



# Where are we in the study of animal emotions?

Amber J. de Vere\* and Stan A. Kuczaj II

The study of emotion is rife with debate over issues as fundamental as how to define emotion, and such disputes are particularly common in the nonhuman animal emotion literature. Here, we seek to address some of these issues, especially in terms of how they relate to animal research. Definitional issues are prevalent; clear definitions are often not given of crucial terms, including 'emotion,' and even where provided, such terms may be used inconsistently throughout a single paper. Further disagreement over the structure of emotions, and the nature of conscious experiences involved, leads to consistent differences in authors' criteria for emotions. We concur with those who believe that animals experience emotions and believe that animal emotions should be studied in their own right, not only as they compare to those of humans. We also propose several avenues for future research that we believe will further our understanding of animal emotions. First, the use of multiple measurement methods to assess emotional responses is most likely to provide the information necessary to distinguish between various states and opens the field to more research in harder-to-study species, such as marine mammals. Second, researchers should also endeavor to increase the range of emotions studied, particularly positive ones, in order to move toward a more balanced range of studied states. Finally, we believe that several aspects of personality research would prove beneficial to the study of animal emotions, particularly the distinction between trait and state emotion and the use of the rating method. © 2016 Wiley Periodicals, Inc.

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## INTRODUCTION

Suppose you were asked to answer true or false when presented with the following statement: 'Animals have emotions.' It is possible that you feel strongly one way or another and so have no problem deciding. However, you might hesitate because you believe the term 'animals' is too encompassing and so would answer true for some species and false for other species if given the choice, or you might want to specify which emotions animals have, believing that some animals possess certain emotions but lack others. Regardless of which camp you fell into, there

would be ample company in the literature on animal emotions. Some scholars believe that most animals have emotions; others argue that emotions are uniquely human, and still others fall somewhere between the two extremes. Although we will present our views on the topic, our primary purpose here is not to definitively argue one way or the other but to discuss a few of what we feel are key issues in current animal emotional research, and to consider several proposals for the future.

## EMOTIONS, AFFECT, AND FEELINGS: DEFINITIONAL ISSUES IN ANIMAL AND HUMAN RESEARCH

Perhaps a major reason that there is much dispute about animal emotions concerns the considerable confusion in both the human and nonhuman animal

\*Correspondence to: [amberdevere@googlemail.com](mailto:amberdevere@googlemail.com)

Department of Psychology, University of Southern Mississippi, Hattiesburg, MS, USA

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literature about how to best define emotion (see Kuczaj et al.<sup>1</sup> for a recent discussion of this state of affairs). This includes debate over the components that make up an emotion as well as an overall lack of consensus over whether the term ‘emotion’ is interchangeable with affect. Some suggest that a distinction be made between affect and emotion, where emotions refer to affective states that are responses to particular events.<sup>2</sup> Others use the terms in the opposite manner, where emotion is the ‘umbrella term’ that encompasses affective states.<sup>3</sup> Still others identify a possible distinction but define the terms as synonymous,<sup>4</sup> which appears to be the way in which emotion and affect are used elsewhere<sup>5</sup> (see Table 1 for a summary of these distinctions).

To further complicate matters, particularly in animal research, there is often ambiguity about the actual denotation of terms, even where definitions are provided. For example, Boissy et al.<sup>2</sup> define emotions as processes that evolved from mechanisms that allowed animals to seek out reward and avoid harm and include several components: behavioral, autonomic, and subjective ‘feeling.’ They also describe emotions as affective responses to events, which seems to indicate that affect will be used as a more general term. Thereafter, however, affect appears to be used in this way in some cases but synonymously with emotion in others. Mendl et al.<sup>6</sup> describe the components of ‘emotional or affective’ states as including changes in cognition, physiology, behavior, and neurology as well as the separate, subjective component of ‘core affect’; however, they also state that the subjective component of discrete emotions is not completely described by the emotion’s core affect position and can also involve other subjective components such as ‘urges.’ That these issues occur even

in some of the best literature on animal emotions demonstrates the real need for authors to clearly define what they mean when using these terms and to ensure that they use them consistently.

