroscience 12, 232. doi:10.3389/fnbeh.2018.00232.
- Baker, K.C., Bloomsmith, M.A., Oettinger, B., Neu, K., Griffis, C. et al. (2012) Benefits of pair housing are consistent across a diverse population of rhesus macaques. American Journal of Primatology 76, 30–42. doi:10.1016/j.applanim.2011.09.010.
- Baker, K.C., Bloomsmith, M.A., Oettinger, B., Neu, K., Griffis, C. et al. (2014) Comparing options for pair housing rhesus macaques using behavioral welfare measures. American Journal of Primatology 76, 30–42. doi:10.1002/ajp.22190.
- Barker, D.J., Sanabria, F., Lasswell, A., Thrailkill, E.A., Pawlak, A. P., et al. (2010) Brief light as a practical aversive stimulus for the albino rat. Behavioural Brain Research 214, 402–408. http://dx.doi.org/10.1016/ j.bbr.2010.06.020.
- Baumans, V., Van Loo, P.L.P., Pham, T.M. (2010) Standardisation of environmental enrichment for laboratory mice and rats: Utilisation, practicality and variation in experimental results. Scandinavian Journal of Laboratory Animal Science 37, 1–14. doi:10.23675/sjlas.v37i2.209.
- Bellhorn, R.W. (1980) Lighting in the animal environment. *Laboratory Animal Science* 30, 440–450.
- Berdoy, M. (2003) The laboratory rat: A natural history. Available at: www.ratlife.com (accessed 22 November 2018).
- Brambell, R. (1965) Report of the Technical Committee to Enquire into the Welfare of Animals Kept under

C. Elkhoraibi *et al.*

- Intensive Livestock Husbandry Systems. Her Majesty's Stationary Office, London, UK.
- Burghardt, G.M. (1996) Environmental enrichment or controlled deprivation? In: Bielitzki, J.T., Boyce, J.R., Burghardt, G.M., Schaefer, D.O. (eds.) *The Wellbeing of Animals in Zoo and Aquarium Sponsored Research*. Scientists Center for Animal Welfare, Greenbelt, Maryland, USA.
- Carbone, L. (2004) What Animals Want: Expertise and Advocacy in Laboratory Animal Welfare Policy. Oxford University Press, New York, USA. doi:10.1093/acprof: oso/9780195161960.001.0001.
- Carbone, L. (2011) Pain in laboratory animals: The ethical and regulatory imperatives. *PLoS ONE* 6(9), e21578. doi:10.1371/journal.pone.0021578.
- Carbone, L. and Austin, J. (2016) Pain and laboratory animals: Publication practices for better data reproducibility and better animal welfare. *PLoS ONE* 11, e0155001. doi:10.1371/journal.pone.0155001.
- Coleman, K. and Novak, M.A. (2017) Environmental enrichment in the 21st century. *ILAR Journal* 58, 295–307. doi:10.1093/ilar/ilx008
- Collymore, C., Towani, R.J., Rasmussen, S. (2015) The behavioral effects of single housing and environmental enrichment on adult zebrafish (*Danio rerio*). *Journal of the American Association of Laboratory Animal Sciences* 54, 280–285.
- Fenton, A. (2014) Can a chimp say 'No'? Re-envisioning chimpanzee dissent in harmful research. *Cambridge Quarterly of Healthcare Ethics* 23, 130–139.
- Gaskill, B.N., Gordon, C.J., Pajor, E.A., Lucas, J.R., Davis, J.K., et al. (2013a) Impact of nesting material on mouse body temperature and physiology. *Physiology and Behavior* 110, 87–95. doi:10.1016/j. physbeh.2012.12.018.
- Gaskill, B.N., Pritchett-Corning, K.R., Gordon, C.J., Pajor, E.A., Lucas, J.R., et al. (2013b) Energy reallocation to breeding performance through improved nest building in laboratory mice. PLoS ONE 8(9), e74153. doi:10.1371/journal.pone.0074153.
- Gouveia, K. and Hurst, J. (2013) Reducing mouse anxiety during handling: Effect of experience with handling tunnels. *PLoS ONE* 8(6), e66401. doi:10.1371/journal.pone.0066401.
- Hannibal, D.L., Bliss-Moreau, E., Vandeleest, J., McCowan, B., Capitanio, J. (2016) Laboratory rhesus macaque social housing and social changes: Implications for research. *American Journal of Primatology* 79:e22528. doi:10.1002/ajp.22528.
- Hattar, S., Liao, H.W., Takao, M., Berson, D.M., Yau, K.W. (2002) Melanopsin-containing retinal ganglion cells: Architecture, projections, and intrinsic photosensitivity. *Science* 295, 1065–1070. doi:10.1126/science. 106960.
- Heffner, H.E. and Heffner, R.S. (2007) Hearing ranges of laboratory animals. *Journal of the American Association* of Laboratory Animal Sciences 46, 20–22.

- Hubrecht, R.C. (1993) A comparison of social and environmental enrichment methods for laboratory housed dogs. *Applied Animal Behavioral Science* 37, 345–361. doi:10.1016/0168-1591(93)90123-7.
- Hurst, J. and West, R. (2010) Taming anxiety in mice by non-aversive handling. *Nature Methods* 7, 825–826. doi:10.1038/nmeth.1500.
- Institute for Laboratory Animal Research. (2011) *Guide* for the Care and Use of Laboratory Animals, 8th edn. National Academies Press, Washington, DC, USA.
- Institute of Medicine and National Research Council. (2011) Chimpanzees in Biomedical and Behavioral Research: Assessing The Necessity. National Academies Press, Washington, DC, USA.
- Kappel, S., Hawkins, P., Mendl, M.T. (2017) To group or not to group? Good practice for housing male laboratory mice. *Animals* 7, 88. doi:10.3390/ani7120088.
- Karatsoreos I.N., Bhagat, S., Bloss, E.B., Morrision, J.H., McEwen, B.S. (2011) Disruption of circadian clocks has ramifications for metabolism, brain, and behavior. *Proceedings of the National Academy of Sciences* 108, 1657–1662. doi:10.1073/pnas. 10183751.
- Kemp, C., Thatcher, H., Farningham, D., Witham, C., MacLarnon, A. et al. (2017) A protocol for training group-housed rhesus macaques (*Macaca mulatta*) to cooperate with husbandry and research procedures using positive reinforcement. *Applied Animal Behavior Science* 197, 90–100. doi:10.1016/j. applanim.2017.08.006.
- Kilkenny, C., Browne, W., Cuthill, I.C., Emerson, M., Altman, D.G. (2010) Animal research: Reporting in vivo experiments: The ARRIVE guidelines. *British Journal of Pharmacology* 160, 1577–1579. doi:10.1111/j.1476-5381.2010.00872.x.
- Kokolus, K.M., Capitano, M.L., Lee, C.T., Eng, J.W., Waight, J.D. et al. (2013) Baseline tumor growth and immune control in laboratory mice are significantly influenced by subthermoneutral housing temperature. Proceedings of the National Academy of Sciences (USA) 110, 20176–20181. doi:10.1073/ pnas.1304291110.
- LaFollette, M., O'Haire, M., Cloutier, S., Blakenberger, W., Gaskill, B.N. (2017) Rat tickling: A systematic review of applications, outcomes and moderators. *PLoS ONE* 12(4), e0175320. doi:10.1371/journal.pone. 0175320.
- Latham, N.R. and Mason, G.J. (2004) From house mouse to mouse house: The behavioural biology of free-living *Mus musculus* and its implications in the laboratory. *Applied Animal Behavior Science* 86, 261–289. doi:10.1016/j.applanim.2004.02.006.
- Li, S., Jin, M., Zhang, D., Yang, T., Koeglsperger, T., et al. (2013) Environmental novelty activates beta2adrenergic signaling to prevent the impairment of hippocampal LTP by Abeta oligomers. Neuron 77, 929–941. doi:10.1016/j.neuron.2012.12.040.

- Lukkes, J.L., Mokin, M.V., Scholl, J.L., Forster, G.L. (2009) Adult rats exposed to early-life social isolation exhibit increased anxiety and conditioned fear behavior and altered hormonal stress responses. *Hormones and Behavior* 55, 248–256. doi:10.1016/j.yhbeh.2008.10.014.
- Mason, G., Clubb, R., Latham, N., Vickery S. (2007) How and why should we use enrichments to tackle stereotypic behavior? *Applied Animal Behaviour Science* 102, 163–188. doi:10.1016/j.applanim.2006.05.041.
- National Research Council. (2009) Recognition and Alleviation of Pain in Laboratory Animals. The National Academies Press, Washington, DC, USA. doi.org/ 10.17226/12526.
- Newberry, R.C. (1995) Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science* 44, 229–243. doi:10.1016/0168-1591(95)00616-Z.
- Olsson, A. and Dhalborn, K. (2002) Improving housing conditions for laboratory mice: A review of 'environmental enrichment'. *Laboratory Animals* 36, 243–270. doi:10.1258/002367702320162379.
- Olsson, A. and Westlund, K. (2007) More than numbers matter: The effect of social factors on behaviour and welfare of laboratory rodents and non-human primates. *Applied Animal Behavior Science* 103, 229–254. doi:10.1016/j.applanim.2006.05.022.
- Patterson-Kane, E.G., Hunt, M., Harper, D. (2002) Rats demand social contact. *Animal Welfare* 11, 327–332.
- Perlman, J.E., Bloomsmith, M.A., Whittaker, M.A., McMillan, J.L., Minier, D.E., et al. (2012) Implementing positive reinforcement animal training programs at primate laboratories. Applied Animal Behavior Science 137, 114–126. doi:10.1016/j.applanim.2011.11.003.
- Reynolds, R.P., Randall, P., Kinard, W.L., Degraff, J.J., Leverage, N., et al. (2010) Noise in a laboratory animal facility from the human and mouse perspectives. Journal of the American Association for Laboratory Animal Science 49, 592–597.
- Richter, S.H., Garner, J.P., Würbel, H. (2009) Environmental standardization: Cure or cause of

- poor reproducibility in animal experiments? *Nature Methods* 6, 257–261. doi:10.1038/nmeth.1312.
- Ros-Simo, C. and Valverde, O. (2012) Early-life social experiences in mice affect emotional behavior and hypothalamic-pituitary-adrenal axis function. *Pharmacology Biochemistry and Behavior* 102, 434–441. doi:10.1016/j.pbb.2012.06.001.
- Russell, W.M.S. and Burch, R.L. (1959) *The Principles of Humane Experimental Technique*. Methuen & Co. Ltd., London. UK.
- Sales, G.D., Wilson, K.J., Spencer, K.E.V., Milligan, S.R. (1988) Environmental ultrasound in laboratories and animal houses: A possible cause for concern in the welfare and use of laboratory animals. *Laboratory Animals* 22: 369–375. doi:10.1258/002367788780746188.
- Toth, L.M., Kregel, K., Leon, L., Musch, T.I. (2011) Environmental enrichment of laboratory rodents: The answer depends on the question. *Comparative Medicine* 61, 314–321.
- Van Loo, P.L.P., Van Zutphen, L.F., Baumans, V. (2003) Male management: Coping with aggression problems in male laboratory mice. *Laboratory Animals* 37, 300–313. doi:10.1258/002367703322389870.
- Van Praag, H., Kempermann, G., Gage, F.H. (2000) Neural consequences of environmental enrichment. Nature Reviews Neuroscience 1, 191–198. doi:10.1038/ 35044558.
- Walton, J.C., Wei, Z.M., Nelson, R.J. (2011) Influence of photoperiod on hormones, behavior, and immune function. *Frontiers in Neuroendocrinology* 32, 303–319. doi:10.1016/j.yfrne.2010.12.00.
- Würbel, H. (2007a) Publications should include an animal-welfare section. *Nature* 446, 257. doi:10.1038/ 446257a
- Würbel H. (2007b) Environmental enrichment does not disrupt standardisation of animal experiments (letter). *Altex* 24 Special Issue, 70–73.
- Würbel, H. and Garner, J.P. (2007) Refinement of rodent research through environmental enrichment and systematic randomization. *NC3Rs* 9, 1–9.

C. Elkhoraibi et al.

20 Mental Health Issues in Captive Birds

LYNNE M. SEIBERT

Veterinary Behavior Consultants, Roswell, Georgia, USA

Mental states in birds involve a wide range of cognitive abilities and emotions. Due to the popularity of psittacine birds as pets, there is a need for understanding and further scientific study of their emotional needs. Psittacine birds do not have the extensive history of domestication that many other species that are kept as pets, such as dogs and cats, have experienced.

Emotional well-being in pet birds is affected by additional unique challenges. Many psittacine species have the capacity to live as long as humans, requiring a lifelong commitment on the part of their caregivers. Unlike dogs and cats in the United States, most pet birds remain reproductively intact, which creates behavioral challenges, especially at puberty and during breeding seasons when new behaviors appear. The intelligence of psittacine birds has been documented in numerous studies and illustrates the importance of providing intellectual challenges for these highly intelligent species (Pepperberg, 1987, 1994).

Understanding the behavioral and emotional needs of psittacine birds has important applications. First, we can improve the conditions for birds kept in captivity and provide for the expression of speciestypical behaviors. We can reduce the incidence of behavior problems in pet birds, such as screaming, repetitive behaviors, feather-damaging behaviors, self-trauma, and aggression. Inadequate attention to birds' mental health is an important welfare issue as it can lead to emotional suffering and poor quality of life. Boredom and social deprivation are examples of the negative influences on birds' mental well-being.

A better understanding of the emotional requirements of psittacine birds could enhance the success of captive breeding programs for endangered psittacine species. Parrots possess the largest number of threatened species of any avian family. There are at least 90 psittacine species at risk for extinction (Collar and Juniper, 1992). The *Psittacidae* family contains more threatened species than would be expected by chance, with an increased extinction

risk with increasing body size and deceasing fecundity (Bennett and Owens, 1997). Threats include habitat destruction, live bird trade, introduced species (cats and rats), persecution, hunting for food, and fluctuations in environmental conditions.

This chapter discusses the importance of mental health and well-being in captive birds, with practical recommendations for bird caregivers to maximize the mental wellness of birds in their care.

20.1 Species Diversity

The large variety of psittacine species presents an important limitation to generalizing about their behavioral needs and mental health. There are three families within the order Psittaciformes: *Psittacidae*, *Cacatuidae*, and *Loriidae*. The family *Psittacidae* is the largest, including approximately 280 species of parrots, macaws, parakeets, rosellas, and lovebirds. The family *Cacatuidae* includes more than 20 species of cockatoos and a single species of cockatiel. *Loriidae* includes more than 50 species of lories and lorikeets (Forshaw, 1989).

Psittacine birds exhibit considerable range in appearance, with wide variations in size (from 10 g to >1500 g), structure (crested or noncrested), and coloration. Some species are sexually dimorphic. Some are primarily arboreal (yellow-winged Amazon, *Amazona aestiva xanthopteryx*), while others are terrestrial foragers (budgerigar, *Melopsittacus undulatus*).

Psittacine birds occupy diverse habitats, living anywhere from tropical rain forest to dry savannah. Tropical and subtropical lowland forested areas offer the most species diversity. Psittacine birds are neither sedentary, nor migratory, but mobile within a geographical area. Many travel substantial distances between roosting and feeding sites.

Social behavior varies among the different species as well. Some appear to be solitary (kakapo, *Strigops habroptilus*), while most species are highly social. With so much variation in habitat and life history, recommendations for maintaining

emotional health would need to be specific for the species and individuals involved.

20.2 Mental States and Experiences of Birds

It is important to recognize both positive and negative mental states in birds. Unfortunately, there are very few published ethograms for psittacine birds. Studies are needed that illustrate the meanings of various postures and actions of captive birds so that caregivers can more accurately assess mental and physical well-being. Fear or anxiety in captive birds is generally associated with increased vocalizations, defensive postures (such as crouching or flight intention movements), avoidance, frantic behaviors, displacement behaviors (such as preening), aggression, or escape attempts. Anxiety can also suppress normal behaviors, manifesting as freezing behavior or lack of interaction with the environment.

In a study evaluating neophobia, or latency to approach a novel object, Mettke-Hofmann *et al.* (2002) found that the natural ecology of the species influences neophobia. Sixty-one parrot species with different habitat preferences were studied in aviaries. The species with the shortest latency and longest duration of exploration were species inhabiting complex habitats and species that fed on seasonal foods (nectar, fruit, and nuts). The species with the longest latency and shortest duration of exploration were seed eaters. This study documents behavioral differences in captive species based on their natural habitats that must be considered when providing ideal captive environments.

In clinical situations, caregivers often report fearful behaviors with no known etiology. Fears can develop as a result of classical conditioning, in which the bird associates the owner with an aversive event. This situation has been reported in a case study of a Goffin's cockatoo (*Cacatua goffini*) that developed a persistent fear response toward its owner following an episode of fear-evoking construction noises (Seibert *et al.*, 2001).

20.3 Importance of Social Interactions

The importance of providing some forms of social companionship must be considered for captive birds. Psittacine birds often form flocks. The benefits of flock membership include improved defense against predators, increased competitive ability, increased feeding efficiency, and access to mates (Wilson, 1975).

Feeding together in organized flocks may be advantageous to the individual, who is able to benefit from the collective knowledge of the group. By following the flock, an individual has a better chance of locating adequate amounts of food when resources are unpredictable. Small foraging groups are better able than individual birds to exclude competitors from feeding sites. There is some evidence that birds with more limited fasting ability, smaller birds, are more likely to flock than larger birds (Gill, 1995).

Indefensible areas also promote flocking behavior in birds. There is increased security in a large group, with individuals nearest the center of the flock having the least chance of becoming the victim of a predator. Flocking improves the efficiency of predator detection, allowing the individual more time for other activities. Alarm calling is common within flocks and serves to alert other members of the group to possible danger.

South and Pruett-Jones (2000) studied feral flocks of Monk parakeets in a natural environment. The birds formed foraging groups of 2 to 31 birds (mean <10). Individual vigilance declined with increasing flock size, indicating that the flock serves an important function for predator detection.

The number of birds in the flock appears to be very important to the breeding success of large macaw species. Only a portion of the flock will be engaged in breeding activity during any one season, with the nonbreeding birds appearing to form a buffer zone of territorial defense (Harrison, 1994).

20.4 Pair Bonding

Pair bonding has been defined as a mutually beneficial relationship between sexually mature female and male birds (Doane and Qualkinbush, 1994). Wilson (1975) defines pair bonding as a close and long-lasting association between a male and a female, serving the primary function of cooperative rearing of young. Pairs are characterized by allopreening, courtship feeding (also called allofeeding), pair participation in agonistic encounters, and close spatial associations (Levinson, 1980).

Allopreening has been cited as the most important behavior for maintenance of social bonds. Close spatial associations are also evidence of a bond. Among bonded pairs of canary-winged parakeets (*Brotogeris v. versicolurus*), mates maintained very close proximity and were usually touching (Arrowood,

292 L.M. Seibert

1988). Many psittacine species maintain pair bonds throughout the year.

In captive environments, many birds do not have the opportunity to form close social bonds with conspecifics. In other situations, social pairings between birds can increase stress due to incompatibility. Captive environments should provide some opportunities for the expression of social behaviors and the maintenance of healthy social relationships with humans or other birds.

Meehan *et al.* (2003a) evaluated the influence of isosexual pairing of orange-winged Amazon parrots (*Amazona amazonica*) on the development of abnormal behaviors. Paired parrots used inanimate enrichment devices more than singly housed cohorts. Paired parrots also spent less time screaming, less time preening, and were more active. Parrots housed in pairs did not develop stereotypic behaviors, were less fearful of human handlers, and had reduced latency to approach a novel object. This study demonstrates the potential importance of social bonds between nonreproductive pairs of birds (Fig. 20.1).



Fig. 20.1. Isosexual pairing between two female cockatoos of different species.

20.5 Predictable Environments

The general daily activities (feeding, maintenance, and roosting behaviors) of flocks of orange-fronted parakeets (Hardy, 1965) and white-fronted Amazons (Levinson, 1980) were highly predictable. Two activity peaks were commonly observed, one in the early morning and one in the late afternoon. During the periods of high activity, the birds engaged in feeding, agonistic behaviors, increased mobility, and increased vocalizations.

Pet birds are often exposed to unpredictable environments. Feedings, photoperiods, baths, attention, exercise, and social interactions are often provided based on the varying schedules of the caregivers. This unnatural state of affairs does not allow the bird to develop a sense of control, or the skills for coping with stress and challenges. McMillan (2002) has discussed the adverse effects of unpredictability on the mental well-being of animals.

20.6 Developmental Factors

Many psittacine offspring have relatively long infancies. Weaning may require up to a year in some species, increasing the requirements for parental care (Doane and Qualkinbush, 1994). The detrimental effects of early maternal deprivation on neural development and adult functioning are well-documented in primate species (Ruppenthal *et al.*, 1976; Suomi *et al.*, 1976).

Captive psittacine breeding programs have historically involved removal of the newly hatched birds from their parents and hand weaning by humans, due to the notion that this practice produces better quality pet birds. However, the rearing of baby birds by human surrogates may not be sufficient for the development of healthy adult coping skills and stress responses. The justifications for the practice of hand weaning are beginning to be questioned and alternatives considered.

Aengus and Millam (1999) studied the effects of neonatal handling of parent-raised orange-winged Amazon parrots. One group was handled daily for 10 to 30 minutes from day 10 to fledging. The control group was handled only to obtain their weights. There were significant differences in tameness between these groups, documenting that tameness toward humans is possible for parent-raised birds that are exposed to human handling. Sensitive periods for socialization to humans need to be determined.

There may be effective interventions for individuals that were deprived of maternal care. Bredy et al. (2003) evaluated the effects of environmental enrichment in rats that were deprived of early maternal care and found that peripubertal enrichment did compensate for some of the effects of early maternal deprivation. Francis et al. (2002) also found that environmental enrichment helped to compensate for the negative effects of postnatal maternal separation.

20.7 Foraging Opportunities

Psittacine flocks generally maintain separate foraging and roosting sites. Levinson (1980) observed separate roosting and feeding areas in white-fronted Amazon parrots. In their observations of sulphur-crested cockatoos (*Cacatua galerita*), Lindenmayer *et al.* (1996) noted that the birds traveled considerable distances between roosting sites and areas where foraging occurred. Orange-fronted parakeets (*Aratinga canicularis*) in natural habitats maintained separate roosting and feeding sites 1 mile apart (Hardy, 1965).

Pet birds are often fed commercially prepared diets on a free-choice feeding schedule, drastically reducing the amount of time spent in feeding behaviors. Meal feeding has been suggested to simulate natural feeding behavior more closely (Fig. 20.2). In addition, captive birds may prefer foraging devices that require them to perform work for food (Coulton *et al.*, 1997). Opportunities to forage have been shown to reduce feather picking behavior in Amazon parrots (Meehan *et al.*, 2003b).



Fig. 20.2. Macaws receiving meal feeding on a schedule.

Foraging enrichments required the subjects to manipulate objects with openings, chew through barriers for food, sort through inedible materials, and open containers. In addition to preventing the development of feather-damaging behaviors in the enriched group, the same enrichments were used to reverse the development of feather-damaging behaviors in control birds. In this study, the foraging enrichments were used more than physical enrichments, which provided perching, swinging, and climbing opportunities.

20.8 Photoperiod, Lighting, and Sleep Deprivation

Sleep deprivation can have detrimental effects on the mental health of captive birds. Most psittacine species are diurnal prey species, with an acute sense of vision and hearing. These characteristics present avian caregivers with the challenge of providing for an adequate amount of uninterrupted rest for the birds in their care. Pet birds are often housed in common areas of the home and covered when the caregivers retire for the evening, or at dusk. Given the level of vigilance and reactivity that is characteristic of prey species, it is highly unlikely that the birds receive adequate sleep in these environments. In addition to the stress associated with sleep deprivation, exposure to lengthy photoperiods (increased daylight or artificial light) can increase the incidence of undesirable reproductive behaviors.

Wilson (1999) has discussed sleep requirements for pet birds. It is generally accepted that natural photoperiod variation is ideal for the mental and physical health of pet birds. A two-cage system, including a sleeping cage in a quiet room, provides pet birds with a quiet secluded sleeping area.

In addition to the proper amount of light, the type of lighting can also affect a bird's sensory experience. There is evidence that birds' perceptive abilities extend into the ultraviolet range (Bennett and Cuthill, 1994; Hausmann *et al.*, 2003). Hausmann *et al.* (2003) found that 68% of psittacine birds surveyed have fluorescent plumage. A bird housed in a room with windows that block ultraviolet light has a more limited sensory experience than one that is exposed to full-spectrum or natural lighting. Housing birds strictly indoors without adequate exposure to UVB light exposure may contribute to feather-damaging behavior (West *et al.*, 2018).

294 L.M. Seibert

20.9 Consequences of Poor Mental Health

Emotional suffering and poor quality of life are evidenced by the prevalence of behavior problems in pet birds and the reduction or absence of speciestypical behaviors. Abnormal behaviors include feather-damaging behavior, barbering and self-mutilation, screaming, aggression and biting, misdirected sexual behaviors, and phobias (Davis, 1991).

20.9.1 Feather picking and self-mutilation

Feather-damaging behavior, also called behavioral feather picking or pterotillomania (Lumeji and Hommers, 2008) is one of the most common behavior problems seen in captive psittacine birds (Lawton, 1996). It is characterized by feather removal, feather damage, and/or soft tissue trauma with no apparent medical, nutritional, or physical explanation (Fig. 20.3).

Boredom, defined as a lack of stimulation (Rushen et al., 1993), or a lack of opportunity to interact with the environment (Wemelsfelder, 1993), is often presumed to be the cause of feather-damaging behavior. This presents an overly simplistic view of



Fig. 20.3. Goffin's cockatoo (Cacatua goffiniana) with chronic pterotillomania.

the behavior. Many of the individual birds presented for feather picking problems do not meet the criteria for boredom. They play with toys, interact with humans and other birds, and some are even in breeding programs and allowed free-flight opportunities. Successful treatment of feather-damaging behavior will need to incorporate a broader approach, evaluating early developmental deficiencies, the needs of individual birds, neurochemical correlates, and species-specific interventions.

Excessive preening may be evidence of conflict. Conflict-induced displacement behaviors are behavioral patterns that appear to have no contextual relevance and result from the ambivalence of a conflict situation (Wilson, 1975). Orange-chinned parakeets exposed to stressful situations increased preening, head scratching, ruffling of the plumage, beak wiping, and flight intention (repeated crouching and leaning forward on the perch) (Power, 1966). Inappropriate housing conditions, frustration, stress, sexual behavior, attention-seeking behavior, overcrowding, separation anxiety, and changes in routines have also been implicated as causes of self-inflicted feather damage (Rosenthal, 1993; Welle, 1999). Feather-damaging behavior may result from management conditions that do not allow the bird to engage in species-typical behaviors, or do not provide appropriate target stimuli for these behaviors (Jenkins, 2001).

Feather-damaging behavior has been compared to a condition in humans affecting impulse control, with noted behavioral similarities (Bordnick *et al.*, 1994). Trichotillomania, an impulse-control disorder of humans, is characterized by removal of hair resulting in alopecia, hence the use of the term pterotillomania when birds are affected. Additional characteristics of the disorder include hair twirling, chewing or mouthing the hair, trichophagia, and skin picking (Stein *et al.*, 1995). Avian practitioners have observed oral manipulation of removed feathers by psittacine birds with pterotillomania.

Obsessive—compulsive disorder is characterized by obsessions, intrusive thoughts or images, and compulsions, repetitive behaviors performed in an attempt to reduce anxiety. Hand washing is an example of a compulsive behavior in humans, which may share similarities with repetitive grooming behaviors in animals, including feather picking in birds (Grindlinger, 1991; Stein, 1996). Identifying similarities between avian disorders and human conditions may contribute to our understanding of the etiology of the disorder and the negative emotional experiences of the affected individual.

In addition to feather-damaging behaviors, captive birds engage in a variety of nonproductive, repetitive behaviors (stereotypies) that are often interpreted as evidence of poor welfare or poor mental health. Stereotypic behaviors observed in captive birds include pacing, spot pecking, beak wiping, perch running, repetitive vocalization, head shaking, head bobbing, weaving, and flight intention movements (crouching, posing) (Sargent and Keiper, 1967).

Dilger and Bell (1982) postulated that the stereotypic head movements seen in some birds might be an early sign of neurosis, which could eventually lead to further behavioral abnormalities. The importance of stereotypic behaviors in captive birds as an indicator of poor emotional health is currently unclear and warrants further study.

20.9.2 Screaming and excessive vocalization

Because many parrots are noisy and communicate vocally, excessive vocalization is a common complaint of avian caregivers. Intense calling and vocalization are typical when arriving or departing from roosting sites. It is generally considered normal for pet psittacine birds to vocalize loudly several times a day (Harrison and Davis, 1986). However, there are species differences in noisiness and differences in caregivers' tolerance of noise. Excessive vocalizations are often made worse when the caregiver responds directly to the noisy bird, providing positive reinforcement for the behavior. Birds lacking environmental enrichment may be predisposed.

While screaming is often evidence of normal or exuberant behavior, it can also be a symptom of an environmental or emotional deficiency, indicating fear, undesirable changes to the environment, boredom, or frustration. It is important to determine the temporal patterns, eliciting stimuli, housing conditions, and opportunities for social interaction, as well as other potential causes for excessive vocalization, before recommending any interventions.

Contact calling occurs in avian species when they are separated from flock members. In some cases, it will be appropriate for the caregiver to answer the bird when it vocalizes, and in other cases, this intervention will be ineffective.

Captive birds may present with fear- or stress-induced screaming. Alarm vocalizations have been measured in wild birds, documenting similarities across species in responses to flying predators and other threats (Jurisevic and Sanderson, 1994). Captive birds may also vocalize to indicate distress

or injury. It is crucial that safe housing and accessories be provided and that pet birds be treated like curious toddlers with attention paid to bird-proofing the environment.

Treatment considerations for excessive vocalization should target the needs, both physical and emotional, of the individual bird. It is helpful for the caregiver to keep a diary of excessive vocalization behavior, including date, time of day, location, duration of screaming without intervention, and persons and stimuli present during the episodes. If there is a pattern to the behavior, feeding, play time, or training sessions can be scheduled just before the bird's 'loud times'. Enriching the environment and rewarding appropriate behaviors can lessen the severity of screaming problems. The environment should be modified to maximize stress-reduction, which might include the provision of environmental sounds, exposure to other birds and household activities, hiding places, quiet times, predictable schedules, and reduced confinement. When necessary, a time-out or removal of attention (a form of negative punishment) can be used to discourage screaming.

20.9.3 Aggression problems

Aggression problems are reported in pet birds, although not as commonly as feather picking and screaming. The relatively heavy jaw musculature allows parrots to crack seeds and nuts and inflict injuries. Psittacine birds have evolved flexible necks that allow rapid movement and detection of predators, and along with the beak, allow the bird to rapidly inflict injury during restraint. Parrots also tend to use their beaks as 'hands' to explore the environment.

The causes of intraspecific and interspecific aggression in psittacine birds have not been systematically classified. The author uses a similar classification system as that used for other species, with some modifications for species differences (Beaver, 1983; Overall, 1993). Possible causes of human-directed aggression in birds include territorial defense, fear, intolerance of handling, hormonally induced aggression, redirected aggression, play, attention seeking, lack of learned bite inhibition, and inappropriate mouthing.

20.9.4 Territorial aggression

A territory is defined as an area occupied exclusively by an individual by means of repulsion through overt defense (Wilson, 1975). Many avian species establish, maintain, and protect access to particular

296 L.M. Seibert

areas in their natural habitats. However, the prevalence of territorial behavior among psittacine species has not been determined. Territorial defense may involve defense of feeding areas, roosting positions, or nesting sites. Nest defense should be differentiated from mate guarding – close association with mates to ensure paternity – a common feature of the early stages of nesting in some species.

Aggression may be directed against any intruder, regardless of familiarity. Pet birds with territorial aggression may be fine when taken away from the vicinity of their cages. Treatment involves working in a neutral area on cue training with positive reinforcement and gradually moving training sessions closer to the cage area (desensitization and counterconditioning).

20.9.5 Fear aggression

Many situations can predispose a pet bird to a fearinduced aggressive episode: inconsistent use of reprimands or punishment by the caregiver, confinement to restrictive areas (cages) that do not allow escape, inappropriate housing conditions contributing to stress, absence of flock support, inadequate socialization to humans, and unstable perching surfaces. Aggressive responses can be modified by learning over time (negative reinforcement of aggressive displays), such that aggression becomes the distanceincreasing behavior of choice any time the bird feels threatened.

Redirected aggression occurs when the caregiver is present, the bird is exposed to an offensive stimulus, and the caregiver becomes the recipient of aggression. Redirected aggression can occur when strangers approach the cage, during veterinary visits, or during exposures to unfamiliar environmental stimuli. Through classical conditioning the bird can learn an association between the caregiver and the fear-evoking stimulus, resulting in persistent fear of the caregiver and aggression whenever that person is present.

The treatment of fear-induced aggression involves avoidance of fear-evoking situations, gradual desensitization and counterconditioning, and favorite treats and toys provided only when the feared individual is present (Seibert *et al.*, 2001).

20.9.6 Play aggression, inappropriate mouthing, and lack of bite inhibition

Play behaviors, seen most commonly in juveniles, imitate essential adult activities without consummating

any serious goals (Wilson, 1975). Juveniles of several psittacine species have been observed to engage in social play in the wild (Levinson, 1980). Play behaviors include clawing, play biting, and mock fighting.

During play with conspecifics, young birds would presumably learn the maximum amount of beak force that can be applied without injuring their playmates. Restricted early contact with clutch mates could jeopardize this early learning, resulting in excessive mouthing of human caregivers. Inappropriate responses to this behavior by human caregivers can cause fear.

Young birds should be provided with chew toys and opportunities for locomotor, object, and interactive play. Simply discontinuing interactions when mouthing becomes excessive will teach the bird to inhibit mouthing behavior.

20.9.7 Reproductive causes of aggressive behavior

Problems may arise as pet birds reach sexual maturity, with reports of behaviors that seem to indicate that the bird is misdirecting sexual behaviors toward a human caregiver. Undesirable behaviors include attempts to allofeed (regurgitate), masturbation, excessive contact seeking or calling, aggressive attempts to drive away other members of the family, and defense of the cage as a nesting site (Harrison and Davis, 1986). The onset of these behaviors may coincide with the natural breeding season, increasing day length, or excessive artificial photoperiods.

Treatment may require that other family members assist with feeding and maintenance care while a healthier relationship between the bird and its primary caregiver is cultivated. Reproductive behaviors can be diminished by decreasing the photoperiod, removal of nesting areas, and avoidance of handling that may be stimulating for the bird. Desensitization and counterconditioning have been successful, when the bird is with the preferred caregiver and others gradually approach them.

20.9.8 Dominance in psittacine birds

The term 'dominance' has been grossly misused in the field of avian behavior. Dominance is not synonymous with aggression, and in fact, the formation of stable dominance hierarchies is associated with a reduction in aggression. Stable flock membership requires mutual recognition of members and a system for allocation of group resources. Within a dyadic encounter, a dominance relationship is presumed to exist when the individuals behave with predictable assertive or submissive responses based on previous experiences with each other. By using ritualized postural signaling, overt aggression is avoided. Once relationships are established, there is consistency of the social interactions, resulting in fewer, or less intense, aggressive assertions of dominance (Bernstein, 1981). With the exception of a study of captive cockatiels (*Nymphicus hollandicus*), there are very few studies that have systematically measured dominance relationships in psittacine birds (Seibert and Crowell-Davis, 2001).

Assuming that all aggression is dominance related is counterproductive and sometimes harmful. There is no direct evidence that psittacine birds aggressively challenge the social status of their human caregivers. Most of the aggression observed in psittacine birds does not meet the criteria for a dominance-related problem: aggressive challenges by socially mature birds accompanied by species-specific dominance postures, which are not location or stimulus specific. Cage or resource guarding is not evidence for a dominance-related problem. Frightened birds will often aggressively defend their space. Attempts by caregivers to 'establish dominance over their birds' are likely to increase stress and induce fear responses.

A relationship between perch height and dominance status has not been established for any psittacine species. If a relationship does exist, species differences are likely based on variations in natural habitats and ecology. An inverse relationship between perch height and dominance status may exist with lower ranking birds preferring higher perches. Many birds prefer higher perching sites, which is more likely to be a safety issue than a dominance-related issue. Likewise, difficulty removing a bird from the top of its cage is not an indication of a dominance problem. Lowering cages and perches for a problem bird may result in increased anxiety. For any behavior problem, including aggression, it is crucial to identify and understand the causative factors, take a detailed behavioral history, make a specific behavioral diagnosis, and develop a treatment plan based on accepted practices of behavioral medicine.

20.10 Enhancing the Quality of Care for Captive Birds

Potential bird caregivers should be advised not to purchase a psittacine bird unless they are prepared for a lifelong commitment. Veterinarians and aviculturists can assist in the selection of the appropriate species and individual, taking into consideration longevity, exercise requirements, disease susceptibility, cost to purchase and maintain, and social needs. It is important to locate a reputable source for the bird and obtain a healthy bird that has already been weaned. Providing quality preventive health care and nutrition is critical for maintaining health and emotional well-being.

Early socialization experiences are important for young birds, and caregivers should expose their birds to a variety of people, stimuli, and situations, without causing fear or risking disease exposure. Avian playgroups and social gatherings are commonly available in many communities. Well-socialized birds can take car trips, visit friends, and participate in animal-assisted therapy programs.

Evans (2001) has reviewed housing requirements for pet birds. Enclosures should address the needs of the bird, should be constructed of nontoxic materials, should provide the appropriate bar spacing, and should be large enough to allow a full range of movements. Cages need to provide privacy and security, such that one side of the cage is placed against a wall or partially covered.

The position of the enclosure is also important. Varying the location may be beneficial for some birds. Some birds may require an area with more activity, and some may require a quieter area of the house. Enclosures should be positioned at eye level of standing family members with varying perch heights. The position of the enclosure should also provide exposure to fresh air and natural sunlight, but avoid drafts. Birds should never be exposed to pesticides, aerosols, scented oils, or cigarette smoke.

Birds should be allowed out of their cages on a regular basis, with appropriate supervision, and given opportunities to exercise. This can be accomplished by using playpen stands, tree stands, free-standing perches, cage-top gyms or activity centers, hanging perches, or the caregiver. Harness training allows flighted birds safe access to outdoors and opportunities for flight.

The benefits of enrichment interventions for psittacine birds are well-documented (Coulton *et al.*, 1997; Vanhoek and King, 1997; Meehan *et al.*, 2003b). A stimulating environment can improve emotional well-being and prevent aberrant behaviors. Recommendations include providing stimulating toys, without overcrowding the enclosure, and rotating them on a regular basis. Caregivers must be

298 L.M. Seibert

certain that any toy offered to the bird is safe, non-toxic, and will not be consumed. Some toys should provide the bird with an opportunity to chew, such as wooden ice cream sticks, plain cardboard, paper towel rolls, whiskbrooms, rawhide pieces, pieces of nontoxic wood, or alfalfa cubes. There are a variety of commercially available toys for birds, and individual preferences may require the caregiver to offer several varieties before identifying the most favorable objects. Unique color preferences of individual birds can influence their choice of toys and foods. Less confident birds may initially avoid novel items, so gradual or repeated introductions of novel items and foods may be necessary.

A variety of perching materials of variable diameters are recommended for healthy feet and for behavioral enrichment purposes. Nontoxic, chemical-free, natural branches provide an opportunity to chew, as well as the perch diameter variation that is recommended for optimal pedal health. Other perching options include manzanita wood, PVC pipe, concrete, braided sisal, and cotton rope.

Maintaining a natural to semi-natural photoperiod variation will provide adequate rest and prevent the onset of undesirable reproductive behaviors. Day length can influence hormone production. Providing a sleeping cage in a quiet room will give the bird a quiet, undisturbed sleeping area during dark hours. A minimum of 10 hours of daily sleeping time has been recommended (Evans, 2001).

Avian caregivers should set a regular schedule for daily activities that is somewhat predictable. Scheduled feeding times simulate natural foraging habits. Foraging enrichments include providing chew foods and using food puzzles or toys to hide food and promote searching behavior. Many psittacine species also enjoy bathing. Baths can be provided by misting, taking the bird into the shower, or providing a water bowl.

Avian caregivers often serve the functions of a flock member, and should talk to the bird, interact with the bird, play with the bird, preen the bird, and involve it in family activities. Some birds respond favorably to hearing familiar sounds, especially in the caregivers' absence, such as tape recordings of family activities, other birds, nature sounds, or music.

Pet birds should be taught basic cues using positive reinforcement, such as a highly palatable food treat, praise, a favorite toy, or attention. Cue training can teach the bird appropriate behaviors and can be used to redirect inappropriate behaviors (Fig. 20.4). Birds should be encouraged and rewarded for playing by



Fig. 20.4. Macaw being taught to step up ('up' cue) onto a person's hand.

themselves, for sitting quietly, and for chewing on appropriate objects. Ignoring undesirable behaviors will prevent inadvertent reinforcement of the behaviors. After a pause in the undesirable behavior, the bird can be redirected to obey a cue that has been previously taught. Physical punishment is never appropriate for psittacine birds. Simply leaving the room, withholding attention, or placing the bird in a time-out cage for a few minutes when it misbehaves are often effective interventions.

An understanding of the native behavior of psittacine birds is essential to the prevention and treatment of behavioral disorders of birds in captivity and for optimizing emotional health. The importance of flock social interactions for various species and the effects of isolation on welfare are also pertinent issues. Recognizing that psittacine birds have evolved as prey species should alert caregivers to the importance of environments that provide a sense of security and predictability, particular in the absence of a flock. Caregivers should also be aware that the sensory experiences of birds will be different from that of humans due to their specialized visual capabilities. The intellectual capacity of psittacine birds should not be underestimated and should motivate avian caregivers to provide intellectual stimulation for the birds in their care.

20.11 References

Aengus, W.L. and Millam, J.R. (1999) Taming parentreared orange-winged Amazon parrots by neonatal handling. Zoo Biology 18, 177–187.

- Arrowood, P.C. (1988) Duetting, pair bonding, and agonistic display in parakeet pairs. *Behavior* 106, 129–157. http://dx.doi.org/10.1163/156853988X00133.
- Beaver, B.V. (1983) Clinical classification of canine aggression. *Applied Animal Ethology* 10, 35–43. http://dx.doi.org/10.1016/0304-3762(83)90110-4.
- Bennett, A.T. and Cuthill, I.C. (1994) Ultraviolet vision in birds: What is its function? Vision Research 34, 1471– 1478. http://dx.doi.org/10.1016/0042-6989(94)90149-X.
- Bennett, P.M. and Owens, I.P. (1997) Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proceedings of the Royal Society of London.* Series B: Biological Sciences 264, 401–408. http://dx.doi.org/10.1098/rspb.1997.0057.
- Bernstein, I.S. (1981) Dominance: the baby and the bath water. *Behavioral and Brain Sciences* 4, 419–429. http://dx.doi.org/10.1017/S0140525X00009614.
- Bordnick, P.S., Thyer, B.A., Ritchie, B.W. (1994) Feather picking disorder and trichotillomania: An avian model of human psychopathology. *Journal of Behavior Therapy and Experimental Psychiatry* 25, 189–196. http://dx.doi.org/10.1016/0005-7916(94)90019-1.
- Bredy, T.W., Humpartzoomian, R.A., Cain, D.P., Meaney, M.J. (2003) Partial reversal of the effect of maternal care on cognitive function through environmental enrichment. *Neuroscience* 118, 571–576. http://dx.doi.org/10.1016/S0306-4522(02)00918-1.
- Collar, N.J. and Juniper, A.T. (1992) Dimensions and causes of the parrot conservation crisis. In: Beissinger, S.R. and Snyder, N.F.R. (eds.) New World Parrots in Crisis. Smithsonian Press, Washington, DC, USA, pp. 1–24.
- Coulton, L.E., Waran, N.K., Young, R.J. (1997) Effects of foraging enrichment on the behavior of parrots. *Animal Welfare* 6, 357–363.
- Davis, C.S. (1991) Parrot psychology and behavior problems. *Veterinary Clinics of North America: Small Animal Practice* 21, 1281–1288.
- Dilger, W.C. and Bell, J. (1982) Behavioral aspects. In: Petrak, M.L. (ed.) *Diseases of Cage and Aviary Birds*. Lea and Febiger, Philadelphia, Pennsylvania, USA, pp. 123–141.
- Doane, B.M. and Qualkinbush, T. (1994) My Parrot, My Friend: An Owner's Guide to Parrot Behavior. Macmillan, New York, USA.
- Evans, M. (2001) Environmental enrichment for pet parrots. In Practice 23, 596. http://dx.doi.org/10.1136/inpract.23.10.596.
- Forshaw, J. (1989) *Parrots of the World*, 2nd edn. Lansdowne Press, Melbourne, Australia.
- Francis, D.D., Diorio, J., Plotsky, P.M., Meaney, M.J. (2002) Environmental enrichment reverses the effects of maternal separation on stress reactivity. *Journal of Neuroscience* 22, 7840–7843. http://dx.doi.org/10.1523/JNEUROSCI.22-18-07840.2002.
- Gill, F.B. (1995) *Ornithology*, 2nd edn. W.H. Freeman and Company, New York, USA.

- Grindlinger, H.M. (1991) Compulsive feather picking in birds. Archives of General Psychiatry 48, 857–857. http://dx.doi.org/10.1001/archpsyc.1991.01810330 081012.
- Hardy, J.W. (1965) Flock social behavior of the orangefronted parakeet. *The Condor* 67, 140–156. http:// dx.doi.org/10.2307/1365258.
- Harrison, G.J. (1994) Perspective on parrot behavior. In: Ritchie, B.W., Harrison, G.J., Harrison, L.R. (eds.) Avian Medicine: Principles and Application. Wingers Publishing Inc., Lake Worth, Florida, USA, pp. 96–108.
- Harrison, G.J. and Davis, C. (1986) Captive behavior and its modification. In: Harrison, G.J. (ed.) Clinical Avian Medicine and Surgery. W.B. Saunders Company, Philadelphia, Pennsylvania, USA, pp. 20–28.
- Hausmann, F., Arnold, K.E., Marshall, N.J., Ownes, I.P. (2003) Ultraviolet signals in birds are special. *Proceedings* of the Royal Society of London B Biological Sciences 270, 61–67. http://dx.doi.org/10.1098/rspb.2002.2200.
- Jenkins, J.R. (2001) Feather picking and self-mutilation in psittacine birds. Veterinary Clinics of North America: Exotic Animal Practice 4, 651–668.
- Jurisevic, M.A. and Sanderson, K.J. (1994) Alarm vocalizations in Australian birds: Convergent characteristics and phylogenetic differences. *Emu* 94, 67–77. http://dx.doi.org/10.1071/MU9940067.
- Lawton, M.P.C. (1996) Behavioral problems. In: Beynon, P.H., Forbes, N.A., Lawton, M.P.C. (eds.) BSAVA Manual of Psittacine Birds. Iowa State University Press, Ames, Iowa, USA, pp. 106–114.
- Levinson, S.T. (1980) The social behavior of the white-fronted Amazon (Amazona albifrons). In: Pasquier, R.F. (ed.) Conservation of New World Parrots. Proceedings of the ICBP Parrot Working Group Meeting. Smithsonian Institution Press, Washington, DC, USA, pp. 403–417.
- Lindenmayer, D.B., Pope, M.P., Cunningham, R.B., Donnely, C.F., Ni, H.A. (1996) Roosting of the sulfurcrested cockatoo (*Cacatua galerita*). *Emu* 96, 209–212. http://dx.doi.org/10.1071/MU9960209.
- Lumeij J.T. and Hommers, C.J. (2008) Foraging 'enrichment' as treatment for pterotillomania. *Applied Animal Behaviour Science* 111, 85–94. http://dx.doi.org/10.1016/j.applanim.2007.05.015.
- McMillan, F.D. (2002) Development of a mental wellness program for animals. *Journal of the American Veterinary Medical Association* 220, 965–972. http://dx.doi.org/10.2460/javma.2002.220.965.
- Meehan, C.L., Garner, J.P., Mench, J.A. (2003a) Isosexual pair housing improves the welfare of young Amazon parrots. *Applied Animal Behavior Science* 81, 73–88. http://dx.doi.org/10.1016/S0168-1591(02)00238-1.
- Meehan, C.L., Millam, J.R., Mench, J.A. (2003b) Foraging opportunity and increased physical complexity both prevent and reduce psychogenic feather picking by young Amazon parrots. Applied Animal

300 L.M. Seibert

- Behavior Science 80, 71–85. http://dx.doi.org/ 10.1016/S0168-1591(02)00192-2.
- Mettke-Hofmann, C., Winkler, H., Leisler, B. (2002) Significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108, 249–272. http:// dx.doi.org/10.1046/j.1439-0310.2002.00773.x.
- Overall, K.L. (1993) Canine aggression. *Canine Practice* 18, 29–31.
- Pepperberg, I.M. (1987) Acquisition of the same/different concept by an African grey parrot (*Psittacus erithacus*): Learning with respect to categories, of color, shape, and material. *Animal Learning and Behavior* 15, 423–432. http://dx.doi.org/10.3758/BF03205051.
- Pepperberg, I.M. (1994) Numerical competence in an African gray parrot (*Psittacus erithacus*). *Journal of Comparative Psychology* 108, 36–44. http://dx.doi.org/10.1037/0735-7036.108.1.36.
- Power, D.M. (1966) Agonistic behavior and vocalizations of orange-chinned parakeets in captivity. *The Condor* 68, 562–581. http://dx.doi.org/10.2307/1366264.
- Rosenthal, K. (1993) Differential diagnosis of feather picking in pet birds. In: *Proceedings of the Annual Conference of the Association of Avian Veterinarians*. Nashville, Tennessee, USA, pp. 108–112.
- Ruppenthal, G.C., Arling, G.L., Harlow, H.F., Sackett, G.P., Suomi, S.J. (1976) A 10-year perspective of motherless-mother monkey behavior. *Journal of Abnormal Psychology* 85, 341–349. http://dx.doi.org/10.1037/0021-843X.85.4.341.
- Rushen, J., Lawrence, A.B., Terlouw, E.M.C. (1993) The motivational basis of stereotypies. In: Lawrence, A.B. and Rushen, J (eds.) Stereotypic Animal Behavior: Fundamentals and Applications to Welfare. CAB International, Wallingford, UK, pp. 41–64.
- Sargent, T.D. and Keiper, R.R. (1967) Stereotypies in caged canaries. *Animal Behavior* 15, 62–66.http://dx.doi.org/10.1016/S0003-3472(67)80012-5.
- Seibert, L.M. and Crowell-Davis, S.L. (2001) Gender effects on aggression, dominance rank, and affiliative behaviors in a flock of captive adult cockatiels (*Nymphicus hollandicus*). *Applied Animal Behavior Science* 71, 155–170. http://dx.doi.org/10.1016/S0168-1591(00)00172-6.

