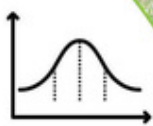


JASON V. WATTERS • BETHANY L. KREBS

# A GUIDE TO MANAGING ZOO ANIMAL WELFARE

A BEHAVIORAL APPROACH



WILEY Blackwell



## **A Guide to Managing Zoo Animal Welfare**



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A Behavioral Approach

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*For every beast whether they have four legs, two, none, or many:  
fins, wings, arms, tentacles, or antennae.*



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# 1

## Background Concepts and Goals

### Keeping Animals

For many reasons, people manage numerous species of animals in what we most frequently refer to as captive conditions. Now, more than ever before, there is a major emphasis on the psychological well-being of the animals cared for in any industry of which they are a part. In this book, it will seem as if we make a distinction between wild or exotic captive animals and domestic animals and focus our examples on the former. This is not to say that the concepts developed here are not also applicable to domestic animals. Our focus on exotics is aimed at the development of a general approach. We develop this approach for two primary reasons. One reason is that the environments and behavioral outcomes associated with them that non-domestic animals live in under human care are a traditional focus of inquiry when it comes to assessing the psychological state of these animals. Less frequently do we compare the domestic animal's environment with their wild counterpart's. Such comparisons are not realistic because, due to artificial selection for domestication, there is no naturally selected wild counterpart to a derived domestic animal. Who is to say that the behavior of the feral mustang is the standard to which the barnyard stallion should be held? A dog is not the same animal as a wolf. Instead, but for subtly different reasons, we compare domestic animals to what we know of their wild ancestors – who are most commonly extinct. The dog and the wolf may have shared an ancestor in the form of some ancient extinct wolf, but they have since gone their separate ways. Nevertheless, an understanding of the evolutionary history of the dog and the wolf is likely to support, not guarantee, caring for either animal in the modern world – regardless of the environment we find them in. Thus, by focusing on wild, exotic animals, we hope to emphasize the point that the psychological care of animals is not dependent on the exact replication of the environmental conditions under which the

animals live in the wild. We also hope to emphasize that it is possible to develop a general approach to thinking about and supporting animals' psychological well-being that can be used to care for individuals of numerous species, wild and domestic.

As a result of evolution's slow progression of tinkering on a core blueprint, there are fundamental similarities across species that support the application of a general approach to promoting animal welfare. Most of us are aware of some of these similarities, such as the generalized vertebrate body plan, but they also include subcortical emotional circuitry that is also widespread in the animal kingdom. The Cambridge Declaration on Consciousness (2012) resulted from a gathering of prominent neuroscientists with varied specializations in anatomy, physiology, pharmacology, and cognition. In developing the Declaration, these experts considered the convergence of evidence that indicates that nonhuman animals, both vertebrate and invertebrate, possess the neuroanatomy that generates and processes affective states. Experimental evidence shows that when these subcortical brain structures are stimulated, behaviors expressed are like those expressed when humans or other animals experience rewarding or punishing affective situations. The Declaration indicates that these emotional brain regions are present in all mammals and birds and that the neural circuits necessary to promote attentiveness, sleep, and decision-making arose long enough ago that they are also present in insects and cephalopod mollusks.

The Declaration states that "emotional feelings" arise from a set of subcortical brain regions that are similar across species and that there is adequate evidence to suggest that humans and nonhuman animals possess "evolutionarily shared primal affective qualia." This is to say that intrinsic self-assessment of positive and negative feelings is evolutionarily old. All animals do this. While the Declaration makes no statement regarding reptiles, amphibians, or fish, the inclusion of insects, cephalopods, birds, and mammals suggests that these taxa would also be included in the thesis of the Declaration were there adequate data to provide examples. Today, evidence is starting to arise that suggests this is the case. This support comes from studies that demonstrate phenomena such as cognitive bias in bees (Bateson et al., 2011) and anticipatory behavior in fish (Reebs and Lague, 2000, Galhardo et al., 2011) and other species (Anderson et al., 2015, McGrath et al., 2016, Clegg et al., 2018, Podturkin et al., 2023). Animal welfare scientists consider these behavioral responses to reflect animals' own perception of their affective state (Moe et al., 2006, Van der Harst and Spruijt, 2007).