The different uses of terminology often correspond with disagreement over the underlying structure of emotions. Some researchers adhere to the discrete approach, where there are a number of distinct, innate emotions, each with specific core affective properties and underlying neural mechanisms that are, to some extent, independent of each other. The positions of these emotions in core affect space result from the autonomic changes associated with each one; a discrete emotion’s affective characteristics are therefore a result of the emotion rather than the cause of it.<sup>7</sup> Others argue that emotions are better explained by a dimensional approach, in which an emotion is generated from a position in core affective space combined with stimuli appraisals.<sup>8</sup> There have been commendable efforts to reconcile the two approaches. For example, an overarching framework has been proposed that incorporates both systems.<sup>6</sup> These authors further extend the idea that core affect is continuously experienced and that there is, therefore, constant interplay between currently experienced emotions and the emergence of new emotions<sup>7</sup>; experiencing a discrete emotion could cause a change in an animal’s position in core affect space, while emotions may also be elicited from a change in core affect position.<sup>6</sup> They therefore argue that the core affective dimensions of valence and arousal provide a ‘common currency’ through which a variety of stimuli can be prioritized; as a result, both the dimensional and discrete emotion systems could exist in humans and some animals and may interact with one another bidirectionally. This framework has experimentally useful applications for animal emotion research in particular; for example, it makes predictions about individual differences that may be seen in response to rewarding and punishing stimuli as a result of differing long-term affective ‘mood’ states. A more recent survey of human emotion researchers also indicates that many now use a combination of both approaches rather than adhering to just one.<sup>9</sup>

There is also major disagreement about whether emotions require conscious experience. Some authors describe emotions as consisting of both the conscious experience and functional processes but that these components may be mediated by different underlying neural mechanisms.<sup>10</sup> Others argue that some emotions may involve conscious experiences but that it is not an essential requirement for experiencing emotions.<sup>4</sup> This appears to be the view of those who make the distinction between basic

**TABLE 1** | Possible Distinctions Identified Between Affect and Emotion by Different Authors

Source	Distinction Identified	Distinction between Affect and Emotion
Boissy et al. <sup>2</sup>	Yes	Emotions are affective responses to events
Izard et al. <sup>5</sup>	No	Used synonymously
Mendl et al. <sup>6</sup>	No	Used synonymously
Panksepp <sup>3</sup>	Yes	Emotion is an umbrella term encompassing affect
Paul et al. <sup>4</sup>	Yes	Emotions are affective states attached to objects
Current authors	No	Emotion used as all-encompassing term, no use of affect

emotions that are processed nonconsciously and emotional schema that consist of basic emotions with the added involvement of conscious and higher-order cognitive processing, such as thought or complex appraisals.<sup>7</sup> However, not all authors make it clear whether they consider all emotions to involve a conscious component; for example, Mendl et al.<sup>6</sup> describe the feeling component of emotions as ‘conscious, subjective experience’ and use core affect as the conceptual construct for this experience and their overarching framework, which includes animals; they then also say that they will discuss animal emotions as ‘states that may or may not be experienced consciously.’ The clarity of such a criterion is key as it significantly affects the requirements for animal emotions.

As if things were not sufficiently messy, there are different standards for what authors consider constituting consciousness, as well as the level of conscious ability that is thought to be involved in emotions. At one extreme, there is no distinction between being conscious and possessing consciousness.<sup>11</sup> However, other authors conclude that being conscious involves just one aspect of consciousness; waking conscious states have been classified as one level, while content consciousness consists of both the ability to know about one’s conscious experience as well as the accompanying subjective, ‘phenomenal’ experience.<sup>10</sup> Others organize consciousness into additional levels, with the ability to experience internal affective states forming the first level. This endows ‘primary process affective consciousness’ on any animal that can experience such states, without requiring the ability to reflect on these experiences.<sup>3</sup> Once again, the terminology used to describe and define consciousness and its relationship to emotional experiences is often vague and not always consistent. For example, the terms ‘subjective’ and ‘conscious’ are often used to refer to experiential components of emotions,<sup>6</sup> but without clarification of exactly what the authors mean by these terms, or whether they are being treated as synonymous. The term ‘feeling’ is also used with differing meanings; some use this to describe a quality of a basic emotion that is not a conscious experience,<sup>7</sup> while others seem to use it interchangeably with ‘subjective’ and therefore ‘conscious.’<sup>6</sup>

There is also debate about how best to label emotions. Some authors are proponents of using individual words, such as fear, to describe particular emotions. The ‘basic’ emotions identified by Izard<sup>12</sup> are each described by single terms: anger, contempt, disgust, distress, fear, guilt, interest, joy, shame, and surprise. However, others believe that this approach

is oversimplified and that the use of single words leaves readers to make too many inferences of their own.<sup>13</sup> We concur with this latter view; while one word can provide a useful base to orient people to the type of emotion being discussed or studied, it can never fully capture all the characteristics of a particular state or the variations that may exist of this state.