- Seibert, L.M., Sung, W., Crowell-Davis, S.L. (2001) Animal behavior case of the month. Fearful behavior in a Goffin's cockatoo. *Journal of the American Veterinary Medical Association* 218, 518–520.
- South, J.M. and Pruett-Jones, S. (2000) Patterns of flock size, diet, and vigilance of naturalized Monk parakeets in Hyde Park, Chicago. *The Condor* 102, 848–854.
- Stein, D.J. (1996) The neurobiology of obsessive-compulsive disorder. *The Neuroscientist* 2, 300–305. http://dx.doi.org/10.1177/107385849600200516.
- Stein, D.J., Simeon, D., Cohen, L.J., Hollander, E. (1995) Trichotillomania and obsessive-compulsive disorder. *Journal of Clinical Psychiatry* 56(S4), 28–35.
- Suomi, S.J., Collins, M.L., Harlow, H.F., Ruppenthal, G.C. (1976) Effects of maternal and peer separations on young monkeys. *Journal of Child Psychology and Psychiatry* 17, 101–112. http://dx.doi.org/10.1111/ j.1469-7610.1976.tb00382.x.
- Vanhoek, C.S. and King, C.E. (1997) Causation and influence of environmental enrichment on feather picking of the crimson-bellied conure (*Pyrrhura per-lata perlata*). Zoo Biology 16, 161–172.
- Welle, K.R. (1999) Clinical approach to feather picking. In: Proceedings of the Annual Conference of the Association of Avian Veterinarians. New Orleans, Louisiana, USA, pp. 119–124.
- Wemelsfelder, F. (1993) The concept of animal boredom and its relationship to stereotyped behavior. In: Lawrence, A.B. and Rushen, J (eds.) Stereotypic Animal Behavior: Fundamentals and Applications to Welfare. CAB International, Wallingford, UK, pp. 65–96.
- West, J.A., Tully, T.N., Nevarez, J.G., Stout, R.W. (2018) Effects of ultraviolet B light exposure on calcifediol and feather damaging behavior in *Amazona ventralis*. *Proceedings of the Annual Exotics Conference*. Atlanta, Georgia, USA, pp. 403.
- Wilson, E.O. (1975) *Sociobiology*. Belknap Press, Cambridge, UK.
- Wilson, L. (1999) Sleep: How much is enough for a parrot? Pet Bird Report 43, 60–62.

21 Psychological Well-being in Zoo Animals

DAVID SHEPHERDSON AND KATHY CARLSTEAD

Oregon Zoo, Portland, Oregon, USA; Center for Species Survival, Smithsonian Conservation Biology Institute, Front Royal, Virginia, USA

When it comes to maintaining mental health, or psychological well-being, zoo animal populations are unique in a number of important ways. In contrast to most other animals in human care, zoo animals are 'wild' rather than domesticated, meaning that they have not been intentionally bred to favor traits compatible with captivity and human management. Certainly, genetic selection must exist in the zoo environment and it may result in small changes that favor survival and reproduction in zoos, but most zoo-held species have not been separated from their natural habitat for many generations and breeding programs exist to maintain genetic diversity and minimize directional selection (reviewed by Hutchins and Wiese, 1991; Maple, 1992).

The number of different 'wild' species that are cared for in zoos results in tremendous variation in ability to adapt to and cope with zoo environments and represents a huge challenge for zoo animal managers. Some species may come from similar environments and climates to the host zoo, whereas others come from radically different ones. Some species have small home ranges and some have large ones. Some species are shy by nature and others are bold. Some species are highly social and others more solitary. Indeed, Mason (2015) has pointed out that this variation could be a powerful comparative tool in identifying the factors that predispose a species to adapt well to captivity and has shown, for example, that species with larger home ranges in the wild tend to spend more time engaged in stereotypic behavior in zoos than those with small home ranges (Clubb and Mason, 2007).

Zoo populations of a species also tend to be relatively small and geographically dispersed, valuable to the zoos that hold them (due to the difficulty of replenishment and emotional attachment of staff and visitors), and, while kept in confined spaces

and in view of the public, are also intensively managed with much higher ratios of husbandry and veterinary staff per individual than most other animals in human care. On the other hand, since these are mostly species that have not been intensively studied in the wild, we often lack basic biological knowledge about them.

In modern zoos, individuals of most species are now captive born and bred. Because one of the central missions of modern zoos is to conserve endangered species, zoos have made major commitments toward research designed to benefit captive populations in fields such as genetics, demographic analysis, reproductive physiology, and assisted reproductive techniques. We would also argue that concern for the welfare of individual animals is and has been a strongly held ethic by most 'good' zoos. The interpretation of good welfare, however, has changed over time. Traditionally, zoos have valued measures such as longevity, breeding success, and physiological health. As the science of zoo animal welfare advances, more measures of psychological well-being are being adopted, environmental enrichment techniques have become an everyday part of husbandry, and welfare assessment and real-time monitoring tools are being developed.

Abnormal Behaviors in **Zoo Animals**

The abnormal ways that many animals behave while confined in zoos was largely accepted by managers and the visiting public before the early to midtwentieth century. One of the first of a new breed of zoo biologists was past director of the Zurich Zoological Garden, Heini Hediger (see obituary by Maple, 1992). He was one of the first to acknowledge, study, and write about abnormal behaviors

and the importance of psychological or mental health in zoo animals, and suggest solutions based on their natural history. Hediger (1950, p.158), wrote that 'Clearly one of the most urgent problems in the biology of zoological gardens arises from the lack of occupation of the captive animal.' Hediger's strategy was to apply his understanding of the biology, behavior, and motivation of a species in the wild to 'see' the zoo environment through their eyes. Hediger was particularly interested in studying stereotyped motor reactions in captive animals, work that was continued by Meyer-Holzapfel (1968) and published, among other places, in M.W. Fox's (1968) seminal publication Abnormal Behavior in Animals. Meyer-Holzapfel spent many years studying abnormal behavior in zoo animals, observing the development and form of mostly locomotor stereotypies in a variety of species, and was one of the first to document the progression through time of some stereotypies from stimulus dependent to 'fixated by habit'. The significance of stereotypic behavior as a potential indicator of stress has been confirmed many times since (Mason et al., 2007; Shepherdson et al., 2013; Kroshko et al., 2016). Other abnormal behaviors observed in zoos include self-mutilation (Pizzutto et al., 2015), regurgitation and re-ingestion (Gould and Bres, 1986), coprophagy (Akers and Schildkraut, 1985), and excessive aggression (Erwin et al., 1976).

21.2 Challenges Particular to Zoo Animals

Zoo environments have challenges to well-being that other contexts may lack. There are many sources of aversive stimulation (stressors) that are known to elicit protective behavioral and/or physiological responses in animals. Many are ultimately associated with space restriction and confinement that limit an animal's ability to escape what is fearinducing or prevent the ability to adapt to it. Some examples are noise, excessive heat or cold, overcrowding, social group instability, and the actions of caretakers (reviewed by Carlstead and Shepherdson, 2000; Morgan and Tromborg, 2007). Hediger (1964) describes situations in which captive animals injured themselves or failed to breed because of the inability to escape from caretakers or visitors. Persistent uncertainty about the actions of caretakers or veterinarians may contribute to the stressfulness of some captive situations if the animals have no reliable predictive cues (Bassett and Buchanan-Smith, 2007;

Thines *et al.*, 2007). Other stressors may be unique to zoos, specifically, olfactory and auditory cues from predators (Buchanan-Smith *et al.*, 1993; Carlstead *et al.*, 1993; Wielebnowski, 2003) and construction noise (Cociu *et al.*, 1974; Powell *et al.*, 2006).

There is one potential stressor that is common to zoos, aquariums, and wild animal parks, and very uncommon or rare in other animal contexts: the presence of zoo visitors. There is evidence that visitor presence, activity, size, and viewing position causes changes in the behavior of zoo-housed mammals (reviewed by Davey, 2007). The 'visitor effect' has been associated with a number of changes suggestive of stress, including increased vigilance, closer social spacing, reductions in affiliative behavior, and increases in aggression (Glatston et al., 1984; Hosey and Druck, 1987; Chamove et al., 1988; Thompson, 1989). Visitor presence can be stressinducing for black rhinoceros (Diceros bicornis) as demonstrated by Carlstead and Brown (2005) in a study of 26 rhinos at ten zoos. They found positive correlations between the degree of public access around rhinos' enclosures and the rhinos' mean fecal corticoid metabolite (FGM) concentrations. An earlier study by Carlstead et al. (1999a) of black rhinos at 23 zoos suggested that high visitor access around the enclosure perimeter was stressful because it correlated with the zoo's 20-year mortality rate for rhinos and with ratings for behavior trait fear. FGM concentrations of eight Indian blackbuck were significantly higher on days when zoo visitor density was extremely high compared to zero or extremely low (Rajagopal et al., 2011), and in spider monkeys (Davis et al., 2005) and Mexican wolves (Pifarré et al., 2012) an increase in the number of visitors was associated with an increase in cortisol. In clouded leopards, FGM concentrations were measured as higher in the individuals kept on public display compared to those maintained off exhibit (Wielebnowski et al., 2002). Obstructing the view of visitors has been reported to decrease fecal corticoids and aggression in black-capped capuchins (Sherwen et al., 2015). Sometimes, however, studies of visitor effects on zoo animals show that the visiting public has no effect (neutral) on animals, or is even enriching (Davey, 2007). The most negative effects of visitors have been found among animals with poor baseline welfare combined with high levels of stereotypic locomotion, intragroup aggression, and self-injurious behavior (Farrand, 2007).

Lack of mental or cognitive stimulation, analogous perhaps to boredom in humans, is often presumed to be a problem for captive exotic animals and has been well documented (Špinka and Wemelsfelder, 2011). Animals in the wild are constantly faced with cognitive challenges. They have to remember the location of important resources that may change through time, and they have to problem solve to find and gain access to the resources that they need. Predators have to outsmart their prey, and prey animals have to avoid predators. Individuals representing a rapidly growing list of species use tools to get what they want (Seed and Byrne, 2010). Information important to survival surrounds wild animals, and finding and interpreting this information correctly can determine the difference between life and death. Exploration is the outward expression of the desire to 'know'. The importance of information seeking and strategies for providing opportunities to meet this need have long been recognized (Shepherdson et al., 1993) and, as we shall see, there are many ways in which zoo environments can be enriched to provide meaningful opportunities for information seeking. However, Meehan and Mench (2007) mount a spirited argument in favor of not just providing information rich environments, but of specifically providing animals with biologically appropriate challenges, the solving of which results in strong positive affect and associated well-being.

21.3 Positive Affective States and Well-being

Animal welfare scientists have become interested in positive emotions and psychological well-being, placing an emphasis on what increases thriving as opposed to reduces suffering. Boissy *et al.* (2007) and Yeates and Main (2008) have proposed a change in focus to a broader perspective of welfare measures that increases the emphasis on positive experiences. For example, they encourage assessment of behavioral indicators of contentment, such as play and exploration, self-grooming and maintenance behaviors, and affiliative relationships between animals as well as between animals and their caretakers (Boissy *et al.*, 2007; Hemsworth, 2007).

Zoo and aquarium industry organizations in America, Europe, British Isles, and worldwide (e.g., Association of Zoos and Aquariums [AZA], European Association of Zoos and Aquaria [EAZA], British and Irish Association of Zoos and Aquariums [BIAZA], World Association of Zoos and Aquariums [WAZA]) have adopted frameworks for assessing and ensuring zoo animal welfare. All of these

frameworks encompass physical and mental health components, including positive and negative experiences such that one can say, in principle, that there is a wide consensus on the importance of mental health for zoo animal welfare. The EAZA (2019) states that welfare should include 'the provision of effective veterinary care, meeting dietary requirements, providing individuals with the opportunity to perform their species-specific behavioral repertoire and promoting positive emotional states'. There is, therefore, an emerging recognition in the zoo and aquarium industry of the importance of considering the experiences of individual animals and promoting subjective affective states; the absence of suffering due to pain, fear, or anxiety alone is not enough to ensure good welfare (Whitham and Wielebnowski, 2013). In fact, some scientists argue that positive experiences may offset the impact of negative experiences (Spruijt et al., 2001; Duncan, 2006; Van der Harst and Spruijt, 2007; Yeates, 2011).

Measures of positive affective state potentially can be determined from responses to signaled events (anticipation) (Watters, 2014), cognitive tests that assess optimism about future events (such as cognitive bias tests; Keen et al., 2013), and even pleasure-associated vocalizations (Panksepp and Watt, 2011) and facial expressions (for a review, see Whitham and Wielebnowski, 2013). Boissy and Lee (2014) discuss investigation of affective states in animals using cognitive approaches, such as tests of judgment bias, which have been developed recently for a variety of species (Boissy and Lee, 2014; Bethell, 2015; see also Chapter 23, this volume). Basically, these methods observe how an animal judges the presentation of an ambiguous stimulus cue after having been trained to distinguish presentations of the same stimulus under conditions in which it is unambiguously rewarding or aversive. The interpretation of reactions to ambiguous cues is considered to reflect whether the animal's emotional state is optimistic or pessimistic. A review of 64 laboratory studies of judgment bias to date indicates that these measures are highly suitable for understudied taxa and can provide new insight into welfare in endangered species housed in zoos and aquariums (Bethell, 2015). The first application of a cognitive bias test to aquariumhoused mammals - bottlenose dolphins - linked the affiliative behavior of synchronous swimming to optimistic judgment of ambiguous cues in a spatial location bias test (Clegg et al., 2017). A study of tufted capuchins (*Cebus apella*) at a research animal center revealed a positive correlation between levels of stereotypic behavior and a pessimistic judgment bias (Pomerantz *et al.*, 2012). Individuals that exhibited a negative bias while judging ambiguous stimuli had higher levels of stereotypic head twirls and had higher levels of fecal corticoids compared to subjects with lower levels of head twirls.

Studies on anticipatory behavior in expectation of predictable events have revealed links with animals' affective states (Van der Harst and Spruijt, 2007). Anticipatory behavior is expressed as an increase in activity in response to a signaled reward such as food or enrichment, and demonstrates the perceived importance of a given reward to the animal. Watters (2014) suggests that zoo animal behaviorists should pay attention to anticipatory behavior, and this technique is beginning to be used to study motivation and related affective state of aquarium-housed cetaceans. Clegg and Delfour (2018) recently used anticipatory behavior of bottlenose dolphins, in this case increased frequencies of surface looking and spy hopping, to demonstrate that they perceive nonfood interactions with humans as more rewarding than toy provisioning. They also found that the frequency of anticipatory behavior is correlated to the level of participation in the following event.

21.4 The Importance of Keeper–Animal Relationships for Psychological Well-being

Optimization of mental health in zoo animals demands better understanding of their psychological needs under human management. We maintain that the daily caretakers of zoo animals are best positioned to meet the challenge of determining what animals feel, and that research on the relationships between keepers and animals is beginning to be a fruitful research approach to understanding animal emotions and psychological well-being. Whitham and Wielebnowski (2013, p.256) state 'it is vital to recognize that animal keepers are a central element of each zoo animal's environment, and that the quality of a given keeper-animal relationship may influence an individual's well-being'. Furthermore, interactions between keepers and animals can be a major source of positive experiences and emotions, in effect becoming a form of environmental enrichment for animals (Claxton, 2011). On a regular basis, individual zookeepers feed, clean, groom, shift, exercise, monitor health, train, and provide enrichment to their animals. Developing a positive keeper–animal relationship (KAR) requires becoming familiar with the communication signals and patterns of the animal toward the keeper and of the keeper towards the animal – from the animal's perspective – and responding appropriately. An important aspect of 'true relationships' is that interactions have reciprocal effects on both partners, which may include benefits to the well-being of each (Hemsworth, 2003; Clegg and Delfour, 2018).

In zoos, there has been limited research on the characteristics of positive KARs. Mellen's (1991, p.99) study of 20 small felid species at eight US zoos was the first to report that 'keepers who spent a great deal of time with each cat, soliciting contact and talking to the cat' had significantly better reproductive success among their cats. Similarly, among 72 clouded leopards, stress, as assessed by fecal corticoids, was lower if keepers spent relatively more time around the animals and higher if there was a greater number of keepers working with the animals (Wielebnowski et al., 2002). A colony of captive common marmosets increased play and grooming activities after a program of daily 20-minute, positive interactions with caretakers was added to their husbandry routine (Manciocco et al., 2009). Keepers anecdotally report the emotional benefits of a caretaker just sitting quietly near an animal. Spending more time around animals could function as 'safety signals', i.e., a learned cue that predicts the nonoccurrence of an aversive event. Safety signals are potent inhibitors of fear and stress responses (Christianson et al., 2012) and are thought to be disrupted in people suffering from posttraumatic stress disorder (Lohr et al. 2007). Keepers' activities are often signals to animals that something is imminent that will affect them, be it feeding, cleaning, shifting, separation from conspecifics, etc., so periods of inactive copresence of a keeper provides a direct safety signal that nothing will happen for a period of time. Hence, this provides the animal an opportunity to visually inspect the keeper, approach in their own time, and relax in keeper presence.

Animals may have varying needs for predictable behavior from keepers, and unpredictable actions may cause stress (Bassett and Buchanan-Smith, 2007). Carlstead (2009) explored KARs among 82 keepers working with four different species: black rhinoceros, cheetah, maned wolf, and great hornbill. She found that the animal's affinity to the keeper (approaching spontaneously and allowing touching, etc.), was modulated by environmental factors

that affect keeper predictability such as keeper visibility to the animal, the frequency and timing of feeding, and whether the keeper enters the enclosure space or not. Rimpley and Buchanan-Smith (2013) have shown that making keeper entries into indoor brown capuchin enclosures more predictable and less startling by providing a reliable entry signal (always knocking on the door before entry) reduces anxiety-related behaviors.

To avoid negative interactions and poor relationships with zoo animals, keepers should be aware of and avoid fear-evoking behaviors. For example, at 32 zoos, keepers were videotaped calling to maned wolves and cheetahs from the visitor area, an unusual location for the keeper to solicit interaction. Both species responded with aggressive behaviors more often to keepers that performed a high amount of locomotion when calling, and they approached keepers less often if the keeper made nonverbal noises (clapping, banging on fence) (Carlstead, 2009). When caretakers spent additional time engaging in positive interactions with chimpanzees, such as playing, grooming, feeding treats, and talking, the animals performed higher levels of allogrooming, exhibited fewer abnormal behaviors, and were less reactive (Baker, 2004). Unstructured affiliative interactions between 12 zookeepers and two resident groups of zoo-housed chimpanzees and two groups of gorillas were associated with the animals exhibiting fewer self-directed and abnormal behaviors (Chelluri et al., 2013). However, after interactions with keepers, agonism in the groups increased, leading the authors to suggest that managers should consider practices that minimize the degree to which zookeepers insert themselves in the social environment of great apes.

Finally, zoo animals and keepers may form mutual bonds that may reflect a psychological need for emotional rewards on both sides of the bond. In a survey of zoo staff working with various species, 92% of zookeepers reported having a bond with a zoo animal (Hosey and Melfi, 2012). Furthermore, the benefits to keepers of bonding were reported to be of two sorts: (i) operational benefits that enabled better, easier, or more efficient management of the animals; and (ii) affective benefits that included general enjoyment of the relationship and emotional rewards. An epidemiological analysis of keeper-elephant relationships (KERs) in North American zoos (Carlstead et al., 2019) revealed that bonds between keeper and elephant are associated with welfare benefits for both. Keepers' attitudes

about interacting with elephants were surveyed at 60 zoos and compared to mean serum cortisol responses of the elephants for which they cared; the more positive the keeper's attitude, the lower the elephants' mean serum cortisol concentrations, indicating that good KERs are associated with lower stress responsiveness of elephants. When queried about the strength of the bonds keepers have with particular elephants, 70% of keepers reported that they have a very strong bond, and the stronger the bond the less likely keepers were to report dissatisfaction with their job. In light of research in occupational medicine demonstrating a strong relationship between job satisfaction and both mental and physical health of workers (Faragher et al., 2005), keepers likely experience multiple benefits from having a bond with a zoo animal.

21.5 Tools for Enhancing Psychological Well-being: Positive Reinforcement Training

The application of positive reinforcement training (PRT) for zoo animals originated in the 1990s and has grown as an enrichment and management technique ever since (Laule, 2003). Described as 'occupational therapy' by Hediger (1950), the benefits of this technique to animals and to husbandry and veterinary management have proven to be numerous. With PRT, animals are reinforced with pleasurable rewards for performing a behavioral response asked for by a trainer. The technique relies on voluntary cooperation by the animal and the animal is not food deprived (Laule, 2003). PRT is welfare enhancing because it provides animals the opportunity to work for food rewards, achieve greater choice and control over daily events, and experience mental stimulation. Also, by using a properly applied PRT training technique called 'cooperative feeding' with socially housed animals, introductions can be enhanced, dominance-related problems mitigated, aggression reduced, and affiliative interactions increased (Laule, 2003).

Few studies have been undertaken to examine the long-lasting impact that PRT has on zoo animals' daily lives. Shyne and Block (2010) examined the effects of PRT on African wild dogs in a zoo, and found reductions in stereotypic pacing behaviors following training sessions. PRT training of chimpanzees decreased abnormal and stress-related behaviors and increased prosocial affiliative behaviors (Pomerantz and Terkel, 2009). Among polar bears at 20 zoos, Shepherdson *et al.* (2013) found

that bears receiving PRT had lower levels of stereotypy and lower fecal corticoid concentrations. All of these studies discuss these long-term effects as being the result of the training process, but evidence suggests that PRT training alters the animal's relationship with the keeper and removes at least one important stressor associated with the keeper's actions that might have been causing anxiety-related behaviors prior to training; examples of such stressors include unpredictability, uncertainty, confusion, need for a safety signal, or even lack of attention. Training provides a stimulating human–animal interface (Reinhardt, 1992; Claxton, 2011). Once training begins, communication with the keeper is improved and stress-related behavior declines.

Studies to establish the impact of PRT on KARs are increasing. Savastano et al. (2003) reported positive changes in keeper-animal rapport among callitrichid primates as a result of PRT, including a reduction in keeper-directed aggression and avoidance. Ward and Melfi (2013) reported shorter latencies to approach keepers and reductions in time to perform novel behaviors after PRT in black rhino, zebra, and Sulawesi macaques, concluding that PRT can decrease fear of humans and contribute to positive KARs. In a later paper, Ward and Melfi (2015) demonstrated that each keeper-animal dyad is unique and animals respond differentially to each keeper's 'stockmanship style', which consists of two factors: attitudes towards animals and knowledge and experience of animals. Therefore, PRT is not only an enriching cognitive challenge for the animal, it is also a means of communicating directly with the keeper in a common language.

Recognition of the importance of the caretaker to the animal's daily life could significantly increase the use of PRT, increase the amount of time the keepers are allowed to spend around animals, and improve positive and reduce negative communication between animal and keeper. We want to emphasize that one of the future directions of zoo animal welfare science is further study of KARs, as evidence is mounting that the benefit to psychological well-being of animals, as well as of keepers, is of major importance.

21.6 Tools for Enhancing Psychological Well-being: Environmental Enrichment

Environmental enrichment has over the last three decades become *de facto* the primary tool for addressing psychological well-being in zoo and

aquarium animals. Compared to other animal contexts, enrichment in a zoo context is permitted to be much more boundless and creative to the extent that zoos perhaps lead the field of enrichment in terms of innovation. However, theory development, formal experimentation, and reporting in the literature may be more restricted than for animals in laboratories and on farms due to the diversity of species kept in zoos, the wide variety of enrichment ideas, and the limited number of subjects in a given zoo. Nevertheless, enrichment methods and successes are widely shared among zoos via scientific publications, newsletters, websites, and workshops.

Many different interpretations of the term 'environmental enrichment' exist today and other names have been used to describe this process. The following definition is commonly accepted by the zoo community and the American Zoo and Aquarium Association:

Environmental enrichment is a process for improving or enhancing zoo animal environments and care within the context of their inhabitant's behavioral biology and natural history. It is a dynamic process in which changes to structures and husbandry practices are made with the goal of increasing behavioral choices available to animals and drawing out their species-appropriate behaviors and abilities, thus enhancing animal welfare. (Shepherdson, 2003, p.119)

A more concise definition is supplied by Newberry (1995, p.229): 'An improvement in the biological functioning of captive animals resulting from modifications to their environment.'

In the 1960s, Desmond Morris, then curator of mammals at the London Zoo, like Hediger took a strong interest in zoo animal behavior and described what we would now call an enrichment device that carried fish around the seal pool before releasing them to the chasing seals (Morris, 1960). More recently, in the 1970s and 1980s, publications arising from experiments conducted by Hal Markowitz and co-workers at what is now the Oregon Zoo in Portland, Oregon, USA, were influential in raising the level of interest in environmental enrichment in zoos (Markowitz, 1982). Markowitz pioneered and popularized the use of machines that required animals to perform complex behavioral tasks in order to obtain a food reward. These ideas were critiqued and built upon by people such as Hutchins et al. (1984) and Maple (1990). They emphasized the importance of providing naturalistic habitats for animals, which allow them to perform many of the

behaviors that would be seen in the wild. Since the 1990s the interest in enrichment, as evidenced by scientific papers, zoo conference programs, and advertised positions, has steadily climbed.

Environmental enrichment encompasses activities in zoos and aquariums that generally proceed with one or more of the following benefits to animals, most of which follow from the challenges discussed already:

- Increasing environmental novelty, change, and complexity to allow animals to establish meaningful interactions with their surroundings, diversify their behavior, and mediate social interactions. More complex environments contain information that is of importance to animals and encourage exploratory behavior (Shepherdson et al., 1993).
- Presenting cognitive challenges such as problem solving, learning new tasks, and participating in training sessions (Meehan and Mench, 2007).
- Meeting specific behavioral needs, such as a need for shelter/hiding, foraging, or a substrate to dig in to encourage the expression of speciesappropriate behavior (Kastelein and Wiepkema, 1989).
- Giving animals choice, control, or 'behavioral contingency'. The goal is to establish in the enrichment program a situation in which the animal achieves its needs through its own behavioral interactions with the environment (Quirke and O'Riordan, 2011).
- Stimulating and mediating social interaction by providing social groupings of appropriate sex ratio, age classes, genetic relatedness, and experience (Meehan *et al.*, 2016a).
- Modulating optimal levels of stress (Wielebnowski, 2003) and reducing abnormal behaviors such as stereotypic behavior (Swaisgood and Shepherdson, 2005).
- Promoting and maintaining positive KARs (Carlstead, 2009).

A heavy emphasis is placed on the importance of providing enrichment that is appropriate to the specific biology of the species under consideration. Biologically appropriate complexity can be increased in many ways, for example, by adding substrates such as dirt, litter, mulch, vegetation, or trees. These substrates increase the 'information content' of the environment and can elicit foraging and exploratory behavior by concealing food, smells, and naturally occurring insects or other wildlife. Barriers

and landscaping can provide privacy, promote territorial behavior, provide escape routes, and interrupt sight lines, thus improving social interactions. Toys and novel objects elicit exploration and creative play. Climbing structures allow more efficient use of space and provide shade and temperature gradients for choice of microclimate. They can also provide hiding places from conspecifics, zoo visitors, and keepers. Cognitive challenges, such as mechanical apparatuses, puzzle feeders, or computer interaction with visitors, put captive animals in a position in which they can learn to actively control and explore some aspects of their environment. Various feeding devices and practices such as carcass and whole-fruit feeding allow animals to acquire and process food in diverse, versatile, and more natural ways (Carlstead and Seidensticker, 1991; McPhee, 2002). More recently, the potential of training, not just as a management tool but as cognitive enrichment for captive animals, has begun to be realized (Westlund, 2013).

Enrichment programs should begin with a thorough understanding of the behavioral biology of the species, from which behavioral goals can be determined. Goals should be well-planned to ensure that enrichment is offered throughout the 24-hour period, and that there is an ample amount of enrichment items and variety of activities to enhance the well-being of each animal within an enclosure. The effectiveness of enrichment should be evaluated on a regular basis to ensure that items and activities offered do indeed meet the animals' behavioral goals (Mellen and Sevenich MacPhee, 2001). Typical measurable behavioral goals include reducing abnormal behavior and increasing feeding behavior, exploration, the range and diversity of natural behaviors, species-specific behavior, space use, and activity.

Assessment is a key step in any adaptive management program. For enrichment, assessment usually involves comparing behavior before, during, and after an enrichment event either through formal behavioral observations or more informally through keeper observation. Programs are being developed to facilitate these and other welfare assessments in zoos, with tools such as Welfare Trak (Whitham and Wielebnowski, 2013) and Zoo Monitor (Lincoln Park Zoo, available online: www.zoomonitor.org) showing promise.

While we must recognize that enrichment is by no means the only tool for improving welfare it has proven to be an effective method (Swaisgood and Shepherdson, 2006) for providing numerous behavioral, cognitive (Carlstead *et al.*, 1999a), and emotional benefits to animals housed in zoos and aquariums.

21.7 Multi-institutional Research in Zoos

In zoo animal welfare science, the most productive approach to determine which environmental factors impact animal well-being are often multiinstitutional studies that compare performance of animals to variations in zoo environments (Wielebnowski et al., 2002). For example, an early study of stereotypy in zoo-housed bear species found that variations in cage size and topography were associated with levels of stereotypic pacing (Van Keulen-Kromhout, 1978). Multi-institutional studies aimed at addressing differences in breeding success have been conducted with red pandas (Roberts, 1989), gorillas (Miller-Schroeder and Paterson, 1989), small felid species (Mellen, 1991), black rhinoceros (Carlstead et al., 1999a,b), and Humboldt penguins (Blay and Côté, 2001). The causal factors of abnormal behaviors such as stereotypy have been investigated multi-institutionally in giraffes (Bashaw et al., 2001), polar bears (Shepherdson et al., 2013), Indian leopards (Mallapur and Chellam, 2002), and elephants in the UK (Harris et al., 2008). The use of noninvasive techniques for analyzing glucorticoid hormones in feces and urine has led to multi-institutional investigations of stress in clouded leopards (Wielebnowski et al., 2002), African rhinoceros species (Carlstead and Brown, 2005), and polar bears (Shepherdson et al., 2013). However, even though multiple zoos participated in all of these studies, they were conducted with relatively small sample sizes and limited investigation of a wide range of factors potentially impacting welfare.

Increasingly, zoo scientists are using epidemiological methods to guide improvements in animal care and well-being. A good example is a recent, large-scale study of almost the entire North American population of 255 Asian and African elephants at 68 zoos accredited by the AZA (Carlstead et al., 2013). A multifactorial approach to measuring elephant welfare was used, and epidemiological methods were applied to determine the risk factors contributing to these indicators of welfare. The first round of study results are published as a collection of nine papers in the online journal *PLoS One* (for

an overview of the results, see Meehan et al., 2016b); subsequent publications are in preparation or published elsewhere (Carlstead et al., 2019). The study identified 22 unique environmental variables that have significant associations with one or more welfare indicators (body condition, foot and joint health, walking rates and recumbence, stereotypy, ovarian cycling, hyperprolactinemia, serum and fecal glucocorticoids, and clinical health). In broad terms, the study provides support that good elephant welfare in zoos is promoted by elephants spending more time in larger, stable social groupings that include both juvenile and adult elephants, reducing time spent in isolation, and experiencing frequent and diverse enrichment. In contrast, there were few associations between welfare measures and the amount of space that elephants experience.

The most important results to come out of the Institute of Museum and Library Services Elephant Welfare Project concerned the impact of humancontrolled management factors. The variety and frequency of enrichment provisioning, the use of alternative feeding methods (e.g., hanging or hiding food), staff-directed walking exercise, time spent interacting with staff, unpredictable feeding schedules, and positive attitudes of keepers all had wellbeing-promoting impacts on the welfare measures assessed in the study (Brown et al., 2016; Greco et al., 2016; Holdgate et al., 2016a,b; Morfeld et al., 2016; Carlstead et al., 2019). While the welfare outcomes used were accepted, 'gold-standard' measures of elephant health and well-being, the results of epidemiological analysis demonstrate, in addition to social factors, that the daily practices of caretaking staff are essential to providing the environmental diversity, stimulation, and attention that elephants need in order to thrive in zoos.

All of this is not to say that case studies of smaller numbers of animals at one or a few institutions are not valuable to help us understand the role of individual differences in the response of zoo animals to our attempts to improve their welfare. These are parallel approaches that complement each other.

21.8 Concluding Remarks

Zoo animals face unique challenges, foremost of which are their recent wild origin and the need for them to be on exhibit to the public. On the other hand, zoo animal welfare is increasingly an integral component of the zoo ethos and considerable resources are already devoted to monitoring and maximizing the welfare of zoo animals. Improvements in our biological understanding of psychological well-being in zoos and other captive circumstances will continue to benefit zoo animals, as will technologies and protocols that improve the monitoring and tracking of welfare.

There is increasing recognition that the quality of interactions and relationships between zoo animals and their caretakers plays an important role in the welfare of animals, as has long been the case for agricultural animals (Hemsworth, 2003). The KAR is an emerging area of study in zoo animal welfare science that promises to deliver increased knowledge of the psychological requirements of animals. Zookeepers are positioned on a daily basis to monitor, interact with, react to, reassure, and provide care for animals; study of these ongoing, reciprocal relationships promises to ensure that all animals will have the opportunity to thrive in zoos.

Enrichment provides an effective and proven tool for addressing many of the challenges of the zoo environment and will continue to increase in effectiveness as it is applied in an institution-wide, programmatic fashion with appropriately dedicated resources.

21.9 References

- Akers, J.S. and Schildkraut, D.S. (1985) Regurgitation/ reingestion and coprophagy in captive gorillas. Zoo Biology 4, 99–109. http://dx.doi.org/10.1002/zoo. 1430040203.
- Baker, K.C. (2004) Benefits of positive human interaction for socially-housed chimpanzees. *Animal Welfare* (South Mimms, England) 13, 239.
- Bashaw, M.J., Tarou, L.R., Maki, T.S., Maple, T.L. (2001) A survey assessment of variables related to stereotypy in captive giraffe and okapi. Applied Animal Behaviour Science 73, 235–247. http:// dx.doi.org/10.1016/S0168-1591(01)00137-X.
- Bassett, L. and Buchanan-Smith, H.M. (2007) Effects of predictability on the welfare of captive animals. Applied Animal Behaviour Science 102, 223–245. http://dx.doi.org/10.1016/j.applanim.2006.05.029.
- Bethell, E.J. (2015) A 'how-to' guide for designing judgment bias studies to assess captive animal welfare. Journal of Applied Animal Welfare Science 18 (suppl 1), S18–S42. http://dx.doi.org/10.1080/10888705.2015.1 075833.
- Blay, N. and Côté, I.M. (2001) Optimal conditions for breeding of captive Humboldt penguins (*Spheniscus humboldti*): A survey of British zoos. *Zoo Biology* 20, 545–555. http://dx.doi.org/10.1002/zoo.10002.

- Boissy, A. and Lee, C. (2014) How assessing relationships between emotions and cognition can improve farm animal welfare. Revue Scientifique et Technique (International Office of Epizootics) 33, 103–110.
- Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., et al. (2007) Assessment of positive emotions in animals to improve their welfare. *Physiology* & *Behavior* 92, 375–397. http://dx.doi.org/10.1016/j. physbeh.2007.02.003.
- Brown, J.L., Paris, S., Prado-Oviedo, N.A., Meehan, C.L., Hogan, J.N., et al. (2016) Reproductive health assessment of female elephants in North American zoos and association of husbandry practices with reproductive dysfunction in African elephants (Loxodonta africana). PloS ONE 11(7), e0145673. http://dx.doi.org/10.1371/journal.pone.0145673.
- Buchanan-Smith, H.M., Anderson, D.A., Ryan, C.W. (1993) Responses of cotton-top tamarins (Saguinus oedipus) to faecal scents of predators and nonpredators. Animal Welfare 2, 17–32.
- Carlstead, K. (2009) A comparative approach to the study of keeper–animal relationships in the zoo. Zoo Biology 28, 589–608.
- Carlstead, K. and Brown, J. L. (2005) Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. Zoo Biology 24, 215–232. http://dx.doi. org/10.1002/zoo.20050.
- Carlstead, K. and Seidensticker, J. (1991) Seasonal variation in stereotypic pacing in an American black bear *Ursus americanus*. *Behavioural Processes* 25, 155–161. http://dx.doi.org/10.1016/0376-6357(91) 90017-T.
- Carlstead, K. and Shepherdson, D. (2000) Alleviating stress in zoo animals with environmental enrichment. In: Moberg, G.P and Mench, J.A. (eds.) The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare. CAB International, Wallingford, UK, pp. 337–354. http://dx.doi.org/10.1079/9780851993 591.0337.
- Carlstead, K., Brown, J.L., Seidensticker, J. (1993) Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). Zoo Biology 12, 321–331. http://dx.doi.org/10.1002/ zoo.1430120403.
- Carlstead, K., Fraser, J., Bennett, C., Kleiman, D.G. (1999a) Black rhinoceros (*Diceros bicornis*) in US zoos: II. Behavior, breeding success, and mortality in relation to housing facilities. *Zoo Biology* 18, 35–52.
- Carlstead, K., Mellen, J., Kleiman, D.G. (1999b) Black rhinoceros (*Diceros bicornis*) in US zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biology* 18, 17–34.
- Carlstead, K., Mench, J.A., Meehan, C., Brown, J.L. (2013) An epidemiological approach to welfare

- research in zoos: The elephant welfare project. *Journal of Applied Animal Welfare Science* 16, 319–337. http://dx.doi.org/10.1080/10888705.2013.827915.
- Carlstead, K., Paris, S., Brown, J.L. (2019) Good keeperelephant relationships in North American zoos are mutually beneficial to welfare. *Applied Animal Behaviour Science* 211, 103–111. http://dx.doi. org/10.1016/j.applanim.2018.11.003.
- Chamove, A.S., Hosey, G.R., Schaetzel, P. (1988) Visitors excite primates in zoos. Zoo Biology 7, 359–369. http://dx.doi.org/10.1002/zoo.1430070407.
- Chelluri, G.I., Ross, S.R., Wagner, K.E. (2013) Behavioral correlates and welfare implications of informal interactions between caretakers and zoohoused chimpanzees and gorillas. *Applied Animal Behaviour Science* 147, 306–315. http://dx.doi. org/10.1016/j.applanim.2012.06.008.
- Christianson, J.P., Fernando, A.B., Kazama, A.M., Jovanovic, T., Ostroff, L.E., *et al.* (2012) Inhibition of fear by learned safety signals: A mini-symposium review. *Journal of Neuroscience* 32, 14118–14124. http://dx.doi.org/10.1523/JNEUROSCI.3340-12. 2012.
- Claxton, A.M. (2011) The potential of the human–animal relationship as an environmental enrichment for the welfare of zoo-housed animals. *Applied Animal Behaviour Science* 133, 1–10. http://dx.doi.org/10.1016/j.applanim.2011.03.002.
- Clegg, I.L. and Delfour, F. (2018) Cognitive judgement bias is associated with frequency of anticipatory behavior in bottlenose dolphins. *Zoo Biology* 37, 67–73. http://dx.doi.org/10.1002/zoo.21400.
- Clegg, I.L., Rödel, H.G., Delfour, F. (2017) Bottlenose dolphins engaging in more social affiliative behaviour judge ambiguous cues more optimistically. Behavioural Brain Research 322, 115–122. http:// dx.doi.org/10.1016/j.bbr.2017.01.026.
- Clubb, R. and Mason, G.J. (2007) Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Applied Animal Behaviour Science 102, 303–328. http://dx.doi.org/10.1016/j.applanim.2006. 05.033.
- Cociu, M., Wagner, G., Micu, N.E., Mihaescu, G. (1974) Adaptational gastro-enteritis in Siberian tigers: Panthera tigris altaica: At Bucharest Zoo. International Zoo Yearbook 14, 171–174. http://dx.doi.org/10.1111/ j.1748-1090.1974.tb00812.x.
- Davey, G. (2007) Visitors' effects on the welfare of animals in the zoo: A review. *Journal of Applied Animal Welfare Science* 10, 169–183. http://dx.doi.org/10.1080/10888700701313595.
- Davis, N., Schaffner, C.M., Smith, T.E. (2005) Evidence that zoo visitors influence HPA activity in spider monkeys (Ateles geoffroyii rufiventris). Applied Animal Behaviour Science 90, 131–141. http://dx.doi.org/ 10.1016/j.applanim.2004.08.020.

- Duncan, I.J. (2006) The changing concept of animal sentience. Applied Animal Behaviour Science 100, 11–19. http://dx.doi.org/10.1016/j.applanim.2006.04.011.
- EAZA (European Association of *Zoos* and Aquaria). (2019) What is welfare? Available at: www.eaza.net/about-us/areas-of-activity/animal-welfare (accessed 22 Mar 2019).
- Erwin, J., Anderson, B., Erwin, N., Lewis, L., Flynn, D. (1976) Aggression in captive pigtail monkey groups: Effects of provision of cover. *Perceptual and Motor Skills* 42, 319–324. http://dx.doi.org/10.2466/pms. 1976.42.1.319.
- Faragher, E.B., Cass, M., Cooper, C.L. (2005) The relationship between job satisfaction and health: A meta-analysis. *Occupational and Environmental Medicine* 62, 105–112. http://dx.doi.org/10.1136/oem.2002.006734.
- Farrand, A. (2007) The effect of zoo visitors on the behaviour and welfare of zoo mammals. Doctoral thesis. Department of Psychology, University of Stirling, Stirling, Scotland.
- Fox, M.W. (1968) *Abnormal Behaviour in Animals*. W.B. Saunders, Philadelphia, Pennsylvania, USA.
- Glatston, A.R., Geilvoet-Soeteman, E., Hora-Pecek, E., Van Hooff, J.A.R.A.M. (1984) The influence of the zoo environment on social behavior of groups of cottontopped tamarins, *Saguinus oedipus oedipus. Zoo Biology* 3, 241–253. http://dx.doi.org/10.1002/zoo. 1430030307.
- Gould, E. and Bres, M. (1986) Regurgitation and reingestion in captive gorillas: Description and intervention. Zoo Biology 5, 241–250. http://dx.doi.org/10.1002/zoo.1430050302.
- Greco, B.J., Meehan, C.L., Miller, L.J., Shepherdson, D.J., Morfeld, K.A., et al. (2016) Elephant management in North American zoos: Environmental enrichment, feeding, exercise, and training. PloS ONE 11(7), e0152490. http://dx.doi.org/10.1371/journal.pone.0152490.
- Harris, M., Sherwin, C., Harris, S. (2008) The welfare, housing and husbandry of elephants in UK zoos. Final Report: DEFRA Science and Research Project WC05007. Department of Food, the Environment and Rural Affairs, University of Bristol, London, UK.
- Hediger, H. (1950) *Wild Animals in Captivity*. Butterworths Scientific Publications. London, UK.
- Hediger, H. (1964) Wild Animals in Captivity. An Outline of the Biology of Zoological Gardens. Translated by G. Sircom. Dover Publications, New York, USA.
- Hemsworth, P.H. (2003) Human–animal interactions in livestock production. Applied Animal Behaviour Science 81, 185–198. http://dx.doi.org/10.1016/ S0168-1591(02)00280-0.
- Hemsworth, P.H. (2007) Ethical stockmanship. Australian Veterinary Journal 85, 194–200. http://dx.doi.org/ 10.1111/j.1751-0813.2007.00112.x.
- Holdgate, M.R., Meehan, C.L., Hogan, J.N., Miller, L.J., Rushen, J., et al. (2016a) Recumbence behavior in zoo elephants: Determination of patterns and frequency

- of recumbent rest and associated environmental and social factors. *PLoS ONE* 11(7), e0153301. http://dx.doi.org/10.1371/journal.pone.0153301.
- Holdgate, M.R., Meehan, C.L., Hogan, J.N., Miller, L.J., Soltis, J., et al. (2016b) Walking behavior of zoo elephants: Associations between GPS-measured daily walking distances and environmental factors, social factors, and welfare indicators. PloS ONE 11(7), e0150331. http://dx.doi.org/10.1371/journal.pone.0150331.
- Hosey, G.R. and Druck, P.L. (1987) The influence of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science* 18, 19–29. http://dx.doi.org/10.1016/0168-1591(87)90251-6.
- Hosey, G. and Melfi, V. (2012) Human–animal bonds between zoo professionals and the animals in their care. Zoo Biology 31, 13–26. http://dx.doi.org/10.1002/ zoo.20359.
- Hutchins, M. and Wiese, R.J. (1991) Beyond genetic and demographic management: The future of the Species Survival Plan and related AAZPA conservation efforts. Zoo Biology 10, 285–292. http://dx.doi.org/10.1002/ zoo.1430100402.
- Hutchins, M., Hancocks, D., Crockett, C. (1984) Naturalistic solutions to the behavioral problems of captive animals. Der Zoologische Garten 54, 28–42.
- Kastelein, R.A. and Wiepkema, P.R. (1989) A digging trough as occupational therapy for Pacific walruses (*Odobenus rosmarus divergens*) in human care. Aquatic Mammals 15, 9–17.
- Keen, H.A., Nelson, O.L., Robbins, C.T., Evans, M., Shepherdson, D.J., et al. (2014) Validation of a novel cognitive bias task based on difference in quantity of reinforcement for assessing environmental enrichment. Animal Cognition 17, 529–541. http://dx.doi. org/10.1007/s10071-013-0684-1.
- Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrenschlager, A., et al. (2016) Stereotypic route tracing in captive Carnivora is predicted by speciestypical home range sizes and hunting styles. Animal Behaviour 117, 197–209. http://dx.doi.org/10.1016/j. anbehav.2016.05.010.
- Laule, G.E. (2003) Positive reinforcement training and environmental enrichment: Enhancing animal wellbeing. *Journal of the American Veterinary Medical* Association 223, 969–973. http://dx.doi.org/10.2460/ javma.2003.223.969.
- Lohr, J.M., Olatunji, B.O., Sawchuk, C.N. (2007) A functional analysis of danger and safety signals in anxiety disorders. *Clinical Psychology Review* 27, 114–126. http://dx.doi.org/10.1016/j.cpr.2006.07.005.
- Mallapur, A. and Chellam, R. (2002) Environmental influences on stereotypy and the activity budget of Indian leopards (*Panthera pardus*) in four zoos in southern India. *Zoo Biology* 21, 585–595. http://dx.doi.org/10.1002/zoo.10063.
- Manciocco, A., Chiarotti, F., Vitale, A. (2009) Effects of positive interaction with caretakers on the behaviour of

- socially housed common marmosets (*Callithrix jacchus*). *Applied Animal Behaviour Science* 120, 100–107. http://dx.doi.org/10.1016/j.applanim.2009.05.007.
- Maple, T.L. (1990) Behavioural enrichment in zoos. In: Proceedings of 45th International Union of Directors of Zoological Gardens Conference. Copenhagen Zoo, Copenhagen, Denmark, pp. 19–24.
- Maple, T.L. (1992) Prof. Dr. Heini Hediger (1908–1992).
 Zoo Biology 11, 369–372. http://dx.doi.org/10.1002/zoo.1430110602.
- Markowitz, H. (1982) Behavioral Enrichment in the Zoo. Van Nostrand Reinhold. New York. USA.
- Mason, G. (2015) Using species differences in health and well-being to identify intrinsic risk and protective factors. WAZA Magazine 16, 2–5.
- Mason, G., Clubb, R., Latham, N., Vickery, S. (2007) Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science* 102, 163–188. http://dx.doi.org/10.1016/j.applanim.2006.05.041.
- McPhee, M.E. (2002) Intact carcasses as enrichment for large felids: Effects on on-and off-exhibit behaviors. Zoo Biology 21, 37–47. http://dx.doi.org/10.1002/zoo.10033.
- Meehan, C.L. and Mench, J.A. (2007) The challenge of challenge: Can problem solving opportunities enhance animal welfare? Applied Animal Behaviour Science 102, 246–261. http://dx.doi.org/10.1016/j. applanim.2006.05.031.
- Meehan, C.L., Hogan, J.N., Bonaparte-Saller, M.K., Mench, J.A. (2016a) Housing and social environments of African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in North American zoos. *PloS ONE* 11(7), e0146703. http://dx.doi. org/10.1371/journal.pone.0146703.
- Meehan, C.L., Mench, J.A., Carlstead, K., Hogan, J.N. (2016b) Determining connections between the daily lives of zoo elephants and their welfare: An epidemiological approach. *PloS ONE* 11(7), e0158124. http:// dx.doi.org/10.1371/journal.pone.0158124.
- Mellen, J. and Sevenich MacPhee, M. (2001) Philosophy of environmental enrichment: Past, present, and future. Zoo Biology 20, 211–226.
- Mellen, J.D. (1991) Factors influencing reproductive success in small captive exotic felids (*Felis* spp.): A multiple regression analysis. *Zoo Biology* 10, 95–110. http://dx.doi.org/10.1002/zoo.1430100202.
- Meyer-Holzapfel, M. (1968). Abnormal behavior in zoo animals. In: Fox, M.W. (ed.) *Abnormal Behaviour in Animals*. W.B. Saunders, Philadelphia, Pennsylvania, USA, pp. 479–484.
- Miller-Schroeder, P. and Paterson, J.D. (1989) Environmental influences on reproductive and maternal behavior in captive gorillas: Results of a survey. In: Segal, E.F. (ed.) Housing, Care and Psychological Well-Being of Captive and Laboratory Primates. Noyes Publications, Park Ridge, New Jersey, USA, pp. 389–415.

