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### Permalink

<https://escholarship.org/uc/item/0h27d45g>

### Journal

Affective Science, 3(4)

### ISSN

2662-2041

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### Publication Date

2022-12-01

### DOI

10.1007/s42761-022-00168-9

Peer reviewed



# Introduction to Special Issue on Affective Science in Animals: Toward a Greater Understanding of Affective Processes in Non-Human Animals

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Received: 20 October 2022 / Accepted: 21 November 2022 / Published online: 3 December 2022  
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## Abstract

How should we characterize the affective lives of non-human animals? There is a large body of work studying affective processes in non-human animals, yet this work is frequently overlooked. Ideas about the affective lives of animals have varied across culture and time and are reflected in literature, theology, and philosophy. Our contemporary ideas about animal affect are philosophically important within the discipline of *affective science*, and these ideas have consequences in several domains, including animal husbandry, conservation, and human and veterinary medicine. The articles contained within this special volume cover several levels of analysis and broad representation of species, from the non-mammalian, to rodents, to primates; but together, these articles are collectively concerned with the topic of affective processes in non-human animals.

**Keywords** Animals · Animal welfare · Emotion · Affect · Behavior · Neuroscience

*‘Well, then,’ the Cat went on, ‘you see, a dog growls when it’s angry, and wags its tail when it’s pleased. Now I growl when I’m pleased, and wag my tail when I’m angry.’ (Carroll, 1865)*

The affective states of non-human animals (hereafter, *animals*) have long been the target of presumption, speculation, denial, and disregard. Animal affect has been reflected upon by authors, philosophers, and theologians; and most laypeople are likely to have some perspective on the topic. It makes sense that we should think about the affective lives of animals. Our own personal affective experiences are deeply rooted in our social lives, and we often think deeply about the affective lives of our social partners. We regularly engage in social

exchanges with nonhuman animals, and at times we cultivate relationships with them, from passing interactions with wild animals to more consistent relationships with livestock or beloved pets. We may even come to regard the latter as members of our extended families (or even describe and often treat them like our own children, e.g., *fur babies*). Through these interactions, many of us seek to attribute affective states to these heterospecific social partners. For some, this attribution of often human-like affective experience to animals is an anthropomorphic overapplication, yet to others, the rejection of animal affect is viewed as anthropocentric. How should we, then, characterize the affective lives of animals?

## Historical Perspectives

The extent to which one attributes affect to animals, or whether one attributes affect to animals at all, is perhaps based in one’s respective views on the nature of affect. These views have been simultaneously cultivated in distinct cultures across several historical periods. For the Western perspective, one might consider the lineage from the ancient Greek philosophical tradition and throughout the development of Christian theology. Aristotle (384–322 BCE, Greece) vacillated in his view of animal affect. On one hand, he believed cognition was a prerequisite for the experience of affect; so when he denied cognitive ability wholesale to animals, he therefore denied affect to animals

Handling editor: Wendy Berry Mendes

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(Fortenbaugh, 1971). Yet on the other hand, he at times attributed fear, pity, and other affective states to nonhuman animals (e.g., “... the eagle expels the nestlings because of jealousy”) (Fortenbaugh, 1971; Sihvola, 1996). Aristotle may have drawn a distinction between affect that is rational versus those that are irrational; and accordingly he attributed the former exclusively to adult humans while applying the latter (e.g., θυμός [*thumos*], or “non-rational, spirited desire”) to animals (and human children) (Sihvola, 1996). This distinction between the rational human and irrational animal was similarly applied by the Stoics (Passmore, 1975; Sihvola, 1996) and later echoed by some Christian theologians (e.g., Augustine of Hippo). This theme continues in the philosophy of Thomas Aquinas who proposed that human rationality gives us the right to govern other, irrational animals. Aquinas taught that it is good to treat animals humanely and with compassion because it promotes such feelings between humans, not because animals experience affective suffering—neither do they, in this view, experience affect more generally nor do they have a capacity for morality (Passmore, 1975). Eastern philosophical traditions developed in parallel to Greek and Christian philosophy, with Confucianism having been established in China at least 100 years prior to the birth of Aristotle and persisting with extensive regional influence over the next two thousand years. By the late Ming Dynasty (1368–1644), Chinese philosophers and writers in the Confucian tradition had cultivated the affective concept of *qing* (情)<sup>1</sup> (roughly translated as feeling or passion), which was at times contrasted with the concept of *xing* (性), or inborn [human] nature (Huang, 1998; Sung, 2016). Animals are characterized as possessing *qing*, but not *xing*. For example, the poet Yang Shen (杨慎) wrote “What will happen if one promotes *xing* but neglects *qing*? He will become dead ashes. What will happen if one is moved by *qing* but forgets about *xing*? He will become an animal” (Huang, 1998, p. 156–157).