These definitional differences are much more than semantic arguments. They result in different standards for animal emotion, with some definitions suggesting that few, if any, animals have emotions, while other definitions extend emotional experiences to many nonhuman species. In an ideal world, we would reach a consensus on the meaning of terms, the best description of the structure of emotion, and the role of consciousness in emotional experience. However, given the level of disagreement in the current literature, as well as the complex nature of the concepts, the likelihood of this consensus being reached in the near future seems somewhat unlikely. This being said, there are authors striving to determine the most widely accepted components and features of emotions<sup>9,14</sup> as well as those who already provide extensive definitions in their work.<sup>15</sup> Until such consensus is achieved, there is an undeniable need for researchers to unambiguously define the terms they use and their criteria for emotional experience.

From this point forward, we will use the term emotion to refer to what others have labelled affect or emotion. We believe that it is more straightforward for emotion to be used as an all-encompassing concept rather than trying to distinguish emotion, affect, feelings, mood, etc. as such distinctions have proven difficult to justify and are too often based on seemingly arbitrary criteria. For example, we do not find attempts to distinguish emotions and affect based on the former’s attachment to objects to be of functional use. We believe that differences between specific states should be specified but that this can be accomplished without belaboring artificial differences in state types (see Paul et al.<sup>4</sup> for an example of this approach). We also commend Mendl et al.<sup>6</sup> for their efforts to reconcile the dimensional and discrete approaches. An overarching framework, such as the one that they put forward, provides a practical way to move forward in animal emotion research. We agree that a combination of these approaches is likely to provide the most complete explanation for emotional phenomena in animals. The use of the valence and arousal dimensions as unifying features of all emotional experiences allows for there to be multiple mechanisms through which different emotions can be elicited, including differing causal

directions and components such as appraisals and action tendencies.

With regard to the conscious component of emotions, it is our belief that the very nature of emotional psychological states requires a subjective, and therefore conscious, component. However, we do not concur with those who propose that in order to experience an emotion, the individual must be able to reflect on the experience. Instead, we perceive emotions as involving a subjective experiential state, along with other components, which may in some cases include such processing. This is in line with Panksepp's view of primary process emotions.<sup>3,16</sup> Emotions vary in intensity and valence, some of which likely evolved to facilitate the ability to avoid harm and punishment and seek out rewards and resources.<sup>4</sup> These processes include physiological, neurological, and potentially behavioral components as well as a subjective, conscious component. We will also be using the terms conscious and subjective interchangeably to refer to primary process emotional consciousness, which we define as the experiential component of an emotion.<sup>4,16</sup> Where necessary, we will also be using the term 'core affect' to refer to the valence and arousal characteristics of emotions. Whether or not the reader agrees with our views, the point that we would like to emphasize most is the need for authors to define their terms clearly, use them consistently, and provide their subsequent criteria for animal possession of emotions.

## STUDYING ANIMAL EMOTIONS

A variety of methods have been used to study emotional experiences in animals. Some researchers have adapted measures similar to those used to study human emotion, such as cognitive biases that result from emotional experiences.<sup>17,18</sup> Others have explored physiological and behavioral indicators of emotion.<sup>19</sup> Unfortunately, it is often difficult to distinguish positive and negative emotional states. For example, anticipation of being rewarded in silver foxes was associated with high levels of stereotypical behavior,<sup>20</sup> but it is not known whether these behaviors indicate positive expectation or frustration.<sup>21</sup> Similarly, inactive behavior has commonly been associated with low cortisol levels, which could indicate positive experience because the animal is at or close to an optimal state, but might also result from learned helplessness.<sup>22</sup> It is possible that the combined study of behavior and physiology will prove most beneficial in differentiating positive and negative experiences.<sup>19</sup> In addition, the integration of

animal emotion research and neuroscience<sup>16</sup> promises to shed additional light on both animal and human emotional experiences. Although this integration involves greater challenges with certain species, fMRI (functional magnetic resonance imaging) imaging has now been used on a number of non-human animals, recently including dogs.<sup>23,24</sup>