- Morfeld, K.A., Meehan, C.L., Hogan, J.N., Brown, J.L. (2016) Assessment of body condition in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in North American zoos and management practices associated with high body condition scores. *PloS ONE* 11(7), e0155146. http://dx.doi.org/10.1371/journal.pone.0155146.
- Morgan, K.N. and Tromborg, C.T. (2007) Sources of stress in captivity. Applied Animal Behaviour Science 102, 262–302. http://dx.doi.org/10.1016/j. applanim.2006.05.032.
- Morris, D. (1960) Automatic seal-feeding apparatus at London Zoo. *International Zoo Yearbook* 5, 70.
- Newberry, R.C. (1995) Environmental enrichment: Increasing the biological relevance of captive environments. Applied Animal Behaviour Science 44, 229– 243. http://dx.doi.org/10.1016/0168-1591(95)00616-Z.
- Panksepp, J. and Watt, D. (2011) What is basic about basic emotions? Lasting lessons from affective neuroscience. *Emotion Review* 3, 387–396. http:// dx.doi.org/10.1177/1754073911410741.
- Pifarré, M., Valdez, R., González-Rebeles, C., Vázquez, C., Romano, M., et al. (2012) The effect of zoo visitors on the behaviour and faecal cortisol of the Mexican wolf (Canis lupus baileyi). Applied Animal Behaviour Science 136, 57–62.
- Pizzutto, C.S., Sgai, M.G., Lopes, D.A., Pessutti, C., Nunes, A., et al. (2015) Relation between the level of self-mutilation and the concentration of fecal metabolites of glucocorticoids in captive chimpanzees (Pan troglodytes). Pesquisa Veterinária Brasileira 35, 62–66.
- Pomerantz, O. and Terkel, J. (2009) Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 71, 687–695. http://dx.doi.org/10.1002/ajp.20703.
- Pomerantz, O., Terkel, J., Suomi, S.J., Paukner, A. (2012) Stereotypic head twirls, but not pacing, are related to a 'pessimistic'-like judgment bias among captive tufted capuchins (*Cebus apella*). *Animal Cognition* 15, 689–698. http://dx.doi.org/10.1007/s10071-012-0497-7.
- Powell, D.M., Carlstead, K., Tarou, L.R., Brown, J.L., Monfort, S.L. (2006) Effects of construction noise on behavior and cortisol levels in a pair of captive giant pandas (*Ailuropoda melanoleuca*). Zoo Biology 25, 391–408. http://dx.doi.org/10.1002/zoo.20098.
- Quirke, T. and O'Riordan, R.M. (2011) The effect of different types of enrichment on the behaviour of cheetahs (*Acinonyx jubatus*) in captivity. *Applied Animal Behaviour Science* 133, 87–94. http://dx.doi.org/10.1016/j.applanim.2011.05.004.
- Rajagopal, T., Archunan, G., Sekar, M. (2011) Impact of zoo visitors on the fecal cortisol levels and behavior of an endangered species: Indian blackbuck (*Antelope cervicapra L.*). Journal of Applied Animal Welfare

- Science 14, 18–32. http://dx.doi.org/10.1080/1088870 5,2011.527598.
- Reinhardt, V. (1992) Improved handling of experimental rhesus monkeys. In: Davis, H. and Balfour, D. (eds.) *The Inevitable Bond: Examining the Scientist-Animal Interactions*. Cambridge University Press, Cambridge, UK, pp. 171–177.
- Rimpley, K. and Buchanan-Smith, H.M. (2013) Reliably signalling a startling husbandry event improves welfare of zoo-housed capuchins (*Sapajus apella*). *Applied Animal Behaviour Science* 147, 205–213. http://dx.doi.org/10.1016/j.applanim.2013.04.017.
- Roberts, M.S. (1989) A survey and analysis of management practices in the North American red panda SSP. In: Glatston, A.R. (ed.) *Red Panda Biology*. SPB Academic Publishing, The Hague, The Netherlands, pp. 85–96.
- Savastano, G., Hanson, A., McCann, C. (2003) The development of an operant conditioning training program for New World primates at the Bronx Zoo. *Journal of Applied Animal Welfare Science* 6, 247–261. http://dx.doi.org/10.1207/S15327604JAWS0603_09.
- Seed, A. and Byrne, R. (2010) Animal tool-use. Current Biology 20, R1032–R1039. http://dx.doi.org/10.1016/j. cub.2010.09.042.
- Shepherdson, D.J. (2003) Environmental enrichment: Past, present and future. *International Zoo Yearbook* 38, 118–124. http://dx.doi.org/10.1111/j.1748-1090.2003.tb02071.x.
- Shepherdson, D.J., Carlstead, K., Mellen, J.D., Seidensticker, J. (1993) The influence of food presentation on the behavior of small cats in confined environments. Zoo Biology 12, 203–216. http://dx. doi.org/10.1002/zoo.1430120206.
- Shepherdson, D., Lewis, K.D., Carlstead, K., Bauman, J., Perrin, N. (2013) Individual and environmental factors associated with stereotypic behavior and fecal glucocorticoid metabolite levels in zoo housed polar bears. *Applied Animal Behaviour Science* 147, 268–277. http://dx.doi.org/10.1016/j.applanim.2013.01.001.
- Sherwen, S.L., Harvey, T.J., Magrath, M.J., Butler, K.L., Fanson, K.V., et al. (2015) Effects of visual contact with zoo visitors on black-capped capuchin welfare. Applied Animal Behaviour Science 167, 65–73. http://dx.doi.org/10.1016/j.applanim.2015.03.004.
- Shyne, A. and Block, M. (2010) The effects of husbandry training on stereotypic pacing in captive African wild dogs (*Lycaon pictus*). *Journal of Applied Animal Welfare Science* 13, 56–65. http://dx.doi.org/10.1080/10888700903372069.
- Špinka, M. and Wemelsfelder, F. (2011) Environmental challenge and animal agency. In: Appleby, M.C., Mench, J.A., Olsson, I.A.S., Hughes, B.O. (eds.) *Animal Welfare*, 2nd edn. CAB International, Wallingford, UK, pp. 27–43. http://dx.doi.org/10.1079/9781845936594.0027.
- Spruijt, B.M., van den Bos, R., Pijlman, F.T. (2001) A concept of welfare based on reward evaluating mechanisms in the brain: Anticipatory behaviour as

- an indicator for the state of reward systems. *Applied Animal Behaviour Science* 72, 145–171. http://dx.doi.org/10.1016/S0168-1591(00)00204-5.
- Swaisgood, R.R. and Shepherdson, D.J. (2005) Scientific approaches to enrichment and stereotypies in zoo animals: What's been done and where should we go next? Zoo Biology 24, 499–518. http://dx.doi. org/10.1002/zoo.20066.
- Swaisgood, R. and Shepherdson, D. (2006) Environmental enrichment as a strategy for mitigating stereotypies in zoo animals: A literature review and meta-analysis. In: Mason, G. and Rushen, J. (eds.) Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare, 2nd edn. CAB International, Wallingford, UK, pp. 256–285.
- Thines, N.J., Shipley, L.A., Bassman, J.H., Fellman, J.K., Mattison, D.S., et al. (2007) Effects of enhanced UV-B radiation on plant chemistry: Nutritional consequences for a specialist and generalist lagomorph. *Journal of Chemical Ecology* 33, 1025–1039. http://dx.doi.org/10.1007/s10886-007-9280-7.
- Thompson, V.D. (1989) Behavioral response of 12 ungulate species in captivity to the presence of humans. *Zoo Biology* 8, 275–297. http://dx.doi.org/10.1002/zoo.1430080308.
- Van der Harst, J.E. and Spruijt, B.M. (2007) Tools to measure and improve animal welfare: Reward-related behaviour. *Animal Welfare* 16, 67–73.
- Van Keulen-Kromhout, G.V. (1978) Zoo enclosures for bears their influence on captive behaviour and reproduction. *International Zoo Yearbook* 18, 177–186.
- Ward, S.J. and Melfi, V. (2013) The implications of husbandry training on zoo animal response rates.

- Applied Animal Behaviour Science 147, 179–185. http://dx.doi.org/10.1016/j.applanim.2013.05.008.
- Ward, S.J. and Melfi, V. (2015) Keeper-animal interactions: Differences between the behaviour of zoo animals affect stockmanship. *PloS ONE* 10(10), e0140237. http://dx.doi.org/10.1371/journal.pone.0140237.
- Watters, J.V. (2014) Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. Zoo Biology 33, 251–256. http://dx.doi.org/10.1002/ zoo.21144.
- Westlund, K. (2014) Training is enrichment—and beyond. Applied Animal Behaviour Science 152, 1–6. http://dx.doi.org/10.1016/j.applanim.2013.12.009.
- Whitham, J.C. and Wielebnowski, N. (2013) New directions for zoo animal welfare science. *Applied Animal Behaviour Science* 147, 247–260. http://dx.doi.org/10.1016/j.applanim.2013.02.004.
- Wielebnowski, N. (2003) Stress and distress: Evaluating their impact for the well-being of zoo animals. *Journal* of the American Veterinary Medical Association 223, 973–977. http://dx.doi.org/10.2460/javma.2003.223.973.
- Wielebnowski, N.C., Fletchall, N., Carlstead, K., Busso, J.M., Brown, J.L. (2002) Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. Zoo Biology 21, 77–98. http://dx.doi. org/10.1002/zoo.10005.
- Yeates, J.W. (2011) Is 'a life worth living' a concept worth having? *Animal Welfare* 20, 397–406.
- Yeates, J.W. and Main, D.C. (2008) Assessment of positive welfare: A review. *The Veterinary Journal* 175, 293–300. http://dx.doi.org/10.1016/j.tvjl.2007.05.009.

22 Mental Health Issues in Captive Cetaceans

LORI MARINO

The Kimmela Center for Animal Advocacy and President, Whale Sanctuary Project, Kanab, Utah, USA

22.1 Introduction

Cetaceans are fully aquatic mammals comprising two suborders: the odontocetes (toothed whales, dolphins, and porpoises) and mysticetes (baleen and rorqual whales). Mental health issues in captive cetaceans, as with all wild animals, are a function of how well the captive environment fits with the adaptive history and characteristics of the animal. Unlike domesticated animals, cetaceans lack any adaptations to domestic or human environments. Moreover, the behaviors and environments cetaceans are adapted to are so disparate from what is on offer in marine parks and aquariums that it is not possible for them to thrive.

In order to address the question of mental health issues in captive cetaceans we need to first understand who they are and what they require for wellbeing. These characteristics should then be compared with what they are afforded in captivity. As we shall see, the gap between their fundamental needs and the captive environment is wide and has profound effects on their mental health and, ultimately, physical health and mortality.

The problem of cetacean mental health in captivity is widespread as there are over 3,000 odontocetes confined to concrete tanks or small pens for entertainment or research globally (Ceta-Base, 2018). (There are no mysticetes in captivity.) The most common species in captivity are orcas (Orcinus orca), who are actually large dolphins, bottlenose dolphins (Tursiops truncatus), and beluga whales (Delphinapterus leucas), although other species, e.g., pilot whales, whitesided dolphins, harbor porpoises, are also kept. This review will, therefore, focus on orcas, bottlenose dolphins, and belugas as more is known about how these species cope with captivity than any other. However, it appears that the impact of captivity on other dolphin and porpoise species is comparable.

22.2 Who are Cetaceans and What Do They Need to Thrive?

22.2.1 Evolutionary history and phylogeny

Cetaceans evolved from ungulate-like terrestrial ancestors ~50 million years ago (mya) (Fordyce, 2009). Their closest living relatives are hippopotamuses (Geisler and Theodor, 2009). And while there were many morphological adaptations to a fully aquatic existence over the first 10-15 million years of their evolution in the oceans the most significant changes relevant to the issue of mental health occurred ~35 mya when early versions of modern cetaceans evolved much larger and more complex brains than their predecessors (Marino et al., 2004a; Montgomery et al., 2013). Moreover, odontocetes were beginning to evolve echolocation at this time as well (Geisler et al., 2011). These changes led to a radically enhanced level of cognitive abilities and social complexity so that, today, many modern cetacean cultures are among the most complex among nonhumans and certainly older than those of humans (Whitehead and Rendell, 2014). These evolutionary changes in brain size and complexity and behavior have direct relevance to their ability to adapt to captivity.

22.2.2 Brain size and complexity Cerebral development

Cetacean brains are highly developed and complex and odontocetes are the most highly encephalized nonhuman taxonomic group known, with encephalization quotients ranging from 1.8 to 5.0, i.e., brain sizes from 1.8 to 5 times above expected size (Marino et al., 2004b). In orcas, for instance, the cerebrum constitutes an average of 81.5% of the total brain volume, compared with an average of 76.2% for humans (Wright et al., 2016). Neocortical surface area, measured by degree of gyrification, is also higher in many cetaceans relative to humans (Ridgway and Brownson, 1984). Cytoarchitectonic patterns in cetacean neocortex are far more varied and complex than previously thought and, although very different, rival the complexity found in humans and other primates (Hof et al., 2005).

In addition to the neocortex, the anterior cingulate and insular cortices, the temporal operculum, and paralimbic regions (all situated deep within the forebrain) are well developed in cetaceans (Hof and Van Der Gucht, 2007). The expansion of these areas in humans and other mammals is associated with high-level cognitive and social functions such as attention, prediction, social awareness, and empathy (Hof *et al.*, 2005; Allman *et al.*, 2011). Moreover, recent studies show that the anterior cingulate and insular cortices in larger cetaceans, such as orcas, contain a type of projection neuron, known as a spindle cell or Von Economo neuron (Hof and Van Der Gucht, 2007), which may be involved in social cognition (Allman *et al.*, 2011).

The limbic system and emotional regulation

Recent work has shown that limbic functions in cetaceans are well integrated with other cortical functions (Pessoa and Hof, 2015). In cetaceans, the limbic system has been elaborated into neighboring regions to form a paralimbic lobe, which forms dense connections between core limbic structures, i.e., region of the brain specializing in emotion, memory, and motivation, and higher-order cerebral information processing, problem solving, and communication areas (Marino *et al.*, 2004b).

Sensory systems

All odontocetes have well-developed auditory capacities using a broader range of frequencies than humans (Madsen and Surlykke, 2013). Acoustics, including echolocation, are their primary perceptual modality and, as such, an integral part of their experience of the world (Madsen and Surlykke, 2013). Vision is also well developed in cetaceans with acuity preserved above and below water in almost all species except freshwater dolphins (Madsen and Herman, 1980). Somatosensory perception (sense of touch, pain, body position, temperature) is also important for cetaceans in a number of contexts, including affiliative. Finally, odontocetes lack olfactory

bulbs and taste buds and, therefore, do not possess smell or taste (Kishida *et al.*, 2015).

22.2.3 Psychology and behavioral adaptations

Orcas, beluga whales, and bottlenose dolphins are among the most cognitively sophisticated and intelligent animals on the planet. Their large complex brain, far from being a protective feature, is a risk factor for poor coping in captivity because it is essentially impossible to meet their complex needs. Orcas, belugas, and bottlenose dolphins are longlived in the wild and experience an extended juvenile period of several years (Whitehead and Rendell, 2014). They are sophisticated problem solvers with high-level capacities for intraspecies and interspecies cooperation, and possess complex communicative functions as well as capacities for comprehending and mimicking human language. They live in complex social networks with individual social roles and learned cultural traditions spanning many generations (Connor, 2007; Lusseau, 2007; Whitehead and Rendell, 2014). In all three species, mothers and their offspring stay together during a protracted weaning and post-weaning stage that lasts several years until reproductive maturity (Fedak et al., 2009). In some populations of orcas, mothers and male offspring stay in the same group for life (Foster et al., 2012). Belugas and orcas experience post-reproductive senescence which aligns with the strong matriarchal nature of their groups (Brent et al., 2015; Ellis et al., 2018).

Cetaceans are generally long-distance and deepdiving animals who fully exploit the three-dimensionality of the water space. For instance, belugas migrate over thousands of kilometers (Lydersen et al., 2001) and orcas can travel over 100-200 km/ day (Pitman and Durban, 2012). They dive to depths of several to hundreds of meters, depending on the species and population (Lydersen et al., 2001; Ford, 2009; Stewart, 2009; O'Corry-Crowe, 2018). While the opportunity to engage in traveling and diving is clearly related to physical health and conditioning, the need to move and travel is equally a psychological one. The free movement in the three-dimensional world of the ocean provides opportunities for hunting and foraging, as well as exploration, socializing, experiencing challenges, and the expression of choice - all of which are critical to mental health in cetaceans, and all of which are either absent or greatly diminished in marine parks.

316 L. Marino

Finally, cetaceans, including all three of the species above, not only have deep emotional attachments to each other, but they show clear and strong capacities for empathy both within and across species. Observations of many cetacean species include reports of long-range contact calling when separated from others, grieving behaviors, and epimeletic behaviors (Reggente *et al.*, 2016; Bearzi and Reggente, 2017).

To conclude, the psychology of cetaceans, and particularly the three species most commonly kept in captivity, is one characterized by a keen intelligence and need for stimulation and new challenges through travel, a high reliance upon learning and group care for juveniles, strong emotional ties, and rich cultural traditions. Therefore, the question of mental health in captivity can be addressed by asking whether these are the kinds of beings whose needs could be met in concrete tanks in entertainment parks.

22.2.4 How well are these needs met in captivity?

Cetaceans in marine parks are typically housed in shallow concrete tanks a miniscule fraction of the size of their natural home ranges (Couquiaud, 2005; Rose et al., 2017). For example, the minimum US space standards for orca enclosures of 15 meters for horizontal distance and 4 meters for depth are grossly inadequate for natural movements and postures for adult orcas, who average 6.0-7.6 meters long (Rose et al., 2017). Marine parks and aquariums have claimed that captive cetaceans do not need to travel or dive extensively because their food is provided for them at the surface, but these statements ignore the physiological adaptations to traveling and diving that need to be met for health and welfare (Clubb and Mason, 2003, 2007; McPhee and Carlstead, 2010). In addition, the barrenness and uniformity of captive display tanks are a striking contrast to the natural environment and do not provide enough challenges or variety in activities to keep an individual stimulated, motivated, and thriving (Couquiaud, 2005).

Captive dolphins and whales are kept in artificially produced groups or 'collections' which do not resemble a natural social group. Commonly, individuals of different species and genetic backgrounds are forced together, bred artificially, and separated by transfers to other facilities without regard for social bonds, including those of mothers and their offspring (Waples and Gales, 2002; Rose *et al.*, 2009). Jett and Ventre (2015) showed that

captive orcas are at the highest risk of dying between ages 2 and 6 years (when juveniles may be weaned but still socially dependent upon their mother) and suggest that mortality would be reduced by avoiding separation of mothers and calves.

Moreover, unlike in the free-ranging situation, captive cetaceans cannot manage conflict by dispersal and are forced to live in a confined space with individuals they may not get along with (Waples and Gales, 2002; Couquiaud, 2005). The result of such unnatural confinement, artificial group composition, and breeding is heightened social tension and aggression (Sweeney, 1990; Waples and Gales, 2002).

Arguably one of the less obvious but more impactful aspects of the captive environment on cetaceans is the lack of control (i.e., loss of autonomy) inherent in a situation in which movement, feeding, social relationships, and every other facet of everyday life is determined by humans. Feeding and show times are highly scheduled daily events and compliance during performances and husbandry practices is linked to outcome (access to social interaction, amount of food, and access to environmental enrichment, etc.). In addition, captive cetaceans are unable to control the noise of audiences, filtration devices, and other physical and sensory aspects of their artificial environment. Dolphins in 'petting pools' and 'swim-with' programs are forced to make physical contact with humans who enter what little space they have to themselves (Couquiaud, 2005; Stewart and Marino, 2009). This ongoing lack of autonomy is not as precisely measurable as tank size but is one of the most insidious sources of stress and poor well-being for captive cetaceans.

In conclusion, there is essentially no correspondence between the artificial environment of entertainment parks and the natural history and adaptative characteristics of cetaceans. The impact is the same for both wild-caught and captive-born individuals, attesting to the deep fundamental discordance between life in concrete tanks and what all cetaceans need to thrive.

22.3 The Effects of Chronic Stress on Mental (and Physical) Health

The mental health of captive cetaceans must be understood in terms of how the maladaptiveness to the conditions of captivity causes chronic stress and, ultimately, a cycle of abnormal behavior and increased morbidity and mortality. Most definitions of stress are rooted in the foundational concept of

homeostasis and the ability of an organism to adapt to various circumstances (Selye, 1976). All animals have evolved to be adapted to their natural environments and, likewise, the stresses found in nature (Tooby and Cosmides, 1990; Panksepp, 2010). The stress responses to these natural situations may be beneficial to the organism, permitting an appropriate response to the stressor (e.g., flight from a predator) and a return to homeostasis once the stressor is no longer present. Other stressors are severe, repetitive, chronic, or outside of the adaptive capabilities of an organism. These types of stressors contribute to a constantly high allostatic load and, therefore, have serious consequences for health and well-being (McEwen, 2017).

A normal stress response involves activation of the hypothalamic-pituitary-adrenal (HPA) axis and a subsequent return to baseline levels and homeostasis. But when the stress is prolonged and severe the physiological effects on the brain and the rest of the body are damaging to organs, the immune system, and the brain (Atkinson et al., 2015). Brain dysfunction, in turn, perpetuates abnormal responses to stress in a cycle of impairment. The HPA axis and its effects are highly conserved across mammals (Morgan and Tromborg, 2007; Lupien et al., 2009). Orcas and other cetaceans share brain mechanisms involved in mounting a stress response with other mammals and adhere to the classic HPA model (Thomson and Geraci, 1986; Romano et al., 2002; Fair et al., 2014; Levin, 2018; for reviews, see Atkinson et al., 2015; Atkinson and Dierauf, 2018). Living in concrete tanks is a situation that produces a constant high level of stress, taking a toll on mental and physical health in captive cetaceans.

The long list of emotional, psychophysiological, and behavioral changes associated with these neurological alterations, in humans and other mammals, includes increased anxiety, posttraumatic stress, cognitive impairment, depression, and mood dysregulation (Buwalda *et al.*, 2005; McEwen, 2006, 2017; Lupien *et al.*, 2009).

Moreover, both acute and chronic stressors that occur early in life have an important impact on an individual's ability to cope with stressors later in life (McEwen, 2017). And therefore, as described below, multigenerational captivity perpetuates cycles of psychopathology in cetaceans.

22.3.1 Behavioral abnormalities

Captive cetaceans exhibit a range of abnormal behaviors that are common sequelae of mental illness in

most complex animals. These include but are not limited to stereotypies, self-harming, hyperaggression, depressive behaviors, and failures in nursing and parent-offspring attachment. These behavioral problems are a consequence of chronic stress and lead to increased morbidity and mortality.

Stereotypies

One of the more prevalent behavioral abnormalities found in captive animals is stereotypic behavior (Mason and Latham, 2004; Mason and Rushen, 2008). There is a recognized correlation between a confined animal's propensity to engage in stereotypical behavior and the size of their natural home range (Clubb and Mason, 2003, 2007).

Although the link between stereotypies and welfare is complex it is generally acknowledged that stereotypies are aberrant repetitive behaviors induced by the frustration of natural impulses, attempts to cope with a stressful environment, and/or brain dysfunction (Mason and Rushen, 2008) and are rarely observed in animals living in a natural habitat (Clegg *et al.*, 2017). Environments that induce or increase stereotypies are typically worse, from a mental health and welfare perspective, than those which do not (Mason and Latham, 2004). Stereotypies, with their inappropriate level of repetition, are not infrequently associated with perseverative behaviors as well (Mason and Latham, 2004).

In captive cetaceans, oral stereotypies are common (Jett *et al.*, 2017). These may include biting, chewing, and jaw-popping on hard tank surfaces and the steel gates used to separate them (Jett and Ventre, 2012; Visser, 2012; Visser and Lisker, 2016; Jett *et al.*, 2017) in a behavior similar to 'cribbiting' in horses (Mason and Latham, 2004). The constant grating of the teeth causes severe wear that results in serious dental problems and subsequent systemic infections and mortality (Jett *et al.*, 2017; see below).

Another common stereotypy in captive cetaceans is circling and repetitive swimming patterns (Jett and Ventre, 2011). These are not simply swimming preferences but repetitive uniform swimming behaviors that follow fixed trajectories and turning at predictable locations. While not studied nearly as well or extensively as they could be, there are reports of swimming stereotypies in captive cetaceans (Gygax, 1993; Ugaz Ruiz et al., 2013). Ugaz Ruiz et al. (2013) found that in closed facilities

318 L. Marino

there were higher rates of circular swimming as well as higher cortisol levels than in open sea pen facilities, where the dolphins tended to swim in straight lines. When interpreting these findings, however, enclosure shape and size should be taken into account to determine how much it influences the formation and morphology of behaviors that look like stereotypies.

Self-harm

Self-harming (whether deliberate or as a result of other abnormal behaviors) is undescribed in freeranging animals yet is one of the most common signs of distress and poor well-being in captive wild animals (Mason, 2010). As mentioned above, common oral stereotypies in orcas and other captive cetaceans result in damaged dentition (Jett et al., 2017). Jett et al. (2017) found that over 60% of captive orcas in the US and Spain had fractured mandibular teeth and 24% exhibited 'major' to 'extreme' mandibular coronal tooth wear down to the gingiva due to oral stereotypies (see Fig. 22.1). Dental pathology in captive orcas requires routine treatment with pulpotomies, drainage, antiseptics, and antibiotics and, even then, stereotypy-induced dental pathology is a major source of systemic infection and mortality in captive orcas (Jett et al., 2017).

In addition to the harmful results of repetitive actions like gate-biting and jaw-popping, captive cetaceans also engage in other forms of self-injurious behavior that inflict severe physical harm and trauma on the individual (Sweeney, 1988). One very young false killer whale (*Pseudorca crassidens*),



Fig. 22.1. Close up of right mandibular dentition in Morgan, a wild-born orca held at Loro Parque in Spain for the past 8 years. The teeth show extensive damage, ranging in severity from mild to extreme and including apical wear (in some cases to the gumline), exposure of the pulp cavity, and fractured teeth.

named Chester, at Vancouver Aquarium exhibited extensive rubbing of his chin against tank walls and other hard objects causing a longstanding abrasion (Lipman, 2016). Another young captive, an orca named Morgan taken from the wild and confined in an entertainment park in Spain, continues to exhibit 'unnatural and self-harming behaviors, including hitting her nose against the concrete tank, chewing the concrete and sliding out of the water – an action known as beaching' (Walters, 2016). One of the more extreme cases of self-injury in a captive cetacean is Hugo, an orca who was captured from the wild in 1968 and held at Miami Seaguarium up until his death. Hugo and his tankmate Lolita performed in shows but Hugo (who was also highly aggressive toward trainers) exhibited very severe self-harm by regularly banging his head against the concrete walls of the tank, which, at one point, resulted in an injury to his rostrum which required surgery and eventually led to his death by brain aneurysm in 1980 (Jett and Ventre, 2011).

In the examples above it is not known whether the individual wanted to self-harm or simply self-harmed in the process of enacting other kinds of abnormal behaviors. In either case the behavior is due to severe mental health issues and results are often devastating. Unfortunately, there have not been any recent comprehensive surveys and studies of self-harming in captive cetaceans as it is known generally through well-publicized and documented case studies such as the ones above. And commercial marine parks and aquariums are not forthcoming with records of animal welfare at their facilities. Nevertheless, it would be reasonable to claim that self-injurious behavior is not uncommon in captive cetaceans.

Hyperaggression

Aggression is a natural part of living in groups but there are very specific stresses associated with living in captivity that encourage aggression both toward conspecifics and toward humans. In free-ranging cetaceans, serious aggression toward members of one's family or social group is kept in check by dispersal and natural social groupings, which act as buffers (Baird and Dill, 1995; Sweeney and Samansky, 1995; Bisther, 2002). But conspecific aggression is frequent in the tanks because of the confined physical characteristics and unstable social relationships that characterize marine park and aquarium life (Waples and Gales, 2002; Frohoff, 2004).

The sole reported orca fatality from conspecific aggression involved two females at SeaWorld San Diego in which one of the whales bled to death from a severed artery (*New York Times*, 1989). Both were wild caught as juveniles and were from different oceans (Icelandic and Pacific), genetic stock, and cultures; they would never have encountered each other naturally. On the other hand, there is not a single case of conspecific death in freeranging orcas even when different populations encounter each other (Rose *et al.*, 2009).

Conspecific aggression is common in captive belugas and bottlenose dolphins as well. In 2015, a beluga whale died at a SeaWorld park after developing an infection in his jaw that was fractured during an aggressive interaction with two other whales (Evans, 2015). Many incidences of conspecific aggression in bottlenose dolphins are caused by dominant adult males toward subordinate adults and juveniles (Wells and Scott, 1999). Samuels and Gifford (1997) noted seasonal peaks in aggression among male dolphins in a captive colony likely to be due to seasonal changes in hormone levels. Johnson and Norris (1986) suggested that adult male aggression toward juveniles may reflect an innate need to herd the young when feeling threatened in the wild (cetaceans, like ungulates, protect juveniles by herding them into the center of a group when threatened). In confinement this behavior may escalate into an obsessive hostility because the young can neither move away nor escape. Therefore, in these cases natural tendencies become pathological because of repeated failed attempts to express them in captive conditions.

In addition to conspecific hyperaggression, captive cetaceans exhibit heightened, and sometimes lethal, aggression toward humans. These frequent attacks in captivity are grossly abnormal compared with the much lower frequency of aggression and threatening behavior initiated by free-ranging cetaceans toward humans (Scheer, 2010). In fact, no free-ranging orca or beluga whale has ever seriously injured or killed a human being despite decades of encounters in the wild and in-water research (Visser, 2005; Pagel et al., 2017). Attacks by free-ranging bottlenose dolphins are highly unusual and typically occur when the dolphin is antagonized or swimmers touch the animal in sensitive body parts like the eyes and blowhole (Frohoff and Packard, 1995; Santos, 1997). To date, there has been only one documented case of lethal aggression toward humans by a free-ranging bottlenose dolphin who rammed a swimmer who was trying to put foreign objects in his blowhole (Santos, 1997).

In contrast, the record of violent attacks, particularly of captive orcas and other dolphins, toward humans is long and demonstrates that this form of hyperaggression is a response to captive circumstances. In just 55 years in marine parks, captive orcas have killed four human beings (three trainers and one member of the public) and seriously injured many more (Parsons, 2012; Wise, 2016). There have been hundreds of aggressive acts toward humans by captive orcas (Lott and Williamson, 2017).

Captive dolphins in 'swim-with' programs are induced to allow humans to touch them and even ride on them. Many visitors in these programs have been seriously injured by bottlenose dolphins (Vail, 2012). There are numerous documented cases of threats, biting, and ramming, including sexual behavior, toward human swimmers by captive bottlenose dolphins (Spradlin *et al.*, 1999) and it is not uncommon for humans to suffer broken bones, severe bruises, severe bites, and fractured ribs requiring hospitalization during captive swim-with activities (Spradlin *et al.*, 1999; Marine Connection, 2008; Rose *et al.*, 2009).

Inadequate maternal attachment and care

In the wild, successful calf rearing is facilitated by mentoring mid-wives or 'aunties' (typically older related females) and stable matrilines. Potentially aggressive adult males are kept at bay by dispersal. In captivity, however, the limited space and artificial social groupings escalate social pressure and stresses (Waples and Gales, 2002). These problems are exacerbated by artificial insemination at unnaturally young ages, as well as the fact that calves are often separated from their mothers at a young age, providing little to no opportunity for new mothers to learn nursing skills. The result is a high incidence of infant mortality, and frequent neglect or rejection of the calf (Couquiaud, 2005; Rose et al., 2009). Infant mortality among cetaceans is also significant in free-ranging populations (Rose et al., 2009), but is explainable by such factors as lack of food, predation, illness, and pollution. However, these factors do not exist in captivity and yet infant mortality is at least as high.

When captive mothers fail to nurse, facility staff typically step in to bottle rear the infant. However, hand rearing of young captive wild animals by

320 L. Marino

humans is generally considered a strategy of last resort and often produces life-long behavioral problems, including poor social and parenting skills (Latham and Mason, 2008, for a review). Moreover, hand rearing has been linked to increased frequency of stereotypic behavior, which can, in turn, serve to prevent or disrupt normal maternal behavior (Sørensen and Randrup, 1986). There is a report of early separation from the mother causing stereotypies in a zoo-housed dolphin (Laule, 1993). This ongoing process of 'de-maternalization' (termed by Lott and Williamson, 2017) in which captive cetaceans and other social long-lived mammals who are rejected by their mothers in turn reject their own offspring is self-perpetuating and extremely difficult, if not impossible, to interrupt.

Depression and the question of suicide

Emotional depression in captive cetaceans is common and can often be associated with a physical illness. However, frequently seemingly healthy individuals may show a 'failure to thrive' and will often suddenly go 'off feed' and die when intense stressors (e.g., the death of a companion or offspring, or a transfer to another facility) are added to the chronic stress of living in captivity (Waples and Gales, 2002). Symptoms of depression in cetaceans are similar to those in other animals and include loss of appetite, lack of motivation, and inactivity (Waples and Gales, 2002).

As mentioned above, one of the most pervasive and insidious stressors in the lives of captive animals is their inability to control most aspects of their surroundings and lives (Sambrook and Buchanan-Smith, 1997; Morgan and Tromberg, 2007). This lack of control or autonomy can lead to a wellknown psychological syndrome called learned helplessness that results in a range of outcomes associated with chronic stress, including depression, 'giving up' or lack of motivation to learn or explore, anorexia, and immune system dysfunction (Maier and Seligman, 2016; see also Chapter 6, this volume). Learned helplessness has been documented across a range of mammals in captivity (Markowitz and Eckert, 2005; Clubb and Mason, 2007; Morgan and Tromborg, 2007; Hodes et al., 2015) and a number of authors have suggested that the chronic stress associated with lack of control in captivity can cause learned helplessness in cetaceans (Couquiaud, 2005; Atkinson and Dierauf, 2018). Extended periods of listless immobility at the surface (commonly termed

'logging') and catatonic-like bottom resting are behaviors reflective of such learned helplessness. An adult male orca at SeaWorld Florida was observed continuously (24 hours/day) for a period of 7 consecutive days, to create an activity budget. The orca spent, on average, 69.6% (16.7 hours) of the day inactive (Worthy et al., 2013) and as such was completely disengaged with his conspecifics, trainers, or environment. Such inactivity is unheard of in the wild, where orca are on the move for more than 99% of their lives (e.g., see Durban and Pitman, 2011; Matthews et al., 2011; Lauriano et al., 2015). Not unexpectedly, captive dolphins who live in concrete tanks show more 'logging' and less activity than those who live in sea pens, suggesting exposure to a more natural environment may help to alleviate depression and other forms of mental illness in captive cetaceans (Ugaz Ruiz et al., 2009, 2013).

Apart from showing overt signs of depression there are several cases of captive cetaceans who seem normal, i.e., eating, interacting with others, moving, who die suddenly without warning. One such example is Maris, a 21-year-old seemingly healthy female beluga at the Georgia Aquarium who died just a few months after losing her second calf in captivity (Markiewicz, 2015). No explanation was ever provided and although much more information is needed, this haunting example – not uncommon – leads to speculation about captive cetaceans losing the will to live.

The above example begs a question which has been getting increasing attention in the scientific literature, that is, whether captive cetaceans can and do commit suicide (Peña-Guzmán, 2017, 2018). Suicide, for the purposes of this discussion, is defined as the intentional ending of one's own life. Key to this definition is intentionality. Motivational states, especially highly complex ones that accompany acts such as suicide, are often difficult to identify, verify, and characterize in other human beings and, thus, are particularly so in nonhuman beings.

To be clear, the debate is not about whether other animals, and, in this case, captive cetaceans lose the 'will to live' or fail to thrive under certain circumstances. The abundant evidence reviewed above arguably settles that issue. Nor does the question of suicide refer to all deaths that result from self-harm. Actual suicide requires an awareness of one's identity and existence and the ability to mentally represent and bring about the ending of existence.

Given these complexities, the suicide question for captive cetaceans needs to be left open but can be approached empirically by noting evidence for mental capacities which would indicate the requisite level of awareness for actual suicide. Cetaceans have large complex brains (Hof et al., 2005), are self-aware (Reiss and Marino, 2001), possess metacognition (the ability to think about their own thoughts; Smith et al., 1995), demonstrate sophisticated social and situational awareness and strong emotional bonds (Bearzi and Reggente, 2017), and engage in goal-directed behaviors (McCowan et al., 2000). Moreover, as voluntary breathers cetaceans have an available mechanism for ending their life by simply not taking the next breath (Kooyman, 1989). Therefore, cetaceans, arguably, possess the mental capacity and physiological means to commit suicide. Whether they do or not is still under debate. There may be a psychological continuum between self-harm and suicide which needs to be explored further in all animals. But certainly, the possibility of intentional suicide in captive cetaceans cannot be ruled out a priori.

22.4 The Use of Psychotropic Drugs to Treat Mental Illness in Captive Cetaceans

One of the bellwethers of mental illness in captive cetaceans is the routine use of psychotropic drugs for 'management'. Psychotropic drugs are ubiquitously given to captive cetaceans in order to treat maladaptive behaviors, control aggression, stimulate appetite, and facilitate handling for procedures. The pills are pushed through the gills of the dead fish they are fed. Marine parks justify the routine use of these drugs with claims that these pharmaceuticals help maintain mental health in captivity (Cronin, 2015). However, the fact that these psychoactive drugs need to be given belies any claims that cetaceans are thriving in concrete tanks and is an implicit confirmation that mental illness is commonplace.

The most widespread of drugs used is diazepam (also known as Valium), a benzodiazepine which calms the animals during clinical procedures and transport. But diazepam is also given routinely to reduce anxiety and control stereotypies (Cornell, 2011). Diazepam is also used to stimulate appetite in sick or depressed individuals by enhancing the taste of food (Dowling, 2015) despite the fact that there is no evidence that odontocetes can taste (Kishida *et al.*, 2015).

The regular use of diazepam and other anxiolytics for these purposes in any captive species can be

hazardous from a general health point of view because of tolerance, reliance, and side-effects, but particularly so for cetaceans, who are voluntary breathers and must be awake to breathe. Diazepam can decrease the responsiveness of the respiratory system (Khan, 2014).

22.5 Concluding Remarks

Cetaceans possess large complex brains and strong social and familial ties. Many species, including orcas and beluga whales, routinely range widely and dive deeply. They are self-aware, cultural beings who differentiate and identify their own groups through dialect, prey preference, group size, and many other learned traditions. They have a prolonged juvenile period of social learning and the emotional bonds between mothers and calves, as well as among other relatives, are as strong as any in the animal kingdom. They also demonstrate the capacity to grieve. While these characteristics are associated with a high degree of intelligence and social sensitivity and complexity, they also mean that cetaceans are inherently ill-suited to thriving in marine parks and aquariums. That is, there is a fundamental incompatibility between who dolphins and whales are and the life they are forced to lead in concrete tanks.

As a result of this mismatch captive cetaceans exhibit multiple signs of chronic stress and mental illness, including behavioral stereotypies, self-harm, hyperaggression, depression, and poor parenting. Despite the inability to meet the needs of these beings, marine parks and aquariums persist in confining them to and breeding them in concrete tanks for entertainment purposes. They 'manage' the mental health issues with regular dosings of diazepam and other psychotropic drugs.

In the end the only way to ameliorate this suffering is to provide a situation that more closely matches their natural habitat. Seaside sanctuaries are now being created in North America, Europe, and elsewhere for the purpose of retiring dolphins and whales in marine parks to an ocean environment while under human care with no performances, breeding, or interaction with the public. Given that most of the captive whales and dolphins cannot simply be released into the ocean, sanctuaries will provide for dolphins and whales an environment that is as close as possible to their natural environment and, in doing so, encourage healthier and more natural expressions of behavior and

322 L. Marino

psychology than is possible in the tanks – just as sanctuaries have done so for wild land animals for decades. Sanctuaries are still captivity but they are designed with the well-being and autonomy of the residents in mind and, therefore, hold out the best hope for currently captive dolphins and whales to achieve better mental and physical health.

22.6 Acknowledgments

I wish to thank Dr. Ingrid Visser, Orca Research Trust, for providing the photograph of Morgan's dentition in Fig. 22.1.

Notes

¹ See, e.g., SeaWorld Responds to Questions About Captive Orcas, Blackfish Film, CNN (October 28, 2013, 11:27 AM). www.cnn.com/2013/10/21/us/seaworld-blackfish-qa, in which SeaWorld's Vice President of Communications, Fred Jacobs, state in a CNN interview: 'While a killer whale can and occasionally might travel as much as 100 miles in a day, it should be said that swimming that distance is not integral to a whale's health and well-being. It is likely foraging behavior... Killer whales living in our parks are given all the food they require.'

22.7 References

- Allman, J.M., Tetreault, N.A., Hakeem, A.Y., Manaye, K.F., Semendeferi, K., et al. (2011) The von Economo neurons in the frontoinsular and anterior cingulate cortex. Annals of the New York Academy of Sciences 1225, 59–71. http://dx.doi.org/10.1111/j.1749-6632. 2011.06011.x.
- Atkinson, S.K.C. and Dierauf, L.A. (2018) Stress and marine mammals. In: Gulland, F.M.D., Dierauf, L.A., Whitman, K.L. (eds.) *CRC Handbook of Marine Mammal Medicine*. CRC Press, Boca Raton, Florida, USA, pp. 141–156.
- Atkinson, S., Crocker, D., Houser, D., Mashburn, K. (2015) Stress physiology in marine mammals: How well do they fit the terrestrial model? *Journal of Comparative Physiology B* 185, 463–486. http://dx.doi.org/10.1007/s00360-015-0901-0.
- Baird, R.W. and Dill, L.M. (1995) Occurrence and behaviour of transient killer whales: Seasonal and pod-specific variability, foraging behaviour, and prey handling. Canadian Journal of Zoology 73, 1300–1311. http://dx.doi.org/10.1139/z95-154.
- Bearzi, G. and Reggente, M.A. (2017) Epimeletic behavior. In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds.) Encyclopedia of Marine Mammals, 3rd edn. Academic Press, San Diego, California, USA, pp. 337–338.

- Bisther, A. (2002) Intergroup interactions among killer whales in Norwegian coastal waters: Tolerance vs. aggression at feeding grounds. *Aquatic Mammals* 28, 14–23.
- Brent, L.J., Franks, D.W., Foster, E.A., Balcomb, K.C., Cant, M.A, et al. (2015) Ecological knowledge, leadership, and the evolution of menopause in killer whales. Current Biology 25, 746–750. http://dx.doi. org/10.1016/j.cub.2015.01.037.
- Buwalda, B., Kole, M.H.P., Veenema, A.H., Huininga, M., De Boer, S.F., et al. (2005) Long-term effects of social stress on brain and behavior: A focus on hippocampal functioning. Neuroscience and Biobehavioral Reviews 29, 83–97. http://dx.doi.org/10.1016/j.neubiorev.2004.05.005.
- Ceta-Base (2018) Captive cetacean database. Living population. Available at: www.ceta-base.org/captive/cetacean (accessed 15 December 2018).
- Clegg, I.L.K., van Elk, C.E., Delfour, F. (2017) Applying welfare science to bottlenose dolphins (*Tursiops truncatus*). Animal Welfare 26, 165–176.
- Clubb, R. and Mason, G. (2003) Captivity effects on wide-ranging carnivores. *Nature* 425, 473–474. http://dx.doi.org/10.1038/425473a.
- Clubb, R. and Mason, G. J. (2007) Natural behavioural biology as a risk factor in carnivore welfare: How analyzing species differences could help zoos improve enclosures. *Applied Animal Behavior Science* 102, 303–328. http://dx.doi.org/10.1016/j.applanim.2006.05.033.
- Connor, R. (2007) Dolphin social intelligence: Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B* 362, 587–602. http://dx.doi.org/10.1098/rstb.2006.1997.
- Cornell, L. (2011) Sworn Affidavit of Dr Lanny Cornell. Seaworld Parks & Entertainment LLC and Marineland of Canada Inc. Ontario Superior Court of Justice. Court File No. 52783/11. Available at: https://www.scribd.com/doc/215567388/Seaworld-v-Marineland-Aff-of-Lanny-Cornell (accessed 16 January 2019).
- Couquiaud, L. (2005) A survey of the environments of cetaceans in human care. Aquatic Mammals 31, 279–385.
- Cronin, M. (2015) Ex-Seaworld trainers: Here's a list of the drugs we fed to orcas. Available at: https://www.thedodo.com/seaworld-orca-drugs-medications-1035364310.html (accessed 21 January 2019).
- Dowling, P. (2015) Drugs affecting appetite (monogastric). Available at: www.merckvetmanual.com/mvm/pharmacology/systemic_pharmacotherapeutics_of_The digestive system/drugs_affecting appetite monogastrichtml (accessed 21 January 2019).
- Durban, J.W. and Pitman, R.L. (2011) Antarctic killer whales make rapid, round-trip movements to subtropical waters: Evidence for physiological maintenance migrations? *Biology Letters* 8, 274–277.
- Ellis, S., Franks, D.W., Nattrass, S., Currie, T.E., Cant, M.A., et al. (2018) Analyses of ovarian activity reveal

- repeated evolution of post-reproductive lifespans in toothed whales. *Scientific Reports* 8, 12833. http://dx.doi.org/10.1038/s41598-018-31047-8.
- Evans, S.J. (2015) Nanuq the beluga whale dies at underfire SeaWorld Orlando after fracturing his jaw and contracting infection while on loan. Available at: www. dailymail.co.uk/news/article-2963937/Nanuq-belugawhale-dies-fire-SeaWorld-Orlando-fracturing-jawcontracting-infection-loan.html (accessed 16 January 2019)
- Fair, P.A., Schaefer, A.M., Romano, T.A., Bossart, G.D., Lamb, S.V., et al. (2014) Stress response of wild bottlenose dolphins (*Tursiops truncatus*) during capture-release health assessment studies. *General and Comparative Endocrinology* 206, 203–212. http:// dx.doi.org/10.1016/j.ygcen.2014.07.002.
- Fedak, M.A., Wilson, B., Pomeroy, P.P. (2009) Reproductive behavior. In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds.) Encyclopedia of Marine Mammals, 2nd edn. Academic Press, San Diego, California, USA, pp. 943–955.
- Ford, J.K.B. (2009) Killer whale (*Orcinus orca*). In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds.) *Encyclopedia* of *Marine Mammals*, 2nd edn. Academic Press, San Diego, California, USA, pp. 650–656.
- Fordyce, R.E. (2009) Cetacean fossil record. In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds.) Encyclopedia of Marine Mammals, 2nd edn. Academic Press, San Diego, California, USA, pp. 207–215.
- Foster, E.A., Franks, D. W., Mazzi, S., Darden, S.K., Balcomb, K.C., et al. (2012) Adaptive prolonged postreproductive life span in killer whales. Science 337, 1313. http://dx.doi.org/10.1126/science.1224198.
- Frohoff, T.G. (2004) Stress in dolphins. In: Bekoff, M. (ed.) Encyclopedia of Animal Behavior. Greenwood Press, Westport, Connecticut, USA, pp. 1158–1164.
- Frohoff, T.G. and Packard, J.M. (1995) Human interactions with free-ranging and captive bottlenose dolphins. *Anthrozoos* 8, 44–53. http://dx.doi.org/10.2752/089279395787156527.
- Geisler, J.H. and Theodor, J.M. (2009) Hippopotamus and whale phylogeny. *Nature* 458, E1. http://dx.doi. org/10.1038/nature07776.
- Geisler, J.H., McGowen, M.R., Yang, G., Gatesy, J. (2011) A supermatrix analysis of genomic, morphological, and paleontological data from crown Cetacea. BMC Evolutionary Biology 11, 112. http://dx.doi.org/10.1186/1471-2148-11-112.
- Gygax, L. (1993) Spatial movement patterns and behavior of two captive bottlenose dolphins (*Tursiops truncatus*): Absence of stereotyped behavior or lack of definition? *Applied Animal Behavior Science* 38, 337–344.
- Hodes, G.E., Kana, V., Menard, C., Merad, M., Russo, S.J. (2015) Neuroimmune mechanisms of depression. *Nature Neuroscience* 18, 1386–1393. http://dx.doi. org/10.1038/nn.4113.