Charles Darwin took great interest in the topic of non-human affect, extensively detailing his perspectives on animal affective expression (Darwin, 1872). He attributed to a variety of non-human animals the experiences of both positive (e.g., joy, affection) and negative (e.g., anger, terror) affective states and the expression thereof to communicate intention, for example:

... *The appearance of a dog approaching another dog with hostile intentions, namely, with erected ears, eyes intently directed forwards, hairs on the neck and back bristling, gait remarkably stiff, with the tail upright and rigid. So familiar is this appearance to us, that an angry man is sometimes said “to have his back “up”.*

(Darwin, 1872, p. 116)

<sup>1</sup> The concept of *qing* has changed over time and the description here is appropriate for the Ming Dynasty, but not necessarily appropriate in earlier texts, for example, those conveyed by Mencius. Interestingly, an early Confucian philosopher Xunzi (荀况, circa 310 – 238 BCE) defined *qing* as five specific emotions of *hao wu xi nu ai le* (好恶喜怒哀乐), or preferences, happiness, anger, grief, and enjoyment (Bruya, 2001).

Paul Ekman would later describe Darwin’s work on expression as “the first pioneering study of emotion” and perhaps even foundational to psychology itself (Ekman, 2009). Darwin, with his evolutionary perspective, registered his objection to the idea that affect is solely experienced and expressed by humans (Darwin, 1872; Ekman, 2009).

## Bridging the Gap

Bridging the gap between our experience of human affect, and our attempt to infer specific states in non-human animals, requires particular philosophical assumptions (Barrett, 2012). That is, because animals cannot describe their affective experiences with language, researchers must instead use various behavioral and physiological indicators of presumed affective states. For example, researchers may register freezing behavior as a proxy for “fear”; or they might alternatively measure neural activity from circuits known a priori to be active during particular human affective experiences or otherwise connected to a particular affectively associated behavior (Barrett, 2012). One perspective is that philosophical assumptions are not necessary if researchers stop attempting to measure specific emotions in animals (in general) or trying to identify hardwired signatures of said emotions in animals; rather, they should study the ingredients of emotion (e.g., *affect*, *conceptual knowledge*, *language*, and *social context*) per the *theories of constructed emotion* (Bliss-Moreau, 2017). In this special issue, Mendl and colleagues provide an alternative perspective in which they consider how to handle these philosophical inferences (Mendl et al., 2022). In this commentary, they argue that it is possible to systematically measure animal affective states with a framework of three pathways of inference through which one might consider how to translate *emotion concepts*, *emotion indicators* and *emotion-generating contexts*. Respectively, Mendl and colleagues consider a series of three questions: What types of emotions are likely to exist in other species? How can one assess animal emotional states? Can one establish an animal’s “ground truth” emotional state at any one time (and use that to identify indicators of animal emotion)? They then consider what might be necessary to determine if such affective states are consciously experienced as *conscious emotional feelings* by animals.

## Of Voles and Men

The successful generation of mental health treatments has relied and continues to rely heavily on the translation of animal research, particularly that in rodent models (Milton & Holmes, 2018). While there is not a perfect rodent model for any particular human affective disorder, the establishment of

assays for behavioral and physiological indicators of negative affect has been foundational to the subsequent generation of pharmacological interventions for affective disorders (e.g., anti-depressants; Robinson, 2018). Advances in genetic, molecular, and other neuroscientific tools have made the generation of improved rodent models and identification of biological markers of psychiatric disorders increasingly promising (Canetta & Kellendonk, 2018). The vast majority of this research is conducted in mice and rats; yet mice and rats are not always the best model for human affective experiences, which are notably rooted in social relationships.