A description of the core mind here may help to understand some of the justification and techniques described in the chapters that follow. A mind is the cumulative set of traits that enable awareness, decision-making, memory, and affective response (i.e. internal reflection). Overall – the mind, like other traits, serves a developed function – and that is to assess and relate to the individual information

regarding their own state as well as their potential state given their perceived circumstances. An individual's mind determines the interpretation of circumstances, both cumulative and present, and generates from this determination the individual's perception of balance. Balance in this way refers to the aggregate assessment of the internal outcomes associated with events the individual experiences. Other authors have referred to this state as mood-like state (Yang et al., 2013, Mendl and Paul, 2020, Bliss-Moreau and Rudebeck, 2021). The cumulative emotional experience of an animal builds their mood-like state (Kremer et al., 2020, Mendl and Paul, 2020). As we hope to apply this thinking to support animal welfare, we use the term "balance" to describe our approach to measuring and managing this state. Experiences are either affectively positive, negative, or neutral (Gasper et al., 2019, Gasper, 2023). Positive and negatively valenced affect can be driven by either tangible outcomes – as in the cases of procuring food or being injured – or intangible ones – as in the cases of information acquisition or becoming fearful. In either case, tangible or intangible outcomes, there is an affective response – essentially, and very simply put, the individual either feels good about the outcome or does not feel good about it. Neutral affective outcomes result in what would appear to be behavioral indifference or a lack of preference (Gasper et al., 2019, Gasper, 2023). The mind thus serves to evaluate these affective outcomes and determine whether the animal should attempt to promote further similar events or avoid them. Thus, the mind serves the function of monitoring and reporting on affective outcomes. At the very least, a balance between positive and negative outcomes ensures that this core mind remains healthy. In this sense, the mind requires specific nurturing and can be unhealthy even when the body appears healthy. While we acknowledge that the brains of many species have evolved to facilitate advanced cognitive abilities, problem-solving, and even self-recognition (Roth, 2015, Mitchell, 2016, Gallup Jr and Anderson, 2020), we assert that the core mind is the seat of fundamental emotion, and that affect is a driving force in supporting evolutionary fitness.

Minds, like bodies, need to be nurtured. When an animal does not consistently live in a state where they achieve that balance between positive and negative outcomes, they can be in a state of negative welfare. This negative state is psychologically damaging (Désiré et al., 2002). The primary goal of this book is to provide a general technique to assess animals' own perspectives of their welfare state and to suggest techniques to provide positive opportunities when an animal is negatively out of balance. Throughout the book, we will refer to animals' core behavioral Needs, investigating, acquiring rewards, and managing one's own processes. These core Needs are evolutionarily old and the logic that we will lay out in this book suggests that ensuring that the Needs are met provides for a balanced state of welfare. Our approach is thus a focus on the fifth domain – mental state – of the five domains model of animal welfare (Mellor and Beausoleil, 2015). Throughout,

we will capitalize the word Need when we refer to these three Needs as a means to set these Needs apart from other needs that animals may have.

Our concept of animal welfare is a kingdom-level individual property. It occurs across phyla and is not a species-level property. There is a reasonable amount of evidence supporting the notion that the three motivational Needs described herein are shared across species and that they are thus of fundamental importance at the level of the kingdom. Phenomena such as cognitive bias in species ranging from bees to bears, anticipatory behavior in species as disparate as rhinoceroses and fish, contra-freeloading of numerous species of birds and mammals, preferences for enriched spaces from turtles to rats, and widespread reward seeking behaviors support the notion that individuals across the animal kingdom share the motivational Needs we describe. This understanding is core to the cross-species applicability of our approach (Pacheco et al in prep). Our approach centers on assessing the three Needs in each animal who draws our focus. We specifically attempt to determine if the animal is showing us, with their behavior, if they are able to meet the three Needs. However, because the mechanism by which each animal interfaces with the environment differs, we seek to understand species typical behaviors that reflect engaging the motivations that underly the three Needs. We often ask, “What does investigatory behavior look like in the species we are currently observing?”

Applied animal welfare workers often approach adjusting animals’ mental state through the application of environmental or behavioral enrichment (Brydges et al., 2011, Douglas et al., 2012). However, this book is not aimed at being a clearinghouse for animal enrichment ideas. Many of those are already available. In its simplest sense, an animal’s mind is nurtured when the animal acquires meaningful and sometimes novel information, occasional and predictable success and has behavioral options that permit them to express agency. This novel information may be related to understanding one’s environment or understanding the consequences of one’s actions. The following chapters will elaborate on topics related to understanding what minds need and how to give it to them. Part of the book is written as a handbook for those caring for numerous species of animals in zoos, aquariums, and sanctuaries. Thus, while the primary concepts are general, there are specific sections pointed directly at this intended audience. These sections aim to further convince this audience that the psychological well-being of the individual animal is of utmost importance to meeting their institutional goals. Throughout the book, we will attempt to provide necessary background but not excessive details in the hope that this will facilitate quick understanding of the key points while not dwelling on minutia and specific details of the supporting research. The goal, after all, is to support the practice of caring for animals’ minds, not to justify it.