- Hof, P.R. and van der Gucht E. (2007) Structure of the cerebral cortex of the humpback whale, *Megaptera* novaeangliae (Cetacea, Mysticeti, Balaenopteridae). The Anatomical Record 290, 1–31. http://dx.doi. org/10.1002/ar.20407.
- Hof, P.R., Chanis, R., Marino, L. (2005) Cortical complexity in cetacean brains. *The Anatomical Record Part A* 287, 1142–1152.
- Jett, J. and Ventre, J. (2011) Keto and Tilikum express the stress of orca captivity. Available at: https://theorcaproject.wordpress.com/2011/01/20/keto-tilikumexpress-stress-of-orca-captivity (accessed on 15 January 2019).
- Jett, J. and Ventre, J.M. (2012) Orca (Orcinus orca) captivity and vulnerability to mosquito-driven viruses. Journal of Marine Animals and Their Ecology 5, 9–16.
- Jett, J. and Ventre, J.M. (2015) Captive killer whale (Orcinus orca) survival. Marine Mammal Science 31, 1362–1377. http://dx.doi.org/10.1111/mms.12225.
- Jett, J., Visser, I.N., Ventre, J., Waltz, J., Loch, C. (2017) Tooth damage in captive orcas (*Orcinus orca*). Archives of Oral Biology 84, 151–160. http://dx.doi. org/10.1016/j.archoralbio.2017.09.031.
- Johnson, C.M. and Norris, K.S. (1986) Delphinid social organization and social behavior. In: Schusterman, R.J., Thomas, A.J., Wood, F.G. (eds.) Dolphin Cognition and Behavior: A Comparative Approach. Lawrence Erlbaum, Hillsdale, New Jersey, USA, pp. 335–346.
- Khan, S.A. (2014) Tranquilizers, antidepressants, sleep aids and anticonvulsants (toxicity). Available at: www.merckvetmanual.com/mvm/toxicology/toxicities_from_human_drugs/tranquilizers_antidepressants_sleep_aids_and_anticonvulsants_toxicity.html (accessed 21 January 2019).
- Kishida, T., Thewissen, J.G.M., Hayakawa, T., Imai, H., Agata, K. (2015) Aquatic adaptation and the evolution of smell and taste in whales. *Zoological Letters* 1, 9. http://dx.doi.org/10.1186/s40851-014-0002-z.
- Kooyman, G.L. (1989) Diverse Divers: Physiology and Behavior. Springer-Verlag, Berlin, Germany. http:// dx.doi.org/10.1007/978-3-642-83602-2.
- Latham, N.R., Mason, G.J. (2008) Maternal deprivation and the development of stereotypic behavior. *Applied Animal Behaviour Science* 110, 84–108. http://dx.doi.org/10.1016/j.applanim.2007.03.026.
- Laule, G. (1993) Using training to enhance animal care and welfare. Animal Welfare Information Center Newsletter 4, 8–9.
- Lauriano, G., Eisert, R., Panigada, S., Ovsyanikova, E., N, Visser, I.N., et al. (2015) Activity, seasonal site fidelity, and movements of Type-C killer whales between the Ross Sea (Antarctica) and New Zealand. Proceedings of the Convention on the Conservation of Antarctic Marine Living Resources, Hobart, Tasmania, Australia.
- Levin, M. (2018) Marine mammal immunology. In: Gulland, F.M.D., Dierauf, L.A., Whitman, K.L. (eds.)

324 L. Marino

- CRC Handbook of Marine Mammal Medicine. CRC Press, Boca Raton, Florida, USA, pp. 197–218.
- Lipman, S. (2016) Exclusive: Self-mutilation by a young whale at Vancouver Aquarium. Available at: https://www.onegreenplanet.org/animalsandnature/exclusive-self-mutilation-by-a-young-whale-at-vancouver-aquarium (accessed 22 February 2019).
- Lott, R. and Williamson, C. (2017) Cetaceans in captivity.
 In: Butterworth, A. (ed.) Marine Mammal Welfare.
 Springer, Cham, Switzerland, pp. 161–181. http://dx.doi.org/10.1007/978-3-319-46994-2_11.
- Lupien, S.J., McEwen, B.S., Gunnar, M.R., Heim, C. (2009) Effects of stress throughout the lifespan on the brain, behaviour and cognition. *Nature Reviews Neuroscience* 10, 434–445. http://dx.doi.org/10.1038/ nrn2639.
- Lusseau, D. (2007) Evidence for social role in a dolphin social network. *Evolutionary Ecology* 21, 357–366. http://dx.doi.org/10.1007/s10682-006-9105-0.
- Lydersen, C., Martin, A.R., Kovacs, K.M., Gjertz, I. (2001) Summer and autumn movements of white whales (*Delphinapterus leucas*) in Svalbard, Norway. *Marine Ecology Progress Series* 219, 265–274. http://dx.doi.org/10.3354/meps219265.
- Madsen, C. and Herman, L.M. (1980) Social and ecological correlates of cetacean vision and visual appearance. In: Herman, L. (ed.) Cetacean Behavior: Mechanisms and Functions. Wiley Interscience, New York, USA, pp. 101–147.
- Madsen, P.T. and Surlykke A. (2013) Functional convergence in bat and toothed whale biosonar. *Physiology* 28, 276–283. http://dx.doi.org/10.1152/physiol.00008.2013.
- Maier, S F. and Seligman, M.E.P. (2016) Learned helplessness at fifty: Insights from neuroscience. *Psychological Review* 123, 349. http://dx.doi.org/10.1037/rev0000033.
- Marine Connection (2008) Dolphin 'accident' at Dolphin Academy, Curacao. Available at: https://www.youtube.com/watch?v=rjUwL1I1YCc (accessed 16 January 2019).
- Marino, L., McShea, D., Uhen, M.D. (2004a) The origin and evolution of large brains in toothed whales. *The* Anatomical Record 281A, 1247–1255.
- Marino, L., Sherwood, C.C., Tang, C.Y., Delman, B.N., Naidich, T.P., et al. (2004b) Neuroanatomy of the killer whale (*Orcinus orca*) from magnetic resonance imaging. *The Anatomical Record* 281A, 1256–1263.
- Markiewicz, D. (2015) Maris, much-loved beluga whale at Georgia Aquarium, dies. Available at: https://www.ajc.com/news/local/maris-much-loved-beluga-whale-georgia-aquarium-dies/SSLoik1xPS4unDpPjDUcBO (accessed 16 January 2019).
- Markowitz, H. and Eckert, K. (2005) Giving power to animals. In: McMillan, F.D. (ed.) *Mental Health and Well-Being in Animals*. Wiley-Blackwell, Ames, Iowa, USA, pp. 201–209. http://dx.doi.org/10.1002/9780470384947.ch14.
- Mason, G. (2010) Species differences in responses to captivity: Stress, welfare and the comparative method.

- Trends in Ecology and Evolution 25, 713–721. http://dx.doi.org/10.1016/j.tree.2010.08.011.
- Mason, G. J. and Latham, N. R. (2004) Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare* 13, S57–S69.
- Mason, G.J. and Rushen, J. (2008) Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. CAB International, Wallingford, UK.
- Matthews, C. J., Luque, S. P., Petersen, S. D., Andrews, R. D., Ferguson, S.H. (2011) Satellite tracking of a killer whale (*Orcinus orca*) in the eastern Canadian Arctic documents ice avoidance and rapid, long-distance movement into the North Atlantic. *Polar Biology* 34, 1091–1096. http://dx.doi.org/10.1007/s00300-010-0958-x.
- McCowan, B., Marino, L., Vance, E., Walke, L., Reiss, D. (2000) Bubble ring play of bottlenose dolphins: Implications for cognition. *Journal of Comparative Psychology* 114, 98–106. http://dx.doi.org/10.1037/0735-7036.114.1.98.
- McEwen, B.S. (2006) Protective and damaging effects of stress mediators: Central role of the brain. *Dialogues in Clinical Neuroscience* 8, 367.
- McEwen, B.S. (2017) Neurobiological and systemic effects of chronic stress. *Chronic Stress* 1, 1–11. http://dx.doi.org/10.1177/2470547017692328.
- McPhee, M.E. and Carlstead, K. (2010) The importance of maintaining natural behaviors in captive mammals. In: Kleiman, D.G., Thompson, K.V., Baer, C.K. (eds.) Wild Mammals in Captivity: Principles and Techniques for Zoo Management, 2nd edn. University of Chicago Press, Chicago, Illinois, USA, pp. 303–313.
- Montgomery, S.H., Geisler, J.H., McGowen, M.R., Fox, C., Marino, L., et al. (2013) The evolutionary history of cetacean brain and body size. *Evolution* 67, 3339–3353. http://dx.doi.org/10.1111/evo.12197.
- Morgan, K.N. and Tromborg, C.T. (2007) Sources of stress in captivity. Applied Animal Behaviour Science 102, 262–302. http://dx.doi.org/10.1016/j.applanim. 2006.05.032.
- New York Times. (1989) Performing whale dies in collision with another. Available at: https://www.nytimes.com/ 1989/08/23/us/performing-whale-dies-in-collisionwith-another.html (accessed 22 February 2019).
- O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood L, et al. (2018) Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). Public Library of Science One 13, e0194201.
- Pagel, C. D., Scheer, M., Lück, M. (2017) Swim encounters with killer whales (*Orcinus orca*) off Northern Norway: Interactive behaviours directed towards human divers and snorkelers obtained from opportunistic underwater video recordings. *Journal of Ecotourism* 16, 190–200. http://dx.doi.org/10.1080/14724049.2016.1273939.
- Panksepp, J. (2010) Affective neuroscience of the emotional BrainMind: Evolutionary perspectives and

- implications for understanding depression. *Dialogues in Clinical Neuroscience* 12, 533–545.
- Parsons, E.C.M. (2012) Killer whale killers. *Tourism in Marine Environments* 8, 153–160. http://dx.doi.org/10.3727/154427312X13491835451494.
- Peña-Guzmán, D.M. (2017) Can nonhuman animals commit suicide? *Animal Sentience* 20, 1–24.
- Peña-Guzmán, D.M. (2018) Can nondolphins commit suicide? *Animal* Sentience 21, 1–22.
- Pessoa, L. and Hof, P.R. (2015) From Paul Broca's great limbic lobe to the limbic system. *Journal of Comparative Neurology* 523, 2495–2500.
- Pitman, R.L. and Durban, J.W. (2012) Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal Science* 28, 16–36. http://dx.doi.org/10.1111/j.1748-7692. 2010.00453.x.
- Reggente, M.A., Alves, F., Nicolau, C., Freitas, L., Cagnazzi, D., et al. (2016) Nurturant behavior toward dead conspecifics in free-ranging mammals: New records for odontocetes and a general review. *Journal of Mammalogy* 97, 1428–1434. http://dx.doi.org/10.1093/jmammal/gyw089.
- Reiss, D. and Marino, L. (2001) Self-recognition in the bottlenose dolphin: A case of cognitive convergence. Proceedings of the National Academy of Sciences USA 98, 5937–5942. http://dx.doi.org/10.1073/ pnas.101086398.
- Ridgway, S.H. and Brownson, R.H. (1984) Relative brain sizes and cortical surface areas of odontocetes. *Acta Zoologica Fennica* 172, 149–152.
- Romano, T.A., Felten, D.L., Stevens, S.Y., Olschowka, J.A., Quaranta, V., et al. (2002) Immune response, stress, and environment: Implications for cetaceans. In: Pfeiffer, C.J. (ed.) Molecular and Cell Biology of Marine Mammals. Krieger Publishing Co., Inc., Malabar, Florida, USA, pp. 253–279.
- Rose, N.A., Parsons, E.C.M., Farinato, R. (2009) *The Case Against Marine Mammals in Captivity*, 4th edn. The Humane Society of the United States and the World Society for the Protection of Animals, Washington DC, USA.
- Rose, N.A., Hancock Snusz, G., Brown, D.M., Parsons, E.C.M. (2017) Improving captive marine mammal welfare in the United States: Science-based recommendations for improved regulatory requirements for captive marine mammal care. *Journal of International Wildlife Law and Policy* 20, 38–72. http://dx.doi.org/1 0.1080/13880292.2017.1309858.
- Sambrook, T.D. and Buchanan-Smith, H.M. (1997) Control and complexity in novel object enrichment. *Animal Welfare* 6, 207–216.
- Samuels, A. and Gifford, T. (1997) A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science* 13, 70–99. http://dx.doi.org/10.1111/j.1748-7692.1997.tb00613.x.

- Santos, M.C. de O. (1997) Lone sociable bottlenose dolphin in Brazil: Human fatality and management. *Marine Mammal Science* 13, 355–356. http://dx.doi.org/10.1111/j.1748-7692.1997.tb00642.x.
- Scheer, M. (2010) Review of self-initated behaviors of free-ranging cetaceans directed towards human swimmers and waders during open water encounters. *Interaction Studies* 11, 442–466.
- Selye, H. 1976. *The Stress of Life*. McGraw-Hill Book Company, New York, USA.
- Smith J.D., Schull J., Strote J., McGee K., Egnor R., Erb L. (1995) The uncertain response in the bottlenosed dolphin (*Tursiops truncatus*). *Journal of Experimental Psychology: General* 124, 391–408.
- Sørensen, G. and Randrup, A. (1986) Possible protective value of severe psychopathology against lethal effects of an unfavourable milieu. Stress Medicine 2, 103–105.
- Spradlin, T.R., Drevenak, J.K., Terbush, A.D., Nitta, E.T. (1999) Interactions between the public and wild dolphins in the United States: Biological concerns and the Marine Mammal Protection Act. Proceedings of the 13th Biennial Conference on the Biology of Marine Mammals, Wild Dolphin Swim Program Workshop. Wailea, Maui, Hawaii, USA. Available at: https://nmssanctuaries.blob.core.windows.net/sanctuaries-prod/media/archive/dolphinsmart/pdfs/spradlin_1999.pdf (accessed 22 February 2019).
- Stewart, B.S. (2009) Killer whale (Orcinus orca). In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds.) Encyclopedia of Marine Mammals, 2nd edn. Academic Press, San Diego, California, USA, pp. 321–326.
- Stewart, K.L. and Marino, L. (2009) Dolphin-human interaction programs: Policies, problems, and practical alternatives. Available at: http://whalesanctuaryproject.org/content/uploads/Dolphin-Human-Interaction-Programs-Policies-Problems-Alternatives-ASI.pdf (accessed 29 January 2019).
- Sweeney, J.C. (1990) Marine mammal behavioral diagnostics. In: Dierauf, L.A. (ed.) Handbook of Marine Mammal Medicine: Health, Disease and Rehabilitation. CRC Press, Boca Raton, Florida, USA, pp. 53–72.
- Sweeney, J.C. (1988) Specific pathologic behavior in aquatic mammals: Self-inflicted trauma. Soundings: Newsletter of the Intl Marine Animal Trainers Assoc 13, 7.
- Sweeney, J.C. and Samansky, T. (1995) Elements of successful facility design: Marine mammals. In: Gibbons, Jr., E.F., Durrant, B.S., Demarest, J. (eds.) Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. State University of New York Press, Albany, New York, USA, pp. 465–477.
- Thomson, C.A. and Geraci, J.R. (1986) Cortisol, aldosterone, and leucocytes in the stress response of bottlenose dolphins, *Tursiops truncatus*. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 1010–1016. http://dx.doi.org/10.1139/f86-125.

326 L. Marino

- Tooby, J. and Cosmides, L. (1990) The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology* 11, 375–424. http://dx.doi.org/10.1016/0162-3095(90)90017-Z.
- Ugaz Ruiz, C., Sánchez, A., Maldonado, F.G. (2009) Social and individual behavior of a group of bottlenose dolphins (*Tursiops truncatus*) in open and closed facilities. *Veterinaria Mexico* 40, 381–387.
- Ugaz Ruiz, C., Valdez, R.A., Romano, M.C., Galindo, F. (2013) Behavior and salivary cortisol of captive dolphins (*Tursiops truncatus*) kept in open and closed facilities. *Journal of Veterinary Behavior* 8, 285–290. http://dx.doi.org/10.1016/j.jveb.2012.10.006.
- Vail, C.S. (2012) The mixed messages of captivity. Available at: https://uk.whales.org/2012/12/03/the-mixed-messages-of-captivity (accessed 16 January 2019).
- Visser, I.N. (2005) Swimming with Orca: My Life with New Zealand's Killer Whales. Penguin Books, Auckland, New Zealand.
- Visser, I.N. (2012) Report on the physiological and behavioural status of Morgan, the wild-born orca held in captivity at Loro Parque, Tenerife, Spain. Available at: www.freemorgan.org/wp-content/uploads/2012/11/Visser-2012-Report-on-the-Physical-Status-of-Morgan-V1.2.pdf (accessed 29 January 2019).
- Visser I.N. and Lisker, R.B. (2016) Ongoing concerns regarding the SeaWorld orca held at Loro Parque, Tenerife, Spain. Available at: www.freemorgan.org/wp-content/uploads/2016/07/Visser-Lisker-2016-Ongoing-concerns-regarding-Seaworld-orca-held-at-Loro-Parque-V1.3.pdf (accessed 29 January 2019).

- Walters L. (2016) Orca's 'unnatural behaviour' has experts worried. Available at: https://www.stuff.co.nz/ world/europe/80846875/orcas-continuous-unnaturalbehaviour-has-experts-worried (accessed 22 February 2019).
- Waples, K.A. and Gales, N.J. (2002) Evaluating and minimising social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). Zoo Biology 21, 5–26. http://dx.doi.org/10.1002/zoo.10004.
- Wells, R.S. and Scott, M.D. (2009) Common bottlenose dolphin: *Tursiops truncatus*. In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds.) *Encyclopedia of Marine Mammals*, 2nd edn. Academic Press, San Diego, California, USA, pp. 249–255.
- Whitehead, H. and Rendell, L. (2014) The Cultural Lives of Whales and Dolphins. University of Chicago Press, Chicago, Illinois, USA. http://dx.doi.org/10.7208/chicago/ 9780226187426.001.0001.
- Wise, H.T. (2016) All is whale that ends whale? The deficiencies in National protection for orca whales in captivity. Akron Law Review 49, 926–954.
- Worthy, G.A., Worthy, T.A., Yochem, P.K., Dold, C. (2013) Basal metabolism of an adult male killer whale (*Orcinus orca*). *Marine Mammal Science* 30, 1229–1237.
- Wright, A., Scandeng, M., Stec, D., Dubowitz, R., Ridgway, S.H., et al. (2016) Neuroanatomy of the killer whale (*Orcinus orca*): A magnetic resonance imaging investigation of structure with insights on function and evolution. *Brain Structure and Function* 222, 417–436.

23 Assessing Affective States in Animals

MICHAEL MENDL AND ELIZABETH S. PAUL

Bristol Veterinary School, University of Bristol, Bristol, UK

23.1 Introduction: Mental Health, Well-being and Emotional States

What is it to be mentally healthy and well? We all know that many aspects of our lives can impinge on our mental health including the ups and downs of our daily existence, how well or otherwise we are getting on with friends and family, how much control we have over our choices, and how well we function, both cognitively and socially. In this book, a similar range of influences on nonhuman animal (hereafter animal) mental health and wellbeing are identified; the extent of control that an animal has, the quality of its social relationships, the opportunities it has to express a wide behavioral repertoire and to choose how to allocate its time, and the degree to which it is prey to apparent disorders of cognitive function such as compulsions, hyperaggression, and forgetfulness.

One potential consequence of this perspective is that in order to comprehensively assess mental health and well-being, we need to monitor the status of each individual with respect to all these factors. How supportive are their social relationships? Do they show symptoms of cognitive and behavioral disorders? Do they have outlets that allow expression of different needs and desires? However, a different view, also articulated in this book, is that what ultimately really matters to the animal is how it feels – whether it is in a positive or negative emotional or affective state. Thus, a hyperaggressive sow in a group who is able to access resources freely due to her unusually despotic style may actually be in a relatively positive affective state. Likewise, a stereotyping animal may be in a more positive state than a nonstereotyper in the same captive environment (Mason and Latham, 2004).

A similar discussion is evident between psychological theorists studying human quality of life.

Norman Bradburn's (1969) seminal research viewed the balance between positive and negative affect as the critical determinant of how well a person felt. However, more recent theories propose that a range of other factors including 'accomplishment', 'positive relationships', 'engagement', 'environmental mastery', 'life satisfaction', and 'meaning and purpose' are also important determinants of well-being (Diener et al., 1999; Ryff and Singer, 2008; Seligman, 2011; Franks and Higgins, 2012). One possibility that unites both views is that it is the impact these factors have on an individual's emotional state that is key (Fig. 23.1). Affective state may be thought of as a 'common currency' (McNamara and Houston, 1986; Cabanac, 1992) which integrates the influence of a range of experiences and provides the best indication of an individual's current well-being. A semantic resolution might consider 'wellbeing' as principally determined by affective state, while 'mental health' is also affected by cognitive (dys)function including, for example, cognitive or behavioral disorders that are not necessarily linked to well-being in a predictable way.

The purpose of this brief discussion is to illustrate that assessment of animal mental health and well-being is conceptually as well as technically challenging, but also that the affective state of the animal will be one of its key determinants. Accurate assessment of emotional or affective state therefore provides a foundation for scientific investigations into the mental health and well-being of animals and is the focus of the rest of this chapter. We begin by discussing what emotion actually is and the inherent challenges of studying a phenomenon that has its roots in human conscious experience. We then briefly describe two ways of conceptualizing emotion in humans and the pros and cons of translating these to animals. At this point, we clarify the



Fig. 23.1. Putative contributing factors (outer boxes) that may influence overall well-being and mental health by altering affective state. See text for details

animal emotion terminology that we will employ in the rest of the chapter, and then discuss ways in which we can infer the occurrence of different affective states in animals, including the use of theoretical and operational definitions that can provide a framework for studying animal affect. In the second half of the chapter, we go on to summarize a variety of methods that have been used to assess animal affect, focusing in particular on new developments in the use of expressive behavior and cognitive markers.

23.2 What is Animal Emotion: Consciousness and Concepts

23.2.1 Emotions as conscious subjective experiences: a potential barrier to their study in animals?

Our concept of animal emotion inevitably stems from our own experience of emotions - feelings that we label with terms such as 'happy', 'serene', 'anxious', 'embarrassed', 'guilty', 'angry', and so on. Emotions are therefore a category of subjective mental experience, the key defining characteristic of which is that we experience them as positive or negative, pleasant or unpleasant, rewarding or punishing - they have 'valence'. Transferring this concept to other species is of course tricky and open to the accusation of uncritical anthropomorphism. We cannot know for certain what private mental states, including emotions, another individual is experiencing, or even whether they are capable of having such subjective experiences (see 'Problem of other minds' [Farah, 2008]). When considering other people, language helps us to tackle this obstacle (although people can of course lie), but this option is not available for nonhuman animals.

So, can we proceed beyond this potential impasse to study animal emotions? One approach is to take

an alternative philosophical stance, and this has been followed by Wemelsfelder (1997), who argues that animal subjectivity can be revealed to an observer through the expressive quality of the animal's behavior and hence can be studied directly. Another more commonly agreed upon approach is to accept that mental experiences are not directly accessible in other species, but that evidence from behavioral, cognitive, and neurophysiological studies is sufficient to argue that at least some species are highly likely to be consciously aware (Griffin and Speck, 2004). The 2012 Cambridge Declaration on Consciousness by consciousness researchers and neuroscientists (Low, 2012) is a good example in which the signatories argue, in contrast to others (Macphail, 1998; Key, 2016), that possession of a neocortex is unlikely to be necessary for conscious experience, and that all mammals and birds, and some other species such as octopuses, possess the neural substrates of consciousness, show the capacity for intentional behaviors, and hence are capable of conscious experience.

If we accept that certain taxa and species have the capacity for conscious experience – and there are differing views as to the range of species that should be included (Panksepp, 1998; Rolls, 2005; Barron and Klein, 2016; Key, 2016) – we next need to develop measures that can give us an insight into what emotional state an animal may be experiencing at any one time (the *contents* of its putative conscious experience). This requires us to become more specific about what we mean by emotion.

23.2.2 Discrete emotions and the dimensional view of emotion

Human psychologists have adopted two main approaches to conceptualizing emotion. The *discrete emotions* approach reflects our usage of 'emotion

words' such as 'sad', 'happy', 'angry', and so on, by arguing that these words describe the subjective experience of distinct emotional states that are instantiated in the activity of specific neural circuits in the brain. Advocates argue that there are a limited number of such discrete emotion systems and that these form the building blocks for all emotional experience. Although researchers vary in their beliefs about how many and which basic emotional states exist (Ekman, 1992; Plutchik, 2001; Izard, 2007), they concur that each state is grounded in the functioning of a modular neurobehavioral system that is activated by particular stimuli and generates behavioral changes such as specific facial expressions, and a distinctive profile of physiological responses.

An alternative dimensional view of human emotion stems from studies that use factor analysis to analyze the clustering in time of reported emotional experiences, or the categorization of discrete emotion words. Most studies detect two or three underlying dimensions that account for much of the variation in the data. Valence (positivity or negativity of the experience) is one of these dimensions and, as mentioned above, can be thought of as the defining characteristic of subjective emotions (Cacioppo and Berntson, 1999; Watson et al., 1999; Carver, 2001; Russell, 2003). Another commonly detected dimension is arousal, the degree of activation experienced. Both these dimensions characterize the prominent core affect model of emotion (Russell, 2003; Fig. 23.2).

Both models of human emotion have their supporters. They can be combined by, for example,

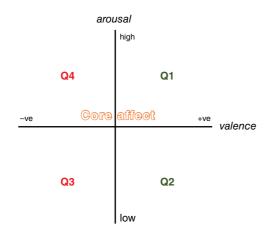


Fig. 23.2. The core affect dimensional model of emotion (Russell, 2003). See text for details.

visualizing discrete emotions as being located in dimensional space. For example, 'sadness' would lie in the low arousal/negative valence quadrant of the core affect model (Q3 in Fig. 23.2). However, ongoing arguments contest the primacy of each view. For example, do core affect processes combine with other information about current context and past experience to construct the experience of an emotion that falls in the 'sad' category, or is 'sadness' a basic discrete emotion that contributes to a 'higher level' abstraction of overall valence and arousal? Whether one set of processes gives rise to the other, or *vice* versa, or both influence each other, remain the subject of vigorous debate (Izard, 2007; Panksepp, 2007; Adolphs, 2017; Barrett, 2017). For example, reliable co-occurrence of particular reported discrete emotions and specific behavioral, physiological, and neural changes is found in some reviews of the literature (Kreibig, 2010; Vytal and Hamann, 2010; Kragel and Labar, 2016), but others suggest that such changes map more closely to dimensional concepts (Mauss and Robinson, 2009; Lindquist et al., 2012).

23.2.3 Translating discrete and dimensional concepts to animals

In terms of translating these ideas to animals, our view is that the dimensional core affect model has some advantages. One reason is that the discrete emotions approach relies on the use of human emotion words. This is problematic because these words are not universal across human cultures (e.g., age-otori - the Japanese feeling of having had a bad haircut), hence questioning the wisdom and validity of generalizing them across species. While it is plausible that, for example, fear-like states are widespread across the animal kingdom, as species' sensory, perceptual, and cognitive abilities become increasingly different from ours, and their evolved behavioral repertoires also diverge, the chances that they will share other discrete emotions are likely to diminish. Second, human emotion words inevitably imply felt subjective states whereas, as we have discussed, we cannot be sure that such states are consciously experienced in other species. Consequently, in a comparative context, the use of discrete emotion words like 'happiness', 'sadness', and especially terms such as 'jealousy' or 'guilt', becomes increasingly questionable as we move away from humans along the phylogenetic tree.

The dimensional core affect model avoids some of these problems by identifying four simple states

that are not founded on human emotion words (Q1-4 in Fig. 23.2), and which can be readily translated to other species. Although this might seem too simple a perspective from which to summarize the emotional lives of at least some other species, the four states can be viewed as the source from which a potentially wide range of affective states can be constructed in combination with other contextual information (Barrett, 2017). Such states will be influenced by species' sensory, perceptual, and cognitive capacities and hence species-unique and not always easily captured by human emotion words (Bliss-Moreau, 2017). Furthermore, the core affect model provides a framework for conceptualizing how different types of emotional states are related to each other (e.g., joy and contentment may primarily differ in arousal), while the discrete emotions approach treats individual emotional states separately and in a piecemeal fashion. Finally, as we will describe below, the core affect approach also fits closely with a simple operational definition of animal emotion that avoids the complicating issue of conscious experience and provides a behavioral grounding that makes studying animal affect empirically tractable. Although we personally favor the dimensional perspective, we will consider both views in the rest of this chapter.

23.3 Animal Emotion Terminology

Given the above discussion, we propose the following use of terms. We will use 'animal emotion' and 'animal affect' as umbrella terms for the general area of study. Because 'emotion' and emotion words ('happy', 'sad', 'angry', etc.) are often assumed to imply conscious feelings, we add the suffix '-like' when using these to indicate that we cannot be certain of whether they are subjectively experienced in other species (cf. 'episodic-like memory' in animals [Clayton and Dickinson, 1998]). We also restrict their use to short-term states generated by specific stimuli or events, as is often the case in human psychology research (Russell, 2003; Scherer, 2005). Similarly, we add the '-like' suffix when we use the word 'mood', which we reserve for longer-term states that are 'free-floating' and not caused by a specific object or event. We use 'affect' or 'affective state' as overarching terms for both short- and long-term valanced states. These therefore cover emotions and moods, but also sensations (e.g., pain) that have a valanced component. Although affective states are usually considered to be consciously experienced in

humans, the technical as opposed to colloquial provenance of the term 'affect' means that it is less likely to be assumed to imply conscious experience in animals. For ease of use, we therefore employ this term without a '-like' suffix, but also without any implication that it denotes a conscious experience. Finally, we use 'feelings' only when referring specifically to the felt component of an affective state.

23.4 From Animal Emotion Concepts to Animal Emotion Assessment

Having laid the groundwork, we now consider how we might measure the concepts that we have discussed. In doing so, we follow the componential view of emotion espoused in human psychology that affective states comprise subjective, behavioral, physiological, and neural 'components' (Paul et al., 2005; Scherer, 2005). While we cannot directly assess the subjective component, we can objectively measure the others. The challenge is to establish which changes in these components are reliable indicators of which discrete or dimensional affective states. This requires an inferential or theoretical framework and we briefly identify three interrelated approaches: translating human affective responses to animals, inferring affect from behavior (responses) or situations (events), and using prescriptive theories or definitions (Paul and Mendl, 2018). A similar schema is discussed and developed in more detail by Mason and Mendl (2019, manuscript in preparation). Irrespective of the details of the schema employed, the main point here is that a rigorous science of animal emotion requires clearly stated theory and/or rationale for exactly how emotion-like states in animals are to be inferred.

A 'translation from humans' perspective involves identifying the behavioral, physiological, and neural indicators of specific reported emotional states in humans and then monitoring these biological markers in animals under the assumption that they are associated with the same affective states. The advantage of this approach is that people provide our best model of how objectively measurable indicators co-vary with subjectively experienced feelings. The disadvantages, as discussed earlier, include that there is still debate as to whether there actually are repeatable and reliable indicator profiles for specific discrete emotions or emotional dimensions in humans, and that other species may not share the same discrete emotion-like states with humans.

An alternative approach is to infer affective states from the animal's behavior or the situation that it is in (Paul et al., 2005). An example of 'behavioral inference' is the common assumption that playing animals are in a 'happy', 'joyful', or otherwise positive affective state. However, the links between play and positive affect are not always straightforward or well understood (Held and Spinka, 2011; Ahloy-Dallaire et al., 2018). An example of 'situation inference' is the notion that exposure to a brightly lit open field or the unprotected arms of an elevated plus maze induces 'fearlike' or 'anxiety-like' states in burrow-dwelling nocturnal rodents. This can be reasonably supported by arguments based on knowledge of the biology of these species, but our anthropocentric perspective makes us prone to errors. For example, we may be unaware that a certain olfactory stimulus generates a 'pleasure-like' state in our animals and, consequently, misinterpret or misattribute behavior in situations where the odor is present. Overall, the utility and validity of these, often intuitive, inferences are likely to depend on how well we know the biology and behavioral ecology of our animals, and on the quality of our argument for why a particular set of circumstances is likely to lead to a particular emotion-like state. Increasing phylogenetic distance between ourselves and our study species is likely to diminish the accuracy of our inferences.

Proposing a prescriptive theoretical framework or operational definition can provide an explicit rationale for our behavioral or situation inferences about animal affect (Paul and Mendl, 2018). One example is Wemelsfelder's (1997) argument that animal subjectivity, including affective states, can be directly observed in the expressive behavior of animals. This provides a basis for behavioral inference grounded in a particular philosophical theory. Another example is the 'cognitive bias' approach that translates the relationship observed between human affective valence and cognitive function to animals and combines it with arguments from evolutionary theory to generate a rationale for inferring affective valence from decision-making behavior (Mendl et al., 2009, 2010b; see later). A third example translates human appraisal theory ideas which posit that particular discrete emotions result when a person appraises a stimulus or event in a specific way. For example, fear arises if a situation is appraised as sudden and of low predictability, pleasantness, or familiarity (Scherer, 2001). Desiré et al. (2002) proposed that a fear-like state would therefore occur in animals exposed to sudden, unpredictable, unpleasant, and unfamiliar events, with other discrete emotion-like states occurring in response to other event profiles based on appraisal theory (Veissier et al., 2009). If one accepts translation of the links between stimulus appraisal profiles and human discrete emotions to animals, this provides a theoretical grounding for situation inference of discrete emotion-like states.

Finally, reinforcement theory concepts of emotion (Millenson, 1967; Gray, 1987; Rolls, 2005) offer an operational definition of emotion which has been articulated by Rolls (2005, p. 72): 'emotions are states elicited by rewards and punishers', where rewards are things that animals will work to acquire and punishers are things that they will work to avoid. This prescriptive definition allows researchers to infer that an animal is in a positive state if exposed to situations that it will work to acquire, and in a negative state if exposed to situations that it will work to avoid. It thus provides a theoretical basis for situation inference of affective valence which sidesteps the question of whether the identified affective states are consciously experienced and hence has clear value in the study of animal emotion. Strengths and limitations of this definition are discussed by Paul and Mendl (2018), alongside prescriptive definitions of animal emotion in terms of 'emotion primitives' or emotional building blocks (Anderson and Adolphs, 2014), and states that mediate goal-directed learning (Dickinson and Balleine, 2009).

We believe that clear and logical arguments for how we infer discrete emotion-like states or affective valence in animals are essential for development of a rigorous science of animal emotion. This may best be achieved by combining theoretical frameworks with translation of findings from human studies to generate operational definitions and/or a clear rationale for why particular behaviors or situations indicate particular affective states.

23.5 Assessing Animal Affect: New Developments in the Use of Expressive Behavior and Cognitive Markers

Scientists in a range of disciplines including neuroscience, psychopharmacology, drug development, and animal welfare science have been using a variety of indicators to assess animal affect for many decades. Prominent among these are measures of

stress physiology (Mormede et al., 2007; von Borell et al., 2007; Palme, 2012), reflecting the long-standing notion that bodily physiological changes are intimately involved in human emotional experience (James, 1884; Critchley et al., 2004). Behavior in standardized testing paradigms such as the open field, elevated plus maze, startle, novel object, sucrose consumption, tail-suspension, and forced-swim tests (Pellow et al., 1985; Ramos and Mormede, 1997; Cryan and Mombereau, 2004; Forkman et al., 2007), and neural markers of affective processes involved in, for example, fear-conditioning, and responses to reward (LeDoux, 1996; Panksepp, 1998; Rolls, 2005) have also been used.

Because there are many excellent reviews of these 'traditional' measures, including those cited above, we focus on approaches that have been developed more recently. These have emerged partly because of limitations of existing indicators, including that physiological stress responses are better indicators of arousal than affective valence (Paul et al., 2005; Buwalda et al., 2012), behavioral tests developed for rodents often have limited relevance in other species due to differences in species' behavioral biology (Paul et al., 2005), and the invasive techniques needed to tap the undoubted potential of neural markers are often not appropriate in animal emotion studies. A number of the new measures considered here have been conceived by animal welfare scientists with a specific interest in animal well-being, including the neglected area of positive affect, and hence are particularly relevant for this book. We identify two main categories - expressive behavior and cognitive markers of affective valence – and briefly consider the rationale underpinning these measures and their pros and cons to illustrate the exciting work that is going on in this field.

23.5.1 Expressive behavior

In his book *The Expression of the Emotions in Man and Animals*, Charles Darwin (1872) explored the idea that discrete emotion-like states are expressed behaviorally through postures, vocalizations, and movements. His 'principle of serviceable habits' posited that expressions reflect adaptive movements associated with the emotional state; for example, opening eyes wide to gather more information when fearful, or closing the nostrils to avoid aversive stimuli in disgust (Susskind *et al.*, 2008). If discrete emotions have particular adaptive functions that can be facilitated by behavioral

expression, then links between affect and expression may occur across species.

In humans, the psychologist Paul Ekman (1992) argued that there were specific human facial expressions reflecting discrete emotions such as happiness, sadness, fear, disgust, anger, and surprise, and that these were conserved across countries and cultures. In animals, there has been increasing interest in the utility of expressive behavior as a marker of affective state. Here we briefly consider facial expressions, vocalizations, and whole-body expressive behavior.

Facial expressions

Facial expressions have been studied in nonhuman primates (hereafter primates) for many years, often using a 'situation inference' rationale. In seminal studies, van Hoof (1976) observed that the primate bared teeth 'grin face' often occurred when animals were under threat and appeared to communicate a submissive state. The open-mouthed 'play face', on the other hand, was expressed during bouts of play fighting and hence might function to communicate nonserious intent. van Hoof argued that human smiling and laughter evolved from these expressions, raising the possibility that the ancestral displays might also be linked to emotional experience. Objective methods for recording and categorizing primate expressions, based on Ekman et al.'s (2002) human facial action coding system (FACS), have allowed systematic description of the precise shifts in facial musculature that occur in particular contexts, providing solid groundwork for further studies of the emotional, communicative, and functional significance of different expressions (Parr et al., 2007; Waller et al., 2012; Caeiro et al., 2013). For example, a chimpanzee FACS was used to demonstrate that the same facial movements occur during both primate play faces and human laughter (Parr et al., 2007), just as van Hoof argued and supporting a 'translation from humans' argument.

Further research has investigated whether these expressions may be linked to emotional states. Parr (2001) demonstrated that chimpanzees were able to match the positivity or negativity of a scenario (e.g., image of hypodermic needle or favorite food) to images of facial expressions assumed to share the same emotional valence (e.g., bared teeth 'grin face' or open mouth 'play face'). Such findings support the idea that primate facial expressions may be useful indicators of affective valence, although

Waller et al. (2017) caution against assuming that primate facial expressions have evolved solely to reflect current emotion-like states which can be 'read' by others.

The use of facial expressions as indicators of affective states now extends to nonprimate species. A particularly active area of research has focused on assessing facial expressions as indicators of pain, including in mice (Langford et al., 2010), rats (Sotocinal et al., 2011), rabbits (Keating et al., 2012), horses (Dalla Costa et al., 2018), cattle (Gleerup et al., 2015), and sheep (McLennan et al., 2016). Most of the resulting 'grimace scales' are based on a 'situation inference' rationale linking facial changes to, for example, naturally occurring conditions assumed to be painful, postoperative recovery, and the presence or absence of analgesia. Some of the observed facial changes (e.g., orbital tightening) occur in putatively painful situations in several species including humans, suggesting that they may be conserved across mammalian taxa.

Facial changes in other situations also show similarities across species. For example, Berridge and Robinson (2003) argued that expressions of gustatory 'liking' (e.g., tongue protrusion, lip-licking) and disgust (e.g., mouth gaping) are conserved across humans, primates, and rodents. Similarly, orbital widening appears to occur in threatening or otherwise aversive situations in species including humans (Susskind et al., 2008), sheep (Reefmann et al., 2009), and cattle (Sandem et al., 2006), and open mouth 'play faces' are observed in dogs (Palagi and Scopa, 2017) and other carnivores (Poole, 1978) as well as primates and humans. Crossspecies similarity of expressions suggests that they may have adaptive value, for example in detecting danger (Susskind et al., 2008), and this allows theoretical arguments to be built for why particular expressions should be associated with particular affective states.

Facial expressions thus hold considerable promise as indicators of animal affect. Many questions remain to be resolved including whether specific expressions map to particular discrete emotion-like states and/or can be used as markers of affective valence, whether they reliably co-occur with such states, are sometimes not expressed, are expressed in other contexts in the absence of such states, whether they reflect longer-term as well as short-term affect, and whether they can tell us anything about emotional feelings in other species. In terms of this last question, Langford *et al.* (2010) showed

that mice with damage to the rostral anterior insula, an area of the brain implicated in human conscious experience of the affective unpleasantness of pain, showed attenuated grimace expressions but continued to display other behaviors such as abdominal constriction that also co-occur with assumed pain states. One speculative interpretation of these findings is that facial expressions are more than just reflex behavioral responses to nociceptive stimulation, and instead reflect an affective and even conscious pain state.

Vocalizations

'Situation inference' approaches have been used to investigate whether vocalizations reflect animal affective states. For example, rats emit characteristic 22 kHz calls in aversive contexts such as social defeat and exposure to noxious stimuli, while they produce 50 kHz calls in response to rewarding stimuli including social play, sex, and manual 'tickling' by a human for which individual-housed animals in particular will learn to work (Panksepp and Burgdorf, 2000). Clear avoidance of and preference for these contexts accords with the operational definition of affective valence described earlier and hence provides a theoretical basis for these inferences from situation. It is therefore plausible that these ultrasonic vocalizations are reliable indicators of negatively and positively valanced affect, respectively, although there appear to be some exceptions, for example the production of 50 kHz calls during aggressive interactions.

The notion that vocalizations reflect affective state is also supported by studies of audible calls in a variety of mammalian species. In a review of research in which affect was principally inferred from situation, Briefer (2012) concluded that vocal features such as elevated call rate, fundamental frequency range, and peak frequency were reliable cross-species indicators of high affective arousal. However, due to a relative lack of study, there was less evidence for any conserved vocal markers of affective valence. Recent studies of pigs have detected a tendency for animals exposed to aversive situations such as castration and isolation to emit higher frequency calls (Weary et al., 1997; Puppe et al., 2005), particularly calls that are modulated (Tallet et al., 2013), than pigs in more positive situations. However, there may be a nonlinear link between affective valence and call characteristics in this species, with high frequency vocalizations

occurring in both strongly positive and negative states and lower frequency calls in less intense states (Tallet *et al.*, 2013).

Further research is required to determine whether there are universal vocal markers of affective valence in mammalian species, or whether calls are more context, and perhaps emotion, specific as suggested by Dupjan *et al.* (2008), who showed that pig call structure changed in response to the same aversive stimulus depending on whether it was anticipated or unexpected. The complexity and flexibility of vocal expressions, coupled with between-species differences in vocal tract morphology, make it challenging to establish simple rules for the relationship between affect and calls. Nevertheless, vocalizations remain a very promising topic for research into behavioral expressions of animal affect (Briefer, 2012).

Qualitative behavioural assessment (QBA)

Wemelsfelder (1997), along with her colleagues, pioneered the development of a method (QBA) for assessing whole-body expressive behavior in animals. Human observers watch the animal and either rate it against specific affective descriptors such as 'happy', 'calm', 'bored', 'fearful', and 'frustrated' on a visual analog scale (Camerlink et al., 2016), or generate their own terms to describe the animal's behavior (Wemelsfelder et al., 2001). Analysis of the resulting ratings often generates factor dimensions or consensus axes that show similarities to core affect valence and arousal dimensions (Camerlink et al., 2016; Minero et al., 2016). Numerous studies on a range of mammalian species including pigs, sheep, cows, horses, goats, dogs, and elephants have indicated good interobserver agreement in ratings of specific affective descriptors, even when observers have different backgrounds (Wemelsfelder and Mullen, 2014; though see Bokkers et al., 2012).

Evidence from studies relying on 'situation inference' and investigating links between QBA and other affect indicators supports the notion that QBA can pick up on behavioral changes that reflect affective states. For example, Hintze *et al.* (2017) adopted a 'situation inference' rationale using grooming to induce an assumed positive state in horses, and a waved plastic bag to induce an assumed negative state. They found higher 'calm' and 'relaxed' observer ratings in the former context and higher 'stressed' and 'nervous' ratings in the

latter. Similarly, observers rated pigs that had been given an anxiolytic drug to be higher on an emergent dimension of 'curiosity' and 'confidence' than control animals (Rutherford *et al.*, 2012).

QBA has been adopted by welfare assurance scheme protocols (e.g., EU Welfare Quality®) as a practical indicator of animal affect. It remains to be seen whether this innovative approach can be extended to taxa whose expressive behavior humans may find more difficult to 'read' (e.g., reptiles, fish, crustacea).

Conclusions

The study of expressive behaviors such as those discussed above and others including inactivity (Fureix and Meagher, 2015) and play (Held and Spinka, 2011) represents a growing area of animal affect research that has already yielded new markers of affective state. These are particularly valuable because they occur spontaneously and hence do not require specific testing situations to be imposed, can be recorded noninvasively, and offer opportunities for automated monitoring, which are already being developed (Schön *et al.*, 2004; Sotocinal *et al.*, 2011; Dalla Costa *et al.*, 2018; Tuttle *et al.*, 2018).

23.5.2 Cognitive markers of affective valence

One disadvantage of expressive behaviors is that many are likely to be species specific, making the search for generalities challenging and the translation of findings across species difficult. Cognitive markers are a new category of animal affect indicator that stem from empirical and theoretical links between affective states and objectively measurable cognitive functions such as decision making, anticipation, and attention that may hold across species and even across diverse taxa. Here we briefly consider anticipatory behavior, lateralized information processing, and cognitive biases.

Anticipatory behavior

A 'cognitive' marker of affective valence based on a theoretical rationale has been proposed by Spruijt *et al.* (2001). The approach draws on ideas about the neuroscience of reward (Berridge and Robinson, 2003; Cabib and Puglisi-Allegra, 2012) and posits that relatively mild or short-term negative states can elevate an animal's reward sensitivity. Spruijt

et al. (2001) hypothesized that this increases an animal's chances of reward acquisition and 'rebalancing' of state toward 'neutral' or positive, and can be detected by measuring 'anticipatory behavior' expressed during presentation of a Pavlovian cue that signals arrival of reward after a short time delay (e.g., 30 seconds). Animals in a short-term negative state are predicted to show enhanced 'anticipatory behavior' while the cue is present. 'Anticipatory behavior' is determined empirically and is quantified as an increase in activity and transitions between behaviors in rodents, horses, and chickens (van den Berg et al., 1999; Peters et al., 2012; Moe et al., 2013), but a decrease in these transitions in cats (van den Bos et al., 2003). Several studies indicate that induction of putatively negative short-term states do indeed appear to result in increased anticipatory behavior (van der Harst et al., 2003; van der Harst and Spruijt, 2007; Makowska and Weary, 2016).