At this point, it is worth noting that while it remains a controversial topic, it is our view that animal emotions do exist. We are not alone in this; in fact, it seems that the majority of the animal emotion literature is based on the assumption that animals experience emotions,<sup>25</sup> the disputes concerning the nature and range of these experiences. These disagreements show little sign of abating as there is currently no definitive way to determine the nature of an animal's subjective experience of emotions, let alone assess its similarity to the human experience. Parallels between human and certain animal species are observed in behavior, brain structure, and biochemistry, suggesting that at least some animals may have experiences that are similar to our own,<sup>2,16</sup> but animal and human emotions need not overlap significantly for animal emotion to be meaningful. For example, claims that some animals possess language skills similar to those of humans did little to increase our understanding of animal communicative capacities. Studies of animals' natural communication efforts contributed much more to this understanding than did attempts to teach animals aspects of human language systems. Claims that some species have language skills comparable to humans have little empirical support, and although comparisons to human language are inevitable, statements that equate animal and human language are virtually nonexistent in contemporary scientific literature, a much healthier state of affairs for this scientific field. We believe that the study of animal emotion would also benefit from an increased focus on studying them in their own right and not solely as they compare to human emotions. We recognize that such comparisons are inevitable and can be theoretically significant, as well as that animal emotions likely do share many similarities with those of humans. However, there may also be important species differences that are overlooked when comparisons to human emotions are the single focus of research. Discovering the ways in which the emotional experiences of species are different, as well as the ways in which they are similar, is essential for the advancement of the study of animal emotion.

In addition to increasing the emphasis on species-specific animal emotions, we urge scholars to broaden the range of emotions that are studied. Perhaps because they are viewed as more salient or

easier to investigate, negative emotions are much more likely to be studied than positive ones.<sup>2,6</sup> A recent review found that 74% of articles since 1990 that referred to animal emotions arose from searches using just five keywords, all of which represented negative states: fear, stress, pain, anxiety, and depression.<sup>25</sup> Furthermore, only 6% of studies that assumed the presence of emotional states in animals concerned positive states. Even when the authors excluded studies with the primary aim of studying nonhuman animals in order to further knowledge of human emotions, only 19% had positive states as their core topic. The result of this bias is that we know little about the underlying mechanisms of positive emotions in animals.<sup>2</sup> The need for expansion of studies on positive emotion is important for theories of animal emotion and for attempts to improve animal welfare. Good welfare consists not only of the lack of negative states but also of the presence of positive ones<sup>26</sup>; therefore, even without the presence of specifically negative state indicators, a lack of positive states alone could be indicative of poor welfare.<sup>2</sup> Furthermore, where some change from a norm is indicative of reduced welfare, species differences in baseline norms must be taken into account in order to accurately interpret these indices.<sup>27</sup> Where welfare initiatives attempt to increase the experience of positive states, knowledge of species-specific positive emotional repertoires would therefore be required for such differing baselines to be taken into account.

The significance of studying positive emotions has been illustrated in a number of recent studies. For example, Panksepp and Burgdorf<sup>28</sup> examined the homologs between an ultrasonic ‘chirping’ vocalization produced by rats in response to tickling and laughter in humans. Homologs have also been identified between tickling-induced vocalizations in several primate species and humans.<sup>29</sup> Certain changes in acoustic parameters of African elephant ‘rumble’ vocalizations may indicate positive as well as negative emotion, although the extent to which these changes reflect valence or arousal is not clear.<sup>30</sup> Specific call types have been implicated as indicators of positive states in farmed silver foxes.<sup>31</sup> In pigs, cognitive biases have been used to study both negative and positive emotions, and some vocalizations have been tentatively associated with positive experiences.<sup>32</sup> Play has been suggested as potentially useful to induce or be indicative of positive states in pigs as well as in other species.<sup>32,33</sup> Several studies of sheep have identified behavioral and physiological differences between individuals in presumably positively versus negatively and neutrally valenced scenarios.<sup>34–36</sup> Ear postures and visible eye white

suggest low arousal positive states in cows,<sup>37,38</sup> and nasal temperatures of dairy cows were found to decrease in increasingly positively valenced states.<sup>39</sup> Specific behavioral and vocal parameters have also been found to correlate with valence in goats, including presumably positively as well as negatively valenced situations.<sup>40</sup> Interestingly, these correlates in goats were largely independent of arousal level, and a different combination of parameters correlated with arousal irrespective of valence. Some fascinating results have also emerged from fMRIs studies of dogs. The activity level of several brain regions has been correlated with the emotional valence of both dog and human vocal stimuli,<sup>23</sup> and the greatest caudate activation was seen in response to the scent of a familiar human, indicating positive expectation and, tentatively, the experience of a positive emotional state.<sup>24</sup>

## THE SIGNIFICANCE OF INDIVIDUAL DIFFERENCES

Human personality and emotion are intertwined. Humans exhibit individual propensities to experience certain emotional states,<sup>41</sup> leading to the distinction often being made between trait and state emotion.<sup>5</sup> The content of several of the human Five Factor Model personality factors have since been shown to contain emotional terms; for example, Neuroticism contains items such as anxiety and depression.<sup>42</sup> Strong correlations have also been found between measures of trait emotion and some of these personality factors, such as anger with low Agreeableness<sup>43</sup> and excitement and energy with high Extraversion.<sup>44</sup> The possibility of trait emotion in animals is largely unexplored, despite such individual propensities being likely to affect the results of assessments of emotion.