One alternative to more common murine models is the prairie vole (*Microtus ochrogaster*), which is central to two papers included in this special issue. Early work by Getz and Carter established that prairie voles have relatively rich social lives, with wild prairie voles often integrated into large social networks of extended families, life-long mating, and biparental care, all indicative of their socially monogamous and cooperatively breeding social strategy (Carter & Getz, 1993; Getz & Carter, 1996; Getz et al., 1981; Roberts et al., 1998; Williams et al., 1992). Some intriguing similarities exist between prairie voles and humans, some of which may be less expected. For instance, the same sort of misattribution of arousal observed in human men by Dutton and Aron in their “shaky bridge” experiment (Dutton & Aron, 1974) is also observed in gonadally male prairie voles (DeVries et al., 1996), such that anxiogenic experiences preceding interaction with an sexually attractive stimulus are found to yield heightened sexual arousal and social approach in both species.<sup>2</sup> Yet, beyond their social behavior alone, prairie voles have proven a useful model for understanding the neurobiology of pair bonding and paternal care (Rogers & Bales, 2019; Seelke et al., 2018; Young & Wang, 2004).

The advent of the COVID-19 pandemic and associated stay-at-home orders fueled increased interest in the negative affective consequences of social isolation (Bland et al., 2022; Palgi et al., 2020), building on previous seminal work on loneliness (Ernst & Cacioppo, 1999). Here, Akinbo and colleagues (Akinbo et al., 2022) apply several levels of analysis at the behavioral, physiological, and neurobiological levels to illustrate the detrimental affective consequences

of prolonged social isolation in prairie voles, as well as the potential for environmental enrichment to partially ameliorate these deleterious effects. They demonstrated that four weeks of social isolation effectively increases depression- and anxiety-like behavior in the forced swim task and elevated plus maze as well as physiological markers of long-term stress (e.g., adrenal weight) in prairie voles. Moreover, socially isolated prairie voles showed altered dendritic morphology in the basolateral amygdala (BLA), a region of the brain associated with the processing of negative affect. Akinbo et al. further demonstrate that an intervention of environmental enrichment substantially ameliorated the aforementioned negative behavioral and physiological outcomes of social stress, yet it did not reverse the associated outcomes in dendritic morphology in the BLA.

For species like humans and prairie voles, our social attachments are deeply important to our mental and physical health. Recent advancements in molecular and genetic tools have allowed researchers to more deeply probe the neural mechanisms of attachment in rodent models of attachment, principally prairie voles. In a review included in this special issue, Berendzen and Manoli (2022) guide us through the relevant developmental and neurobiological concepts necessary to understand the genetic and neuroendocrine factors (e.g., the oxytocinergic system) that subservise social attachment in animals and humans. They synthesize historical findings with new perspectives and elegantly juxtapose the orthodox model of oxytocinergic action on processes of attachment with new, updated models which intriguingly redefine the role of the oxytocinergic system.

## Our Closest Relatives

We often attribute a similarity of affective experience between non-human primates and humans, due to our phylogenetic closeness (Darwin, 1872; Preuschoft & van Hooff, 1995). This issue contains several articles which explore the affective processes of monkeys and apes. Kim and colleagues (In Press) explored the social context of the bared-teeth display in chimpanzees (*Pan troglodytes*). The bared-teeth display is a facial expression which bears a resemblance to the human smile. Dominants directed these displays towards subordinates during affiliation, suggesting a reassurance function, while the same display was directed by subordinates towards dominance in aggressive contexts, suggesting an appeasement function. The authors thus found multicontextual use for this communicative signal, as well as slight variations in the display that may have different communicatory meanings.

Comparative research that includes physiological data measurable in both humans and animals, as well as

<sup>2</sup> In the study by Dutton and Aron (1974), male gendered (assumed heterosexual) human participants crossed a subjectively dangerous bridge, an anxiogenic experience, followed by an interaction with a subjectively attractive female interviewer. Compared to controls who crossed a subjectively safer bridge or interacted with a male interviewer, these participants demonstrated outcomes consistent with heightened sexual arousal. In the study of gonadally male prairie voles (DeVries et al., 1996), formation of a pair bond with a prospective female mate was facilitated by prior anxiogenic experiences of either the forced swim task or having been injected with corticosterone. In both cases, anxiogenic experiences promoted sexual arousal and social approach.

non-verbal tasks that both humans and animals can perform, can be especially enlightening regarding animal affect. For instance, differing pupil sizes can be an indicator of state of arousal or other social information. In addition, the dot-probe task is utilizable in similar ways in humans and animals (van Rooijen et al., 2017). Zijlstra and colleagues (2022) utilized a dot-probe task to investigate attentional bias towards an affective cue (i.e., differing pupil size), collecting similar data in both humans and bonobos (*Pan paniscus*). In this task, two stimuli are presented simultaneously, followed by a dot where one of the stimuli was displayed. If attention was consistently on one of the stimuli, the delay to touch the dot when it appears on the same side should be shorter than to touch the dot when it appears on the other side which is receiving less attention. Humans displayed a significant bias towards individuals with larger pupils, while bonobos did not display a bias. While the bonobo results were based on a relatively small sample size, if replicable they will indicate an interesting evolutionary difference in the role of pupil size in social interactions.