However, in longer-term negative states, there is evidence from some rodent studies (van den Berg et al., 1999; von Frijtag et al., 2000) that sensitivity to, and valuation of, reward decreases (cf. anhedonia) and hence anticipatory behavior in response to a Pavlovian cue actually reduces (van der Harst and Spruijt, 2007). This biphasic relationship between negative affect and anticipatory behavior means that using the approach as a measure of affective valence is best done when there is knowledge of the time course of the subject's experiences. In addition, a reliable measure of anticipatory behavior needs to be determined for each species. Given this information, anticipatory behavior can be a useful indicator of affective valence.

Understanding the role of anticipation in affect may also enable us to generate positive affective states or protect against negative ones. It has been proposed that signaling the arrival of reward activates the mesolimbic dopaminergic 'reward system' and that the consequent release of dopamine during the reward anticipation phase can act to induce a relatively positive affective state and to counteract depression-like states (van der Harst and Spruijt, 2007). For example, announcing food arrival or transfer to an enriched cage prevented the onset of depression-like anhedonic symptoms in rats subjected to social defeat, and appeared to be more effective than presenting the reward without announcement (van der Harst et al., 2005). In a study of pigs, cueing the arrival of enrichment was found to increase play in newly weaned pigs, and to decrease stress-related post-weaning behavior (Dudink et al., 2006).

Lateralization

Empirical findings from human studies have generated a variety of hypotheses about potentially different functions of the left and right hemispheres of the brain, including emotional processes. One such hypothesis is that the right hemisphere plays a dominant role in processing negatively valanced, novel, or threatening events, while the left hemisphere is dominant in processing more positive events ('emotional valence lateralization') (Davidson and Irwin, 1999; Leliveld *et al.*, 2013).

Following a 'translation from humans' rationale, these ideas have been investigated in animals (Rogers, 2010; Leliveld et al., 2013). While direct recording of brain activity (e.g., using EEG or MRI) would be the gold standard measure of hemispheric functional lateralization, this is impractical in most contexts and instead researchers use proxy measures such as whether the animal turns to the left or right when inspecting a rewarding or aversive stimulus. Because signals from the left visual and auditory fields project contralaterally to the right hemisphere and vice versa, the prediction is that punishing events will be inspected and detected more readily in the left sensory field, and rewarding stimuli in the right sensory field. The opposite prediction is made for olfactory stimuli because neurons in the right and left nostrils project ipsilaterally to the right and left hemisphere, respectively.

Leliveld et al. (2013) reviewed evidence from studies that inferred affective valence from contexts that involved threat ('fear-like'), aggression (negative), or food, sex, and positive social interactions (positive). The work encompassed a range of taxa, including mammals, birds, reptiles, and fish, and used proxy measures of laterality. Support for the emotional valence lateralization hypothesis was found in 'fear-like', aggression, and food contexts. For example, lizards preferentially used their left eye when inspecting predators (Martin et al., 2010), dogs showed right-hemisphere bias by favoring use of the left visual field when faced with novel or threatening stimuli (Siniscalchi et al., 2010), and black winged stilts preferentially used their right eye to inspect food (Ventolini et al., 2005). However, there were exceptions to these findings and no clear lateralization was observed in the sex and positive social interaction contexts.

As well as reflecting the affective impact of the current situation, lateralized brain activity or behavior has also been suggested to indicate an individual's background affective state. For example, lower left relative to right frontal activity is characteristic of depressed human patients (Bruder et al., 2017). In animals, there is some evidence for similar associations. For example, right-handed marmosets, suggesting left-hemisphere dominance, were bolder in their response to novel food and showed shorter 'fear-like' freeze responses to a predator call (Braccini and Caine, 2009), perhaps indicating a more positive background affective state. Likewise, pigs showing consistent right biases in the use of their snouts and how their tails curl were bolder and more exploratory (Goursot et al., 2018). However, links between putative background affective state and laterality are not always observed (Kappel et al., 2017).

Measures of lateralization as markers of affective valence have advantages that include not usually requiring any training of the animal and hence being potentially quick to assess. They can also be used in a range of vertebrate taxa, and potentially in any species with bilateral symmetry of brain structures. However, there is still uncertainty in both the human and animal literature as to the strength of the relationship between affective valence and lateralization, as evidenced by the range of hypotheses about the functions of brain asymmetry (Brancucci et al., 2009) and the increasing focus on functional networks of activity within the brain that involve communication between hemispheres and hence may not be inherently predisposed to lateralization (Shanahan, 2012).

Cognitive bias

The rationale for the most well-used cognitive bias method for assessing animal affective valence – 'judgment bias' – is based on both 'translation from humans' and theoretical arguments. The former includes findings that people in negative states make more negative judgments ('pessimistic') about ambiguous events and situations than happier people (Mathews and MacLeod, 1994; Mineka *et al.*, 1998; Paul *et al.*, 2005). The latter include arguments that, following the reinforcement theory definition of animal affect described earlier, an animal's affective valence reflects its experience of past rewarding or punishing events. Affective valence may also, therefore, act as a Bayesian prior

for the likelihood of these events occurring in future; it makes adaptive sense for individuals who have experienced a preponderance of aversive events and hence are in a more negative state to also predict that such events are more likely to occur in future ambiguous situations, and hence to make negative judgments under ambiguity (Mendl *et al.*, 2010b; Nettle and Bateson, 2012).

Over 100 studies have been published using the judgment bias assay initially developed for rats by Harding et al. (2004; Fig. 23.3). Because the theoretical basis of the approach generates predictions that are expected to hold across taxa, studies have been performed in a wide range of species including mammals (e.g., rats, mice, sheep, dogs, pigs, horses, cattle, monkeys, humans), birds (e.g., starlings, chickens), and even insects (e.g., bumblebees, honeybees) - see reviews by Mendl et al. (2009), Gygax (2014), Baciadonna and McElligott (2015), Bethell (2015), and Roelofs et al. (2016). The majority of studies support the hypothesis that induced affective states are associated with the expected judgment bias, although some studies have null or even opposite results. Our ongoing meta-analyses are identifying this heterogeneity in findings, and seeking to evaluate the influence of different moderators on results.

There are also theoretical reasons to believe that affect can exert its influence on decision making in a number of ways. For example, affective states may not just alter estimates of the likelihood of positive and negative decision outcomes, but also their value, and these two factors will interact to determine a final decision. Computational approaches combined with sophisticated task designs can be used disentangle these influences in human studies (Iigaya et al., 2016) and we are now applying these methods to animal studies, too. From a methodological perspective, it is plausible that in some studies affect manipulations have induced different states than those that the researchers intended, and that this may explain unexpected results. For example, pre-test withdrawal of an acute manipulation designed to induce a negative affective state might instead result in the animal being in a relatively positive 'relief-like' state during the judgment bias test (Doyle et al., 2010; see also Burman et al., 2011). This type of problem is relevant to studies of any affect indicators that use pretest acute manipulations to induce affective states.

Judgment bias tests are promising new indicators of affective valence with a theoretical underpinning

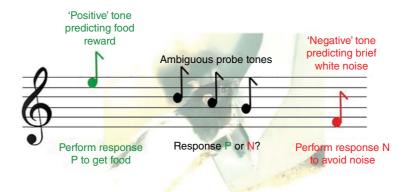


Fig. 23.3. Schematic of the judgment bias assay. In this variant, animals are trained to perform response P when they hear a positive tone to get a reward (food pellet), and response N when they hear a negative tone to avoid an aversive stimulus (brief white noise). Once trained they are presented with occasional ambiguous intermediate tones to see whether they make response P indicating anticipation of a rewarding outcome and hypothesized to reflect a positively valanced affective state, or response N indicating anticipation of an aversive outcome and hypothesized to reflect a negative state. The effects of affect-induction treatments on these responses can be tested.

that allows them to be utilized across species. More work is needed to better understand some of the interpretational complexities listed above. The approach requires animals to be trained on the basic discrimination task (Fig. 23.3) and this can take from about 1 hour (e.g., dogs; Mendl et al., 2010a) to many training sessions across days to achieve. Consequently, development of quicker and automated tests is an important focus of research (Brydges and Hall, 2017; Hintze et al., 2018; Jones et al., 2018). Attention-bias tasks, based on empirical findings from human psychology and theoretical predictions that detection of threatening stimuli is particularly valuable and likely in individuals who are in a negative state, offer another cognitive bias approach (Bethell et al., 2012; Lee et al., 2016). They may also involve nontrained spontaneous behavior such as orientation toward threat, and hence be quicker to implement.

Conclusions

Cognitive markers of affective valence are a new growth area in the assessment of animal affect, and the animal welfare research community has been influential in their development. They are based on theoretical and/or 'translation from humans' rationales and their strengths include translatability across species, a specific focus on affective valence – a key determinant of animal welfare –

and, in some cases, clear *a priori* predictive frameworks for how cognitive functions should alter in different affective states. A limitation of some of these approaches is the need to train animals on cognitive tasks prior to assessment, and the development of quicker and automated methods is therefore an important current goal.

23.6 Concluding Remarks

The evaluation of animal mental health and wellbeing necessarily involves accurate assessment of affective states. This is a challenging enterprise that requires clear definitions of concepts and terms, recognition of the logic by which human emotion theories and models can be applied to animals, and awareness that inferences about the conscious experience of affective states in nonhuman animals should be made carefully and rationally. For example, findings of predicted affect-induced judgment biases in insects naturally raise the question of whether such biases tell us anything about conscious experience of the inferred states. In this case, we suggest that judgment bias tests, like all the other indicators that we have discussed here, can be reliable markers of affective states that are instantiated in the activity of underlying neurophysiological systems, but that whether these states also comprise a conscious component requires evidence from different types of study that specifically

address the possibility of consciousness in other species. Such studies may focus on, for example, the presence or absence of neural structures and functions thought to be involved in human conscious experience, and the occurrence of particular behavioral and cognitive abilities such as metacognition, episodic memory, future planning, and theory of mind that can be argued to require consciousness (Clayton and Dickinson, 1998; Boly et al., 2013). We believe that the framework for developing a scientific study of animal affect outlined here can provide a basis for identifying new and better affect indicators, and that expressive behavior and cognitive marker measures exemplify the novel and exciting developments taking place in this important enterprise.

23.7 Acknowledgments

We thank the UK Biotechnology and Biological Sciences Research Council for funding ESP on grant BB/P019218/1 during the writing of this chapter.

23.8 References

- Adolphs, R. (2017) How should neuroscience study emotions? By distinguishing emotion states, concepts, and experiences. Social Cognitive and Affective Neuroscience 12, 24–31. http://dx.doi.org/10.1093/scan/nsw153.
- Ahloy-Dallaire, J., Espinosa, J., Mason, G. (2018) Play and optimal welfare: Does play indicate the presence of positive affective states? *Behavioural Processes* 156, 3–15. http://dx.doi.org/10.1016/j.beproc.2017.11.011.
- Anderson, D.J. and Adolphs, R. (2014) A framework for studying emotions across species. *Cell* 157, 187–200. http://dx.doi.org/10.1016/j.cell.2014.03.003.
- Baciadonna, L. and Mcelligott, A.G. (2015) The use of judgement bias to assess welfare in farm livestock. *Animal Welfare* 24, 81–91. http://dx.doi.org/10.7120/ 09627286.24.1.081.
- Barrett, L.F. (2017) The theory of constructed emotion: An active inference account of interoception and categorization. *Social Cognitive and Affective Neuroscience* 12, 1–23. http://dx.doi.org/10.1093/scan/nsx060.
- Barron, A.B. and Klein, C. (2016) What insects can tell us about the origins of consciousness. *Proceedings of the National Academy of Sciences of the United States of America* 113, 4900–4908. http://dx.doi.org/10.1073/pnas.1520084113.
- Berridge, K.C. and Robinson, T.E. (2003) Parsing reward. *Trends in Neurosciences* 26, 507–513. http://dx.doi.org/10.1016/S0166-2236(03)00233-9.

- Bethell, E.J. (2015) A 'how-to' guide for designing judgment bias studies to assess captive animal welfare. Journal of Applied Animal Welfare Science 18, S18—S42. http://dx.doi.org/10.1080/10888705.2015.1075833.
- Bethell, E., Holmes, A., Maclarnon, A., Semple, S. (2012) Evidence that emotion mediates social attention in rhesus macaques. *PloS ONE* 7(8), e44387. http://dx.doi.org/10.1371/journal.pone.0044387.
- Bliss-Moreau, E. (2017) Constructing nonhuman animal emotion. *Current Opinion in Psychology* 17, 184–188. http://dx.doi.org/10.1016/j.copsyc.2017.07.011
- Bokkers, E.A.M., De Vries, M., Antonissen, I., De Boer, I.J.M. (2012) Inter- and intra-observer reliability of experienced and inexperienced observers for the Qualitative Behaviour Assessment in dairy cattle. *Animal Welfare* 21, 307–318. http://dx.doi.org/ 10.7120/09627286.21.3.307.
- Boly, M., Seth, A. K., Wilke, M., Ingmundson, P., Baars, B., et al. (2013) Consciousness in humans and non-human animals: Recent advances and future directions. Frontiers in Psychology 4, 625. http://dx.doi.org/10.3389/fpsyg.2013.00625.
- Braccini, S.N. and Caine, N.G. (2009) Hand preference predicts reactions to novel foods and predators in marmosets (*Callithrix geoffroyi*). *Journal of Comparative Psychology* 123, 18–25. http://dx.doi.org/10.1037/ a0013089.
- Bradburn, N.M. (1969) The Structure of Psychological Wellbeing. Aldine, Chicago, Illinois, USA.
- Brancucci, A., Lucci, G., Mazzatenta, A., Tommasi, L. (2009) Asymmetries of the human social brain in the visual, auditory and chemical modalities. *Philosophical Transactions of the Royal Society B Biological Sciences* 364, 895–914. http://dx.doi.org/10.1098/rstb.2008.0279.
- Briefer, E.F. (2012) Vocal expression of emotions in mammals: Mechanisms of production and evidence. *Journal of Zoology* 288, 1–20. http://dx.doi.org/10.1111/j.1469-7998.2012.00920.x.
- Bruder, G.E., Stewart, J.W., McGrath, P.J. (2017) Right brain, left brain in depressive disorders: Clinical and theoretical implications of behavioral, electrophysiological and neuroimaging findings. *Neuroscience and Biobehavioral Reviews* 78, 178–191. http://dx.doi.org/ 10.1016/j.neubiorev.2017.04.021.
- Brydges, N.M. and Hall, L. (2017) A shortened protocol for assessing cognitive bias in rats. *Journal of Neuroscience Methods* 286, 1–5. http://dx.doi.org/10.1016/j.jneumeth.2017.05.015.
- Burman, O., McGowan, R., Mendl, M., Norling, Y., Paul, E., et al. (2011) Using judgement bias to measure positive affective state in dogs. *Applied Animal Behaviour Science* 132, 160–168. http://dx.doi.org/10.1016/j.applanim.2011.04.001.
- Buwalda, B., Scholte, J., De Boer, S.F., Coppens, C.M., Koolhaas, J.M. (2012) The acute glucocorticoid stress response does not differentiate between rewarding

- and aversive social stimuli in rats. *Hormones and Behavior* 61, 218–226. http://dx.doi.org/10.1016/j. yhbeh.2011.12.012.
- Cabanac, M. (1992) Pleasure: The common currency. Journal of Theoretical Biology 155, 173–200. http://dx.doi.org/10.1016/S0022-5193(05)80594-6.
- Cabib, S. and Puglisi-Allegra, S. (2012) The mesoaccumbens dopamine in coping with stress. *Neuroscience and Biobehavioral Reviews* 36, 79–89. http://dx.doi.org/10.1016/j.neubiorev.2011.04.012.
- Cacioppo, J.T. and Berntson, G.G. (1999) The affect system: Architecture and operating characteristics. *Current Directions In Psychological Science* 8, 133–137. http://dx.doi.org/10.1111/1467-8721.00031.
- Caeiro, C C., Waller, B.M., Zimmermann, E., Burrows, A.M., Davila-Ross, M. (2013) OrangFACS: A muscle-based facial movement coding system for orangutans (*Pongo* spp.). *International Journal of Primatology* 34, 115–129. http://dx.doi.org/10.1007/s10764-012-9652-x.
- Camerlink, I., Peijnenburg, M., Wemelsfelder, F., Turner, S.P. (2016) Emotions after victory or defeat assessed through qualitative behavioural assessment, skin lesions and blood parameters in pigs. *Applied Animal Behaviour Science* 183, 28–34. http://dx.doi.org/ 10.1016/j.applanim.2016.07.007.
- Carver, C.S. (2001) Affect and the functional bases of behavior: On the dimensional structure of affective experience. *Personality and Social Psychology Review* 5, 345–356. http://dx.doi.org/10.1207/ S15327957PSPR0504 4.
- Clayton, N.S. and Dickinson, A. (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272–274. http://dx.doi.org/10.1038/26216.
- Critchley, H.D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R.J. (2004) Neural systems supporting interoceptive awareness. *Nature Neuroscience* 7, 189–195. http://dx.doi.org/10.1038/nn1176.
- Cryan, J.F. and Mombereau, C. (2004) In search of a depressed mouse: Utility of models for studying depression-related behavior in genetically modified mice. *Molecular Psychiatry* 9, 326–357. http://dx.doi. org/10.1038/sj.mp.4001457.
- Dalla Costa, E., Pascuzzo, R., Leach, M.C., Dai, F., Lebelt, D., et al. (2018) Can grimace scales estimate the pain status in horses and mice? A statistical approach to identify a classifier. PloS ONE 13(8), e0200339. http://dx.doi.org/10.1371/journal.pone.0200339.
- Darwin, C.R. (1872) The Expression of the Emotions In Man and Animals. John Murray, London, UK. http:// dx.doi.org/10.1037/10001-000.
- Davidson, R.J. and Irwin, W. (1999) The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences* 3, 11–21. http://dx.doi.org/10.1016/ S1364-6613(98)01265-0.
- Desiré, L., Boissy, A., Veissier, I. (2002) Emotions in farm animals: A new approach to animal welfare in applied ethology. *Behavioural Processes* 60, 165–180.

- Dickinson, A. and Balleine, B. (2009) Hedonics: The cognitive-motivational interface. In: Kringelbach, M.L. and Berridge, K.C. (eds.) *Pleasures of the Brain*. Oxford University Press, Oxford, UK, pp. 74–84.
- Diener, E., Suh, E.M., Lucas, R.E., Smith, H.L. (1999) Subjective well-being: Three decades of progress. *Psychological Bulletin* 125, 276–302. http://dx.doi.org/10.1037/0033-2909.125.2.276.
- Doyle, R.E., Fisher, A.D., Hinch, G.N., Boissy, A., Lee, C. (2010) Release from restraint generates a positive judgement bias in sheep. *Applied Animal Behaviour Science* 122, 28–34. http://dx.doi.org/10.1016/j.applanim.2009.11.003.
- Dudink, S., Simonse, H., Marks, I., De Jonge, F.H., Spruijt, B.M. (2006) Announcing the arrival of enrichment increases play behaviour and reduces weaning-stress-induced behaviours of piglets directly after weaning. *Applied Animal Behaviour Science* 101, 86–101. http://dx.doi.org/10.1016/j. applanim.2005.12.008.
- Dupjan, S., Schoen, P.C., Puppe, B., Tuchscherer, A., Manteuffel, G. (2008) Differential vocal responses to physical and mental stressors in domestic pigs (*Sus scrofa*). *Applied Animal Behaviour Science* 114, 105– 115. http://dx.doi.org/10.1016/j.applanim.2007.12.005.
- Ekman, P. (1992) An argument for basic emotions. Cognition and Emotion 6, 169–200. http://dx.doi. org/10.1080/02699939208411068.
- Ekman, P., Friesen, W.V., Hager, J.C. (2002) *The Facial Action Coding System (FACS)*. Research Nexus, Salt Lake City, Utah, USA.
- Farah, M.J. (2008) Neuroethics and the problem of other minds: Implications of neuroscience for the moral status of brain-damaged patients and nonhuman animals. *Neuroethics* 1, 9–18. http://dx.doi.org/10.1007/ s12152-008-9006-8.
- Forkman, B., Boissy, A., Meunier-Salauen, M.C., Canali, E., Jones, R.B. (2007) A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiology and Behavior* 92, 340–374. http://dx.doi.org/10.1016/j.physbeh.2007.03.016.
- Franks, B. and Higgins, E.T. (2012) Effectiveness in humans and other animals: A common basis for wellbeing and welfare. In: Olson, J.M. and Zanna, M.P. (eds.) Advances in Experimental Social Psychology, Vol 46. Academic Press, Cambridge, Massachusetts, USA, pp. 285–346. http://dx.doi.org/10.1016/B978-0-12-394281-4.00006-4.
- Fureix, C. and Meagher, R.K. (2015) What can inactivity (in its various forms) reveal about affective states in non-human animals? A review. *Applied Animal Behaviour Science* 171, 8–24. http://dx.doi.org/10.1016/j.applanim.2015.08.036.
- Gleerup, K.B., Andersen, P.H., Munksgaard, L., Forkman, B. (2015) Pain evaluation in dairy cattle. *Applied Animal Behaviour Science* 171, 25–32. http://dx.doi.org/10.1016/j.applanim.2015.08.023.

- Goursot, C., Dupjan, S., Kanitz, E., Tuscherer, A., Puppe, B., et al. (2018) Assessing animal individuality: Links between personality and laterality in pigs. Current Zoology, https://doi.org/10.1093/cz/zoy071.
- Gray, J.A. (1987) *The Psychology of Fear and Stress*, 2nd edn. Cambridge University Press, Cambridge, UK.
- Griffin, D.R. and Speck, G.B. (2004) New evidence of animal consciousness. *Animal Cognition* 7, 5–18. http://dx.doi.org/10.1007/s10071-003-0203-x.
- Gygax, L. (2014) The A to Z of statistics for testing cognitive judgement bias. *Animal Behaviour* 95, 59–69. http://dx.doi.org/10.1016/j.anbehav.2014.06.013.
- Harding, E.J., Paul, E.S., Mendl, M. (2004) Animal behaviour: Cognitive bias and affective state. *Nature* 427, 312–312. http://dx.doi.org/10.1038/427312a.
- Held, S.D.E. and Spinka, M. (2011) Animal play and animal welfare. *Animal Behaviour* 81, 891–899. http://dx.doi.org/10.1016/j.anbehav.2011.01.007.
- Hintze, S., Murphy, E., Bachmann, I., Wemelsfelder, F., Würbel, H. (2017) Qualitative Behaviour Assessment of horses exposed to short-term emotional treatments. *Applied Animal Behaviour Science* 196, 44–51. http:// dx.doi.org/10.1016/j.applanim.2017.06.012.
- Hintze, S., Melotti, L., Colosio, S., Bailoo, J.D., Boada-Sana, M., et al. (2018) A cross-species judgement bias task: Integrating active trial initiation into a spatial Go/No-go task. Scientific Reports 8, 5104. http://dx.doi.org/10.1038/s41598-018-23459-3.
- ligaya, K., Jolivald, A., Jitkrittum, W., Gilchrist, I.D., Dayan, P., et al. (2016) Cognitive bias in ambiguity judgements: Using computational models to dissect the effects of mild mood manipulation in humans. PloS ONE 11(11), e0165840. http://dx.doi.org/10.1371/ journal.pone.0165840.
- Izard, C.E. (2007) Basic emotions, natural kinds, emotion schemas, and a new paradigm. Perspectives on Psychological Science 2, 260–280. http://dx.doi. org/10.1111/j.1745-6916.2007.00044.x.
- James, W. (1884) What is an emotion? Mind 9, 188-205.
- Jones, S., Neville, V., Higgs, L., Paul, E.S., Dayan, P., et al. (2018) Assessing animal affect: An automated and self-initiated judgement bias task based on natural investigative behaviour. Scientific Reports 8, 12400. http://dx.doi.org/10.1038/s41598-018-30571-x.
- Kappel, S., Mendl, M.T., Barrett, D.C., Murrell, J.C., Whay, H.R. (2017) Lateralized behaviour as indicator of affective state in dairy cows. *PloS ONE* 12, e0184933. http://dx.doi.org/10.1371/journal.pone.0184933.
- Keating, S.C.J., Thomas, A.A., Flecknell, P.A., Leach, M.C. (2012) Evaluation of EMLA cream for preventing pain during tattooing of rabbits: Changes in physiological, behavioural and facial expression responses. *PloS ONE* 7(9), e44437. http://dx.doi.org/10.1371/journal. pone.0044437.
- Key, B. (2016) Why fish do not feel pain. *Animal Sentience* 1, 1.

- Kragel, P.A. and Labar, K.S. (2016) Decoding the nature of emotion in the brain. *Trends in Cognitive Sciences* 20, 444–455. http://dx.doi.org/10.1016/j.tics.2016.03.011.
- Kreibig, S.D. (2010) Autonomic nervous system activity in emotion: A review. *Biological Psychology* 84, 394–421. http://dx.doi.org/10.1016/j.biopsycho.2010.03.010.
- Langford, D.J., Bailey, A.L., Chanda, M.L., Clarke, S.E., Drummond, T.E., et al. (2010). Coding of facial expressions of pain in the laboratory mouse. *Nature Methods* 7, 447–449. http://dx.doi.org/10.1038/nmeth.1455.
- LeDoux, J. (1996) The Emotional Brain: The Mysterious Underpinnings of Emotional Life. Simon and Schuster, New York, USA.
- Lee, C., Verbeek, E., Doyle, R., Bateson, M. (2016) Attention bias to threat indicates anxiety differences in sheep. *Biology Letters* 12(6), 20150977.
- Leliveld, L.M.C., Langbein, J., Puppe, B. (2013) The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science* 145, 1–14. http://dx.doi.org/10.1016/j.applanim.2013.02.002.
- Lindquist, K.A., Wager, T.D., Kober, H., Bliss-Moreau, E., Barrett, L.F. (2012) The brain basis of emotion: A metaanalytic review. *Behavioral and Brain Sciences* 35, 121–143.http://dx.doi.org/10.1017/S0140525X11000446.
- Low P. (2012) The Cambridge Declaration on Consciousness. Available at: http://fcmconference.org/img/CambridgeDeclarationOnConsciousness.pdf (accessed 2 March 2019).
- Macphail, E.M. (1998) The Evolution of Consciousness. Oxford University Press, Oxford, UK. http://dx.doi. org/10.1093/acprof:oso/9780198503248.001.0001.
- Makowska, I.J. and Weary, D.M. (2016) Differences in anticipatory behaviour between rats (*Rattus norvegicus*) housed in standard versus semi-naturalistic laboratory environments. *PloS ONE* 11(1), e0147595. http://dx.doi.org/10.1371/journal.pone.0147595.
- Martin, J., Lopez, P., Bonati, B., Csermely, D. (2010) Lateralization when monitoring predators in the wild: A left eye control in the common wall lizard (*Podarcis muralis*). Ethology 116, 1226–1233. http://dx.doi.org/10.1111/j.1439-0310.2010.01836.x.
- Mason, G.J. and Latham, N.R. (2004) Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare* 13, S57–S69.
- Mathews, A. and Macleod, C. (1994) Cognitive approaches to emotion and emotional disorders. *Annual Review* of *Psychology* 45, 25–50. http://dx.doi.org/10.1146/ annurev.ps.45.020194.000325.
- Mauss, I. and Robinson, M. (2009) Measures of emotion: A review. Cognition and Emotion 23, 209–237. http:// dx.doi.org/10.1080/02699930802204677.
- McLennan, K.M., Rebelo, C.J.B., Corke, M.J., Holmes, M.A., Leach, M.C., et al. (2016) Development of a facial expression scale using footrot and mastitis as models of pain in sheep. Applied Animal Behaviour Science 176, 19–26. http://dx.doi.org/10.1016/j.applanim.2016.01.007.

- McNamara, J.M. and Houston, A.I. (1986) The common currency for behavioral decisions. *American Naturalist* 127, 358–378. http://dx.doi.org/10.1086/284489.
- Mendl, M., Burman, O.H.P., Parker, R.M.A., Paul, E.S. (2009) Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science* 118, 161–181. http://dx.doi.org/10.1016/j. applanim.2009.02.023.
- Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., et al. (2010a) Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. Current Biology 20, R839–R840. http://dx.doi.org/10.1016/j.cub.2010.08.030.
- Mendl, M., Burman, O.H.P., Paul, E.S. (2010b) An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B-Biological Sciences* 277, 2895–2904. http://dx.doi.org/10.1098/rspb.2010.0303.
- Millenson, J.R. (1967) *Principles of Behavioral Analysis*. Macmillan, New York, USA.
- Mineka, S., Watson, D., Clark, L.A. (1998) Comorbidity of anxiety and unipolar mood disorders. *Annual Review* of Psychology 49, 377–412.
- Minero, M., Dalla Costa, E., Dai, F., Murray, L.A.M., Canali, E., et al. (2016) Use of Qualitative Behaviour Assessment as an indicator of welfare in donkeys. Applied Animal Behaviour Science 174, 147–153. http://dx.doi.org/10.1016/j.applanim.2015.10.010.
- Moe, R.O., Nordgreen, J., Janczak, A.M., Spruijt, B.M., Bakken, M. (2013) Effects of signalled reward type, food status and a mu-opioid receptor antagonist on cue-induced anticipatory behaviour in laying hens (*Gallus domesticus*). Applied Animal Behaviour Science 148, 46–53. http://dx.doi.org/10.1016/j. applanim.2013.08.001.
- Mormede, P., Andanson, S., Auperin, B., Beerda, B., Guemene, D., et al. (2007) Exploration of the hypothalamic-pituitary-adrenal function as a tool to evaluate animal welfare. *Physiology and Behavior* 92, 317–339. http://dx.doi.org/10.1016/j.physbeh.2006.12.003.
- Nettle, D. and Bateson, M. (2012) The evolutionary origins of mood and its disorders. *Current Biology* 22, R712– R721. http://dx.doi.org/10.1016/j.cub.2012.06.020.
- Palagi, E. and Scopa, C. (2017) Integrating Tinbergen's inquiries: Mimicry and play in humans and other social mammals. *Learning and Behavior* 45, 378–389. http://dx.doi.org/10.3758/s13420-017-0278-x.
- Palme, R. (2012) Monitoring stress hormone metabolites as a useful, non-invasive tool for welfare assessment in farm animals. *Animal Welfare* 21, 331–337. http://dx.doi.org/10.7120/09627286.21.3.331.
- Panksepp, J. (1998) Affective Neuroscience. Oxford University Press, Oxford, UK.
- Panksepp, J. (2007) Neurologizing the psychology of affects: How appraisal-based constructivism and basic emotion theory can coexist. Perspectives on

- Psychological Science 2, 281–296. http://dx.doi.org/10.1111/j.1745-6916.2007.00045.x.
- Panksepp, J. and Burgdorf, J. (2000) 50-kHz chirping (laughter?) in response to conditioned and unconditioned tickle-induced reward in rats: Effects of social housing and genetic variables. *Behavioural Brain Research* 115, 25–38. http://dx.doi.org/10.1016/ S0166-4328(00)00238-2.
- Parr, L.A. (2001) Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglo-dytes*). *Animal Cognition* 4, 223–229. http://dx.doi. org/10.1007/s100710100085.
- Parr, L.A., Waller, B.M., Vick, S.J., Bard, K.A. (2007) Classifying chimpanzee facial expressions using muscle action. *Emotion* 7, 172. http://dx.doi.org/ 10.1037/1528-3542.7.1.172.
- Paul, E.S. and Mendl, M. (2018) Animal emotion: Descriptive and prescriptive definitions and their implications for a comparative perspective. *Applied Animal Behaviour Science* 205, 202–209.
- Paul, E.S., Harding, E.J., Mendl, M. (2005) Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews* 29, 469–491. http://dx.doi.org/10.1016/j. neubiorev.2005.01.002.
- Pellow, S., Chopin, P., File, S.E., Briley, M. (1985) Validation of open:closed arm entries in an elevated plus-maze as a measure of anxiety in the rat. *Journal of Neuroscience Methods* 14, 149–167. http://dx.doi.org/10.1016/0165-0270(85)90031-7.
- Peters, S.M., Bleijenberg, E.H., van Dierendonck, M.C., van der Harst, J.E., Spruijt, B.M. (2012) Characterization of anticipatory behaviour in domesticated horses (*Equus caballus*). *Applied Animal Behaviour Science* 138, 60–69. http://dx.doi.org/10.1016/j.applanim.2012.01.018.
- Plutchik, R. (2001) The nature of emotions: Human emotions have deep evolutionary roots, a fact that may explain their complexity and provide tools for clinical practice. *American Scientist* 89, 344–350. http://dx.doi.org/10.1511/2001.4.344.
- Poole, T.B. (1978) Analysis of social play in polecats (Mustelidae) with comments on form and evolutionary history of open mouth play face. *Animal Behaviour* 26, 36–49. http://dx.doi.org/10.1016/0003-3472(78)90006-4.
- Puppe, B., Schön, P.C., Tuchscherer, A., Manteuffel, G. (2005) Castration-induced vocalisation in domestic piglets, Sus scrofa: Complex and specific alterations of the vocal quality. Applied Animal Behaviour Science 95, 67–78. http://dx.doi.org/10.1016/j.applanim. 2005.05.001.
- Ramos, A. and Mormede, P. (1997) Stress and emotionality: A multidimensional and genetic approach. *Neuroscience and Biobehavioral Reviews* 22, 33–57. http://dx.doi.org/10.1016/S0149-7634 (97)00001-8.

- Reefmann, N., Wechsler, B., Gygax, L. (2009) Behavioural and physiological assessment of positive and negative emotion in sheep. *Animal Behaviour* 78, 651–659. http://dx.doi.org/10.1016/j.anbehav.2009.06.015.
- Roelofs, S., Boleij, H., Nordquist, R.E., van der Staay, F.J. (2016) Making decisions under ambiguity: Judgment bias tasks for assessing emotional state in animals. Frontiers in Behavioral Neuroscience 10, 119. http:// dx.doi.org/10.3389/fnbeh.2016.00119.
- Rogers, L.J. (2010) Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science* 127, 1–11. http://dx.doi.org/10.1016/j.applanim.2010.06.008.
- Rolls, E.T. (2005) Emotion Explained. Oxford University Press, Oxford, UK. http://dx.doi.org/10.1093/acprof: oso/9780198570035.001.0001.
- Russell, J.A. (2003) Core affect and the psychological construction of emotion. *Psychological Review* 110, 145–172. http://dx.doi.org/10.1037/0033-295X.110.1.145.
- Rutherford, K.M.D., Donald, R.D., Lawrence, A.B., Wemelsfelder, F. (2012) Qualitative Behavioural Assessment of emotionality in pigs. *Applied Animal Behaviour Science* 139, 218–224. http://dx.doi.org/10.1016/j.applanim.2012.04.004.
- Ryff, C.D. and Singer, B.H. (2008) Know thyself and become what you are: A eudaimonic approach to psychological well-being. *Journal of Happiness Studies* 9, 13–39. http://dx.doi.org/10.1007/s10902-006-9019-0.
- Sandem, A.I., Janczak, A.M., Salte, R., Braastad, B.O. (2006) The use of diazepam as a pharmacological validation of eye white as an indicator of emotional state in dairy cows. Applied Animal Behaviour Science 96, 177–183. http://dx.doi.org/10.1016/j. applanim.2005.06.008.
- Scherer, K.R. (2001) Appraisal considered as a process of multi-level sequential checking. In: Scherer, K.R., Schorr, A., Johnstone, T. (eds.) Appraisal Processes In Emotion: Theory, Methods, Research. Oxford University Press, New York, USA, pp. 92–120.
- Scherer, K.R. (2005) What are emotions? And how can they be measured? Social Science Information 44, 695–729.http://dx.doi.org/10.1177/0539018405058216.
- Schön, P.C., Puppe, B., Manteuffel, G. (2004) Automated recording of stress vocalisations as a tool to document impaired welfare in pigs. *Animal Welfare* 13, 105–110.
- Seligman, M.E.P. (2011) Flourish: A New Understanding Of Happiness And Well-Being And How To Achieve Them. Free Press, London, UK.
- Shanahan, M. (2012) The brain's connective core and its role in animal cognition. *Philosophical Transactions of the Royal Society B Biological Sciences* 367, 2704–2714. http://dx.doi.org/10.1098/rstb.2012.0128.
- Siniscalchi, M., Sasso, R., Pepe, A.M., Vallortigara, G., Quaranta, A. (2010) Dogs turn left to emotional stimuli. Behavioural Brain Research 208, 516–521. http://dx.doi.org/10.1016/j.bbr.2009.12.042.

- Sotocinal, S.G., Sorge, R.E., Zaloum, A., Tuttle, A.H., Martin, L.J., et al. (2011) The Rat Grimace Scale: A partially automated method for quantifying pain in the laboratory rat via facial expressions. *Molecular Pain* 7, 55.
- Spruijt, B.M., van den Bos, R., Pijlman, F.T.A. (2001)
 A concept of welfare based on reward evaluating mechanisms in the brain: Anticipatory behaviour as an indicator for the state of reward systems. *Applied Animal Behaviour Science* 72, 145–171. http://dx.doi.org/10.1016/S0168-1591(00)00204-5.
- Susskind, J.M., Lee, D.H., Cusi, A., Feiman, R., Grabski, W., et al. (2008) Expressing fear enhances sensory acquisition. Nature Neuroscience 11, 843–850. http://dx.doi.org/10.1038/nn.2138.
- Tallet, C., Linhart, P., Policht, R., Hammerschmidt, K., Šimeček, P., et al. (2013) Encoding of situations in the vocal repertoire of piglets (Sus scrofa): A comparison of discrete and graded classifications. PLoS ONE 8(8), e71841.http://dx.doi.org/10.1371/journal.pone.0071841.
- Tuttle, A.H., Molinaro, M.J., Jethwa, J.F., Sotocinal, S.G., Prieto, J.C., et al. (2018) A deep neural network to assess spontaneous pain from mouse facial expressions. Molecular Pain 14, 1744806918763658. http:// dx.doi.org/10.1177/1744806918763658.
- van den Berg, C.L., Pijlman, F.T.A., Koning, H.A.M., Diergaarde, L., van Ree, J.M., et al. (1999) Isolation changes the incentive value of sucrose and social behaviour in juvenile and adult rats. Behavioural Brain Research 106, 133–142. http://dx.doi.org/10.1016/S0166-4328(99)00099-6.
- van den Bos, R., Meijer, M.K., van Renselaar, J.P., van der Harst, J.E., Spruijt, B.M. (2003) Anticipation is differently expressed in rats (*Rattus norvegicus*) and domestic cats (*Felis silvestris catus*) in the same Pavlovian conditioning paradigm. *Behavioural Brain Research* 141, 83-89.
- van der Harst, J.E. and Spruijt, B.M. (2007) Tools to measure and improve animal welfare: Reward-related behaviour. *Animal Welfare* 16, 67–73.
- van der Harst, J.E., Baars, A.M., Spruijt, B.M. (2003) Standard housed rats are more sensitive to rewards than enriched housed rats as reflected by their anticipatory behaviour. *Behavioural Brain Research* 142, 151–156. http://dx.doi.org/10.1016/S0166-4328(02)00403-5.
- van der Harst, J.E., Baars, A.M., Spruijt, B.M. (2005) Announced rewards counteract the impairment of anticipatory behaviour in socially stressed rats. Behavioural Brain Research 161, 183–189. http:// dx.doi.org/10.1016/j.bbr.2005.02.029.
- van Hoof, J.A.R.A.M. (1976) A comparative approach to the phylogeny of laughter and smiling. In: Bruner, J.S., Jolly, A., Sylva, K. (eds.) *Play, Its Role In Development And Evolution*. Penguin Books, London, UK, pp. 209–241.
- Veissier, I., Boissy, A., Desire, L., Greiveldinger, L. (2009) Animals' emotions: Studies in sheep using appraisal theories. *Animal Welfare* 18, 347–354.

- Ventolini, N., Ferrero, E.A., Sponza, S., Chiesa, A.D., Zucca, P., et al. (2005) Laterality in the wild: Preferential hemifield use during predatory and sexual behaviour in the black-winged stilt. Animal Behaviour 69, 1077– 1084. http://dx.doi.org/10.1016/j.anbehav.2004.09.003.
- von Borell, E., Langbein, J., Despres, G., Hansen, S., Leterrier, C., et al. (2007) Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals A review. *Physiology and Behavior* 92, 293–316. http://dx.doi.org/10.1016/j.physbeh.2007.01.007.
- von Frijtag, J.C., Reijmers, L., van der Harst, J.E., Leus, I.E., van den Bos, R., et al. (2000) Defeat followed by individual housing results in long-term impaired reward-and cognition-related behaviours in rats. Behavioural Brain Research 117, 137–146. http://dx.doi.org/10.1016/S0166-4328(00)00300-4.
- Vytal, K. and Hamann, S. (2010) Neuroimaging support for discrete neural correlates of basic emotions: A voxelbased meta-analysis. *Journal of Cognitive Neuroscience* 22, 2864–2885. http://dx.doi.org/10.1162/ jocn.2009.21366.
- Waller, B.M., Lembeck, M., Kuchenbuch, P., Burrows, A.M., Liebal, K. (2012) GibbonFACS: A musclebased facial movement coding system for hylobatids.

- International Journal of Primatology 33, 809–821. http://dx.doi.org/10.1007/s10764-012-9611-6.
- Watson, D., Wiese, D., Vaidya, J., Tellegen, A. (1999) The two general activation systems of affect: Structural findings, evolutionary considerations, and psychobiological evidence. *Journal of Personality and Social Psychology* 76, 820–838. http://dx.doi.org/10.1037/ 0022-3514.76.5.820.
- Weary, D.M., Ross, S., Fraser, D. (1997) Vocalizations by isolated piglets: A reliable indicator of piglet need directed towards the sow. Applied Animal Behaviour Science 53, 249–257. http://dx.doi.org/10.1016/ S0168-1591(96)01173-2.
- Wemelsfelder, F. (1997) The scientific validity of subjective concepts in models of animal welfare. *Applied Animal Behaviour Science* 53, 75–88. http://dx.doi.org/10.1016/S0168-1591(96)01152-5.
- Wemelsfelder, F. and Mullen, S. (2014) Applying ethological and health indicators to practical animal welfare assessment. Revue Scientifique Et Technique-Office International Des Epizooties 33, 111–120.
- Wemelsfelder, F., Hunter, T.E.A., Mendl, M.T., Lawrence, A.B. (2001) Assessing the 'whole animal': A free choice profiling approach. *Animal Behaviour* 62, 209–220. http://dx.doi.org/10.1006/anbe.2001.1741.

24 Treatment of Emotional Distress and Disorders – Nonpharmacologic Methods

PAMELA J. REID

Anti-Cruelty Behavior Team, American Society for the Prevention of Cruelty to Animals, New York, USA

Emotional distress underlies many of the behavior disorders suffered by companion animals. While stress is a normal part of everyday life, stress becomes distress when the animal's ability to cope compromises its well-being (Moberg, 2000). Distress-related behaviors can be challenging for pet owners, prompting them to seek professional help from certified behaviorists and veterinary behaviorists (Tiira et al., 2016; Cannas et al., 2018). They also rank high among reasons owners give for relinquishing their pets to shelters and rescues (Patronek et al., 1996; Segurson et al., 2005). The most common distress disorders reported by pet owners include fears and phobias, generalized or free-floating anxiety, separation anxiety, and defensive aggression.

Most problematic fears in companion animals are learned, although there is suggestion that fear of loud percussive noises may be innate in some dogs (Lindsay, 2005). Learned fears develop when an animal associates a previously innocuous stimulus or situation with the threat or the occurrence of an aversive event. The stimulus or situation comes to elicit fear and fear-related responses. This learning can take place in as few as one trial (Jarvik and Essman, 1960; Fanselow, 1990). As an example, it is not uncommon for a pet to learn to fear the sight of nail clippers after one painful experience of having a nail cut too short. A fear is labeled a phobia if the fearful response is far more intense than what is appropriate for the situation (Hothersall and Tuber, 1979) - for instance, a dog that repeatedly throws itself against confinement barriers in an effort to avoid contact with a person, causing itself iniury.

Generalized anxiety disorder is characterized by distress that is not associated with any specific stimuli. Instead, the animal is in a chronic state of apprehension, agitation, heightened sensitivity, and hypervigilance (Lindsay, 2001; Ferdowsian et al., 2012), sharing many of the same symptoms as posttraumatic stress disorder in humans (Foa et al., 1992; see also Chapter 14, this volume). This type of disorder often develops from exposure to traumatic events but can also result from chronic experience with low level aversive stimuli.

While most dogs, and some cats, may experience some degree of discomfort when separated from their person (or people), an animal is considered to suffer from separation anxiety when it becomes so distressed that it engages in destruction, vocalization, elimination, and/or attempts to escape. These animals are often hyper-attached to their people as well, exhibiting anxiety even when separated by a door or gate and displaying effusive greeting behavior when reunited.

Defensive aggression develops when an animal learns that an effective means for fending off a frightening person or conspecific is to adopt the strategy of 'the best defense is a good offense'. Most fearful animals will prefer to escape, but if escape is prevented, aggression is a viable defensive tactic. Unfortunately, defensive aggression often results in the threatening stimulus moving away and so the behavior is reinforced, with the result that this can become the go-to strategy for the frightened animal. Without knowing the history of the animal, this type of aggression can be misidentified as offensive.

Whether an animal is vulnerable to developing a particular distress disorder depends on factors such as temperament, early experience, prior exposure to stressors, and the interactions of these (Mineka and Oehlberg, 2008). There is solid evidence that there are genetic or epigenetic predispositions for fearfulness. In a classic demonstration, Murphree (1973) artificially selected for fearful behavior and produced a strain of 'nervous' pointer dogs that exhibited intense avoidance of humans, regardless of their socialization history. Deficits in socialization and environmental exposure during development can result in profoundly debilitating neophobia (Scott and Fuller, 1965). Dogs originating from substandard commercial breeding operations often suffer severe impoverishment in early life, resulting in a variety of maladaptive distress disorders that sometimes cause the dogs to be described as 'autisticlike' by their owners (McMillan et al., 2011, 2013; McMillan, 2017). Experiencing an acute stressor, such as a startling or traumatic event, can lead to rapid conditioned fear of any stimuli associated with the event (Haeson et al., 2017). However, repeated exposures to lower level aversive stimuli can also result in conditioned fear. For instance, Schilder and Van der Borg (2004) found that dogs trained with the use of low-intensity shock experienced distress during training sessions and came to associate the painful events with their owners, even outside of the training context. Finally, chronic experience with uncontrollable and/or unpredictable aversive events can, in some animals, lead to generalized anxiety disorder (Dess et al., 1983).

24.1 Components of Treatment

Nonpharmacological procedures designed to reduce emotional distress and distress-related behaviors in companion animals consist of two components: management and treatment. The purpose of management is to decrease the opportunities for the expression of negative emotion-laden behaviors. Effective management serves to: (i) reduce the likelihood that the animal will continue to experience distress; (ii) halt the strengthening of any associations and patterns of responding that may result from the animal's repeated exposure to distressing events; (iii) reduce the likelihood that the animal's display of emotional behavior will result in damage to people, other animals, or property; and (iv) empower clients with a strategy they can use to reduce the risks associated with their pet's undesired behaviors. Clients may be more willing to embark on a treatment program if they can be provided with at least some degree of respite from the anguish of experiencing their pet's undesired, and sometimes dangerous, behavior.

The purpose of the treatment component is to diminish the animal's distress and the associated emotional behaviors, and replace them with positive emotions and their associated emotional behaviors. Separating problem behavior into its affective and behavioral components is helpful in conceptualizing how to assess and approach treatment. Parceling out emotional state from emotional behavior forms the basis for much of the following discussion of treatment options.

24.2 Treatment Options for Distress-Related Behaviors

24.2.1 Flooding or implosion therapy

Flooding, also known as implosion therapy, involves exposing an animal to the full-intensity distress-eliciting stimulus while at the same time preventing the animal from escaping the situation. The goal is for escape and avoidance behaviors to extinguish, thereby enabling the animal to learn that its fear is unfounded. Blocking the animal's ability to escape or avoid the feared stimulus, called response prevention, is a necessary component of flooding, as otherwise responding is very resistant to extinction. As long as the animal's escape/avoidance response is blocked, this procedure leads to rapid extinction of fear responding (Lindsay, 2000). However, because the animal is forced to experience the full-intensity stimulus, it is extremely frightened during the initial stages of treatment (Fig. 24.1). Similarly, human patients find implosion therapy most unpleasant (Thyer et al., 1988).