The argument for the core behavioral Needs is developed here with consideration of the findings of three primary research disciplines. The disciplines use differing and sometimes overlapping techniques to evaluate behavior, its drivers, and its

outcomes. Where techniques overlap, they help to demonstrate generality and where techniques are novel to a discipline, they help to validate findings. Some techniques are not practiced across fields because of their invasiveness or varied feasibility with certain subjects. For example, human psychology researchers can hold conversations with their subjects while animal behavior researchers cannot. Similarly, affective neuroscientists can stimulate specific brain regions and observe responses.

Several disciplines separately indicate similar factors that lead to positive psychological and behavioral outcomes for both animals and people. Taken together, these disciplines suggest a simple set of core behavioral Needs. Specifically, these disciplines are Affective Neuroscience, Motivation Psychology, and Animal Behavior. In essence, we use these disciplines' emphasis on similar goals to build support for our approach through a triangulation wherein we look for the overlap of findings across fields or the application of those from one field to another. Jaak Panksepp is our inspiration for applying this approach.

In the end, we hope to provide a way to observe and measure animal behavior that is informed by these disciplines and that helps the observer to understand if animals' core Needs are met. Another goal of the book is to suggest a general technique that can be useful for monitoring and improving animal welfare and is not reliant on expensive technology or testing. Its efficacy is observable through animals' behavior. In the sections that describe animals' Needs, we will present evidence from each of these areas in support of that Need's importance.

## **Affective Neuroscience**

Affective neuroscientists focus their efforts on understanding the neurological mechanisms of emotion. They often use techniques that directly measure the neural responses to specific stimuli. For example, Jaak Panksepp, whose work demonstrated seven basic mammalian emotions used a combination of neurostimulation and recording techniques coupled with various stimuli to track the seat of several emotions in the brain as well as the situations that stimulate them and the behavioral responses associated with them (Panksepp, 2005a, 2011). We follow Panksepp in using a triangulation approach. He included evidence from behavioral, psychological, and neuroscientific studies to elucidate what he called core affective states (Panksepp, 2005b). Specifically, Panksepp was a pioneer in the field of affective neuroscience, demonstrating that raw affects arise from the sub-neocortical neurophysiologies of emotional action systems in the mammalian brain. These findings were in stark contrast to the assumptions of behavioral neuroscience and cognitive neuroscience that placed the development of affect as a higher order brain process (Panksepp, 2005b). As a result of these disparities across neuroscience fields, Panksepp believed that affect was overlooked in

studies of basic animal biology. Though affect is becoming a central paradigm of animal welfare research.

Panksepp and colleagues' work lays a foundation for understanding that there are evolutionarily old behavioral Needs. His findings suggest that the core emotions are subcortical and not the result of higher order cognitive function. It is this work that demonstrates the locations in the brain where stimuli generate affective responses and associated behaviors that suggest that mind and emotion do not require higher order cognitive capability. In addition, work in this field suggests that when certain basic emotions are not experienced, psychological welfare is compromised (Alcaro and Panksepp, 2011).

## **Motivation Psychology**

Human psychologists are interested in how the state of a person's mind drives their behavior. Scientists studying humans can interview their subjects and ask informed questions. This process, where the subject of study describes to the researcher their feelings and actions, is referred to as self-reporting (Paulhus and Vazire, 2007). Those who work on understanding the connections between emotional states and behavior advance these understandings with the self-report process. While the credibility of self-reported data is sometimes criticized (Paulhus and Vazire, 2007), the self-report procedure is perhaps the sole technique that allows the direct coupling of affective state with behavior. Given the possibility of widespread affect-driven behavior as proposed in the Cambridge Declaration on Consciousness, it seems possible that educated observers could use animals' behavior as a sort of a self-report and a means to assess animals' emotional state.