Our reading of the flourishing animal personality literature suggests that trait emotion in animals has only been studied indirectly through the trait rating method; this requires human judges to rate individual animals on their tendencies on a set of trait words. While we believe that, as with animal emotions, there is great value in studying animal personality in its own right, inherent in this method is the tendency for greater reliance on human models compared to its alternative, behavioral coding. While there have been commendable efforts to incorporate more species-specific traits, in most cases, selection of trait words is based on the human Five Factor Model<sup>45</sup> and therefore includes a large selection of terms referring to trait emotion. As a result, the use

of these terms assumes (at least implicitly) that the animals assessed are capable of experiencing such states. This is true unless the terms are assigned operational definitions that differ from those used in human personality assessments, but we are not aware of any examples of studies in which this is the case. This being said, some studies may do this indirectly, where statements clarifying trait words are phrased in terms of behaviors rather than internal state tendencies (e.g., bottlenose dolphins<sup>46</sup>); however, it seems likely that raters interpret trait words as they are typically used and so assume the experience of emotions. Other significant similarities have also already been identified between the overlapping areas of emotion and personality; both ultimately aim to assess underlying constructs that cannot be observed directly and focus on characteristics of individuals that are expected to be largely consistent across both time and contexts.<sup>1</sup>

We believe it is important to distinguish the ability to experience a particular state from individual propensities to experience that state and so encourage both animal personality and animal emotion researchers to include the trait versus state emotion distinction in their efforts. In animal emotion research, acknowledging that variation between individuals in their responses to a certain stimulus may reflect personality differences could help to reduce the ambiguity as to whether or not a type of animal is capable of experiencing a certain emotional state. It would also allow the likely species-specific nature of emotional repertoires to be incorporated into research in both areas. As a result of the significant similarities that exist for animal personality and animal emotion research, including the existing overlap in content, we believe that there is much to be gained from researchers studying one area to also consider aspects of the other.

## ADDITIONAL PROPOSALS/ CONSIDERATIONS FOR THE FUTURE

We conclude by expanding on some of our earlier recommendations as well as adding some additional proposals for future animal emotion research. First, we advocate greater use of vocalizations as potential indicators of emotional states. There is already some evidence that particular features of mammalian vocalizations may be associated with experiencing positive states as well as communicating these states to others, although, as in the other animal emotion literature, there is a bias toward the study of negative states (see review by Briefer<sup>47</sup>). Some species, such as

marine mammals, are more challenging subjects for emotion research as it is difficult to collect physiological or neurological measures, particularly without potentially affecting the valence of the animal's experiential state. For such species, measures of vocalizations in combination with behavior may prove most useful in investigating both positive and negative states. Further study of emotions in all animals, particularly these types of understudied groups, may therefore be advanced by measuring vocal parameters in positive, neutral, and negative situations of approximately equal arousal levels. In fact, features of vocalizations that may indicate arousal have already been identified in a small number of these species (e.g., Weddell seals<sup>48</sup>), and we suspect future research will identify such features in the valence dimension and in other species.

Related to this proposal, we would like to emphasize that the use of multiple measurement methods is likely to yield the most persuasive results with regard to characterizing animal emotions. Many authors agree that it is unlikely that one mode of measurement will provide a reliably accurate way in which to assess emotions.<sup>1,19</sup> The use of vocal indicators, as discussed above, is likely to be of limited use if not measured alongside other factors, such as physiological and behavioral measures. Similarly, behavioral or physiological indicators alone must be interpreted with caution as similar behaviors may be produced in a variety of contexts, and physiological measures often correlate to more than one type of state.<sup>4,19</sup> In addition to multiple types of measurements, we would like to stress the importance of recording the context in which animals are studied and of assessing emotions across a range of contexts that appear to have the same valence.

We have not provided a comprehensive review of the literature on positive emotions here, but it is clear that there remains a huge bias toward the study of negative states. It should therefore remain a goal for researchers to include more positive states in their studies of animal emotion. This could often be achieved by adding an extra condition with a positive stimulus to a study that utilizes neutral and negative stimuli to provoke measurable responses. It is also evident that the primary focus of positive emotion research has concerned farmed animals. While the reasons for this are obviously relevant, we believe that it is also important to make a greater variety of species the subjects of such research. Increasing the range of species studied would permit more cross-species comparisons to be made of the types of responses to stimuli across

more taxonomically diverse groups than is currently possible.