Despite the effectiveness of flooding in experimental set-ups and in human therapy, few reports exist of its efficacy for treating companion animals. One notable exception is the successful treatment of stranger aggression in three dogs by Williams and Borchelt (2003). They developed a form of flooding and response blocking with their use of a 'grain box' to prevent aggressive responses in dogs undergoing repeated presentations of the triggering stimulus. As a form of response prevention, at the American Society for the Prevention of Cruelty to Animals (ASPCA) Behavioral Rehabilitation Center (BRC), dogs are initially provided an airline crate in which to hide from feared stimuli, but early in treatment the top of the crate is removed to prevent the dog from

346 P.J. Reid



Fig. 24.1. A demonstration of flooding a dog that is frightened of being handled by people. (Photograph credit: Pamela Reid.)

continued hiding. However, this can hardly be likened to flooding because dogs at the BRC are never exposed to full-intensity stimuli during treatment.

There are two reasons why this author does not recommend flooding/response blocking. First, flooding can be a tricky procedure to put into practice. In addition to needing a way to prevent the animal from escaping (or, in the case of defensive aggression, from attacking the stimulus), it is critical that sessions continue until the animal not only ceases attempting to escape but also relaxes in the situation. This can take an unreasonably lengthy amount of time. If the animal is still fearful at the end of the session, there is unlikely to be any beneficial effect and, in fact, the animal's fear may intensify (Metja et al., 1974). Second, flooding can be severely traumatizing for both the animal and the client. Clients do not want to see their pets in distress, even if they are advised that the end will justify the means. And there is the very real risk that the procedure can backfire and the fear will worsen. This author feels that there are equally effective and more humane methods from which to choose.

24.2.2 Desensitization and counterconditioning

According to Wolpe and Lazarus (1966), desensitization and counterconditioning (DSCC) involves the 'breaking down of neurotic anxiety-response habits, employing a physiological state incompatible with anxiety to inhibit the anxiety response to the stimulus that evokes it weakly, repeating the exposure until the stimulus loses completely its anxietyprovoking ability'. To say that is a complicated description would be an understatement! First, DSCC works to change an animal's response to a stimulus by repeatedly presenting the stimulus at such a low level that the animal's arousal is kept to a minimum, thereby setting the animal up to habituate (or 'desensitize') to the stimulus. At the same time, however, the stimulus is paired with the presentation of another stimulus that elicits responses motivationally and/or physically incompatible with the distress response. The distress response originally exhibited by the animal to the stimulus is 'countered' by this new and very different association.

The first report of the clinical use of DSCC, also known as graduated exposure therapy (Antony and Barlow, 1997), described its use in eliminating fear in children (Jones, 1924). Children temporarily housed in an institution were assessed for their reactions to a variety of stimuli, including a snake, a rat, a rabbit, a frog, loud noises, and scary faces. Iones (1924) subjected children, who responded with extreme distress to one or more of the stimuli, to procedures designed to eradicate their fear. The most successful intervention consisted of the therapist bringing the child to the cafeteria, then placing the feared stimulus sufficiently far away that it did not interfere with the child's desire to eat, and feeding the child a favorite food, such as ice cream. While the child ate, the stimulus was slowly brought nearer the table, then placed on the table and, finally, brought close enough for the child to touch. In one instance, the child ate ice cream while a rabbit, which initially had terrified the child, sat in the child's lap. Jones also found that increasing the children's hunger enhanced the effectiveness of the procedure (Dickinson and Pearce, 1977 also confirm that, at least when it comes to food, deprivation leads to more effective counterconditioning).

Wolpe (1958) documented the eradication of conditioned fear in cats using DSCC. He established 'experimental neurosis' in hungry cats by associating the act of feeding with the delivery of electric

shock. After the initial conditioning, the cats refused to eat in the experimental room, despite 1 to 2 days of food deprivation. This inhibition of feeding generalized to rooms that were similar in appearance to the experimental room. Wolpe identified a room that was sufficiently unlike the experimental room in which the cats were able to eat despite still being visibly anxious. Successive feedings in the new room eliminated all signs of distress. The cats were then moved to a room slightly closer in appearance to the experimental room and offered food. The same routine was repeated in a series of rooms of increasing similarity to the experimental room, remaining in each room until the cats no longer showed signs of distress before progressing to the next. With some cats, Wolpe paired an auditory stimulus with the delivery of shock and found that the same procedure successfully eliminated the cats' fear of the sound. The cat was initially moved far enough away from the source of the sound that it was able to eat. Much the same as in Jones's study with children, the cat was gradually moved closer to the sound until the sound no longer elicited fear nor inhibited feeding.

A classic example of DSCC in clinical animal behavior can be provided through the example of a dog that fears the sound of thunder (Fig. 24.2).

First there must be a way of presenting the noise at a volume so low that it fails to evoke a distress response. For instance, some dogs will react to an audio recording of thunder. While the dog hears the recording at a very quiet level, it is fed especially tasty food. The dog comes to learn a new association between thunder and food. Anticipation of the food elicits responses that are motivationally incompatible with fear and these responses eventually come to replace the distress responses. In other words, the dog comes to expect food when it hears thunder at a low volume. Gradually, the volume of the recording is increased while the dog's arousal is maintained at a low level. Distress responses continue to decline while appetitive behaviors predominate. Eventually, the dog can tolerate the sound of thunder at realistic volumes without becoming afraid. Like Pavlov's dogs, a dog successfully undergoing DSCC for thunder phobia presumably salivates upon hearing thunder.

A cat that becomes distressed when a new kitten is introduced into the home can be treated in much the same way as Jones treated the children. For example, imagine a cat that flattens its ears and hisses at the sight of the kitten. If the kitten ventures too close, the cat will spit and swat at the kitten before running away. To employ DSCC in this case,



Fig. 24.2. Dogs at the ASPCA's Behavioral Rehabilitation Center being desensitized and counterconditioned to accept leashing. (Photograph credit: ASPCA.)

348 P.J. Reid

the cat is positioned, on a harness and leash or in a wire crate, at one end of a room or hallway, while the kitten is held far enough away that the cat is willing to eat its favorite treats. The cat is fed continuously while the kitten is in view. The session can consist of one lengthy period of exposure, as Jones did, or of a series of discrete exposures (trials) in which the kitten is periodically removed from sight and the treats are discontinued. This further draws the cat's attention to the positive association between the kitten and the treats, such that the kitten becomes a discriminative stimulus for food. As with any type of conditioning, the time between stimulus presentations (the intertrial interval) should be longer than the duration of exposure to the stimulus itself (Mackintosh, 1974). For instance, if the kitten is in view for 10 seconds, the time the kitten is removed from the cat's view should be noticeably longer than 10 seconds.

In practical applications, the components of desensitization (DS) and counterconditioning (CC) can be employed together or separately. Analyses of CC applications further reveal that there are two similar, but theoretically and procedurally distinct, methods in use. Next, I describe how DS and CC procedures each work separately and in concert and outline their benefits and limitations.

Desensitization alone

The use of DS alone relies on the processes of habituation to the feared stimulus and/or extinction of an association between the feared stimulus and a second frightening stimulus that historically were linked. In a typical study of habituation, a stimulus is presented repeatedly. Over presentations, there is a relatively permanent decline in responding to the stimulus, presumably reflecting a general reduction in the animal's attention to the stimulus. In a typical extinction study, the animal first undergoes a series of conditioning trials to establish an association between a stimulus and an outcome, and then that link is subsequently abolished. The underlying learning process is the same as flooding, in that fear reduction occurs as a result of the response extinguishing first and then the underlying emotion following suit.

In a clinical application of DS alone, the animal experiences repeated presentations of the feared stimulus, but at such a low intensity that it does not elicit distress responses. No attempt is made to countercondition by pairing the stimulus with a

reinforcer such as food. For instance, a dog that fears the sound of thunder could be continuously exposed to a recording of thunder played at a very low volume. The dog would likely initially alert to the sounds but eventually would learn to ignore it. Gradually, probably over the course of many days, the volume may be increased, with the goal that the dog ceases alerting to the sound or showing any signs of distress.

Aside from the fact that it is logistically simpler to implement, there are few, if any, situations where it makes sense to use DS alone to treat distress disorders. The addition of CC invariably makes behavior change more probable.

Counterconditioning alone

CC involves an explicit attempt to counter the animal's distress by associating the feared stimulus with a second stimulus that elicits an incompatible motivational state and/or physical response. When CC is implemented alone, the feared stimulus is presented at full intensity. This is comparable to flooding, but with the addition of reinforcement to 'counter' the original association. Sometimes graded exposure (desensitization) is simply not possible, as there is no way to lower the intensity of the stressor (e.g., fear of flying in an airplane).

For an example of CC alone, consider a dog that has learned to fear children because of a history of punishment whenever children were present. If a child is nearby, the dog attempts to hide. The dog could be counterconditioned by associating the presence of a child with a game of fetch. The motivational state elicited by ball play is incompatible with the distress elicited by the child. If the dog's desire to play ball is stronger than the motivation to hide, anticipation of play will come to override the original anticipation of punishment. If it is not, the fear association will remain intact. In classic opponent-process style, the desire to play and the motivation to hide are assumed to exert antagonistic influences on each other until arousal in one system inhibits arousal in the opposing system and interferes with its motivating, reinforcing, and responseproducing capabilities (Stein, 1964). Although it should be acknowledged that there are problems with this conceptualization (Capaldi et al., 1983), delving into the exact nature of the mechanisms underlying CC is unnecessary for this discussion.

The scientific literature on CC is confusing because the term is used to describe two theoretically and procedurally distinct CC methods: classical and operant. The following describes each individually.

CLASSICAL COUNTERCONDITIONING. In the examples presented thus far, the feared stimulus (the conditioned stimulus [CS]) is linked with a pleasant unconditioned stimulus (UCS), such as food, in an attempt to replace distress responses with conditioned appetitive responses (CRs or conditioned emotional responses [CERs]). This is more accurately termed *classical counterconditioning* (CCC) because the two stimuli are presented contiguously, with no explicit conditioning of a target behavior. In other words, the UCS (food) is presented in conjunction with the CS (the feared stimulus), noncontingently, regardless of the animal's behavior. The objective is, of course, to change behavior but this is expected to occur as a result of a change in the animal's emotional or motivational state. For instance, in the example presented in the previous section, the dog is exposed to a child and then the dog is invited to play. The play is offered regardless of the dog's behavior toward the child; the dog might initially be trembling, panting, pacing, growling, barking, or any number of behaviors designed to increase distance between itself and the child. Provided play is a sufficiently powerful motivator, the dog will come to associate play, rather than punishment, with the presence of children, and so the responses elicited by the child will come to reflect this new association responses that are elements of the play behavior system, such as tail wagging, play bowing, etc. In a nutshell, CCC focuses on altering the emotional state of the animal with the assumption that the form of the behaviors elicited by the emotions, the CERs, will also emerge.

CCC is an extremely powerful agent for behavior change. Laboratory studies of CCC are often referred to as cross-motivational transfer experiments. In most demonstrations, an initially neutral stimulus is first paired with one UCS such as shock, and then, at a later time, the stimulus is paired with a motivationally disparate UCS such as food. In other demonstrations, though, two biologically relevant but incompatible UCSs are paired together. For instance, Erofeeva (1921) used a strong electric shock to signal the delivery of food to hungry dogs. Erofeeva reported that the dogs initially responded with defensive behaviors such as struggling and yelping. Yet, as conditioning progressed, the dogs began to show typical appetitive responses toward the shock, including lip licking and

salivating. Even more surprising, Dearing and Dickinson (1979) found that after counterconditioning an aversive stimulus to signal an appetitive one, the aversive stimulus was incapable of functioning as a punishing stimulus in an instrumental paradigm. This supports the interpretation that CCC can actually produce a change in the motivational and reinforcing properties of a UCS.

OPERANT COUNTERCONDITIONING. The second CC approach is to explicitly condition a volitional behavior that is physically incompatible with the undesirable distress behavior, with the goal that the new behavior increases in frequency while the distress behavior fades away. Tarpy (1982) defines CC as a form of training in which 'a new behavior, counter to the original response, is reinforced, while at the same time the original response is not rewarded'. Defined as such, this CC is the result of instrumental contingencies and should correctly be referred to as *operant counterconditioning* (OCC). The focus is on replacing behaviors rather than changing emotions.

OCC, although identified simply as counterconditioning, is the method often described in the applied animal behavior literature. For instance, Overall (1997) writes that 'in counterconditioning The dog is taught to engage in a behavior that competitively inhibits the performance of the undesirable behavior.' Overall provides an example of OCC in the treatment for submissive urination: 'as soon as the dog's rump touches the ground without any leakage, the treat is released. Clearly, if the dog rolls, grovels, or leaks, it does not get the food.' In this example, delivery of the UCS (food) is contingent on the dog displaying or inhibiting a specific response. Contrast that with a CCC approach to submissive urination. Suppose the CS (the stressor) is identified as direct eye contact from a person. The dog experiences direct eve contact followed immediately by the delivery of a treat, regardless of whether the dog urinates or not. With sufficient pairings, the objective is for the dog to associate eye contact with treats and, if the dog finds the treats pleasurable enough, then urinating should be replaced with solicitous behaviors such as approaching, lip licking, and tail wagging.

DIFFERENTIATING OPERANT AND CLASSICAL COUNTER-CONDITIONING. Why is the distinction between CCC and OCC important? To start, a significant

350 P.J. Reid

difference exists in how these procedures play out in an applied setting. Take, for instance, the example of a dog that experiences fear at the sound of the vacuum cleaner. This negative emotion prompts the dog to flee under the bed, where it pants and trembles. In a CCC paradigm, the behaviorist's task is to identify a UCS, such as food or play, that is emotionally incompatible with the emotion of fear, and pair the sound of the vacuum with the new UCS. This pairing can be accomplished every time: present the vacuum, present the food. If the food is sufficiently appealing, the expectation of food will come to replace the fear associated with the sound of the vacuum. And as a result, approach behavior will take the place of avoidance behavior. Contrast this with an OCC paradigm. Imagine that the dog is required to sit-stay before receiving the UCS. The dog hears the vacuum and is then cued to sit and stay. If it does, it gets a treat. If it does not, it does not get a treat (no UCS).

With CCC, a correlation of 1.0 exists between CS presentation (vacuum) and UCS presentation (food). With OCC, the correlation between CS and UCS may be <1.0, because it is up to the animal whether or not to perform the requisite behavior. If the animal does not perform the behavior, the UCS is not presented in conjunction with the feared stimulus. Conditioning is shown to be stronger when there is a greater contingency between CS and UCS (Mackintosh, 1974).

The second primary distinction between CCC and OCC is the matter of what changes first, emotions or behavior? In CCC, the goal is to change emotion, with the assumption that a change in behavior will follow. In OCC, the goal is to change behavior, with the assumption that a change in the underlying emotional state is inevitable. Because emotion 'drives' most serious distress disorders such as aggression, fear, and separation anxiety, it is reasonable to conclude that conditioning procedures which focus on changing the quality and intensity of the animal's emotional state first will ultimately lead to conditioned emotional responses that are reflective of the altered emotion. A convincing illustration is the guard dog that barks aggressively and lunges at the fence when the next-door neighbor enters the adjacent yard. If the neighbor tosses a delicious steak over the fence every time she comes out, it will not be long before the guard dog comes running happily toward the fence the instant he detects her door opening.

Instrumental contingencies may change the animal's behavior but they are not guaranteed to produce a shift in the underlying affective state. In other words, while the animal's behavior may be altered, the feelings of distress remain, and the original problematic behavior is likely to reoccur. Barlia (1988) provides an illustration of this in his report of a dog that behaved aggressively toward unfamiliar people. The client trained the dog to adopt specific postures (sit, down) with such high reliability that the dog would remain in position even when approached directly by a stranger. However, Barlia notes that the dog remained stiff and tense during interactions, despite the extensive training and exposure to people. Although the dog's response toward the feared stimulus had been transformed through OCC, the underlying fear remained intact. Similarly, it is not uncommon for human subjects to report that, after therapy, although they are able to function more effectively in the presence of a feared stimulus, such as sitting through an airplane flight, they still experience extreme anxiety and fear (Hersen, 1973).

VOLUNTARY AND INVOLUNTARY BEHAVIOR. Another factor that comes into play is the nature of the behavior or behaviors linked to the animal's distress. Specific behaviors can be thought of as ranging on a continuum of voluntary-involuntary, although, in reality, things may not be as clear cut as this (De Havas et al., 2016) (Fig. 24.3). Certain behaviors, such as sit and down, are under good volitional control and amenable to operant conditioning, whereas behaviors such as trembling or freezing are closely linked to underlying emotional states and are much more difficult, if not impossible, for an animal to control. Involuntary responses are easily classically conditioned but far less sensitive to instrumental contingencies (Skinner, 1957; Thompson, 1958). Other behaviors are more likely to fall somewhere in the middle. For instance, a dog's bark can be highly emotive, yet still the dog may exercise some control over whether to bark. Although it is recognized that emotionally charged behaviors are sometimes placed under operant control (Salzinger and Waller, 1962), the typography of the behavior is altered and the response becomes emancipated from the emotion. An example of this is the dog that has been taught to bark on cue. The sound of the bark is often noticeably different from the bark produced by the dog, for instance, in response to an intruder. Likewise, a dog taught to





Fig. 24.3. This dog has suffered motion sickness from driving in the car in the past. Despite being on an antiemetic, she is anticipating nausea. Her avoidance behavior is voluntary; her excessive salivation is involuntary. (Photograph credit: Pamela Reid.)

growl for the reward of a tidbit can do so, but the growl sounds quite different from a growl the same dog produces when it is experiencing the associated affect.

The fact that behaviors are differentially sensitive to classical and operant contingencies goes unrecognized by some behaviorists and trainers, forming the basis for a basic misconception about treating distress disorders in animals. Historically, there was reluctance to use CCC because of the belief that the inclusion of noncontingent reinforcement might inadvertently reinforce the fearful behavior, that 'coddling' the animal will reward anxious or fearful behavior (see, for example, Aloff, 2001; Miller, 2001; Price, 2001). It is exceedingly difficult to instrumentally condition anxietyrelated behaviors, and even if a client were particularly adept at teaching his or her dog to react as though afraid of a stimulus, the resulting behaviors would be unfettered by the underlying emotion of fear. Fortunately, few behaviorists and trainers still adhere to this way of thinking (Lindsay, 2000; Clothier, 2005; McConnell, 2005), although statements like '...reducing inadvertent reinforcement of anxious behaviors by an owner' still appear in the literature (Calder, 2019).

Perhaps the best way to conceptualize the infeasibility of reinforcing distress behaviors is to examine CCC in the laboratory. The procedure typically consists of two phases. In phase 1, a neutral stimulus,

such as a tone, is paired with an aversive UCS, usually shock. Conditioning continues until the animal reacts fearfully in response to the tone by itself. Animals typically freeze because the shock in unavoidable. In phase 2, the animal learns that the exact same tone now reliably precedes the delivery of food. At first, the animal reacts by freezing when it hears the tone, even though food is delivered. From an instrumental conditioning perspective, the animal receives reinforcement for the behavior of freezing; however, the behavior of freezing does not increase in frequency, as would be expected if the behavior were susceptible to the instrumental contingency. Instead, freezing at the sound of the tone decreases in intensity while orienting to the feeder and salivating become predominant. This is true even when the conditioned responses are not mutually exclusive for instance, if the animal can freeze and eat in the same location (Scavio, 1974).

24.2.3 Which procedure is best?

First and foremost, graded exposure should be used whenever possible. DS is not only more effective but also more humane than flooding. Human patients report more comfort with graded exposure than with exposure to anxiety-provoking stimuli at full intensity (Antony and Barlow, 1997). And DS combined with CC is considered to more effectively facilitate behavior change than either DS or CC by itself.

352 P.J. Reid

Poppen (1970) contrasted the effectiveness of the four procedures: (i) flooding (extinction); (ii) DS alone; (iii) CC alone; and (iv) DSCC, for eliminating rats' fearful responses to a tone that had previously been paired with shock. In the extinction condition, rats were exposed to repeated presentations of the full-volume tone in the absence of shock. In the DS condition, rats were presented with graded presentations of the tone in the absence of shock; the volume of the tone was increased only when the rats no longer showed a fearful reaction at the current volume. In the CC condition, rats were exposed to the tone at full volume, followed by the noncontingent delivery of food. In the DSCC condition, the rats experienced graded tones paired with the noncontingent delivery of food, with an increase in the volume of the tone only when the rats no longer showed a fearful reaction at the current volume. The DSCC procedure was superior to the others, although all four procedures were effective in reducing the rats' fear of the tone to varying degrees.

Gambrill (1967) compared extinction with OCC by first teaching rats to run on a wheel to avoid shock. Once wheel running was well established, shocks were no longer delivered. The *extinction* rats were then permitted to run on the wheel until wheel running extinguished. The OCC rats had similar access to the wheel, but they were also taught to press a bar to obtain food. Did this group, with the opportunity to engage in a physically incompatible response, learn more quickly that they need not bother running on the wheel? Both groups extinguished the wheel running response at roughly the same rate. In this study, providing an incompatible response did not facilitate elimination of the avoidance behavior.

The next decision is whether to use CCC or OCC. Is it better to focus on the animal's emotional state and deliver noncontingent reinforcement or to make reinforcement contingent upon a behavior that is physically incompatible with the distress response? Thomas *et al.* (2012) explored this question by using a conditioned suppression procedure. They first trained rats to bar press for sucrose, then quite separately, they taught the rats to associate lights-off with shock. In the final CC phase, the lights were periodically turned off but no shocks were delivered. One group of rats received chocolate milk noncontingently whenever the lights were out, regardless of whether they pressed the bar or not. The other group had to press the bar to earn

chocolate milk. In a subsequent experiment, a completely novel behavior, chain pulling, was incorporated into the CC phase. The researchers found that requiring the rats to engage in an operant response to earn the chocolate milk (OCC) was equally as effective in eliminating the avoidance response (freezing) as providing the chocolate milk noncontingently (CCC). However, they did discover that the rats' fear reduction generalized more readily to new contexts after the OCC procedure.

Thomas et al. (2012) point out that laboratory demonstrations of CCC with animals tend to generate mixed results, whereas clinical behavior therapy with humans is dramatically effective in reducing fear (Rachman, 1990; Ougrin, 2011). Success rates are reported to fall between 70 and 92% (Thomas et al., 2012). The critical difference between the procedures appears to be that human behavior therapy typically involves reinforcement for behavior incompatible with anxiety, such as relaxation. Wolpe (1984) believed that a state of deep relaxation was a necessary component of DSCC for human patients. While relaxation techniques exist for companion animals, there has yet to be a systematic comparison of the effectiveness of including relaxation into CC procedures. Examples of fear-reduction treatment protocols that include a relaxation component are provided in Overall (1997) and Lindsay (2005). Behavior specialists at the ASPCA's BRC do not explicitly incorporate relaxation techniques into their treatment regimens, yet they are able to transform roughly 84% of the extremely fearful, undersocialized dogs entering their facility into comfortable pet dogs within an average of 12 weeks of treatment (K. Miller et al., 2019, manuscript in preparation).

For most types of distress disorders, the author recommends a combined approach of CCC in the early stages of treatment, followed by a switch to OCC once there are signs of an emotive change. For instance, consider a dog that becomes distressed, barking and lunging, when approached by other dogs during leashed walks. DS is achieved by maintaining enough distance from passing dogs to keep arousal low. As soon as the dog detects the oncoming stimulus (the other dog), the client delivers a constant stream of tasty food until the stimulus passes by. The food is delivered regardless of the dog's behavior. If the procedure proves successful, the first observable change is likely that the dog

orients toward the client when detecting another dog. This is a new conditioned response, reflecting the expectation of food. At this point, the author would switch to OCC and require that the dog perform the orienting response to earn the treats. This further strengthens the new conditioned response, which is incompatible with barking and lunging. In this way, the animal's emotion changes first but there is also an explicit contingency for behavior change. If successful, the new orienting response will morph into sustained attention on the client and this behavior will supersede the original fearful reaction even as proximity to the passing dog gradually increases. This merged process is illustrated by McDevitt (2007) in her book, Control Unleashed.

24.2.4 Procedural considerations

Ease of use

CCC is certainly easier for most clients to implement than OCC because no response-dependent contingencies exist. On the other hand, clients feel more engaged and impactful if they are actively targeting a specific behavior. It is helpful to identify for clients in advance the types of conditioned emotional responses that are likely to appear so that they can detect even small advances in the reduction of their pet's distress.

Session duration and frequency

Any fear-reduction procedure is more likely to be successful if sessions are long (prolonged exposure to the fear-eliciting stimulus is best) and if treatment sessions are scheduled frequently (Mackintosh, 1974). The one caveat is that if the animal is still experiencing considerable anxiety, frequent sessions can actually cause sensitization. While it is unavoidable for animals to experience some distress during sessions, it should be kept to a minimum and sessions should end on a high (positive) note, when the animal is as relaxed as possible (Thyer *et al.*, 1988).

Choice of reinforcement

The importance of identifying powerful reinforcement cannot be underestimated when it comes to treating distress disorders. Laboratory examples of CC invariably involve food as an appetitive stimulus, but Premack (1965) clarified that any pleasurable activity can function as reinforcement in the right circumstances. Therapists use a variety of activities, such as martial arts, relaxation, book reading, and inducing laughter to successfully treat anxiety, fear, and anger in human patients (Spiegler and Guevremont, 1993). At the ASPCA's BRC, some fearful dogs are encouraged to explore novel environments by arranging for urine overmarking or scent rolling opportunities.

D.F. Tortora (New Jersey City University, 1998, personal communication) argues that, whenever possible, play should be preferred over food when treating distress in animals because he believes play is more emotionally incompatible with fear than feeding (Fig. 24.4). Indeed, the author's dog exhibited extreme distress while in the car when it was going through an automated car wash. Several repetitions of the car wash experience combined with the dog's favorite treats had no discernible impact on the dog's fear. The dog ate the food but still shivered in terror. A switch to play had an immediate and dramatic effect. The use of certain phrases that had already been conditioned to predict games like tug and fetch completely changed the dog's emotional state so that within one session, the dog was barking with glee and chasing the water that was spraying on the windows. Furthermore, the change was relatively permanent. Years later, the dog still wagged his tail and got excited at the prospect of going through a car wash. Owners can often identify a hierarchy of phrases (i.e., 'walkies!', 'wanna go for a car ride?', etc.) that reliably produce changes in their pets' emotions and can be used as reinforcement in a CC application.

Incorporating some type of appetitive stimulus, whether it is food, play, or something else the animal finds pleasing seems to function to encourage the animal to maintain proximity with the fear-eliciting stimulus. Be aware, however, that reinforcing behaviors that are compatible with avoidance can actually backfire and intensify the animal's fear.

Maintenance

The most serious limitation of fear-reduction procedures is that the resulting behavior change is highly susceptible to relapse. After a great deal of effort to countercondition a switch from a fearful association to an appetitive one, the undesired fearful responses can easily emerge again because the original learning is never 'erased' but rather is inhibited by new learning. For instance, a change in the physical

354 P.J. Reid



Fig. 24.4. An example of using play to reinforce approach behavior in a dog that fears human interaction. (Photograph courtesy of the ASPCA's Behavioral Rehabilitation Center.)

context can prompt a renewal of fearful responses (Peck and Bouton, 1990). A dog may have undergone DSCC to overcome a fear of driving in the owner's car but the dog may experience a full-blown fear response in a novel car. Simply not driving in the owner's car for a time can result in spontaneous recovery of the fear (Bouton and Peck, 1992). If fear of the car was initially established because of a traumatic event such as an accident, experiencing some component of that event, say slamming on the brakes, can reinstate the original fear (Brooks et al., 1995). The first-learned fear is always susceptible to rapid reacquisition so treatment regimens must incorporate measures, such as generalization across multiple contexts and lifetime maintenance, to guard against relapse (Bouton, 2014).

24.3 Adjunct Treatment Options

There are various other treatment options that can be used in conjunction with the previous procedures or, in some cases, on their own.

24.3.1 Social buffering

It is well established in a variety of species that fearful responses in an animal can be attenuated by the presence of a calm companion (Epley, 1974;

Chapter 8, this volume). Just as fear can be socially transmitted between individuals (Mineka and Cook, 1993; D'Aniello et al., 2018), so can feelings of safety and reduced fear (Kikusui et al., 2006). Baum (1969) and Uno et al. (1973) showed that when an animal is first conditioned to perform a response to escape or avoid shock and then the shock is turned off, the conditioned animal performs fewer avoidance responses during the extinction phase if accompanied by a nonfearful conspecific. This social buffering may be the result of distracting the conditioned animal from attending to the fear-eliciting stimulus and/or of pairing the fear-eliciting stimulus with safety cues emitted by the companion (Morozov and Ito, 2018). It appears that animals emit multisensory safety cues – physical, visual, olfactory, auditory - that provide a buffer for the otherwise frightened animal (Morozov and Ito, 2018).

Human patients undergoing therapy for phobias benefit from observing the therapist or another individual confidently approaching and interacting with the fear-eliciting stimulus (Bandura *et al.*, 1967). Rats benefit from similar observation even if the nonfearful companion is separated by a wiremesh partition and a gap of 5 cm to prevent the rats from making physical contact (Kiyokawa *et al.*, 2009). However, social buffering is enhanced if the

animals are permitted to interact (Liu and Yuan, 2016). Familiarity is a factor as well; Kiyokawa *et al.* (2014) found that the more familiar the companion, the greater the social buffering effect.

Social buffering is a powerful component of the treatment program implemented with fearful, unsocialized dogs at the ASPCA's BRC. Fearful dogs are paired up with more confident 'helper' dogs until the final stages of treatment. Not only does the helper dog shield the fearful dog from experiencing full-blown anxiety; a social facilitation effect may be at work as well. The fearful dog observes the helper dog confidently approaching people and obtaining treats or playing with a toy and is more likely to get caught up in the action. On walks in novel places, the presence of the helper dog exploring the environment and investigating smells encourages the fearful dog to do the same. If incorporating helper companions into a treatment regimen, it is best to use a nonfearful helper with a solid history of positive interactions with people so as not to risk a reverse effect, in which alarm cues from the fearful dog facilitate the acquisition of fear in the helper (Kiyokawa et al., 2014; Morozov and Ito, 2018). Social buffering is highly context specific, so it can be tricky to fade out the use of the helper animal (Mikami et al., 2016). It is not surprising that integration of these fearful dogs into adoptive homes is more successful if there is a nonfearful dog already in the home (Fig. 23.5).

24.3.2 Competing response training

There are techniques that appear to be slight variations on OCC. Competing response training, or

countercommanding, is a technique in which the animal is presented with the feared stimulus and then explicitly cued to perform an already-trained incompatible behavior (Borchelt, 1987). For instance, the client cues the dog to back away from a stranger rather than lunging forward. The goal is for the stranger to eventually function as a discriminative stimulus, cueing the new incompatible behavior without the aid of the client. Schwartz and Robbins (1995) claim that the main difference from OCC is that users of competing response training emphasize generalization of the new behaviors to a realistic range of stimuli.

Differential reinforcement of incompatible behavior (DRI), in practical terms, is likely the same as OCC, although to be precise, differential schedules only reinforce the target behavior if it occurs within a specified period of time (Lindsay, 2000). Instead of targeting a behavior that is naturally elicited by the appetitive stimulus, such as orienting to the client, an incompatible behavior in the animal's repertoire is identified and reinforced when it occurs, while unwanted behavior is ignored. No effort is made to elicit the incompatible response, so it must be a behavior that has some probability of occurring on its own. For instance, suppose the dog typically vacillates between hiding under the bed and peering around the doorway when a guest is in the home. If the client were to implement a DRI schedule, they would reward the dog each time it pokes its head around the doorway and ignore hiding and, if the schedule is effective, the frequency of peering out will increase while the frequency of hiding decreases. It is also conceivable to implement a DRO (differential rein-





Fig. 24.5. A dog is reluctant to navigate the stairs on its own but willingly follows a confident helper dog. (Photograph credit: Pamela Reid.)

356 P.J. Reid

forcement of other behavior) or a DRH (differential reinforcement of high rates of any behavior other than the undesired behavior) but these procedures are less targeted and more complicated for clients to put into practice.

24.3.3 Backward chaining

Backward chaining can be used to establish new sequences of behavior in a distressing situation (Martin and Pear, 1996). This technique is most useful for teaching animals to move through frightening environments, such as conditioning a dog to navigate stairs. Backward chaining starts with the final link of the behavior chain so that the animal is always moving toward a familiar, safe place. In the case of a dog that is frightened to navigate a set of stairs, the final link is the top step of the stairway. The client begins by carrying the dog up to the step before the top. The dog is motivated to take the one step because it is moving toward the safety of level ground. Over repetitions, the dog is carried less far up the stairs. Navigating each step is reinforced because the dog is moving closer to safety, along an increasingly familiar sequence of steps. Eventually the dog can navigate the stairs on its own. From the dog's perspective, it is always moving toward the level ground at the top, even though it is now starting from the bottom. Backward chaining is also useful for treating animals that are afraid to walk through a room or step on certain substrates, such as tiled or slippery floors, provided the dog does not rush frantically through the sequence.

A slightly different but related procedure, used at the ASPCA's BRC, is to teach the dog to perceive something, such as a crate, as a secure base or safe haven and then bring the crate along when exposing the dog to unfamiliar environments (Fig. 24.6). Much like Harlow's monkeys with their surrogate terry-cloth-covered inanimate mothers (Harlow and Suomi, 1970), an animal that is frightened of a novel environment is more willing to venture into unfamiliar territory if it has a safe, secure base from which to start (Kraemer, 1992). At the ASPCA's BRC, dogs are coaxed to move in novel environments alongside a rolling crate-on-wheels, into which they can retreat if they become overwhelmed. This technique has served to kickstart some dogs that



Fig. 24.6. At the ASPCA's Behavioral Rehabilitation Center, a dog learns to move through a novel environment more comfortably when accompanied by its safe haven, the crate. (Photograph courtesy of the ASPCA's Behavioral Rehabilitation Center.)

were reluctant to walk outside of their kennels, even with a confident helper dog.

24.3.4 Clicker training/shaping by successive approximations

Clicker training is a technique that can facilitate the replacement of distress behaviors with desirable ones. Technically, clicker training means operant conditioning, using a clicker as an auditory conditioned reinforcer. Through classical conditioning, the animal is first taught to associate the sound of the clicker (the CS) with food (the UCS) until the clicker comes to take on secondary reinforcing properties. The clicker is then inserted into the training sequence to mark the desired behavior and bridge the time between the behavior and the delivery of the food reinforcement. Use of a conditioned reinforcer is generally considered to enhance learning when compared to the same training procedure without a conditioned reinforcer (Williams and Dunn, 1991), however a recent review by Dorey and Cox (2018) suggests that the superiority of clicker training is unsubstantiated by research.

Clicker training is often a euphemism for a handsoff form of operant conditioning that involves shaping new behavior topographies by differentially reinforcing successive approximations (shaping by successive approximations, or SBSA) to the desired

behavior. SBSA can be extremely helpful when working with animals suffering from distress disorders because of the hands-off nature of the technique, as handling can sometimes interfere with a fearful animal's ability to learn. For example, a dog that displays hand shyness can be shaped, with the use of a clicker, to approach, and even touch, an outstretched hand without the person making any movement toward the dog (Fig. 24.7). Exotic species that cannot be handled safely by people are shaped to comply with minor veterinary procedures by offering certain parts of their bodies for examination, a technique called body targeting (Young and Cipreste, 2004). SBSA can be particularly useful for teaching an animal to perform behaviors such as entering a crate or wearing a muzzle. Many animals show reluctance, or even fear, during crating or muzzling, further retarding their treatment progress. Because the use of SBSA never involves forcing or even tempting the animal with treats to enter the crate or put its face in the muzzle, fear is not elicited, and training can proceed at a rate that is comfortable for the animal.

24.3.5 Pressure-release

Pressure—release is a response prevention technique that is based on the process of negative reinforcement, in conjunction with extinction. While exposed



Fig. 24.7. A fearful dog at the ASPCA's Behavioral Rehabilitation Center learning to hand target. (Photograph credit: ASPCA.)

358 P.J. Reid

to the fear-eliciting stimulus, the animal is prevented from escaping with some sort of pressure. As soon as the animal offers an alternative behavior, it is negatively reinforced by relief from the pressure. Imagine a dog that balks when going through doorways. The handler applies just enough pressure on the leash to make it mildly uncomfortable for the dog and releases it the moment the dog takes a step forward. If the dog balks again, the process repeats until the dog has moved through the doorway. Moving forward is negatively reinforced by relief from pressure and with repetitions, fear of doorways extinguishes.

Much of traditional horse training is based on pressure-release procedures. A classic example is Monty Roberts' round-pen technique for working with unsocialized horses (Roberts, 1997). The horse is contained in a circular pen and Roberts applies pressure by moving toward the horse. The horse runs away. This persists until the horse finally stops running, at which point Roberts immediately relieves the pressure by turning away from the horse. If the horse remains at a distance, Roberts resumes applying pressure. At some point, the horse takes a step toward Roberts and he moves away. The horse quickly learns that it can relieve its distress by moving toward the frightening stimulus rather than from it. In short order, the horse accepts contact from Roberts. The horse's escape response is ineffective, so undergoes extinction, while at the same time, behaviors that move the horse closer to the feared stimulus are negatively reinforced. Recent work by Valenchon et al. (2017) suggests there may be a nonintuitive interaction between horse personality and responsiveness to training with negative reinforcement. They found that, provided there were no additional stressors in the environment, fearful horses performed best with negative reinforcement techniques whereas nonfearful horses responded best to positive reinforcement techniques.

Like Roberts (1997), Snider's (2017) constructional aggression treatment incorporates an element of pressure–release negative reinforcement. The dog is prevented from contacting the feared stimulus (a stranger) or from escaping the situation. The stranger remains in the situation (essentially applying pressure by his presence) until the dog ceases responding aggressively. The instant the dog stops, the stranger leaves. The stranger's departure serves to negatively reinforce the dog's alternative behavior. After an interval, the stranger returns

and the process repeats until the dog recognizes that the way to get rid of the stranger is to offer nonaggressive behaviors. Eventually the dog's fear of the stranger diminishes, and the client can switch to a procedure more akin to OCC.

24.3.6 Predictability and control

Considerable evidence has accumulated in humans and animals indicating an array of benefits from having a perception of being able to predict and/or control exposure to fear-provoking stimuli and the autonomy to terminate the experience at any time it becomes too much to handle (for reviews, see Peterson, 1999; Franks and Higgins, 2012; Chapter 6, this volume). Some inconsistent findings have been reported, however; for instance, Thompson (1981) found little evidence to support that knowing something bad is going to happen lessens the perception of unpleasantness, and Grillon et al. (2004) reported that if the feared event cannot be avoided, then being able to anticipate that it is coming just seems to make things worse. Overall, the experimental evidence suggests that the effects of predictability and controllability are extraordinarily complicated and interdependent (Averill, 1973; Mineka and Henderson, 1985).

Select techniques that have been popularized in the behavior and training literature emphasize the importance of teaching the animal that it is able to predict and control its contact with the fear-inducing stimulus. Stewart's (2016) behavior adjustment training is an amalgamation of DSCC, negative reinforcement (in the form of providing 'relief' by moving away from the feared stimulus), and enabling the animal to control whether or not to attend to or approach the stimulus. Patel's 'bucket game' is also focused on providing the dog with control over whether it is prepared to accept graded handling and for how long (Cartlidge, 2018). The dog is taught that when it attends to the bucket, it will be handled (with handling 'countered' by treats). Looking away from the bucket causes the handling to stop (and the treats). Attention to the bucket functions as the dog giving the person 'permission' to perform the handling maneuvers. The ASPCA's BRC uses body targeting in conjunction with counterconditioning to teach fearful dogs to offer parts of their body up for physical contact with a person's hand, thereby controlling the initiation, intensity, and duration of contact. Nonetheless, it has yet to be demonstrated whether providing the animal with some degree of autonomy over its exposure to feared stimuli is any more efficacious than procedures that are entirely out of the animal's control.

24.4 Concluding Remarks

The nonpharmacologic treatment of emotional distress and disorders in companion animals involves a careful assessment of the etiology of the fear, the typography of the fear-related behaviors, the eliciting stimuli, and the contexts in which the fear is exhibited. Treatment programs leading to the reduction of emotionally based behaviors consist of both behavior management and behavior change techniques designed to reduce negative emotional states and replace them with positive emotional states. Combined CCC and OCC procedures are expected to be most effective for changing and sustaining reductions in emotional distress.

24.5 References

- Aloff, B. (2001) Positive Reinforcement: Training Dogs in the Real World. T.F.H. Publications, Neptune City, New Jersey, USA.
- Antony, M.M. and Barlow, D.H. (1997) Social and specific phobias. In: Tasman, A. and Lieberman, J.A. (eds.) *Psychiatry*. WB Saunders, Philadelphia, Pennsylvania, USA, pp. 1037–1059.
- Averill, J.R. (1973) Personal control over aversive stimuli and its relationship to stress. *Psychological Bulletin* 80, 286–303. http://dx.doi.org/10.1037/h0034845.
- Barlia, E. (1988) A case study on aggression in dogs.

 Animal Behavior Consultant's Newsletter 5, 2.
- Bandura, A., Grusec, J.E., Menlove, F.L. (1967) Vicarious extinction of avoidance behavior. *Journal of Personality and Social Psychology* 5, 16–23. http://dx.doi.org/10.1037/h0024182.
- Baum, M. (1969) Extinction of an avoidance response motivated by intense fear: Social facilitation of the action of response prevention (flooding) in rats. Behaviour Research and Therapy 7, 57–62. http:// dx.doi.org/10.1016/0005-7967(69)90049-7.
- Borchelt, P.L. (1987) Counterconditioning and countercommanding. *Animal Behavior Consultant's Newsletter* 4, 3.
- Bouton, M.E. (2014) Why behavior change is difficult to sustain. *Preventive Medicine* 68, 29–36. http://dx.doi.org/10.1016/j.ypmed.2014.06.010.
- Bouton, M.E. and Peck, C.A. (1992) Spontaneous recovery in cross-motivational transfer (counterconditioning). *Animal Learning & Behavior* 20, 313–321. http://dx.doi.org/10.3758/BF03197954.

- Brooks, D.C., Hale, B., Nelson, J.B., Bouton, M.E. (1995) Reinstatement after counterconditioning. *Animal Learning & Behavior* 23, 383–390. http://dx.doi.org/10.3758/BF03198938.
- Calder, C.D. (2019) Animal Behavior Case of the Month. Journal of the American Veterinary Medical Association 254, 213–216. http://dx.doi.org/10.2460/javma.254.6.676.
- Cannas, S., Talamonti, Z., Mazzola, S., Minero, M., Picciolini, A., et al. (2018) Factors associated with dog behavioral problems referred to a behavior clinic. Journal of Veterinary Behavior 24, 42–47. http://dx.doi.org/10.1016/j.jveb.2017.12.004.
- Capaldi, E.D., Viveiros, D.M., Campbell, D.H. (1983) Food as a contextual cue in counterconditioning experiments: Is there a counterconditioning process? *Animal Learning & Behavior* 11, 213–222. http://dx.doi.org/10.3758/BF03199651.
- Cartlidge, R. (2018) Chirag Patel Domesticated Manners (The bucket game). Available at: https:// www.animaltrainingacademy.com/podcast/trainingtidbits/chirag-patel (accessed 31 March 2019).
- Clothier, S. (2005) Bones Would Rain From the Sky: Deepening Our Relationships With Dogs. Warner Books, New York, USA.
- D'Aniello, B., Semin, G.R., Alterisio, A., Aria, M., Scandurra, A. (2018) Interspecies transmission of emotional information via chemosignals: From humans to dogs (Canis lupus familiaris). Animal Cognition 21, 67–78.
- De Havas, J., Ghosh, A., Gomi, H., Haggard, P. (2016) Voluntary motor commands reveal awareness and control of involuntary movement. *Cognition* 155, 155–167. http://dx.doi.org/10.1016/j.cognition.2016.06.012.
- Dearing, M.F. and Dickinson, A. (1979) Counterconditioning of shock by a water reinforcer in rabbits. Animal Learning & Behavior 7, 360–366. http://dx.doi.org/10.3758/BF03209685.
- Dess, N.K., Linwick, D., Patterson, J., Overmier, J.B., Levine, S. (1983) Immediate and proactive effects of controllability and predictability on plasma cortisol responses to shocks in dogs. *Behavioral Neuro*science 97, 1005–1016. http://dx.doi.org/10.1037/ 0735-7044.97.6.1005.
- Dickinson, A. and Pearce, J.M. (1977) Inhibitory interactions between appetitive and aversive stimuli. *Psychological Bulletin* 84, 690–711. http://dx.doi.org/10.1037/0033-2909.84.4.690.
- Dorey, N.R. and Cox, D.J. (2018) Function matters: A review of terminological differences in applied and basic clicker training research. *PeerJ* 6, e5621. http:// dx.doi.org/10.7717/peerj.5621.
- Epley, S.W. (1974) Reduction of the behavioral effects of aversive stimulation by the presence of companions. *Psychological Bulletin* 81, 271. http://dx.doi.org/ 10.1037/h0036389.
- Erofeeva, M.N. (1921) Additional data on nocuous conditioned reflexes. *Isvestiga Petrogradskogo Nauchnago Instituta im. PF Lesgafta* 3, 69–73.

360 P.J. Reid

- Fanselow, M.S. (1990) Factors governing one-trial contextual conditioning. *Animal Learning & Behavior* 18, 264–270. http://dx.doi.org/10.3758/BF03205285.
- Ferdowsian, H.R., Durham, D.L., Johnson, C.M., Brüne, M., Kimwele, C., et al. (2012) Signs of generalized anxiety and compulsive disorders in chimpanzees. Journal of Veterinary Behavior 7, 353–361. http://dx.doi.org/10.1016/j.jveb.2012.01.006.
- Foa, E.B., Zinbarg, R., Rothbaum, B.O. (1992) Uncontrollability and unpredictability in post-traumatic stress disorder: An animal model. *Psychological Bulletin* 112, 218–238. http://dx.doi.org/10.1037/0033-2909. 112.2.218.
- Franks, B. and Higgins, E.T. (2012) Effectiveness in humans and other animals: A common basis for wellbeing and welfare. In: Olson, J.M. and Zanna, M.P. (eds.) Advances in Experimental Social Psychology, Vol. 46. Academic Press, Burlington, Massachusetts, USA, pp. 285–346. http://dx.doi.org/10.1016/B978-0-12-394281-4.00006-4.
- Gambrill, E. (1967) Effectiveness of the counterconditioning procedure in eliminating avoidance behavior. Behavioural Research and Therapy 5, 263–273. http://dx.doi.org/10.1016/0005-7967(67)90018-6.
- Grillon, C., Baas, J.P., Lissek, S., Smith, K., Milstein, J. (2004) Anxious responses to predictable and unpredictable aversive events. *Behavioral Neuroscience* 118, 916–924. http://dx.doi.org/10.1037/0735-7044. 118.5.916.
- Haesen, K., Beckers, T., Baeyens, F., Vervliet, B. (2017) One-trial overshadowing: Evidence for fast specific fear learning in humans. *Behaviour Research and Therapy* 90, 16–24. http://dx.doi.org/10.1016/j.brat. 2016.12.001.
- Harlow, H.F. and Suomi, S.J. (1970) Nature of love: Simplified. American Psychologist 25, 161–168. http://dx.doi.org/10.1037/h0029383.
- Hersen, M. (1973) Self-assessment of fear. Behavior Therapy 4, 241–257. http://dx.doi.org/10.1016/S0005-7894(73)80034-6.
- Hothersall, D.A. and Tuber, D.S. (1979) Fears in companion dogs: Characteristics and treatment. *Psychopathology* in Animals: Research and Clinical Implications. Academic Press. New York, USA.
- Jarvik, M.E. and Essman, W.B. (1960) A simple one-trial learning situation for mice. *Psychological Reports* 6, 290. http://dx.doi.org/10.2466/pr0.1960.6.2.290.
- Jones, M.C. (1924) The elimination of children's fears. Journal of Experimental Psychology 7, 382–390. http://dx.doi.org/10.1037/h0072283.
- Kikusui, T., Winslow, J.T., Mori, Y. (2006) Social buffering: Relief from stress and anxiety. *Philosophical Transactions* of the Royal Society B: Biological Sciences 361, 2215– 2228. http://dx.doi.org/10.1098/rstb.2006.1941.
- Kiyokawa, Y., Hiroshima, S., Takeuchi, Y., Mori, Y. (2014) Social buffering reduces male rats' behavioral and corticosterone responses to a conditioned stimulus.

