Anthropomorphism in Comparative Affective Science: Advocating a Mindful Approach

Lisa A. Williams,[a*] Sarah F. Brosnan,[b] & Zanna Clay[c]

[a] School of Psychology, University of New South Wales, Sydney, NSW 2052 Australia

[b] Department of Psychology, Language Research Center, and Center for Behavioral Neuroscience, Georgia State University, PO Box 5010, Atlanta, GA 30302-5010 United States

[c] Psychology Department, Durham University, South Rd, Durham DH1 3LE, United Kingdom

* Corresponding Author: Lisa A. Williams
School of Psychology, University of New South Wales, Sydney, NSW 2052,
lwilliams@unsw.edu.au

Highlights

- Anthropomorphism is the attribution of human-like capacities to non-human entities.
- Anthropomorphism is both beneficial and problematic for comparative research.
- We advocate a mindful approach to anthropomorphizing in comparative science.

Abstract

Anthropomorphism is the attribution of human-like capacities and traits to non-human entities. Anthropomorphism is ubiquitous in everyday life and in scientific domains, operating both implicitly and explicitly as a function of the human lens through which we view the world. A rich history of work in psychology, animal behavior, cognitive science, and philosophy has

highlighted the negative and, to a lesser degree, the positive implications of anthropomorphism. In this article, we aim to provide a nuanced perspective of how anthropomorphism impacts the work of comparative affective science. Specifically, we discuss three domains of empirical inquiry in which lessons can be drawn about the benefits and pitfalls of anthropomorphism: responses to death, inequity aversion, and prosocial behavior. On balance, we advocate a mindful approach to anthropomorphizing in comparative affective science, and comparative science more generally.

Keywords: anthropomorphism; comparative psychology; comparative science; comparative thanatology; inequity aversion; prosocial behavior

1. Introduction

The scientific investigation into the basis of emotion or affect has, to date, largely taken a human perspective, where the quest to understand the basis of human experience has influenced which questions are asked, how experiments are designed, and how the ensuing data are interpreted. When humans are the target of study, this 'anthropocentric' perspective is relatively innocuous – indeed, 'seeing human' in other humans is entirely sensible. Put simply – when aiming to understand human affective processes, adopting a human mindset is both rational and defensible. However, when other species are the focus of scientific inquiry, this human perspective can impact the scientific process in a way that might ultimately be a disservice to uncovering the veridical truths about the cognitive or affective processes at hand. This tension is especially relevant to the field of Comparative Affective Science, a newly emerging inter-disciplinary branch of affective science that is concerned with understanding the evolutionary

basis of affect through comparing how animals produce, perceive, and experience affective states and, potentially, emotions.

Of particular relevance to the arena of comparative affective science is *anthropomorphism* – the attribution of human-like capacities and traits to non-human entities (Epley et al., 2007). Comparative affective science is in many ways an inherently anthropomorphic endeavor, adopting a starting point from the human perspective. Consider common research questions asked in comparative affective science: can non-human animals (henceforth animals) experience emotion – or is animal experience better characterized as affect? How are such states expressed by animals? Are the physiological signatures of human affective experience similar to those observed in animals? Do human expressions of emotion overlap with those observed in other animals?

Since Darwin debated such questions in his seminal work, *The Expression of the Emotions in Man and Animals* (1872), one view is that one should expect evolutionary continuities in both the capacities and the underlying mechanisms driving affective processes for closely related species. In this regard, a legitimate starting point of many such research questions may in fact be the anthropomorphic view that animals with close phylogenetic relationships to humans should experience some affect and emotions similar to what is seen in humans (Bekoff, 2000; Burghardt, 2004; de Waal, 2016, 1999). However, this anthropomorphic approach has also been widely criticized as inherently flawed and to be avoided (Wynne, 2006, 2004), particularly as human emotions themselves have also been proposed to be socially and/or culturally constructed (e.g., Barrett, 2013; Barrett and Russell, 2014; Boiger and Mesquita, 2012; Mesquita and Boiger, 2014). Our view is that the best path most likely lies in the middle of these views, acknowledging that anthropomorphism can sometimes be beneficial (Bruni et al., 2018;

Burghardt, 2006; de Waal, 2016, 1999) – at least when undertaken mindfully and judiciously. At the same time, anthropomorphism must be treated with caution, especially for processes that are not yet well understood in our own species, such as how individuals come to experience and perceive emotions.