Although we strongly encourage additional research in positive emotions, we recognize that it is difficult to identify stimuli that elicit positive affective responses reliably across individuals.<sup>36</sup> One problem is that such responses may provide the opportunity to improve fitness but do not necessarily decrease fitness if the individual does not respond to the positive stimulus. In fact, positive emotional responses are expected to be less intense<sup>2</sup> and show greater interindividual variation than those to negative stimuli.<sup>49</sup> Future research, then, should expand the literature on positive emotions in order to fully capture the range of animal experiences but should also continue to identify stimuli that consistently elicit positive emotional responses in individuals or whole groups of individuals. In particular, we encourage researchers to explore the possibility of play as a useful window into the study of positive animal emotions (see Kuczaj and Horback<sup>33</sup> for a discussion of this topic), as has been done in a few select species, such as pigs.<sup>32</sup>

The potential for interindividual variation in emotional responses in animals should not be ignored in future research. Researchers should assess an animal's capacity to experience a certain state and compare this capacity to that of the animal's conspecifics as well as to that of other species. The possibility that emotional responses to stimuli may not be completely uniform across individuals is in itself an interesting topic for future research. For example, one reason suggested to explain the performance of stereotypical behavior is that the captive environment induces internal states that trigger the behavior. In many cases, this is indicative of poor welfare caused by the experience of negative emotional states.<sup>50</sup> Therefore, if individuals differ in their propensity to experience these states, differing adjustments to their environment may be required in order to induce the same reduction in negative states, such as frustration or fear, and increase in positive states. This variation is therefore not meaningless and, in fact, could prove to be an important consideration for those striving to improve captive animal welfare in particular.

Methodology from personality research should also prove useful in future attempts to assess animal emotions. For example, human raters have proven capable of rating animals' behavioral tendencies on a range of traits with reliabilities comparable to those in human research.<sup>51</sup> It has already been suggested that, due to the similarity of the goal of both personality and emotion research of assessing

unobservable underlying constructs, the rating method may have applications in animal emotion research.<sup>1</sup> Animals capable of experiencing emotions should be able to read the emotional states of others in order to avoid unnecessary conflicts. This should be especially true for members of social species. Indeed, many potential behavioral indicators of emotional states have been identified in a range of taxa; for example, in cows, ear postures have been linked to the experience of positive states.<sup>37</sup> Humans who are familiar with individual animals may be able to rate emotional states reliably using cues that signal emotions to conspecifics. If this method is implemented in the future, it will be important to carefully consider raters' experiences with the rated animals as this can affect their ratings.<sup>52</sup> Of course, we need to beware of assuming that cues reliably assessed by humans exhaust those actually used by a species; it is likely that the cues animals use to assess the emotional states of others are quite different from those humans use and recognize. Nevertheless, investigation of the possibility of reliable emotional assessment by raters could allow the practical applications of this less time-intensive and noninvasive method to be explored.

Finally, we believe it is important to ask the question: given the current unobservable nature of these subjective mental states, is it possible for animal emotions to be studied without anthropomorphism? Again, we feel that the study of animal personality provides useful insights. In this field, underlying latent constructs have been successfully measured using behavioral observations and human ratings rather than any physiological measures.<sup>45</sup> Of course, this does not take into account the subjective nature of emotional states. However, again, the significant numbers of personality trait words that refer to such states seem to indicate that we are already, albeit somewhat unintentionally, measuring individual tendencies to experience some emotions. The fact that ratings of these states in animals have proven to be, on average, as reliable as ratings made in humans suggests that we are able to judge these subjective states with reasonable reliability. However, this reliability does not eliminate the possibility of anthropomorphism, or ensure accuracy, for it is possible that all raters across all animal personality studies that have found ratings to be reliable could have anthropomorphized the animals under study in similar ways across all reliably rated traits. This seems somewhat unlikely, but the extent to which human ratings of animal personality and animal emotions reflect our own emotional experiences requires further investigation.

## CONCLUDING REMARKS

Despite the difficulties inherent in studying emotion, particularly in animals, we believe such research is necessary if we wish to understand the manner in which other species make sense of their world. There are many questions that await answers: How do species other than humans experience emotions? Are there universal characteristics of emotion that occur in all species that experience them? How does emotional experience differ from species to species? How do members of social species assess the emotional states of conspecifics and via which sensory systems?

Are animals able to use this information to guide social interactions? What is the role of individual differences in all of this?

Again, we have no doubt that other species experience emotions, but this does not mean that all emotional experiences are equivalent, let alone human-like. Determining the similarities and differences of emotional states across species and individuals, as well as the manner in which such states govern social behavior, is essential for a comparative psychology of emotions. We eagerly look forward to the results of future research that addresses these issues.