- Hormones and Behavior 65, 114–118. http://dx.doi.org/10.1016/j.yhbeh.2013.12.005.
- Kiyokawa, Y., Takeuchi, Y., Nishihara, M., Mori, Y. (2009) Main olfactory system mediates social buffering of conditioned fear responses in male rats. *European Journal of Neuroscience* 29, 777–785. http://dx.doi.org/10.1111/j.1460-9568.2009.06618.x.
- Kraemer, G.W. (1992) A psychobiological theory of attachment. Behavioral and Brain Sciences 15, 493– 511. http://dx.doi.org/10.1017/S0140525X00069752.
- Lindsay, S.R. (2000) Handbook of Applied Dog Behavior and Training, Vol. 1: Adaptation and Learning. Iowa State University Press, Ames, Iowa, USA. http:// dx.doi.org/10.1002/9780470376874.
- Lindsay, S.R. (2001) Handbook of Applied Dog Behavior and Training, Vol. 2: Etiology and Assessment of Behavior Problems. Iowa State University Press, Ames, Iowa, USA. http://dx.doi.org/10.1002/9780470376997.
- Lindsay, S.R. (2005) Handbook of Applied Dog Behavior and Training, Vol. 3: Procedures and Protocols. Iowa State University Press, Ames, Iowa, USA. http://dx.doi.org/10.1002/9780470344514.
- Liu, H. and Yuan, T.F. (2016) Physical interaction is required in social buffering induced by a familiar conspecific. Scientific Reports 6, 39788. http://dx.doi. org/10.1038/srep39788.
- Mackintosh, N.J. (1974) *The Psychology of Animal Learning*. Academic Press, London, UK.
- Martin, G. and Pear, J. (1996) *Behavior Modification:* What It Is and How To Do It, 5th edn. Prentice Hall Upper Saddle River, New Jersey, USA.
- McConnell, P.B. (2005) The Cautious Canine: How To Help Dogs Conquer Their Fears, 2nd edn. McConnell Publishing, Black Earth, Wisconsin, USA.
- McDevitt, L. (2007) Control Unleashed: Creating a Focused and Confident Dog. Clean Run Productions, South Hadley, Massachusetts, USA.
- McMillan, F.D. (2017) Behavioral and psychological outcomes for dogs sold as puppies through pet stores and/or born in commercial breeding establishments: Current knowledge and putative causes. *Journal of Veterinary Behavior* 19, 14–26. http://dx.doi.org/10.1016/j.jveb.2017.01.001.
- McMillan, F.D., Duffy, D.L., Serpell, J.A. (2011) Mental health of dogs formerly used as 'breeding stock' in commercial breeding establishments. *Applied Animal Behaviour Science* 135, 86–94. http://dx.doi.org/10.1016/ j.applanim.2011.09.006.
- McMillan, F.D., Serpell, J.A., Duffy, D.L., Masaoud, E., Dohoo, I.R. (2013) Differences in behavioral characteristics between dogs obtained as puppies from pet stores and those obtained from noncommercial breeders. *Journal of the American Veterinary Medical Association* 242, 1359–1363. http://dx.doi.org/10.2460/javma.242.10.1359.
- Metja, C., Reid, L., Coon, K., Paxton, R. (1974) Methods of deconditioning avoidance: II. JSAS Catalogue of Selected Documents in Psychology 4, 119–120.

- Mikami, K., Kiyokawa, Y., Takeuchi, Y., Mori, Y. (2016) Social buffering enhances extinction of conditioned fear responses in male rats. *Physiology & Behavior* 163, 123–128. http://dx.doi.org/10.1016/j.physbeh. 2016.05.001.
- Miller, P. (2001) *The Power of Positive Dog Training*. Hungry Minds, New York, USA.
- Mineka, S. and Cook, M. (1993) Mechanisms involved in the observational conditioning of fear. *Journal of Experimental Psychology: General* 122, 23-38.
- Mineka, S. and Hendersen, R.W. (1985) Controllability and predictability in acquired motivation. *Annual Review of Psychology* 36, 495–529. http://dx.doi. org/10.1146/annurev.ps.36.020185.002431.
- Mineka, S. and Oehlberg, K. (2008) The relevance of recent developments in classical conditioning to understanding the etiology and maintenance of anxiety disorders. *Acta Psychologica* 127, 567–580. http:// dx.doi.org/10.1016/j.actpsy.2007.11.007.
- Moberg, G.P. (2000) Biological response to stress: Implications for animal welfare. In: Moberg, G.P. and Mench, J.A. (eds.) *The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare*. CABI Publishing, Wallingford, UK, pp. 1–22. http://dx.doi.org/10.1079/9780851993591.0000.
- Morozov, A. and Ito, W. (2019) Social modulation of fear: Facilitation vs buffering. *Genes, Brain and Behavior* 18, e12491. http://dx.doi.org/10.1111/gbb.12491.
- Murphree, O.D. (1973) Inheritance of human aversion and inactivity in two strains of the pointer dog. *Biological Psychiatry* 7, 23–29.
- Ougrin, D. (2011) Efficacy of exposure versus cognitive therapy in anxiety disorders: Systematic review and meta-analysis. BMC Psychiatry 11, 200. http://dx.doi.org/ 10.1186/1471-244X-11-200.
- Overall, K.L. (1997) Clinical Behavioral Medicine for Small Animals. Mosby-Year Book, Inc., St. Louis, Missouri, USA.
- Patronek, G.J., Glickman, L.T., Beck, A.M., McCabe, G.P., Ecker, C. (1996) Risk factors for relinquishment of dogs to an animal shelter. *Journal of the American Veterinary Medical Association* 209, 572–581.
- Peck, C.A. and Bouton, M.E. (1990) Context and performance in aversive-to-appetitive and appetitive-to-aversive transfer. *Learning and Motivation* 21, 1–31. http://dx.doi.org/10.1016/0023-9690(90)90002-6.
- Peterson, C. (1999) Personal control and well-being. In: Kahneman, D., Diener, E., Schwarz, N. (eds.) Wellbeing: The Foundations of Hedonic Psychology. Russell Sage Foundation, New York, USA, pp. 288–301.
- Poppen, R. (1970) Counterconditioning of conditioned suppression in rats. *Psychological Reports* 27, 659– 671. http://dx.doi.org/10.2466/pr0.1970.27.2.659.
- Premack, D. (1965) Reinforcement theory. In: Nevine, D. (ed.) Nebraska Symposium on Motivation. University of Nebraska Press, Lincoln, Nebraska, pp. 123–180.

- Price, C. (2001) Understanding the Rescue Dog: All You Need to Know about Rehoming a Dog with a Past. Broadcast Books. Bristol. UK.
- Rachman, S. (1990) The determinants and treatment of simple phobias. Advances in Behaviour Research and Therapy 12, 1–30. http://dx.doi.org/10.1016/ 0146-6402(90)90005-B.
- Roberts, M. (1997) *The Man Who Listens To Horses*. Random House, New York, USA.
- Salzinger, K. and Waller, M.B. (1962) The operant control of vocalization in the dog. *Journal of the Experimental Analysis of Behavior* 5, 383–389. http://dx.doi. org/10.1901/jeab.1962.5-383.
- Scavio, M.J. (1974) Classical-classical transfer: Effects of prior aversive conditions upon appetitive conditioning in rabbits (*Oryctolagus cuniculus*). *Journal of Comparative and Physiological Psychology* 86, 107–115. http://dx.doi.org/10.1037/h0035966.
- Schilder, M.B. and van der Borg, J.A. (2004) Training dogs with help of the shock collar: Short and long term behavioural effects. Applied Animal Behaviour Science 85, 319–334. http://dx.doi.org/10.1016/j. applanim.2003.10.004.
- Schwartz, B. and Robbins, S.J. (1995) *Psychology of Learning and Behavior*, 4th edn. WW Norton, New York, USA.
- Scott, J.P. and Fuller, J.L. (1965) *Genetics and the Social Behavior of the Dog*. University of Chicago Press, Chicago, Illinois, USA.
- Segurson, S.A., Serpell, J.A., Hart, B.L. (2005) Evaluation of a behavioral assessment questionnaire for use in the characterization of behavioral problems of dogs relinquished to animal shelters. *Journal of the American Veterinary Medical Association* 227, 1755–1761. http://dx.doi.org/10.2460/javma.2005.227.1755.
- Skinner, B.F. (1957) Verbal Behavior. Appleton-Century Crofts, New York, USA. http://dx.doi.org/10.1037/11256-000.
- Snider, K. (2017) Turning Fierce Dogs Friendly: Using Constructional Aggression Treatment to Rehabilitate Aggressive and Reactive Dogs. Companion House Books, Mount Joy, Pennsylvania, USA.
- Spiegler, M.D. and Guevremont, D.C. (1993) *Contemporary Behavior Therapy*, 2nd edn. Brooks/Cole, Pacific Grove, California, USA.
- Stein, L. (1964) Reciprocal action of reward and punishment mechanisms. In: Heath, R.G. (ed.) The Role of Pleasure In Behavior. Harper and Row, New York, 1194
- Stewart, G. (2016) Behavior Adjustment Training 2.0: New Practical Techniques for Fear, Frustration, and Aggression. Direct Book Service, Wenatchee, Washington, USA.
- Tarpy, R.M. (1982) Principles of Animal Learning and Motivation. Scott, Foresman, Glenview, Illinois, USA.
- Thomas, B.L., Cutler, M., Novak, C. (2012) A modified counterconditioning procedure prevents the renewal

362 P.J. Reid

- of conditioned fear in rats. Learning and Motivation 43,24–34.http://dx.doi.org/10.1016/j.lmot.2012.01.001.
- Thompson, S.C. (1981) Will it hurt less if I can control it?
 A complex answer to a simple question. *Psychological Bulletin* 90, 89–101. http://dx.doi.org/10.1037/0033-2909.90.1.89.
- Thompson, W.R. (1958) Social behavior. In: Roe, A. and Simpson, G. (eds.) Behavior and Evolution. Yale University Press, New Haven, Connecticut, USA.
- Thyer, B.A., Baum, M., Reid, L.D. (1988) Exposure techniques in the reduction of fear: A comparative review of the procedure in animals and humans. *Advances in Behaviour Research and Therapy* 10, 105–127. http://dx.doi.org/10.1016/0146-6402(88)90011-2.
- Tiira, K., Sulkama, S., Lohi, H. (2016) Prevalence, comorbidity, and behavioral variation in canine anxiety. *Journal of Veterinary Behavior* 16, 36–44. http://dx.doi.org/10.1016/j.jveb.2016.06.008.
- Uno, T., Greer, S.E., Goates, L. (1973) Observational facilitation of response prevention. *Behaviour Research and Therapy* 11, 207–212. http://dx.doi.org/10.1016/S0005-7967(73)80007-5.
- Valenchon, M., Lévy, F., Moussu, C., Lansade, L. (2017) Stress affects instrumental learning based on positive or negative reinforcement in interaction with

- personality in domestic horses. *PLoS ONE* 12, e0170783. http://dx.doi.org/10.1371/journal.pone.0170783.
- Williams, N.G. and Borchelt, P.L. (2003) Full body restraint and rapid stimulus exposure as a treatment for dogs with defensive aggressive behavior: Three case studies. *International Journal of Comparative Psychology* 16, 226–236.
- Williams, B.A. and Dunn, R. (1991) Substitutability between conditioned and primary reinforcers in discrimination acquisition. *Journal of the Experimental Analysis of Behavior* 55, 21–35. http://dx.doi.org/ 10.1901/jeab.1991.55-21.
- Wolpe, J. (1958) Psychotherapy by Reciprocal Inhibition. Stanford University Press, Stanford, California, USA.
- Wolpe, J. (1984) Deconditioning and ad hoc uses of relaxation: An overview. *Journal of Behavior Therapy* and Experimental Psychiatry 15, 299–304. http://dx. doi.org/10.1016/0005-7916(84)90092-2.
- Wolpe, J. and Lazarus, A.A. (1966) *Behavior Therapy Techniques: A Guide to the Treatment of Neuroses*. Pergamon Press, New York, USA.
- Young, R.J. and Cipreste, C.F. (2004) Applying animal learning theory: Training captive animals to comply with veterinary and husbandry procedures. *Animal* Welfare 13, 225–232.

25 Treatment of Emotional Distress and **Disorders – Pharmacologic Methods**

SHARON CROWELL-DAVIS

Department of Veterinary Biosciences and Diagnostic Imaging, College of Veterinary Medicine, University of Georgia, Athens, Georgia, USA

25.1 Why Use Medications?

All of the emotions are a consequence of chemical reactions within the central nervous system (CNS). Ideally, an animal's genetics, diet, experience, and environment are such that the various neurochemicals that affect emotion are in the appropriate amount and location for the animal to primarily experience positive affect, and only experience negative affect when there is a strong reason to, such as a cat being attacked by a dog. In this situation, the emotion of fear, the well-known 'fight-orflight' response, will occur. If it is able to, the cat will likely run away, climb a tree, or hide in a location where the dog cannot reach it. If it cannot escape, it will begin using its teeth and claws to defend itself. In this case fear is normal, and facilitates actions that maximize the likelihood of survival.

If the cat experiences the same fear upon seeing an unknown dog through a window, or encountering an unfamiliar human who is visiting the home and represents no threat of harm to the cat, its wellbeing may be adversely affected. Returning to a normal state of mental health, i.e., the cat does not experience fear when there is no danger, requires a change in the chemical reactions in the animal's brain. In many cases, this can be achieved satisfactorily without using pharmacologic treatments, as is discussed in Chapter 24, this volume. However, in severe cases, or to make recovery occur faster, pharmacologic medications are often needed.

While for various reasons many individuals oppose the use of medication, if we are focusing on optimizing the patient's welfare we must consider the potential benefits of pharmacologic agents, especially anxiolytic medications in animals that have developed disorders of anxiety or fear. Important

considerations include the type of problem, severity of the problem, medical problems the animal has (e.g., diabetes), the owner's ability to medicate the patient, existing evidence of potential benefits, and potential adverse side-effects. In many cases, the use of appropriate medication increases – often dramatically - the patient's welfare. Sometimes medications are used in good part because the patient's behavior is disturbing to the owner. For example, a storm phobic dog may howl and destroy things in the house. In contrast, many storm phobic cats simply hide. Is the welfare of the cat that is hiding any less compromised than that of the dog that is showing signs of distress? Probably not. The author has one cat with storm phobia. In the case of mild storms, we simply ensure that she has a good place to hide. With a mild storm and the availability of a good hiding spot, such as under a particular desk, her body language does not show substantial fear; however, signs will become evident if she is taken out of her hiding place. In the case of severe storms, or if her body language shows that she is fearful even while hiding, she is given an anxiolytic, not for the convenience of the author, but for the welfare of the cat.

It is beyond the scope of this single chapter to cover all indications, contraindications, dosing protocols, costs, and other issues for all medications that may benefit a patient's psychological well-being. For a more comprehensive resource, see Veterinary Psychopharmacology, 2nd edition (Crowell-Davis et al., 2019b).

25.2 Decisions to Use Medication: Legal, Ethical, and Cost Issues

Prescription medications intended for animals must be prescribed by a veterinarian. The veterinarian

must make the decision to recommend medication based on their own medical and behavioral examination and their own diagnostic assessment. Additional information that may be used in making a diagnosis includes reports of the patient's behavior and mental status from the pet owner, trainers who have worked with the animal, animal behaviorists who are not veterinarians who have directly observed the animal, and others who have directly observed the animal. The prescribing veterinarian must perform their own direct examination of the patient, as it is both illegal and unethical for a veterinarian to provide a prescription based solely on the recommendation of another individual, even if they are a highly experienced animal behaviorist.

Not all of the psychoactive medications available on the market are in regular use in veterinary medicine or, most importantly, have evidence-based documentation of their efficacy and side-effect profile. Therefore, in the sections covering specific medications, only the more commonly used medications which currently have evidence-based documentation of their effects on at least one species of common veterinary patients are included.

25.2.1 The Animal Medicinal Drug Use Clarification Act (AMDUCA)

In the United States, the use of most psychoactive medications in animals is extra-label, i.e., the medication is not approved by the U.S. Food and Drug Administration (FDA) for the species and problem being treated. There are only a few exceptions at this time, i.e., Clomicalm (clomipramine) for separation anxiety in dogs, Anipryl (l-deprenyl) for cognitive dysfunction in elderly dogs, Sileo (dexmedetomidine) for noise aversion in dogs, and Reconcile (fluoxetine) for separation anxiety in dogs. All other uses of these medications are extralabel, for example, fluoxetine use in cats to treat separation anxiety and clomipramine use in dogs to treat storm phobia.

In all cases of extra-label use, the client should be informed of the extra-label status of the medication. It is advisable to accompany verbal explanations with a printed information sheet that discusses the extra-label use of medications, the reasons for this medication being used, the potential benefits, and the potential adverse effects. Have two copies, one of which the client signs, indicating that they have been

given the information and understand it; this copy goes in the patient's record. The other copy is for the client to take home to reread at their leisure.

25.2.2 Cost

Owners are usually paying for their pet's medication out of their own pocket. As a consequence, it is important to follow changes in price of the various psychoactive medications that are useful for pets. Substantial price changes can occur, sometimes very quickly. Therefore, current price of a medication, in addition to potential benefits and side-effects, should be taken into consideration when making a decision on which medication to prescribe.

25.2.3 Medicating the patient

Many psychoactive medications are given daily, or at least frequently. Getting patients to take medications on such a regular basis can be challenging. In some cases, the manufacturer has placed the active ingredient in a chewable form that the patient finds at least acceptably palatable. For dogs and cats, hiding the pill in one of the various snack 'pockets' that are available over the counter will facilitate voluntary consumption.

Usually, dogs are the easiest, as many dogs will gulp food, and can be relied on to do so if there is a routine that facilitates gulping. For example, begin by giving the dog a highly palatable treat at a particular time of day. The treat should be of the sort that can be used to hide medication, such as a meatball, piece of hot dog, or pocket. If the dog needs the treat to be tossed in order to gulp it without tasting, begin with gentle tosses at a short distance. Then proceed to tossing at a greater distance and with the style that is most likely to result in the dog gulping without chewing or otherwise pausing to taste. Once this is accomplished, hide the medication inside the treat, and medicate the dog this way.

Cats can be more difficult, as they do not often gulp without tasting the way dogs do. Nevertheless, a highly palatable food can be an excellent motivator for cats. One can train a cat to accept being given a pill or a liquid medication. In a similar fashion to training dogs, begin by taking the cat to a specific location, at about the same time of day, and giving it a highly palatable treat. This does not have to be something labeled as a 'treat' in the commercial cat food market. It can be a teaspoon of a wet food that the cat is particularly fond of, a bit of fish, or anything

else that the cat really likes, does not routinely get, and is safe to eat. After that habit is established, if the cat has to be given a pill it is not going to voluntarily consume, the owner starts the training by briefly placing their hands over the head and jaw of the cat the same way they would if they were going to open the cat's mouth to pill it. At this stage, the mouth is not opened. Immediately follow that action with the special treat. Once the cat is comfortable with this, the owner can open the mouth slightly and then give the cat the treat. Gradually, open the mouth more and more, followed by giving the treat. Once the cat's mouth can be opened as much as is needed for a pill to be placed in the back of the mouth, the owner should quickly stick their finger in, then again give the cat the treat. Finally, give the pill, and follow up with the special treat. Many cats will tolerate mildly aversive medical procedures if they anticipate a special food treat immediately following the procedure.

Medications that do not have a bitter or aversive taste can often be given to horses in their feed. For example, fluoxetine is available in capsules. The horse's daily dose of fluoxetine can be emptied into their grain, and stirred in. All of the horses that the author has treated this way have readily consumed it.

25.3 Fast-acting Medications

Fast-acting medications can be used on an as needed basis, or daily, depending on the species, the disorder, and the medication. For patients with major anxiety disorders, such as severe separation anxiety or severe storm phobia, fast-acting medications are often used as a supplement to a maintenance medication and behavior modification, especially during the first weeks of treatment. These products are most useful being used on an as needed basis, with no other

medication, when the situation that triggers anxiety or fear is uncommon, especially if it can be anticipated in advance. All of them typically work best if given in advance of the fear-inducing stimulus or situation. While the owner's departure or a visit to the veterinary hospital can be predicted in advance, aversive stimuli such as storms are usually much less predictable. However, modern weather monitoring systems, combined with various apps that can notify an owner on their smart phone or their computer that a storm is likely, have made it much easier to anticipate when a fast-acting medication is needed for a storm phobic patient.

25.3.1 Benzodiazepines

The benzodiazepines comprise the longest used rapidacting medications for anxiety and fear. They also often promote prosocial behavior. Their anxiolytic effects are due to action in the hypothalamus and cerebrum, facilitating the action of gamma-aminobutyric acid (GABA) in the CNS by binding to GABA_A receptors. Clinically, their duration of efficacy varies widely depending on the species, the dose, and whether the medication is given as a single dose or multiple doses.

They are useful for a wide variety of anxiety disorders, including submissive urination and urine marking in dogs, phobias, such as storm phobia and noise phobia, fear of being clipped, separation anxiety, and timidity. While dose recommendations have been offered for diazepam in cats, the author recommends that it not be used in this species due to reports of the drug causing acute hepatic failure and the fact that alternative benzodiazepines are available which have not been recorded as having this adverse effect in cats (Center *et al.*, 1996; Hughes *et al.*, 1996; Park, 2012; van Beusecom *et al.*,

Table 25.1. Doses of various benzodiazepines for dogs and cats.

Medication	Dogs	Cats
Alprazolam (Xanax)	0.02–0.1 mg/kg q4h	0.0125–0.25 mg/kg q8h
Chlordiazepoxide (Librium)	2.0-6.5 mg/kg q8h	0.2-1.0 mg/kg q12h
Clonazepam (Klonopin)	0.1-0.5 mg/kg q8-12h	0.015-0.2 mg/kg q8h
Clorazepate dipotassium (Tranxene)	0.5–2.0 mg/kg q4h	0.5-2.0 mg/kg q12h
Diazepam (Valium)	0.5–2.0 mg/kg q4h	0.1–1.0 mg/kg q4h
Flurazepam (Dalmane)	0.1–0.5 mg/kg q12h	0.1-0.4 mg/kg q12h
Lorazepam (Ativan)	0.02–0.5 mg/kg q8–12h	0.03–0.08 mg/kg q12h
Oxazepam (Serax)	0.04–0.5 mg/kg q6h	0.2-1.0 mg/kg q12-24h

Note: All doses given are orally and as needed until the desired effect is reached. The hourly schedules are the maximum frequency at which the medication should be given. As a general rule, start at the lowest dose and titrate upward if needed. See text for further explanation. From de Souza Dantas and Crowell-Davis (2019a), with permission.

366 S. Crowell-Davis

2015). Doses of eight different benzodiazepines for use in dogs and cats are given in Table 25.1. Diazepam doses for parrots, horses, and rabbits are given in Table 25.2.

25.3.2 Trazodone

Trazodone is a serotonin antagonist/reuptake inhibitor that blocks serotonin 2A and 2C receptors, as well as serotonin reuptake. It is given as needed for fear and anxiety, particularly when the animal is in a fear-inducing situation, such as going to the veterinary hospital.

Side-effects recorded in dogs include colitis, vomiting, increased excitement, sedation, increased appetite, and perceived disinhibition (Gruen and Sherman, 2008). Doses for the dog and cat are given in Table 25.3.

25.3.3 Sympatholytics

Dexmedetomidine

Dexmedetomidine is a sympatholytic medication for which an oral gel (Sileo) has been FDA-approved for use in dogs with noise phobias. It should be

Table 25.2. Dose of diazepam for parrots, horses, and rabbits.

Species	Diazepam dose
Parrot	Two drops of 5 mg/ml solution per ounce of drinking water
Horse	10–30 mg q8h
Rabbit	0.1–0.6 mg/kg

From de Souza Dantas and Crowell-Davis (2019a), with permission.

Table 25.3. Dose of trazodone given orally for dogs and cats.

Species	Dose range
Dog	1.7–19.5 mg/kg/day PO (daily or prn) or
Cat	1.7-9.5 mg/kg PO q8-24h 50-100 mg per cat PO prn or 10.6-33.3 mg/kg PO prn

PO, orally; prn, use when needed. From de Souza Dantas and Crowell-Davis (2019b), with permission. placed on the oral mucosa between the dog's cheek and gums, ideally 30–60 minutes before an anticipated adverse noise event. If unexpected noises occur and the dog begins to show anxiety, the dexmedetomidine should be given immediately. During a prolonged noise event, such as 4th of July fireworks in the United States, up to five doses can be given with a minimum of 2 hours between each dose (Korpivaara *et al.*, 2017).

Propanolol

Propanolol is a sympatholytic agent, blocking beta-1 and beta-2 receptors. In human psychiatry it is used for situations of acute anxiety, such as test anxiety, performance anxiety in musicians, and stage fright. It has been used in dogs and cats in combination with other medications and behavior modification, but there is little information on its use in veterinary behavioral medicine at this time (Walker *et al.*, 1997).

25.3.4 Opioid antagonists

Opioid antagonists are effective in the treatment of some cases of stereotypic behaviors and obsessivecompulsive disorder in animals. A common hypothesis is that carrying out the stereotypic behavior causes the release of endogenous endorphins, giving the patient a kind of 'high'. In this way, carrying out the stereotypic behavior would be positively reinforced. However, studies confirming this theory are lacking. If this were actually happening when the patient was given an opioid antagonist, the intensity and/or frequency of the behavior should initially increase, i.e., the so-called 'extinction burst' would occur. Instead, animals that respond to this treatment decrease or discontinue the stereotypic behavior almost immediately. This response supports another hypothesis, which is that opioids induce stereotypic behavior. If this were the case, giving the patient an opioid antagonist would be expected to cause a rapid or immediate decrease or discontinuation of the behavior.

25.3.5 Antipsychotics

Antipsychotics block the action of dopamine, which is a catecholamine neurotransmitter that is synthesized from tyrosine obtained via the diet. Dopamine regulates motor activities and appetitive behavior. Low levels of dopamine result in behavioral quieting,

depression, and extrapyramidal signs. Excessive dopamine causes psychotic symptoms and the development of stereotypic behaviors. In veterinary medicine in general, antipsychotics are most commonly used to generate temporary decreases in motor activity and/or restraint.

In behavioral medicine, antipsychotics can be useful in cases of intense fear that can lead the individual to harm itself or its environment. However, for such patients it should only be used in conjunction with true anxiolytics, as antipsychotics themselves have little to no anxiolytic effect. In essence, all they do is slow the patient down.

Acepromazine

Acepromazine maleate is probably the most commonly used antipsychotic in veterinary medicine. It should never be used as the sole treatment for fearful or anxious patients. While its use is based upon its slowing down the animal's movement, there have been multiple incidents of idiosyncratic aggression in both dogs and cats treated with acepromazine (Waechter, 1982; Meyer, 1997). Doses for the more commonly used antipsychotics in dogs, cats, and horses are given in Tables 25.4 and 25.5.

Haloperidol

Haloperidol is a butyrophenone antipsychotic. Its most common use in veterinary behavioral medicine is for the treatment of feather-picking and self-mutilation in psittacine birds (Iglauer and Rasim, 1993; Lennox and VanderHeyden, 1993; Cooper and Harrison, 1994; Telles *et al.*, 2015). It also decreases feather-pecking, but not aggression, in chickens (Kjaer *et al.*, 2004) (Table 25.6).

Table 25.4. Doses for antipsychotics for dogs and cats.

Drug	Canine	Feline
Acepromazine Chlorpromazine Promazine Thioridizine Haloperidol Pimozide Clozapine	0.5–2.0 mg/kg PO q8h or prn 0.8–3.3 mg/kg PO q6h 2.0–6.0 mg/kg IM or IV q4–6h prn 1.0–3.0 mg/kg PO q12–24h 0.05–2.0 mg/kg PO q12h 0.03–0.3 mg/kg PO 1.0–70 mg/kg PO	1.0–2.0 mg/kg PO prn 3.0–6.0 mg/kg PO 2.0–4.5 mg/kg IM 0.1–1.0 mg/kg PO
Sulpiride	5.0–10.0 mg/kg PO	

IM, intramuscular; PO, orally; prn, use when needed. From Seibert and Crowell-Davis (2019) with permission.

Table 25.5. Doses of antipsychotics for horses.

Drug	Dose
Acepromazine	0.02–0.1 mg/kg IM
Promazine	0.4–1.0 mg/kg IV or 1.0–2.0 mg/kg PO q4–6h
Haloperidol decanoate	0.004 mg/kg IM

IM, intramuscular; PO, orally.

From Seibert and Crowell-Davis (2019), with permission.

Table 25.6. Doses of antipsychotics for parrots.

Drug	Dose
Haloperidol	0.2 mg/kg-0.4 mg/kg q12h; begin at lowest dose and increase in 0.02 increments q2d to effect
Haloperidol decanoate	1–2 mg/kg IM q14–21d; lower dose for cockatoos, African grey parrots, and Quaker parakeets

From Seibert and Crowell-Davis (2019), with permission.

368 S. Crowell-Davis

25.3.6 CNS stimulants

CNS stimulants are used in the treatment of attention-deficit/hyperactivity disorder (ADHD) in humans. They can also be effective for a similar phenomenon, originally called hyperkinesis, in dogs (Corson *et al.*, 1976).

While some people may be skeptical of this phenomenon actually occurring in dogs, research has shown actual biochemical differences in a group of Telomian dogs which had hyperkinetic syndrome. The dogs that responded positively to treatment with amphetamines were found to have low levels of norepinephrine, dopamine, and homovanillic acid in the brain (Bareggi *et al.*, 1979).

In spite of hyperkinesis or ADHD being identified as being a real phenomenon in dogs, most dogs that present with a complaint of excessive activity or hyperactivity do not have this disorder. Common reasons for the complaint include unrealistic expectations for the dog's readiness to be quiet and calm when the owners want them to be, insufficient exercise for the age and physical type of the dog, the owner playing roughly with the dog and then expecting it to immediately calm down when the owner no longer wants to play with it anymore, and deliberate or inadvertent positive reinforcement of being very active. Many dogs learn that they get attention from family members when running around, jumping, and barking, but are ignored when they sit or lie down quietly. Thus, a very thorough behavior evaluation is required before hyperkinesis is considered.

If the dog does have hyperkinesis and is a positive responder to the medication, a change in behavior should be rapidly observed after the medication has had time to enter the system. However, the fact that the medication eliminates the dog's hyper-reactivity does not cause it to suddenly learn all the things it was unable to learn when off of medication. Thus, identifying that the dog is a positive responder is just a first step. Subsequent positive reinforcement training and behavior modification will be required to change the dog's behavior to that which the owners find desirable. Table 25.7 shows doses for CNS stimulants for dogs with hyperkinesis.

25.3.7 Gabapentin

Gabapentin is an analog of GABA which binds to α 2-delta subunits of voltage activated Ca²⁺ channels. It is primarily used for neuropathic pain, but also has

Table 25.7. Doses of CNS stimulants for dogs with true hyperkinesis or canine ADD.

CNS stimulant	Dose
Dextroamphetamine	0.1–1.3 mg/kg
Levoamphatamine	1–4 mg/kg
Methylphenidate	2–4 mg/kg

Note: Medication should only be given as needed, but can be repeated several times a day.

From Crowell-Davis (2019a), with permission.

Table 25.8. Dose range for gabapentin in cats and dogs.

	Cats	Dogs
Daily medication Situational medication ^a	3–10 mg/kg q8h 5–20 mg/kg	2–20 mg/kg q8h 10–20 mg/kg

^aSituational medication refers to using the medication for particular stressful events, such as visits to the veterinary office. The low dose is a recommended starting point. The dose can be titrated up, as needed.

From Crowell-Davis et al. (2019a), with permission.

anxiolytic and anti-epileptic properties. In veterinary patients it is sometimes difficult to differentiate pure anxiety from anxiety secondary to neuropathic pain. In these cases in particular, gabapentin can be very useful. Gabapentin can also be useful as an adjunctive treatment to other therapies when neuropathic pain is suspected. For example, Bain and Fan (2012) used gabapentin as an adjunct to fluoxetine in a tail-chasing bull terrier. The doses for gabapentin for dogs and cats are given in Table 25.8.

Pregabalin (Lyrica) has a similar mode of action to gabapentin. At this time it is substantially more expensive than gabapentin and therefore not commonly used in animal patients.

25.3.8 Hormones Oxytocin

Oxytocin has a positive effect on a variety of prosocial and cooperative behaviors in many species (Romero *et al.*, 2016). While its use in behavioral medicine is in its infancy, it is worth mentioning because of its potential. There is an oxytocin–gaze positive loop in which oxytocin levels in both dogs and humans increase when they gaze at each other (Fiset and Plourde, 2015; Nagasawa *et al.*, 2015). This loop has probably been important in the

evolution of the human–dog social relationship (Buttner, 2016; Kekecs *et al.*, 2016). Over our long history of selectively breeding dogs for particular types of interactions and social relationships with humans, we have altered the distribution of oxytocin receptor gene polymorphisms. For example, border collies, which have been selectively bred to engage in complex cooperative behavior with humans, have a stronger response to intranasal administration of oxytocin than do Siberian huskies, a breed that has been developed to work more independently (Kis *et al.*, 2014, 2017).

In cats, variation in the oxytocin receptor gene has been identified as being related to personality. However, further studies are needed to delineate the relationship between oxytocin activity and temperament (Arahori *et al.*, 2016).

Progestins

Progestins were used to treat a wide variety of behavior problems back in the 1970s and 1980s. However, since that time many medications have become available that have been shown to be as or more effective than the progestins, economical, and free of the extensive and serious side-effects that can result from progestin use. At this time, use of progestins to treat behavior problems is not the standard of practice.

25.4 Long-term or Maintenance Medications

25.4.1 Selective serotonin reuptake inhibitors

The selective serotonin reuptake inhibitors (SSRIs) are a class of antidepressants that, at clinically usual doses, exclusively inhibit the reuptake of serotonin. Serotonergic neurotransmission is therefore facilitated by the serotonin molecules being able to act for long periods of time. Over time, downregulation of the serotonergic receptors also occurs.

In veterinary medicine, the SSRIs are used for their anxiolytic, anti-compulsive, and anti-aggressive effects. They are also antidepressants and are sometimes used in that capacity, for example when an animal is exhibiting prolonged and significant depression following the death of a companion (Charney *et al.*, 1990; Coccaro *et al.*, 1990; Kavoussi *et al.*, 1994; Sánchez and Hyttel, 1994; Stein and Stahl, 2000; Walsh and Dinan, 2001).

SSRIs should be given once a day, every day. It can take several weeks after starting an SSRI for an animal to exhibit a change in behavior. Clients should be educated about this so that they are not disappointed by the lack of an immediate change. If an immediate change is needed, many of the short-acting medications can be used simultaneously with the SSRI, and their dose decreased once the SSRI has had sufficient time to show effect.

Mild sedation and decreased appetite are two of the most commonly observed side-effects. These are often transient, and in most cases can be avoided entirely if the patient is started on a subclinical dose for a week, then increased to a low clinical dose, with subsequent dose increases until a middle range dose is achieved, so long as there are no side-effects. If insufficient improvement is noted at the middle range dose, the dose can be gradually increased until the desired level of improvement or adverse side-effects occur. Other side-effects include aggression, agitation, anorexia, anxiety, constipation, decreased libido, diarrhea, hyponatremia, mania, nausea, seizures, and tremor. For patients in which undesired sexual behavior, such as persistently mounting toys or other animals in the house, occurs, the decrease in libido can actually be a beneficial effect. The combined anti-compulsive effect and decreased libido can make SSRIs very useful in cases where excessive sexual behavior is a manifestation of obsessive-compulsive disorder.

SSRIs can alter blood glucose levels. Therefore, caution should be used in diabetic patients, and blood glucose should be monitored regularly during treatment. Dose ranges for the most commonly used SSRIs are given in Table 25.9.

25.4.2 Tricyclic antidepressants

The tricyclic antidepressants (TCAs) inhibit the reuptake of both serotonin and norepinephrine. There is wide variation between the different TCAs in the effect on serotonin and norepinephrine, explained by the differences in molecular structure. The tertiary amines have two methyl groups at the end of their side chain while the secondary amines only have one. Tertiary amines have a greater effect on blocking serotonin reuptake, while secondary amines have a greater effect on blocking norepinephrine transport (Bolden-Watson and Richelson, 1993; Tatsumi *et al.*, 1997; Nelson, 2004). Of all the commercially available TCAs, clomipramine has the strongest serotonin reuptake effect.

370 S. Crowell-Davis

Table 25.9. Doses of various SSRIs for dogs, cats, horses, and parrots.

SSRI	Dog	Cat	Parrot	Horse
Citalopram	0.5–1.0 mg/kg			
Fluoxetine	1.0-2.0 mg/kg	0.5-1.5 mg/kg	2.0-5.0 mg/kg	0.25-0.5 mg/kg
Fluvoxamine	1.0-2.0 mg/kg	0.25–0.5 mg/kg		
Paroxetine	1.0-1.5 mg/kg	0.5-1.5 mg/kg	2.0 mg/kg q12h	0.5 mg/kg
Sertraline	0.5-4.0 mg/kg	0.5–1.5 mg/kg		

Note: All doses given are orally, once daily, unless otherwise specified. Do not evaluate efficacy until the patient has received the medication daily for at least 1 full month.

From Ogata et al. (2019), with permission.

TCAs also affect a number of other molecules, resulting in their having antihistaminic effects and anticholinergic effects. They are also α -1 adrenergic antagonists. As with serotonin and norepinephrine, there is wide variation in these three effects. For example, amitriptyline has a stronger antihistaminic effect than does clomipramine. It also has a weaker serotonin reuptake inhibition effect. The diversity of biochemical activity of six of the most commonly used TCAs is shown in Table 25.10. Doses are given in Tables 25.11 and 25.12.

As with the SSRIs, the TCAs have anxiolytic, anticompulsive, anti-aggressive, as well as antidepressant effects. Clomipramine, as Clomicalm, is FDA-approved for the treatment of separation anxiety in dogs. The effect of clomipramine on feather-picking in several species of cockatoos was investigated using a double-blind, placebo-controlled clinical trial with the drug administered in raspberry syrup at an oral dose of 3 mg/kg q12h. Results showed that significantly more improvement occurred in the birds that were on clomipramine as compared to birds receiving a placebo (Seibert *et al.*, 2004).

With the wide variation in beneficial effects for TCAs there is a comparable variation in side-effects. Some of the most common are sedation, emesis, pupillary dilation, decreased appetite, decreased frequency of urination, and decreased frequency of defecation (Seksel and Lindeman, 1998; Landsberg, 2001; Landsberg and Wilson, 2005; Martin, 2010). Other effects include diarrhea, constipation, urinary retention, changes in appetite, mydriasis, decreased tear production, ataxia, and cardiovascular effects such as arrhythmias, tachycardia, and changes in blood pressure.

With long-term use, the number of serotonin receptors and ß-adrenoceptors at the post-synaptic membrane steadily decreases, i.e., downregulation occurs. In addition to downregulation, prolonged use of TCAs changes the function of various serotonin

receptors in the forebrain (Vetulani and Sulser, 1975; Sulser *et al.*, 1978; Heninger and Charney, 1987; Potter *et al.*, 1995).

Table 25.10. Acute *in vitro* biochemical activity of selected tricyclic antidepressants (TCAs).

TCA drug	NE	5-HT	α-1	α-2	H ₁	Musc
Amitriptyline	±	++	+++	±	++++	++++
Clomipramine	+	+++	++	0	+	++
Desipramine	+++	0	+	0	0	+
Doxepin	++	+	++	0	+++	++
Imipramine	+	+	++	0	+	++
Nortriptyline	++	±	+	0	+	++

NE, norepinephrine; 5-HT, serotonin; α -1, α -1 adrenergic antagonists; α -2, α -2 adrenergic antagonists; H_1 , antihistaminic; Musc, antimuscarinic.

From Crowell-Davis (2019b), with permission.

Table 25.11. Doses of selected tricyclic antidepressants (TCAs) in dogs and cats.

TCA	Cat	Dog
Amitriptyline	0.5–2.0 mg/kg q12–24h	1–6 mg/kg q12h
Clomipramine	0.25–1.3 mg/kg q24h	1.0–3.0 mg/kg q12h
Desipramine		1.5-3.5 mg/kg q24h
Doxepin	0.5–1.0 mg/kg q12h	3.0–5.0 mg/kg q8–12h
Imipramine	0.5–1.0 mg/kg q12–24h	0.5–2.0 mg/kg q8–12h
Nortriptyline	0.5–2.0 mg/kg q12–24h	1.0-2.0 mg/kg q12h

Note: Always start with a low dose and titrate up as necessary if the patient does not exhibit side-effects. All doses are given orally.

From Crowell-Davis (2019b), with permission.

Table 25.12. Doses of selected tricyclic antidepressants (TCAs) in horses and parrots.

Animal	Dose
Parrots Clomipramine	2.0–4.0 mg/kg q12h
Doxepin	0.5–5.0 mg/kg q12h
Horses Imipramine	0.75-2.0 mg/kg

Note: Always start with a low dose and titrate up as necessary if the patient does not exhibit side-effects. All doses are given orally. From Crowell-Davis (2019b), with permission.

25.4.3 Azapirones: buspirone

The azapirones are serotonin 1A agonists. Buspirone is the only azapirone currently commercially available in the United States. It can be useful in a wide variety of anxiety disorders, including generalized anxiety disorder, and specific anxieties such as separation anxiety. It is very useful in the treatment of timid cats; these cats usually become steadily more confident when on this medication. Owners also often report increased prosocial behavior when their cat is on buspirone, including increased solicitation of petting. It is anxioselective and side-effects are uncommon, although sedation and paradoxical increased anxiety can occur in rare instances. Buspirone should be given every day, not on an 'as needed' basis. Doses are given in Table 25.13.

25.4.4 Monoamine oxidase inhibitors

Monoamine oxidase (MAO) is an enzyme that is part of the outer mitochondrial membrane. As such, it can be found in a wide variety of tissues throughout the body, including the central and peripheral nervous system, as well as platelets, the heart, liver, kidney, and spleen (Obata *et al.*, 1987). There are two major types, MAO-A and MAO-B. In the CNS, MAO, especially MAO-B catabolizes oxidative deamination of catecholamines. This activity includes dopamine, norepinephrine, epinephrine, β-phenylethylamine (2-phenylethylamine), and serotonin.

MAO inhibitors inhibit the actions of MAO-A, MAO-B, or both. In veterinary behavioral medicine, selegiline, an MAO-B inhibitor, is used for the treatment of cognitive decline/dysfunction in both dogs and cats (Knoll, 1972; Yang and Neff, 1974; Glover *et al.*, 1977). It is FDA-approved, as Anipryl, for the treatment of cognitive dysfunction in dogs. While

Table 25.13. Dose of buspirone given orally for various species.

Species	Dose
Dog Cat	0.5–2.0 mg/kg q8–24h 2.5–7.5 mg/cat q12h
	or 0.5—1.0 mg/kg q12h
Rabbit	0.25–1.0 mg/kg q12h

From de Souza Dantas and Crowell-Davis (2019b), with permission.

not FDA-approved for cats, it can provide the same benefit in that species (Landsberg, 1999). Doses for cats and dogs are given in Table 25.14.

The main actions of selegiline, at clinically appropriate doses, are:

- inhibition of the reuptake of dopamine, norepinephrine, and serotonin into presynaptic nerves;
- increase in the turnover of dopamine;
- reduction of oxidative stress caused by the degradation of dopamine;
- enhancement of superoxide dismutase and catalase activity, which increases the elimination of free radicals; and
- potentiation of neural responses to dopamine by increasing levels of phenylethylamine, which is a neuromodulator of dopaminergic responses.

Cognitive dysfunction is characterized by a variety of behavioral changes, which include apparent loss of house training, changes in social behavior, restlessness and vocalization at night, and apparent loss of standard training, for example, responding to the spoken word 'sit' by the act of sitting. In one study of over 600 dogs treated with 0.5-1.0 mg/kg of selegiline, given orally, once daily, 77% of the dogs showed improvement. The most common side-effects were diarrhea (4.2%) and anorexia (3.6%). Less common side-effects were vomiting and hypersalivation. By day 30 of treatment, dogs with primary complaints of disorientation, changes in social behavior, and loss of house training responded to therapy better than dogs with primary complaints of changes in activity or in the sleep/wake cycle (Campbell et al., 2001).

A patient should be on selegiline for at least 1 month before its efficacy is evaluated, as improvement, when it occurs, is gradual. Patients with a positive response may continue to show additional improvement for another month or two before

S. Crowell-Davis

Table 25.14. Doses of selegiline for dogs and cats.

Species	Dose
Cat	0.5–1.0 mg/kg
Dog	0.5–1.0 mg/kg

From de Souza Dantas and Crowell-Davis (2019c), with permission.

their behavior stabilizes. For dogs that have a positive response, substantial improvement in the quality of life can occur.

Because people do not typically train cats to obey commands, and also because cats are normally active at night, the development of cognitive dysfunction can be easily missed. Older cats presenting with elimination behavior problems when they had previously been consistent in their use of the litterbox, or with changes in social behavior should be assessed for overall cognitive function.

25.5 Changing and Combining Medications for Optimal Well-being

At this time, blinded, controlled studies comparing specific medications for the treatment of specific problems in specific species have not been done. Therefore, we do not know, for example, if alprazolam or diazepam would have greater efficacy in dogs with storm phobia. Given the wide variation in drug metabolism of various dog breeds, it is possible that focused studies may reveal differences such as certain breeds responding more positively to alprazolam while other breeds respond better to diazepam.

When deciding which medications to initially use for a given patient, several factors must be considered:

- Whether or not there is a medication that is FDA-approved for the species and disorder being treated.
- What evidence exists regarding the efficacy of the medication being considered for the particular species and breed of patient with that particular disorder.
- What evidence exists regarding type, frequency, and intensity of adverse side-effects for the particular species and breed of patient being treated.
- Specific ongoing health issues that the patient
- The ability of the owner to administer the medication to the patient.
- The cost of the medication.

Because we have no way of verifying in advance which particular medication or medications, and at which particular doses, will best facilitate a given patient's optimal mental health it is not uncommon for the first medication selected to fail to achieve the desired results. It may cause some, but insufficient, improvement, or it may cause no improvement at all. If inadequate benefits are achieved, and assuming that the medication has been used at an appropriate dose for an appropriate amount of time, another medication can reasonably be attempted. Sometimes multiple medications must be tried before the specific drug or drugs which provide the optimal effect can be identified. For example, in treating dogs with storm phobia, the author typically starts with fluoxetine as the maintenance drug. This choice is due to a combination of extensive information on the effect of fluoxetine on dog behavior, emotions and health, and cost. If fluoxetine does not bring about sufficient improvement, clomipramine is usually the second drug attempted. In addition to serotonin reuptake inhibition, clomipramine has norepinephrine reuptake inhibition. In some patients, this added feature is beneficial.

For many patients, two or more different medications provide the optimal benefit to their mental health. For example, fluoxetine can be a useful maintenance medication for a dog with storm phobia, while supplementation with a second, fast-acting medication such as alprazolam or trazodone can enhance treatment effects during severe storms.

25.6 References

Arahori, M., Hori, Y., Saito, A., Chijiiwa, H., Takagi, S., et al. (2016) The oxytocin receptor gene (OXTR) polymorphism in cats (*Felis catus*) is associated with 'Roughness' assessed by owners. *Journal of Veterinary Behavior* 11, 109–112. http://dx.doi.org/10.1016/j.jveb.2015.07.039.

Bain, M.J. and Fan, C.M. (2012) Animal behavior case of the month. *Journal of the American Veterinary Medical* Association 240, 673–675. http://dx.doi.org/10.2460/ javma.240.6.673.

Bareggi, S.R., Becker, R.E., Ginsburg, B.E., Genovese, E. (1979) Neurochemical investigation of an endogenous model of the 'hyperkinetic syndrome' in a hybrid dog. *Life Sciences* 24, 481–488. http://dx.doi.org/ 10.1016/0024-3205(79)90168-1.

Bolden-Watson, C. and Richelson, E. (1993) Blockade by newly-developed antidepressants of biogenic amine uptake into rat brain synaptosomes. *Life Sciences* 52, 1023–1029. http://dx.doi.org/10.1016/0024-3205(93)90194-8.