E. Tory Higgins and colleagues have developed (Higgins, 1997) the conceptual framework of "effectiveness" that describes motivations aimed at generating positive emotional outcomes. The theory of effectiveness describes three primary motivational goals that support positive well-being. Higgins and colleagues refer to these motivational goals as truth, value, and control. Their research demonstrates that supporting these motivations leads to positive well-being. Becca Franks has extended Higgins' approach to the field of animal welfare (Franks and Higgins, 2012). She has demonstrated that the concept of effectiveness carries over to animals.

## **Animal Behavior**

Animal behavior research has expanded humans' understanding of numerous factors including animal movement, communication, mate choice and sexual selection, foraging decisions, predator-prey interactions, and many more areas.

Much animal welfare research is housed within this discipline. Here, specific questions regarding what animals want, one of Marian Stamp Dawkins (Dawkins, 2021) two components of animal welfare (the other being health), are often addressed. Additionally, animal behavior researchers are now frequently asking questions about how animals feel – in part through approaches that draw on other fields but rely on behavioral observation. These two lines of inquiry, what animals want and how they feel, are tools for assessing animals' mental health.

Studies that investigate animals' preferences, anticipatory responses, decision-making, willingness to work, and response to novelty are among those that point to animals' core behavioral Needs. They reinforce our understanding of animals' basic motivations that we believe must be supported to promote animal welfare.

We acknowledge that there are many interpretations of the term animal welfare (Fisher, 2009, Watters et al., 2021). Its definitions vary and, as a result, we feel it is important for those writing on the subject to define it so that their meaning is not misinterpreted by others who are interested in the subject but perhaps ascribe a different meaning to it. Indeed, as animal welfare research expands and takes on more nuanced forms of investigation, this simple description upon planning research or describing it will help workers to justify their choice of variables to measure and the techniques they use to assess them.

In previous work, we have described animal welfare as being a state of balance between animals' positive and negative affective experiences (Watters et al., 2019). We have suggested that animal welfare is the animal's own perception of their psychological state (Watters and Krebs, 2019). We have assessed this reflection with various behaviors and have justified doing so with chains of logic. We consider an animal's welfare to be their cumulative emotional state. Often referred to as an animal's mood-like state (Mendl and Paul, 2020), this cumulative state reflects the overall balance between positive and negative emotional outcomes. Some circumstances lead to positive affective responses while others result in negative ones. It is the state of balance between these positive and negative emotional outcomes that we measure when we ascribe an animal's welfare state. We admit that we do not know exactly the duration that we should assess to determine a cumulative welfare state and suggest that this duration may be dependent upon the presence of very strongly valenced, highly aroused affective outcomes. For example, experiences that produce very strong fear responses are likely to cause shifts to a generally negative affective state that is relatively long lasting compared to episodes that result in brief moments of fear followed by recovery (Jones and Boissy, 2011). We also suggest that because they are built on cumulative outcomes, mood-like states should be observable repeatedly over relatively short time frames and can persist for very long ones, though our key premise is that they can change.

We will provide suggestions for developing protocols aimed at observing animals' cumulative affective state. These protocols will help observers determine the duration of observation necessary to draw conclusions about animals'

own perceptions of their well-being. The approach we will describe combines observation across time with specific situational observation as there are situationally expressed behaviors that reflect some degree of this cumulative state.

## References

- ALCARO, A. & PANKSEPP, J. 2011. The SEEKING mind: primal neuro-affective substrates for appetitive incentive states and their pathological dynamics in addictions and depression. *Neuroscience and Biobehavioral Reviews*, 35, 1805–1820.
- ANDERSON, C., YNGVESSON, J., BOISSY, A., UVNAS-MOBERG, K. & LIDFORS, L. 2015. Behavioural expression of positive anticipation for food or opportunity to play in lambs. *Behavioural Processes*, 113, 152–158.
- BATESON, M., DESIRE, S., GARTSIDE, S. E. & WRIGHT, G. A. 2011. Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology*, 21, 1070–1073.
- BLISS-MOREAU, E. & RUDEBECK, P. H. 2021. Animal models of human mood. *Neuroscience and Biobehavioral Reviews*, 120, 574–582.
- BRYDGES, N. M., LEACH, M., NICOL, K., WRIGHT, R. & BATESON, M. 2011. Environmental enrichment induces optimistic cognitive bias in rats. *Animal Behaviour*, 81, 169–175.
- CLEGG, I. L. K., RÖDEL, H. G., BOIVIN, X. & DELFOUR, F. 2018. Looking forward to interacting with their caretakers: dolphins' anticipatory behaviour indicates motivation to participate in specific events. *Applied Animal Behaviour Science*, 202, 85–93.
- DAWKINS, M. S. 2021. *The Science of Animal Welfare: Understanding What Animals Want*. USA: Oxford University Press.
- DÉSIRÉ, L., BOISSY, A. & VEISSIER, I. 2002. Emotions in farm animals: a new approach to animal welfare in applied ethology. *Behavioural Processes*, 60, 165–180.
- DOUGLAS, C., BATESON, M., WALSH, C., BÉDUÉ, A. & EDWARDS, S. A. 2012. Environmental enrichment induces optimistic cognitive biases in pigs. *Applied Animal Behaviour Science*, 139, 65–73.
- FISHER, M. W. 2009. Defining animal welfare - does consistency matter? *New Zealand Veterinary Journal*, 57, 71–73.
- FRANKS, B. & 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.
- GALHARDO, L., VITAL, J. & OLIVEIRA, R. F. 2011. The role of predictability in the stress response of a cichlid fish. *Physiology & Behavior*, 102, 367–372.
- GALLUP, G. G., Jr. & ANDERSON, J. R. 2020. Self-recognition in animals: where do we stand 50 years later? Lessons from cleaner wrasse and other species. *Psychology of Consciousness: Theory, Research, and Practice*, 7, 46.