## REFERENCES

- Kuczaj SA, Highfill LE, Makecha RN, Byerly HC. Why do dolphins smile? A comparative perspective on dolphin emotions and emotional expressions. In: Watanabe S, Kuczaj SA, eds. *Comparative Perspectives on Human and Animal Emotions*. Tokyo: Springer; 2013, 63–86.
- Boissy A, Manteuffel G, Jensen MB, Moe R, Spruijt B, Keeling L, Winckler C, Forkman B, Dimitrov I, Langbein J, et al. Assessment of positive emotions in animals to improve their welfare. *Physiol Behav* 2007, 92:375–397.
- Panksepp J. Affective consciousness: core emotional feelings in animals and humans. *Conscious Cogn* 2005, 14:30–80.
- Paul ES, Harding EJ, Mendl M. Measuring emotional processes in animals: the utility of a cognitive approach. *Neurosci Biobehav Rev* 2005, 29:469–491.
- Izard CE, Libero DZ, Putnam P, Haynes OM. Stability of emotion experiences and their relations to traits of personality. *J Pers Soc Psychol* 1993, 64:847–860.
- Mendl M, Burman OHP, Paul ES. An integrative and functional framework for the study of animal emotion and mood. *Proc R Soc B* 2010, 277:2895–2904.
- Izard CE. Basic emotions, natural kinds, emotion schemas, and a new paradigm. *Pers Psychol Sci* 2007, 2:260–280.
- Barrett LF. Solving the emotion paradox: categorization and the experience of emotion. *Pers Soc Psychol Rev* 2006, 10:20–46.
- Ekman P. What scientists who study emotion agree about. *Pers Psychol Sci* 2016, 11:31–34.
- Tsuchiya N, Adolphs R. Emotion and consciousness. *Trends Cogn Sci* 2007, 11:158–167.
- Baars BJ. There are no known differences in brain mechanisms of consciousness between humans and other mammals. *Anim Welf* 2001, 10:31–40.
- Izard CE. Basic emotions, relations among emotions, and emotion-cognition relations. *Psychol Rev* 1992, 99:561–565.
- Kagan J. *What is Emotion? History, Measures, and Meanings*. New Haven, CT: Yale University Press; 2007.
- Izard CE. The many meanings/aspects of emotion: definitions, functions, activation, and regulation. *Emotion Rev* 2010, 2:363–370.
- Broom DM. Cognitive ability and awareness in domestic animals and decisions about obligations to animals. *Appl Anim Behav Sci* 2010, 126:1–11.
- Panksepp J. The basic emotional circuits of mammalian brains: do animals have affective lives? *Neurosci Biobehav Rev* 2011, 35:1791–1804.
- Burman OHP, Parker RMA, Paul ES, Mendl M. Sensitivity to reward loss as an indicator of animal emotion and welfare. *Biol Lett* 2008, 4:330–333.
- Mendl M, Burman OHP, Parker RMA, Paul ES. Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. *Appl Anim Behav Sci* 2009, 118:161–181.
- Broom DM. Assessing the welfare of modified or treated animals. *Livestock Prod Sci* 1993, 36:39–54.
- Moe RO, Bakken M, Kittilsen S, Kingsley-Smith H, Spruijt BM. A note on reward-related behavior and emotional expressions in farmed silver foxes (*Vulpes vulpes*)—basis for a novel tool to study animal welfare. *Appl Anim Behav Sci* 2006, 101:362–368.
- Mason G, Mendl M. Do the stereotypies of pigs, chickens and mink reflect adaptive species differences in the control of foraging? *Appl Anim Behav Sci* 1997, 53:45–58.
- Alloy LA, Seligman MEP. On the cognitive component of learned helplessness in animals and man. In: Bower G, ed. *The Psychology of Learning and Motivation*. New York: Academic Press; 1979, 219–276.