- Buttner, A.P. (2016) Neurobiological underpinnings of dogs' human-like social competence: How interactions between stress response systems and oxytocin mediate dogs' social skills. *Neuroscience & Biobehavioral Reviews* 71, 198–214. http://dx.doi.org/10.1016/j. neubiorev.2016.08.029
- Campbell, S., Trettien, A., Kozan, B. (2001) A noncomparative open-label study evaluating the effect of selegiline hydrochloride in a clinical setting. *Veterinary Therapeutics* 2, 24–39.
- Center, S.A., Elston, T.H., Rowland, P.H., Rosen, D.K., Reitz, B.L., et al. (1996) Fulminant hepatic failure associated with oral administration of diazepam in 11 cats. Journal of the American Veterinary Medical Association 209: 618–625.
- Charney, D.S., Krystal, J.H., Delgado, P.L., Heninger, G.R. (1990) Serotonin-specific drugs for anxiety and depressive disorders. *Annual Review of Medicine* 41, 437–446. http://dx.doi.org/10.1146/annurev.me.41.020190.002253.
- Coccaro, E.F., Astill, J.L., Herbert, J.L., Schut, A.G. (1990) Fluoxetine treatment of impulsive aggression in DSM-III-R: Personality disorder patients. *Journal of Clinical Psychopharmacology* 10, 373–374. http://dx.doi.org/10.1097/00004714-199010000-00021.
- Cooper, J.E. and Harrison, G.J. (1994) Dermatology. In: Ritchie, B.W., Harrison, G.J., Harrison, L.R. (eds) Avian Medicine: Principles and Application. Wingers, Lake Worth, Florida, USA, pp. 608–639.
- Corson, S.A., Corson, E.L., Arnold, L.E., Knopp, W. (1976) Animal models of violence and hyperkinesis: Interaction of psychopharmacologic and psychosocial therapy in behavior modification. In: Serban, G. and Kling, A. (eds.) Animal Models in Human Psychobiology. Springer, Boston, Massachusetts, USA, pp. 111–139. http://dx.doi.org/10.1007/978-1-4684-2184-2_8.
- Crowell-Davis, S. (2019a) CNS stimulants. In: Crowell-Davis, S.L, Murray, T.F., de Souza Dantas, L.M. (eds.) *Veterinary Psychopharmacology*, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 217–230. http://dx.doi.org/10.1002/9781119226253.ch15.
- Crowell-Davis, S. (2019b) Tricyclic antidepressants. In: Crowell-Davis, S.L, Murray, T.F., de Souza Dantas, L.M. (eds.) *Veterinary Psychopharmacology*, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 231–256. http://dx.doi.org/10.1002/9781119226253.ch16.
- Crowell-Davis, S. Irimajiri M, de Souza Dantas, L.M. (2019) Anticonvulsants and mood stabilizers. In: Crowell-Davis, S.L., Murray, T.F., de Souza Dantas, L.M. (eds.) *Veterinary Psychopharmacology*, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 147–156. http://dx.doi.org/10.1002/9781119226253.ch10.
- Crowell-Davis, S.L, Murray, T.F., de Souza Dantas, L.M. (2019) *Veterinary Psychopharmacology*, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA. http://dx.doi.org/10.1002/9781119226253.
- de Souza Dantas, L.M. and Crowell-Davis, S. (2019a) Benzodiazepines. In: Crowell-Davis, S.L, Murray, T.F.,

- de Souza Dantas, L.M. (eds.) *Veterinary Psycho-pharmacology*, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 67–102.
- de Souza Dantas, L.M. and Crowell-Davis, S. (2019b) Miscellaneous serotonergic agents. In: Crowell-Davis, S.L, Murray, T.F., de Souza Dantas, L.M. (eds.) Veterinary Psychopharmacology, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 129–146. http://dx.doi.org/10.1002/9781119226253.ch9.
- de Souza Dantas, L.M. and Crowell-Davis, S. (2019c) Monoamine oxidase inhibitors. In: Crowell-Davis, S.L, Murray, T.F., de Souza Dantas, L.M. (eds.) Veterinary Psychopharmacology, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 185–200. http:// dx.doi.org/10.1002/9781119226253.ch13.
- Fiset, S. and Plourde, V. (2015) Commentary: Oxytocingaze positive loop and the coevolution of human-dog bonds. Frontiers in Psychology 6, 1845. http://dx.doi. org/10.3389/fpsyg.2015.01845.
- Glover, V., Sandler, M., Owen, F., Riley, G.J. (1977) Dopamine is a monoamine oxidase B substrate in man. *Nature* 265, 80–81. http://dx.doi.org/10.1038/265080a0.
- Gruen, M.E. and Sherman, B.L. (2008) Use of trazodone as an adjunctive agent in the treatment of canine anxiety disorders: 56 cases (1995–2007). *Journal of the American Veterinary Medical Association* 233, 1902–1907. http://dx.doi.org/10.2460/javma.233.12.1902.
- Heninger, G.R. and Charney, D.S. (1987) Mechanism of action of antidepressant treatments: Implications for the etiology and treatment of depressive disorders. In: Meltzer, H.Y. (ed.) *Psychopharmacology: The Third Generation of Progress*. Raven Press, New York, USA, pp. 535–544.
- Hughes, D.H., Moreau, R.E., Overall, K.L., Winkle, T.V. (1996) Acute hepatic necrosis and liver failure associated with benzodiazepine therapy in six cats, 1986– 1995. Journal of Veterinary Emergency and Critical Care 6, 13–20.
- Iglauer, F. and Rasim, R. (1993). Treatment of psychogenic feather picking in psittacine birds with a dopamine antagonist. *Journal of Small Animal Practice* 34, 564-566. http://dx.doi.org/10.1111/j.1748-5827.1993. tb03550.x.
- Kavoussi, R.J., Liu, J., Coccaro, E.F. (1994) An open trial of sertraline in personality disordered patients with impulsive aggression. *Journal of Clinical Psychiatry* 55, 137–141.
- Kekecs, Z., Szollosi, A., Palfi, B., Szaszi, B., Kovacs, K.J., et al. (2016) Commentary: Oxytocin-gaze positive loop and the coevolution of human–dog bonds. Frontiers in Neuroscience 10, 155. http://dx.doi. org/10.3389/fnins.2016.00155.
- Kis, A., Bence, M., Lakatos, G., Pergel, E., Turcsán, B., et al. (2014) Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (Canis familiaris). PloS ONE 9(1), e83993. http://dx.doi.org/10.1371/journal.pone.0083993.

374 S. Crowell-Davis

- Kis, A., Ciobica, A., Topál, J. (2017) The effect of oxytocin on human-directed social behaviour in dogs (*Canis familiaris*). Hormones and Behavior 94, 40–52. http://dx.doi.org/10.1016/j.yhbeh.2017.06.001.
- Kjaer, J.B., Hjarvard, B.M., Jensen, K.H., Hansen-Møller, J., Larsen, O.N. (2004) Effects of haloperidol, a dopamine D2 receptor antagonist, on feather pecking behaviour in laying hens. *Applied Animal Behaviour Science* 86, 77–91. http://dx.doi.org/10.1016/j.applanim.2003.11.009.
- Knoll, J. (1972) Some puzzling pharmacological demonstration for monoamine oxidase inhibition. Advances in Biochemical Psychopharmacology 5, 393–408.
- Korpivaara, M., Laapas, K., Huhtinen, M., Schöning, B., Overall, K. (2017) Dexmedetomidine oromucosal gel for noise-associated acute anxiety and fear in dogs – A randomised, double-blind, placebo-controlled clinical study. Veterinary Record 180, 356. http://dx.doi.org/ 10.1136/vr.104045.
- Landsberg, G. (1999) Feline house soiling: Marking and inappropriate elimination. In: *Proceedings of the Atlantic Coast Veterinary Conference*. Atlantic City, New Jersey, USA, pp. 315–320.
- Landsberg, G.M. (2001) Clomipramine Beyond separation anxiety. *Journal of the American Animal Hospital Association* 37, 313–318. http://dx.doi.org/10.5326/15473317-37-4-313.
- Landsberg, G.M. and Wilson, A.L. (2005) Effects of clomipramine on cats presented for urine marking. *Journal* of the American Animal Hospital Association 41, 3–11. http://dx.doi.org/10.5326/0410003.
- Lennox, A.M. and VanDerHeyden, N. (1993) Haloperidol for use in treatment of psittacine self-mutilation and feather plucking. In: *Proceedings of the Association* of Avian Veterinarians. Nashville, Tennessee, USA, pp. 119–120.
- Martin, K.M. (2010) Effect of clomipramine on the electrocardiogram and serum thyroid concentrations of healthy cats. *Journal of Veterinary Behavior* 5, 123–129. http://dx.doi.org/10.1016/j.jveb.2009.12.019.
- Meyer, E.K. (1997) Rare, idiosyncratic reaction to acepromazine in dogs. *Journal of the American Veterinary Medical Association* 210, 1114–1115.
- Nagasawa, M., Mitsui, S., En, S., Ohtani, N., Ohta, M., et al. (2015) Oxytocin-gaze positive loop and the coevolution of human-dog bonds. Science 348, 333–336. http://dx.doi.org/10.1126/science.1261022.
- Nelson, J.C. (2004) Tricyclic and tetracyclic drugs. In: Schatzberg, A.F. and Nemeroff, C.B. (eds.) *Textbook of Psychopharmacology*. American Psychiatric Publishing, Washington, DC, USA, pp. 207–230.
- Obata, T., Egashira, T., Yamanaka, Y. (1987) Evidence for existence of A and B form monoamine oxidase in mitochondria from dog platelets. *Japanese Journal of Pharmacology* 44, 105–111. http://dx.doi.org/10.1254/jjp.44.105.
- Ogata, N, de Souza Dantas, L.M., Crowell-Davis, S. (2019) Selective serotonin reuptake inhibitors. In:

- Crowell-Davis, S.L, Murray, T.F., de Souza Dantas, L.M. (eds.) *Veterinary Psychopharmacology*, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 103–128. http://dx.doi.org/10.1002/9781119226253.ch8.
- Park, F.M. (2012) Successful treatment of hepatic failure secondary to diazepam administration in a cat. *Journal of Feline Medicine and Surgery* 14, 158–160. http://dx.doi.org/10.1177/1098612X11432238.
- Potter, W.Z., Manji, H.K., Rudorfer, M.V. (1995) Tricyclics and tetracyclics. In: Schatzberg, A.F. and Nemeroff, C.B. (eds.) *Textbook of Psychopharmacology*. American Psychiatric Publishing, Washington, DC, USA, pp. 141–160.
- Romero, T., Onishi, K., Hasegawa, T. (2016) The role of oxytocin on peaceful associations and sociality in mammals. *Behaviour* 153, 1053–1071. http://dx.doi. org/10.1163/1568539X-00003358.
- Sánchez, C. and Hyttel, J. (1994) Isolation-induced aggression in mice: Effects of 5-hydroxytryptamine uptake inhibitors and involvement of postsynaptic 5-HT1A receptors. European Journal of Pharmacology 264, 241–247. http://dx.doi.org/10.1016/0014-2999(94)00470-6.
- Seibert, L. and Crowell-Davis, S. (2019) Antipsychotics. In: Crowell-Davis, S.L, Murray, T.F., de Souza Dantas, L.M. (eds.) Veterinary Psychopharmacology, 2nd edn. Wiley-Blackwell, Hoboken, New Jersey, USA, pp. 201–216.
- Seibert, L.M., Crowell-Davis, S.L., Wilson, G.H., Ritchie, B.W. (2004) Placebo-controlled clomipramine trial for the treatment of feather picking disorder in cockatoos. *Journal of the American Animal Hospital Association* 40, 261–269. http://dx.doi.org/ 10.5326/0400261.
- Seksel, K. and Lindeman, M.J. (1998) Use of clomipramine in the treatment of anxiety-related and obsessive-compulsive disorders in cats. *Australian Veterinary Journal* 76, 317–321. http://dx.doi.org/10.1111/j. 1751-0813.1998.tb12353.x
- Stein, D.J. and Stahl, S. (2000) Serotonin and anxiety: Current models. *International Clinical Psychopharmacology* 15(suppl. 2), S1–6. http://dx.doi.org/10.1097/00004850-200008002-00002.
- Sulser, F., Vetulani, J., Mobley, P.L. (1978) Mode of action of antidepressant drugs. *Biochemical Pharmacology* 27, 257–261. http://dx.doi.org/10.1016/ 0006-2952(78)90226-5.
- Tatsumi, M., Groshan, K., Blakely, R.D., Richelson, E. (1997) Pharmacological profile of antidepressants and related compounds at human monoamine transporters. *European Journal of Pharmacology* 340, 249–258. http://dx.doi.org/10.1016/S0014-2999(97)01393-9.
- Telles, L.F., Malm, C., Melo, M.M., Vilela, D.A.D.R., Lago, L.A., et al. (2015). Psychogenic feather picking behavioral in parakeet: Haloperidol and environmental enrichment. Ciência Rural 45, 1099–1106.
- van Beusekom, C.D., van den Heuvel, J.J., Koenderink, J.B., Russel, F.G., Schrickx, J.A. (2015) Feline hepatic

- biotransformation of diazepam: Differences between cats and dogs. *Research in Veterinary Science* 103, 119–125. http://dx.doi.org/10.1016/j.rvsc.2015.09.016.
- Vetulani, J. and Sulser, F. (1975) Action of various antidepressant treatments reduces reactivity of noradrenergic cyclic AMP-generating system in limbic forebrain. *Nature* 257, 495–496. http://dx.doi.org/10.1038/257495a0.
- Waechter, R.A. (1982) Unusual reaction to acepromazine maleate in the dog. *Journal of the American Veterinary Medical Association* 180, 73–74.
- Walker, R., Fisher, J., Neville, P. (1997) The treatment of phobias in the dog. *Applied Animal Behaviour*

- Science 52, 275–289. http://dx.doi.org/10.1016/ S0168-1591(96)01128-8.
- Walsh, M.T. and Dinan, T.G. (2001) Selective serotonin reuptake inhibitors and violence: A review of the available evidence. *Acta Psychiatrica Scandinavica* 104, 84–91. http://dx.doi.org/10.1034/j.1600-0447. 2001.00357x.
- Yang, H.Y. and Neff, N.H. (1974) The monoamine oxidases of brain: Selective inhibition with drugs and the consequences for the metabolism of the biogenic amines. *Journal of Pharmacology and Experimental Therapeutics* 189, 733–740.

376 S. Crowell-Davis

Note: Page numbers in **bold** type refer to **figures**Page numbers in *italic* type refer to *tables*Page numbers followed by 'n' refer to notes

acepromazine 368	assessing animal affect
action-driven agency 159	anticipatory beha
adaptive fear responses 184–185	cognitive bias 337
adrenocorticotropic hormone (ACTH) 142	cognitive markers
affect 53, 150n1	expressive behavious
see also assessing animal affect	facial expressions
Affect Balance Model (Bradburn) 11, 328	judgment bias test
affective state 53, 328–344	lateralization 336
affective valence, cognitive markers of	Pavlovian cues 33
335–338	Qualitative Behav
agency 158-159, 164, 268-269	vocalizations 334
aggression 171-173, 317, 320, 345, 346	attention-deficit/hypera
types 170	autism spectrum disorc
aggressive behavior 258	autonomy 244, 317
aging pets 212–230	avoidance behavior 35
alert function, of suffering 148	azapirones, buspirone
allopreening 292	
altricial mammals 126	
Alzheimer's disease 215, 216, 252	backward chaining 35°
American Society for the Prevention of Cruelty to	battery cages 28
Animals (ASPCA), Behavioral Rehabilitation	Bayes' theorem 159–10
Center (BRC) 346, 348, 348, 354, 355, 356,	bears 191–192, 193
356 , 357, 357 , 358, 358	beef cattle 231, 233
American Zoo and Aquarium Association 307	behavior
amygdala 169, 173, 189, 234	aggressive 258
anesthesia 15, 16	anticipatory 305,
anhedonia 157, 163, 264–266, 264	avoidance 352, 3
Animal Liberation (Singer) 23	changes, signs and
Animal Machines (Harrison) 26	control 78n1
Animal Medicinal Drug Use Clarification Act	defined 1
(AMDUCA) 365	displacement 245
animal rights 23–24	expressive 332–3.
animal welfare 53–54, 117	mental health 3–4
definitions 27	ongoing 1
science of 24–28	patterns, mechani
Animal Welfare Act (AWA) 278	problems
anticipation 269	prevention 1
anticipatory behavior 305, 335–336	resolving 13
antipsychotics 367–368, 368	repetitive 176, 26
anxiety 2–3, 175, 220	rewarding 53, 60
Anxiety Intensity Rank (AIR) 175	stereotypic 296
aspirational agency 164	voluntary and inv
assessing affective states 328–344	<i>see also</i> dogs

```
ehavior 335-336
337-338
ters of affective valence 335–338
avior and cognitive markers 332-338
ons 333-334
test 337-338, 338
336-337
336
havioral Assessment (QBA) 335
334–335
peractivity disorder (ADHD) 369
order (ASD) 169, 346
352, 352
ne 372, 372
357-358
9-160
05, 335–336
2, 352
and causes 4, 5
245-246
2-338
3-4
anistic approach 167-168, 168
n 134–136
136
264
60-61
involuntary 351, 352
```

behavioral abnormalities 318–322	psittacine species 291
behavioral conditions 167, 168, 168	pterotillomania 295
behavioral contingency 308	reproductive aggressive behavior 297
behavioral despair 197	screaming and excessive vocalization 296
behavioral diagnoses 171, 172	sleep deprivation, lighting and photoperiod 294
behavioral engineering 268–269	sleeping 299
behavioral health 124	social bonds 293
behavioral needs (Poole and Hetts) 124	social interactions 292
behavioral parameters 42, 42	socialization 298
behavioral phenotypes 167, 168	stereotypic behavior 296
behaviorism 21, 25	territorial aggression 296–297
behaviorist's view 1–7	treatment considerations 296
Beluga whales (<i>Delphinapterus leucas</i>) 315–327	blink rate 249, 250
benzodiazepines 366–367, 367	body targeting 358, 359
bias, cognitive 118, 119, 265, 304, 337–338	bonding 57, 292–293
bile extraction 191–192, 193	boredom 29, 74, 75, 295
biological functioning 50–51	box walking, horses 243
Biological Functioning School, The 27	brain 112, 315–316
biomarkers 42–43, 43	atrophy 217
bipolar continuum phenomenon 11–12	Brambell Report (1965) 26, 280, 283
birds (captive)	breaking horses 73, 162
aggression problems 296, 297	breeding programs 293–294
allopreening 292	bucket game 359
bathing 299	
boredom 295	C
breeding programs 293–294	Cacatua goffini/goffiniana (Goffin's cockatoo) 292, 295
consequences of poor mental health 295–298	Cacatuidae 291
contact calling 296	cages, battery 28
cue training 299, 299	Cambridge Declaration on Consciousness (2012) 329
developmental factors 293–294	Canine Behavioral Assessment and Research
dominance 297–298	Questionnaire 119
enhancing QOL 298–299	canine compulsive disorder 177
enrichment 298	Canis lupus (wolf) 191
fear aggression 297	captive animals 67, 68
fearful behavior 292	captive birds see birds (captive)
feather	captive cetaceans see cetaceans (captive)
damaging 294	caretaker education 134
picking 295–296	Case for Animal Rights, The (Regan) 23-24
flocking 292	cats
foraging 294	DSCC 348-349
hand weaning 293–294	feline interstitial cystitis (FIC) 37, 40, 44
housing 298	hallucinations 176
isosexual pairing 293, 293	informational topics on behavior 135, 135
longevity 291	MRI brain scan 215, 216
meal feeding 294, 294	obsessive-compulsive disorder (OCD) 175-178
mental health issues 291–301	PTSD 192
mental states and experiences 292	socialization phase 128
neonatal handling 293	trauma and OCD 176
neophobia 292	cattle
OCD 295	beef 231, 233
pair bonding 292-293	cows 190
parrots 291	central threat response system (CTRS) 33, 35, 36–37,
perch height 298	39, 41, 42, 42
perching materials 299	cetaceans (captive)
play aggression, inappropriate mouthing, lack of	aggression 317, 320
bite inhibition 297	autonomy 317
predictable environments 293	behavioral abnormalities 318–322
production christianiches 275	Denational achormalities 310 322

brain size and complexity 315–316	neuronal loss 216
cerebral development 315-316	neuropathology in aging dogs 216, 217
depression 321-322	neuropsychological tests 212, 213
evolutionary history and phylogeny 315	pathophysiology 215–216
future - seaside sanctuaries 322–323	pollution 215
hyperaggression 319–320	prevalence 213–214
infant mortality 317, 321	progression 215
learned helplessness 321	risk factors 215
limbic system and emotional regulation 316	senior canine and feline behavior
maternal attachment and care 320–324	questionnaire 214, 214
mental health issues 315–327	Strange Situation Test 213
noise 317	treatment
petting pools 317	enrichment 222
population 315	nutraceuticals 222–223
psychology and behavioral adaptations 316–317	prescription diets 223
self-harm 319	prescription pharmacotherapy 223–224, 224
sensory systems 316	symptom-based anxiolysis 224–225
social tension 317	cognitive functioning 71
stereotypies 318–319	cognitive markers, of affective valence 335–338
oral 318–319, 319	competence building agency 158, 161
swimming 318	competing response training 356–357
stress effects on health 317–322	conditioned fear 161, 246
stressors in captivity 317	conditioned stimulus 184
suicide 321–322	conflict aggression 171
swim-with programs 320	consciousness 141–142, 329
1 0	consecific aggression 320
treatment with psychotropic drugs 322 voluntary breathers 322	contrafreeloading 269
chimpanzees 118, 191, 197, 205, 333	control animals over humans 75
happiness 113–116 studies 112–115	behavioral 78n1
choice 67–68, 133, 308	beneficial effects 71
chronic stress 2, 119, 197, 198, 204, 258, 260,	captive animals 67, 68
264–266, 317–322	cognitive 78n1, 158
chute test 231	functioning 71
clicker training 358	defining and characterizing 67–68
CNS stimulants 369, 369	desirability 69–70
cognitive behavior therapy (CBT) 203–204	distress 149–150
cognitive bias 119, 265, 337–338	effectiveness 159
tests 118, 304	effects of 70–71
cognitive challenges 308	enhancing 73–74, 75
cognitive control 78n1, 158	environments harmful to animals 72–73, 73
cognitive disorders 212–230	event specific versus general 74–75
cognitive dysfunction syndrome (CDS)	hiding places 74, 74
algorithm for diagnosis 219–220, 221	immunizing against adverse effects of
anxiety 220	uncontrollability 76
brain atrophy 217	individualizing the enhancement 75
characteristics 212–213	learned helplessness 72–73, 73
clinical signs 212	locus of control (LOC) 68–69
comorbidity with affective disorders 220-222	loss of 158
diagnosis 216–220	mental health
diet 215, 223	implications 78
DISHAA 212, 213	and well-being benefits 67-81
hyperphosphorylated tau accumulation in cat	methods of enhancing in literature 76, 77
brains 216, 218	optimism 70
medical conditions to rule out 219, 220	perception of 67–68, 68
medical differentials in dogs and cats 218, 219	practical applications 76
MRI scans 215, 216	predictability 71–72

control (continued)	limitations of research-based operational
psychological trauma 200	definitions 143
relationship to mental health and well-being 70	negative affect 142-143
rodents 69–70	specific, discrete or basic emotion 141
therapeutic considerations 76, 78	why important to clarify understanding 143
treatment 359–360	Dog Mentality Assessment test 119
zoo animals 308	dogs
controllability 125	adolescent phase 129
coping 124	anxiety
ability 12, 71	separation 173–175
choices available when it fails 146–147	signs 175
distress 143–144, 144	behavior
reactive styles 119	avoidance 352, 352
cortisol levels 119, 142	informational topics on 135, 135
counterconditioning 349–351	using play to reinforce approach 354, 355
Courage of Lassie (1946) 192–193, 194	voluntary and involuntary 352, 352
cows 190	breeds and OCD 177
Cushing's disease 252	Canine PTSD 192–194
	cognitive bias 119
	commercial breeders 129
depression 196–197, 321–322	desiring human contact/support 105, 105, 106
desensitization 246, 349	DSCC 348, 348
desensitization and counterconditioning (DSCC)	early life experiences 38
procedural considerations 354–355	helper 356, 356
treatment (nonpharmacological)	impulse control aggression 171-173
347–355	learned helplessness 73
development	learning novel environment using a safe haven
altricial mammals 126	357 , 357
mental welfare 125-126	learning to hand target 358, 358
of pathology 144	narcolepsy 177
developmental origins of health and disease	noise 173–175, 345, 348
(DOHaD) 36, 39	OCD 175-178, 197
dexmedetomidine 367	playing 58
diagnosis 167–181, 168, 171	PTSD 191
what is? 167–170	puppy rehoming age 128–129
diazepam 366–367, 366, 367	recidivism 176
diet 215	social buffering 102
	socialization phase 127–128
dishabituation, stress-induced 198	
displacement behaviors 245–246	stranger aggression treatment 346
distress 2, 140–155	dolphins (bottlenose) (Tursiops truncatus) 305,
adversity leads to abnormal or maladaptive	315–327
behaviors 145	dominance 118, 171
affect and motivation 146–147	
any severity of certain mental disorders 141	
any unpleasantness 141	early life, epigenetic influences 36–40
chronic 2	early life adversity (ELA) 144, 199-200
compared with suffering 147–150	eating 44
conceptualizing 141–142	effect habituation 173
consciousness 141–142	elephants 191
control 149–150	emotion in animals 329–332, 330
coping 143–144	emotional disorders 212-230
current conceptualizations 140-141	emotional well-being 9
extreme unpleasantness 140–141	endogenous pharmacology 39
inability to cope 143–144	endophenotypes 168
intensity/threshold question 142	Enlightenment 22
is it a negative, maladaptive state? 145	enrichment 222
laboratory animals 280	environmental enrichment 41, 43, 130, 134
laboratory allillais 200	chynonnental chriefficht 71, 73, 130, 137

1 380

American Zoo and Aquarium Association	causes 167
definition 307	circuits in brain 234
biomarkers 43, 43	conditioned 161, 246
classification scheme 287–288	conditioning 160-161, 163, 184, 185, 189
laboratory animals 279, 287-288	factor in farm animals 233–234
pseudo-enrichment 288	innate 184
publications (NLM) 44, 44	learned 184, 345
shelter animals 268–269	learning and memory 173
term 287	memories 235–236
zoo animals 307–309	pain 157
environmental influences 40–41, 126–130	pathologic 185
environmental interventions 120	predispositions 346
environmental stimuli processing 33, 34	rats 102
environmental threats 37	response in Cacatua goffini 292
epigenetic influences 36–40	structure 185
epigenetic mechanisms 37, 38	fearfulness 231
epigenetic modulation 41	feather
ethology 1	damaging 294
European Association of Zoos and Aquaria (EAZA) 304	picking 295–296
European Welfare Quality Principles 61	feeding methods 309
euthanasia 257, 287	feelings 21–30
exercise 57	Feelings School, The 27
	9
Expression of the Emotions in Man and Animals, The ((Darwin) 333	feline interstitial cystitis (FIC) 37, 40, 44 fetal development 37
	-
expressive behavior 332–338	fight-or-flight response 2
	Five Domains model 51, 53–58, 59–60
(: 1 .: (FACC) 222	Five Freedoms of Animal Welfare (Brambell Report) 43.
facial action coding system (FACS) 333	50, 51
facial expressions 333–334	Five Freedoms (Farm Animal Welfare Council)
Farm Animal Welfare Council 2, 6	2, 6, 280
farm animals	Five Provisions/Welfare Aims framework
acclimating 237	61–63, 62
bucking 235	flank sucking 175–176, 178
chute test 231	flocking, birds (captive) 292
fear	flooding 346–347, 347
factor 233–234	foraging 294
memories 235–236	freedom 51
handling 234, 235, 236–237	frustration 28
human presence 235–236, 236	
human voice 235	
importance of good first experiences 234–235	gabapentin 369, 369
intensive versus intensive environment 238	gene expression 41
locking head stanchions 235	generalized anxiety disorder (GAD) 185, 196, 345
mental health issues 231–241	genetic predispositions 126
need for novelty 237–238	genetics 35–36, 119–120, 177, 199
non-slip flooring 235	graduated exposure therapy 347, 349
novelty paradox 237	grazing, open-field 56
rearing 235	grimace scales 334
separation distress 232	Groundwork of the Metaphysic of Morals (Kant) 22
social behavior 232	Guide for the Care and Use of Laboratory Animals
sound fear memory 236	(National Institute for Health) 278
stimulation 237, 238	
temperament selection 231	
transportation 234	hallucinations 176
fear 28	haloperidol 368
adaptive 184–185	hand shyness 358
behaviors 259	hand weaning 293–294
	σ

handling	human appraisal theory 332
farm animals 234, 236-237	human-animal relationships (HAR) 85
laboratory animals 285	Hume, D. 23
training 236–237	hunter/hunted 56
happiness 8-9, 106, 111-123	hyperaggression 319–320
chimpanzees 113–116, 113	hyperarousal 263–264, 263
health	hypervigilance 189
definition (WHO) 33	hypothalamic-pituitary-adrenal (HPA) axis 2, 37,
quality of life (QOL) 85	97, 103
Health Research Extension Act (1985) 278	
hedonism 11	
helper dogs 356, 356	implosion therapy 346–347
helplessness, learned 72–73, 73, 321	improving mental health 130–131
hens 28, 28	and physical health 43–44
hiding places 74, 74	professional help 133–136
homeostasis 146	impulse control aggression 171–173
Hominoid Personality Questionnaire (Weiss) 115	individuality 75, 84
horse boxes 247	infant mortality 317, 321
horses	intervention 4
adaptive behavior 251	isolation 99, 100, 101
Alzheimer's disease 252	isosexual pairing 293, 293
antipsychotics 367–368, 368	isosexuai pairing 273, 273
autonomy 244	
blink rate 249, 250	iinala ianala muahlam 116
boredom 248–249	jingle jangle problem 116
	judgment bias test 337–338, 338
box walking 243	jumpiness 190
breaking 162	
cognitive dysfunction and associated	1 402 205
problems 251–252	kangaroos 192, 205
conditioned fears 246	Keeper-Animal Relationships (KAR) 305–306
coping in the domestic environment 243–244	kennel environments 73
Cushing's disease 252	
depressed 250	
desensitization 246	laboratory animals
displacement behaviors 245-246	assent 286
dopaminergic activity 249	birth-to-death inventory checklist 281, 282
evolutionarily natural challenges 243	care standards 279
fears, frustrations and anxieties 245–246	consent 286
GAD 251	cross-infection 285
inconsistent communications 249	endpoints 287
insoluble tasks 249	environmental enrichment 279, 287–288
lack of social support 251	euthanasia 287
learned helplessness 73, 246	experiment design 277
maladaptive versus malfunctional responses 244	handling 285
mental health issues 242–256	human-animal interactions 285-286
motivational conflict 245, 246	improvements for well-being 280-288
novel domestic challenges 243-244	light 283
OCD 251	link between welfare and research data 278-280
pain 248	mental health 277-290
physical and psychological threats 242	mice 281
pressure-release 358–359	monkeys 281, 284
separation anxiety 246–247	needs of research project 285
social buffering 101	noise 283
transmission of fears 246	pain 279, 286–287
unmet evolutionary expectations 243	physical environment 281–283
withdrawn states 250	positive reinforcement training 286, 286
house training 135	psychosomiasis 279
nouse training 100	posenosomiasis 277

1 382

regulatory and historical context 278	monkeys 281
rodent housing 284	brown capuchin 116
setting 277	monoamine oxidase inhibitors 372-373, 373
social environment 283–285	motivation, strength of 28–29
social housing 283	
stress 280	
suffering 278	narcolepsy 177
temperature 281–282	National Institute for Health (NIH), Guide for the Care
tight controls 278	and Use of Laboratory Animals 278
vibration 283	National Library of Medicine (NLM), environmental
lateralization 336–337	enrichment publications 44, 44
learned helplessness 72-73, 73, 196-197, 246, 265, 321	National Research Council (NRC)
leopards, clouded and snow 117	Committee on Pain and Distress in Laboratory
Leviathan (Hobbes) 22	Animals (1992) 143, 144, 145, 146
life	Recognition and Alleviation of Distress in
conditions 16	Laboratory Animals (2008) 142
experiences 16	needs
sanctity 84	concept of 124–125
satisfaction, term 9	meeting 12–13
sustaining behaviors 52	negative affect 52, 142–143, 150, 150n1
limited rights 24	negative affective experiences 51–52
lions, African 117	negative emotional states 124
livestock animals 101	neophobia 292
locus ceruleus (LC) 173–174	nesting box 28, 28
locus of control (LOC) 68–69, 200	neuroendocrine mechanisms 102–103
Loriidae 291	neurogenetic dysfunction 176
Editate 271	neurohormones 103
	neuronal loss 216
Macaca fascicularis 286	neuropathology 216, 217
macaques, rhesus 116	neuroticism 117
maladaptive distress disorders 346	noise 173–175, 317
managing welfare 63	nonpharmacologic methods of treatment <i>see</i> treatment
maternal attachment and care 320–324	(nonpharmacologic methods)
maternal experiences 127	nurturing 57
*	nutraceuticals 222–223
meal feeding 294, 294	nutraceuticais 222–223
mechanistic approach, to behavior patterns 167, 168	
mechanistic diagnosis levels 167, 168 mechanistic interaction 170–178	abosity 44
	obesity 44
medications 364	objectivity, well-being terminology 16–17
mental disorder, definition 185	Obligation and Extent of Humanity to Brutes,
Mental Evolution in Animals (Romanes) 25	Principally Considered with Reference to the
mental health	Domesticated Animal, The (Youatt) 24–25
assessing 2	obsessive-compulsive disorder (OCD) 170,
behavior 3–4	175–178, 197
behaviorist's view 1–7	opioid antagonists 367
definitions 2, 33, 123–124, 242	opioids 103
social support/contact 97–98	optimism 70
systemic signs 4	orangutans 116
mental illness, diagnosis 167–181	orbital widening 334
mental and physical health	orcas (Orcinus orca) 315–327
evaluating 42	oxytocin 103, 369–370
improving 43–44	
relationship 33–49	
mental stimulation 125	pain 85, 157, 159–162, 279, 286–287
mental welfare development 125–126	Pain and Distress in Laboratory Animals Committee
mice 129–130, 281	(NRC, 1992) 143, 144, 145, 146
military working dogs (MWD) 192-194, 204	pair bonding 292–293

panic disorder 173	interindividual variability 187
Panksepp Emotional System 231–232, 232	kangaroos 192
parrots 367-368, 368	learned helplessness 196-197
passive/reactive agency 159	models 190–191
pathologic fear 185	neurobiology and pathophysiology 189-190
pathology, development of 144	OCD 197
pathophysiological responses to chronic threat 42, 43	partial 186
Pavlovian cues 336	phobias 195–196
perfectionism 11	predictability 72
personality traits 111, 116–117	proposed schematic 195, 195
personhood 158	qualitatively distinct syndrome 186
pets 4, 212–230	re-exposure to TRCs 190
pharmacologic methods of treatment <i>see</i> treatment	social buffering 102
(pharmacologic methods) 346	subsyndromal 186
pharmacotherapy 204–205	subthreshold 186–187
philosophy 21–32	types 189
phobia 195–196, 345	wolf 191
photoperiod 294	potentially traumatic event (PTE) 183
physical health 33–49	predictability 71–72, 76, 125, 359–360
physical well-being 15–16, 15	predictable behavior 305
physiologic stress 97	pressure-release 358–359
physiological parameters, CTRS 42, 42	preventative veterinary medial care 39
physiological responses, to environmental	prevention, of behavior problems 134–136
enrichment 43, 43	primates 102, 106
pigs 235–236, 236, 237, 238	probability 159–160
placebo effect 160	progestins 370
playing 58	propanolol 367
pleasurable experiences 125	pseudo-enrichment 288
pleasure 30, 57	Psittacidae 291
pollution 215	psychological constructs, measuring 112
population attributable fractions (PAFs) 36	psychological harm 200, 201
positive affective engagement 53, 58, 60	psychological trauma
positive experiences 56	adaptive fear responses 184–185
Positive Reinforcement Training (PRT) 286, 306–307	CBT 203–204
positive welfare experiences 58–61	characteristics of the experiencer 199
posttraumatic psychological disorders in animals 200–203	coexisting conditions 197–198
posttraumatic psychopathology 182–211	comparing humans and animals 183–184
posttraumatic stress 185–187, 186, 186	control 200
posttraumatic stress disorder (PTSD)	early life adversity 199–200
amygdala 189	GAD 185
bears 191–192, 193	genetics 199
brain functions 189	history of understanding 182
canine 192–194	indistinct concepts and terminology 182
chimpanzees 191	meaning 182–183
clinical diagnosis 187	posttraumatic psychopathology 182–211
clinical studies 191–192	potentially traumatic event (PTE) 183
cows 190	risk and resilience 198–200, 201
depression 196–197	social buffering 200
diagnostic criteria in children 187, 188	stress inoculation 200
does it occur? 194–195	stressors 189–190
dogs 191	systematic desensitization (SD) 203-204
elephants 191	treatment 203, 204–205
experimental studies 190–191	psychological well-being 15–16, 15
fear conditioning 189	psychopathologies 100, 101
felines 192	psychosomiasis 279
GAD 196	psychotropic drugs 322
hypervigilance 189	psychotropic medicines 205
0	

pterotillomania 295	response
puppies, rehoming age 128–129	blocking 346–347
	prevention 346
	rewarding behaviors 53, 60–61
Qualitative Behavioral Assessment (QBA)	risk of psychological trauma 198–200
265, 335	rodents 69–70, 101–102, 102
quality of life (QOL)	1040115 05 70, 101 102, 102
animals in veterinary medical practice 82–95	
applications of thinking 88–91	safety signals 305
11 0	
assessment 2, 88–89	sanctuaries 322–323
proxy 86–87	screaming 296
assessment tools 88, 89, 89, 90	seaside sanctuaries 322–323
breadth 83–84	seeking system 264
categorizing 10	selective serotonin reuptake inhibitors (SSRIs) 204,
change under anesthesia 16	370, 371
check sheet 131–133, 132–133	selegiline 372–373, 373
communication 91	self, diminished sense of 164
evaluating multiple inputs 86	self-harm 319
evaluative 82–83	self-injurious behavior (SIB) 191
health 85	self-medicating 44
individualistic 84	self-medication 28
inputs and indicators 85-86	sensitization 2, 36–37, 39, 184
measuring 87	sensory systems 316
mental 84	separation
minimizing bias and error 87	anxiety 173-175, 246-247, 345
pain 85	distress 232
policy 91	serotonin system 173
predictions 89	shaping 358
qualities 82	shaping by successive approximations (SBSA) 358
quality versus quantity 84, 84	shelter animals
recognizing assessment limitations 88	ability to opt out 266
relationships and instrumental value 85	aggressive behavior 258
Robinson scale 117–118	anhedonia and helplessness 264–266, 264
screening 88	background 257
term 8–9, 14	cognitive biases 265
tool validation 87–88	effect of exercise 260
treatment decisions 89–90	environment 259–262
using 86–88	euthanasia 257
what affects 85–86	fear 258, 259
what animals should be free from 83	fear-based aggression 258
what animals should have opportunities for 83	frustration 263–264
what it is not 84–85	human attention 259
WHO 82	human interaction 261
Question of Animal Awareness, The (Griffin) 26	hyperarousal 263–264, 263
Question of Animal Awareness, The (Gillill) 20	
	Italy 257
261	learned helplessness 265
rage system 264	learning body language 266
rats 129–130, 353	length of stay (LOS) 257, 260
reactive depression 197	long term holds 257, 260
recidivism 176	mental health issues 257–276
Recognition and Alleviation of Distress in Laboratory	noise 260
Animals (NRC, 2008) 142	ontogeny 262–263
reinforcement theory 332, 354, 355, 359	personality 266–268
repetitive behaviors 176, 264	play behavior 261–262
research, teaching and testing (RTT) procedures 54	playgroups 261
resilience 41, 198–200	population figures 257
training 134	previous experiences 262

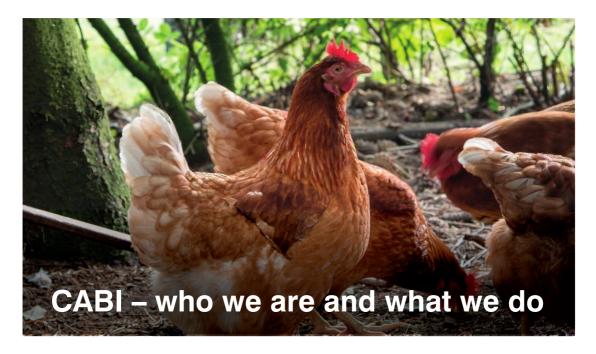
shelter animals (continued)	stress-related versus non-stress-related
psychological environment 263-266	effects 89–90
puppies 262–263, 262	social tension 317
QOL assessments 265	socialization 128-129, 183, 197-198, 205n1
Qualitative Behavioral Assessment 265	phase 127–128
rage system 264	somatic causes, diagnosis 170
recommendations 268–270, 268	stereotypic behavior 296
relinquishment reasons 258–259	stereotypies 318–319, 319
repetitive behaviors 264	stimulus 184
restricted movement 260	Strange Situation Test 213
reward sensitization 264	stranger aggression 346
seeking system 264	stress 2–3
social enrichment 261, 261	chronic 2, 119, 197, 198, 204, 258, 260, 264–266,
stressors 259–260, 259	317–322
visitor access 261	
situation inference 332, 334	coping 71 definition 124
	homeostasis and distress 146
Six Elements to Psychological Wellbeing in Captive	
Animals (USDA) 2	inoculation, psychological trauma 200
sleep deprivation 294	laboratory animals 280
sociability 106	meaning 35
social animal 106n1	stress buffering see social buffering
social buffering 96, 97, 355–356	stress-induced behavioral models 197
adult animals 101–102	stress-induced dishabituation 198
dogs 102, 105, 105, 106	stressful developmental experiences 37
helper 356, 356	subjective well-being (SWB) 8–9, 14, 117
emotional state of social partners 104	subjectivity 332
factors modulating efficacy 103-104	suffering
familiarity of social partner 103-104	academic usage of term 156-157, 157
horses 101	adaptiveness 148
hypothalamic-pituitary-adrenal (HPA) axis 103	agency and the Bayesian mind 156-166
infant and juvenile animals 100–101	alert function of 148
livestock 101	assessing 163–164
neuroendocrine mechanisms underlying 102-103	causes 149
non-social isolation stress and adversity 100–104	character 149
number of social partners 104	compared with distress 147–150
opioids and neurohormones 103	control 149–150
oxytocin 103	cut-off point 148
posttraumatic stress disorder (PTSD) 102	definition 147–148
primates 102	factors likely to contribute to 163
promotion of social affect 104–105	function 148
psychological trauma 200	human descriptions 157–158
rodents 101–102, 102	negative affect 150
social experiences in early life 104	in silence 4
social companionship 125	surgery 162
social interaction 308	understanding states of 28–30
social pain 99	suicide 321–322
social species law (Switzerland) 99, 100	surgery 162
social support/contact 96–110	survival 52–53, 99
alleviation of negative affects of isolation 99-100	survival-critical negative affects 51–52, 55, 62
categorizing effects 98–99	swimming stereotypies 318
general benefits 96	Switzerland, social species law 99, 100
how it benefits mental health and	sympatholytics 367
well-being 98–105	systematic desensitization (SD) 203-204
isolation-related and non-isolation related stress 99 mental health benefits 97–98	
physical health benefits 96–97	tail chasing 175–176
proposed pathways leading to positive effects 98, 98	temperament selection 231
proposed pathways leading to positive critets 70,70	temperament selection 251

1 386 Index

temporality 14-15	selective serotonin reuptake inhibitors (SSRIs)
Terrestrial Animal Health Code (OIE) 13	370, 371
thermoneutral zone (TNZ) 281	selegiline 372–373, 373
threatening environments 35	sympatholytics 367
thriving animals 53	trazodone 367, 367
thunderstorm phobia 174	tricyclic antidepressants (TCAs) 370-371, 371, 372
torture 162	truth effectiveness 158, 161
toys 74	
transportation 234	
trauma related cues (TRCs) 184, 189	United States Department of Agriculture (USDA),
trazodone 367, 367	Six Elements to Psychological Wellbeing in
treatment (nonpharmacologic methods) 345-363	Captive Animals 2
backward chaining 357-358	upbringing, fostering mental and behavioural
clicker training 358	wellness 123–139
competing response training 356–357	Ursus thibetanus 191-192, 193
components of 346	utilitarianism 22–23, 24
control 359–360	
counterconditioning alone 349-351	
desensitization alone 349	value effectiveness 159
desensitization and counterconditioning	visitor effect, zoo animals 303
(DSCC) 347–355	vocalizations 334–335
effective management 346	voluntary behavior 351, 352
emotional distress and disorders in companion	voluntary breathers 322
animals 345–363	
flooding 346–347, 347	
graduated exposure therapy 347	weaning 129
implosion therapy 346-347	welfare
options for distress-related behaviors 346-355	animal 24–28, 53–54, 117
predictability 359–360	concept of needs 124-125
pressure-release 358–359	definitions 10
response blocking 346–347	genetic predispositions 126
shaping 358	term 8–9, 26
social buffering 355–356	well-being
treatment (pharmacologic methods) 346	concepts 9–11, 13–17
acepromazine 368	determinants of 328
Animal Medicinal Drug Use Clarification Act	effects on 11, 11, 13
(AMDUCA) 365	measurements 13
antipsychotics 367–368, 368	states, different terminology 11, 12
azapirones, buspirone 372	terminology 8–9, 10
benzodiazepines 366–367, 367	distinctions in literature 14–17
changing and combining 373	general descriptions 13
CNS stimulants 369, 369	objectivity 16–17
cost 365	physical 15–16, 15
dexmedetomidine 367	problems with 8–20
emotional distress and disorders 364-376	psychological 15–16, 15
fast-acting medications 366–370	summary 17
gabapentin 369, 369	temporality 14–15
haloperidol 368	whales (Beluga) (Delphinapterus leucas) 315-327
hormones 369–370	What is it like to be a bat? (Nagel) 29
legal, ethical and cost issues 364–366	wildcats, Scottish 117
long-term or maintenance medications 370-373	wolf (Canis lupus) 191
medicating the patient 365–366	World Health Organization (WHO) 82, 242
monoamine oxidase inhibitors 372–373, 373	
opioid antagonists 367	
oxytocin 369–370	zoo animals
progestins 370	avoiding negative interactions 306
propanolol 367	behaviors 302–303, 305

zoo animals (continued)
boredom 303-304
challenges particular to 303-304
choice, control, behavioral contingency 308
cognitive bias test 304
cognitive challenges 308
enrichment assessment 308
environmental enrichment 307-309
exploration needs 304
feeding methods 309
food rewards 307
KAR bonding benefits 306
Keeper-Animal Relationships (KAR) 305-306

measuring positive affective state 304 multi-institutional research 309 naturalistic habitats 307 novelty 308 occupational therapy 306 population 302 positive affective states and well-being 304–305 Positive Reinforcement Training (PRT) 306–307 psychological well-being 302–314 safety signals 305 social interaction 308 visitor effect 303 welfare standards 304



This book is published by **CABI**, an international not-for-profit organisation that improves people's lives worldwide by providing information and applying scientific expertise to solve problems in agriculture and the environment.

CABI is also a global publisher producing key scientific publications, including world renowned databases, as well as compendia, books, ebooks and full text electronic resources. We publish content in a wide range of subject areas including: agriculture and crop science / animal and veterinary sciences / ecology and conservation / environmental science / horticulture and plant sciences / human health, food science and nutrition / international development / leisure and tourism.

The profits from CABI's publishing activities enable us to work with farming communities around the world, supporting them as they battle with poor soil, invasive species and pests and diseases, to improve their livelihoods and help provide food for an ever growing population.

CABI is an international intergovernmental organisation, and we gratefully acknowledge the core financial support from our member countries (and lead agencies) including:



Ministry of Agriculture People's Republic of China





Agriculture and Agri-Food Canada





Discover more

To read more about CABI's work, please visit: www.cabi.org

Browse our books at: www.cabi.org/bookshop, or explore our online products at: www.cabi.org/publishing-products

Interested in writing for CABI? Find our author guidelines here: www.cabi.org/publishing-products/information-for-authors/

Mental Health and Well-being in Animals

2nd Edition

Edited by Franklin D. McMillan

Since publication of the first edition of this book, public concern for the well-being of animals has continued to increase throughout the world. In addition, advances in research over the past decade have yielded an enormous amount of knowledge about animal mental health and well-being. Studies on animal stress, distress, emotions, psychological trauma, and mental disorders have brought to light insights on how to care for and treat the animal mind.

The second edition is:

- Fully revised, expanded, and comprehensively updated with the most current knowledge about the full array of mental health issues seen in animals.
- Written by key opinion leaders, internationally-recognized experts and specialists.
- Comprehensive in its coverage, from the basic principles of mental wellness, emotional distress, suffering and mental illness, through to measurement and treatment.
- Packed with even more practical information, wisdom and clinical tips.

This book remains invaluable to veterinary professionals, animal welfare researchers and advocates, and other animal caregivers.