- GASPER, K. 2023. A case for neutrality: why neutral affect is critical for advancing affective science. *Affective Science*, 4, 458–462.
- GASPER, K., SPENCER, L. A. & HU, D. F. 2019. Does neutral affect exist? How challenging three beliefs about neutral affect can advance affective research. *Frontiers in Psychology*, 10, 2476.
- HIGGINS, E. T. 1997. Beyond pleasure and pain. *American Psychologist*, 52, 1280.
- JONES, B. & BOISSY, A. 2011. Fear and other negative emotions. In: APPLEBY, M. C., MENCH, J. A., OLSSON, I. A. S. & HUGHES, B. O. (eds.) *Animal Welfare*. CABI. pp. 78–97.
- KREMER, L., HOLKENBORG, S. E. J. K., REIMERT, I., BOLHUIS, J. E. & WEBB, L. E. 2020. The nuts and bolts of animal emotion. *Neuroscience and Biobehavioral Reviews*, 113, 273–286.
- LOW, P., PANKSEPP, J., REISS, D., EDELMAN, D., VAN SWINDEREN, B. & KOCH, C. 2012. The Cambridge Declaration on Consciousness. *Francis Crick Memorial Conference*.
- MCGRATH, N., BURMAN, O., DWYER, C. & PHILLIPS, C. J. C. 2016. Does the anticipatory behaviour of chickens communicate reward quality? *Applied Animal Behaviour Science*, 184, 80–90.
- MELLOR, D. J. & BEAUSOLEIL, N. J. 2015. Extending the ‘Five Domains’ model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*, 24, 241–253.
- MENDL, M. & PAUL, E. S. 2020. Animal affect and decision-making. *Neuroscience and Biobehavioral Reviews*, 112, 144–163.
- MITCHELL, C. 2016. The evolution of brains and cognitive abilities. In: PONTAROTTI, P. (ed.) *Evolutionary Biology: Convergent Evolution, Evolution of Complex Traits, Concepts and Methods*. Cham: Springer.
- MOE, R. O., BAKKEN, M., KITTILSEN, S., KINGSLEY-SMITH, H. & SPRUIJT, B. M. 2006. A note on reward-related behaviour and emotional expressions in farmed silver foxes (*Vulpes vulpes*): basis for a novel tool to study animal welfare. *Applied Animal Behaviour Science*, 101, 362–368.
- PANKSEPP, J. 2005a. Affective consciousness: core emotional feelings in animals and humans. *Consciousness and Cognition*, 14, 30–80.
- PANKSEPP, J. 2005b. On the embodied neural nature of core emotional affects. *Journal of Consciousness Studies*, 12, 158–184.
- PANKSEPP, J. 2011. The basic emotional circuits of mammalian brains: do animals have affective lives? *Neuroscience & Biobehavioral Reviews*, 35, 1791–1804.
- PAULHUS, D. L. & VAZIRE, S. 2007. The self-report method. *Handbook of Research Methods in Personality Psychology*, 1, 224–239.
- PODTURKIN, A. A., KREBS, B. L. & WATTERS, J. V. 2023. A quantitative approach for using anticipatory behavior as a graded welfare assessment. *Journal of Applied Animal Welfare Science*, 26, 463–477.