Laméris and colleagues (2022) also use the dot-probe methodology in orangutans (*Pongo pygmaeus*) to examine attentional bias towards affective scenes. Using Bayesian analysis, they support the likelihood that orangutans lack this bias which has been found in some other primate species, including rhesus monkeys (Lacreuse et al., 2013) and bonobos (Kret et al., 2016), but significantly not in chimpanzees (Wilson & Tomonaga, 2018). The need for testing of additional subjects, species, and affective contexts provides a promising area for future studies.

Debracque and colleague (2022) utilize a different technology, functional near infrared spectroscopy, to explore cerebral activity in baboons (*Papio anubis*) while hearing aggressive calls from either their own species or a different species (chimpanzee calls). The subjects tested had quite heterogeneous results; however, the technology is promising as a form of non-invasive technology which can be utilized to examine neural reactions to a wide range of affective stimuli.

## Back to our Lizard Brains

On the opposite end of the phylogenetic continuum, it is often more difficult for us to imagine that non-mammals (fish, reptiles, amphibians, invertebrates) experience affect, and the literature in this area is relatively sparse (Braithwaite et al., 2013; Lambert et al., 2019). Paul MacLean suggested that the mammalian limbic system gave mammals superior affective processing and linked this to the mammalian care of their offspring—even calling parental care “the Big News” in mammalian evolution (MacLean, 1977). Maciejewski and Bell (2022) now take the example of parenting

behavior to provide a review of this behavior in non-mammalian vertebrates, as well as evidence that there is a conserved similarity in the neurobiological mechanisms for this affect-linked behavior. They also point out that the relative frequency of male and biparental care in non-mammals provides special opportunities to expand our understanding of this behavior, which is rare in mammals (Kleiman, 1977; Kleiman & Malcolm, 1981).

## Technological Frontiers in the Study of Animal Affect

As technology improves, so does our ability to interrogate affect in animals—for instance, via the dot-probe task used in several of the papers in this issue. Positron emission tomography (PET) scans, as well as other modes of imaging and the fNIRS method used by Debracque and colleagues (2022), give us the ability to non-invasively study affect by putting animals in evocative situations during the radiotracer uptake period (Zablocki-Thomas et al., 2022). Eye-tracking can also be used non-invasively in animals to give measures of attention to videos or photos with affective content (Ryan et al., 2019; Yorzinski et al., 2013). Autonomic tools also give us a non-invasive window into the internal affective lives of animals (Murphy et al., 2019).

## Conclusions and Practical Implications of the Study of Animal Affect

The basic philosophical and scientific consideration of animal affect is on its own important, with significant implications for how we consider both the ultimate (evolutionary) and proximate mechanisms of our own human affect. Yet outside of these academic considerations, the study of animal affect has tangible consequences for practices of animal welfare, husbandry, and conservation, as well as human and animal medicine. For example, meat consumption and standards for animal welfare are influenced by how we conceptualize animals as beings with the ability to experience, think, and *feel* (Braithwaite et al., 2013; Loughnan et al., 2014; Morris et al., 2012; Wilkins et al., 2015). The translation of studies on animal affect into pharmacological treatments to improve human mental health implies a certain amount of shared affective reality between humans and animals (Milton & Holmes, 2018).

The papers published in this special issue span the phylogenetic tree from fish to humans but leave room for a great deal of additional exploration in many new species that have not yet been studied, and more in depth questions in those that have. We particularly hope that this special issue

highlights the strong role that animal research should play in affective science, as well as the openness of this journal to articles on animal affect.

A century and a half ago, Darwin argued that the study of animal emotion deserved further attention: "...we may conclude that the philosophy of our subject has well deserved the attention which it has already received from several excellent observers, and that it deserves still further attention, especially from any able physiologist." (Darwin, 1872). The collection of articles in this special issue suggests a multitude of new directions in which to take the study of animal affect.

## Additional Information

**Funding** Not applicable.

**Conflicts of Interest** The authors declare no competing interests.

**Data Availability** Not applicable.

**Code Availability** Not applicable.

**Authors' Contribution** Both authors contributed to the original draft, editing, and approving the final version.

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