23. Andics A, Gacsi M, Farago T, Kis A, Miklosi A. Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. *Curr Biol* 2014, 24:574–578.
24. Berns GS, Brooks AM, Spivak M. Scent of the familiar: an fMRI study of canine brain responses to familiar and unfamiliar human and dog odors. *Behav Processes* 2015, 110:37–46.
25. Proctor HS, Carder G, Cornish AR. Searching for animal sentience: a systematic review of the scientific literature. *Animals* 2013, 3:882–906.
26. Dawkins MS. Animal minds and animal emotions. *Am Zool* 2000, 40:883–888.
27. Mason GJ. Species differences in responses to captivity: stress, welfare and the comparative method. *Trends Ecol Evol* 2010, 25:713–721.
28. Panksepp J, Burgdorf J. Laughing rats? Playful tickling arouses high-frequency ultrasonic chirping in young rodents. *Am J Play* 2010, 2:357–372.
29. Ross MD, Owren MJ, Zimmermann E. Reconstructing the evolution of laughter in great apes and humans. *Curr Biol* 2009, 19:1106–1111.
30. Soltis J, Blowers TE, Savage A. Measuring positive and negative affect in the voiced sounds of African elephants (*Loxodonta africana*). *J Acoust Soc Am* 2011, 129:1059–1066.
31. Gogoleva SG, Volodin IA, Volodina EV, Kharlamova AV, Trut LN. Sign and strength of emotional arousal: vocal correlates of positive and negative attitudes to humans in silver foxes (*Vulpes vulpes*). *Behavior* 2010, 147:1713–1736.
32. Murphy E, Nordquist RE, van der Staay FJ. A review of behavioral methods to study emotion and mood in pigs, *Sus scrofa*. *Appl Anim Behav Sci* 2014, 159:9–28.
33. Kuczaj SA, Horback KM. Play and emotions. In: Watanabe S, Kuczaj SA, eds. *Comparative Perspectives on Human and Animal Emotions*. Tokyo: Springer; 2013, 87–112.
34. Reefmann N, Bütikofer Kaszàs F, Wechsler B, Gyax L. Ear and tail postures as indicators of emotional valence in sheep. *Appl Anim Behav Sci* 2009a, 118:199–207.
35. Reefmann N, Bütikofer Kaszàs F, Wechsler B, Gyax L. Physiological expression of emotional reactions in sheep. *Physiol Behav* 2009b, 98:235–241.
36. Reefmann N, Wechsler B, Gyax L. Behavioral and physiological assessment of positive and negative emotion in sheep. *Anim Behav* 2009c, 78:651–659.
37. Proctor HS, Carder G. Can ear postures reliably measure the positive emotional state of cows? *Appl Anim Behav Sci* 2014, 161:20–27.
38. Proctor HS, Carder G. Measuring positive emotions in cows: do visible eye whites tell us anything? *Physiol Behav* 2015b, 147:1–6.
39. Proctor HS, Carder G. Nasal temperatures in dairy cows are influenced by positive emotional state. *Physiol Behav* 2015a, 138:340–344.
40. Briefer EF, Tettamanti F, McElligott AG. Emotions in goats: mapping physiological, behavioral and vocal profiles. *Anim Behav* 2015, 99:131–143.
41. Watson D, Tellegen A. Toward a consensual structure of mood. *Psychol Bull* 1985, 98:219–235.
42. Pytlík Zillig LM, Hemenover SH, Dienstbier RA. What do we assess when we assess a big 5 trait? A content analysis of the affective, behavioral, and cognitive processes represented in big 5 personality inventories. *Pers Soc Psychol Bull* 2002, 28:847–858.
43. Kuppens P. Interpersonal determinants of trait anger: low agreeableness, perceived low social esteem, and the amplifying role of the importance attached to social relationships. *Personal Ind Diff* 2005, 38:13–23.
44. Smillie LM, DeYoung CG, Hall PH. Clarifying the relation between extraversion and positive affect. *J Pers* 2015, 83:564–574.
45. Gosling S. From mice to men: what can we learn about personality from animal research? *Psychol Bull* 2001, 127:45–86.
46. Highfill L, Kuczaj S. Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquat Mamm* 2007, 33:380–389.
47. Briefer EF. Vocal expression of emotions in mammals: mechanisms of production and evidence. *J Zool* 2012, 288:1–20.
48. Collins KT, McGreevy PD, Wheatley KE, Harcourt RG. The influence of behavioral context on Weddell seal (*Leptonychotes weddellii*) airborne mother-pup vocalization. *Behav Process* 2011, 87:286–290.
49. Fraser D, Duncan IJH. ‘Pleasures’, ‘pains’ and animal welfare: toward a natural history of affect. *Anim Welf* 1998, 7:383–396.
50. Mason G, Clubb R, Latham N, Vickery S. Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Appl Anim Behav Sci* 2007, 102:163–188.
51. Gosling S, John O. Personality dimensions in nonhuman animals: a cross-species review. *Curr Direct Psychologic Sci* 1999, 8:69–75.
52. Highfill L, Hanbury D, Kristiansen R, Kuczaj S, Watson S. Rating vs. coding in animal personality research. *Zoo Biol* 2010, 29:509–516.