The goal of this article is to discuss and highlight the benefits and drawbacks of anthropomorphism within the emerging field of comparative affective science. Following a review of the concepts and empirical evidence regarding anthropomorphism generally, we review the influence of anthropomorphism on research in three emerging areas: responses to death (comparative thanatology), inequity aversion, and prosocial behavior. Given the implications that anthropomorphism may have for understanding the affective lives of animals, many of these themes discussed in the context of affective science also extend to comparative research more broadly.

2. Anthropomorphism: Concept and Consequences

Discussions of anthropomorphism date back at least to late 6th and early 5th centuries BC, with the Greek philosopher-poet Xenophanes calling out the human-like representation of gods. In the intervening centuries, anthropomorphism has received attention from philosophers, sociologists, and psychologists alike. Social psychological research in particular has produced myriad insights into the nature and consequences of anthropomorphism.

Epley and colleagues (2007) provide a useful definition, proposing that anthropomorphism, "describes the tendency to imbue the real or imagined behavior of nonhuman agents with humanlike characteristics, motivations, intentions, or emotions" (pg. 864). A related process, mind perception, involves the attribution of mental states such as intentions,

consciousness, and emotional experience to nonhuman agents (Gray et al., 2007), though anthropomorphism subsumes mind perception in that anthropomorphized targets can be imbued with human-like traits other than mind (e.g., behaviors and physical forms). The targets of anthropomorphism span animals, technological devices, inanimate objects, nature, and supernatural entities. Standing as the conceptual converse of anthropomorphism, denial of human-like characteristics to animals also occurs, a process termed anthropodenial (de Waal, 2016, 1999). Such denial can also target humans, in which case the process is considered infrahumanization (Leyens et al., 2000) and dehumanization (Haslam et al., 2008).

Research shows that both adults and children readily anthropomorphize non-human entities (Severson and Lemm, 2016; Tahiroglu and Taylor, 2018; Waytz et al., 2010a), though several individual difference and situational contexts promote its occurrence. Epley and colleagues (2007) theorized that anthropomorphism is most likely to occur (1) in contexts in which anthropocentric knowledge is current in the mind and relevant to the situation, (2) when people are motivated to interact effectively with nonhumans, and (3) among individuals who, chronically or situationally, lack a sense of social connection to other humans. A range of empirical data supports these tenets (e.g., Bartz, Tchalova, & Fenerci, 2016; Epley, Akalis, Waytz, & Cacioppo, 2008; Epley, Waytz, Akalis, & Cacioppo, 2008; Severson & Lemm, 2016; Waytz, Morewedge, et al., 2010).

From a social psychological perspective, this trio of reasons reinforces the broader idea that anthropomorphism is a process with functional value (Airenti, 2018). More specifically, anthropomorphism might fulfil the self's need for agency (e.g., competence, Ryan & Deci, 2000; White, 1959; aligning with #1 and #2 above) and for communion (e.g., belonging, Bakan, 1966; Baumeister & Leary, 1995; Ryan & Deci, 2000; aligning with #3 above). Thus, at least from an

anthropocentric standpoint on individual wellbeing, anthropomorphism may confer some benefits. We will return later to consideration of whether anthropomorphism is good or bad (or rather, in what contexts it may be so) for science itself.

Anthropomorphism and the related processes of mind perception are considered to have particular impact on the domains of moral reasoning, decision making, and action (Gray et al., 2012). The granting –or, indeed, denial– of human-like traits and capacities to others dictates inclusion or exclusion in the circle of moral regard, or the boundary between those to whom we extend moral consideration and those to whom we do not (Graham et al., 2017; Laham, 2009). Entities granted full humanity, so to speak, are deemed to be within the circle or 'in-group', whereas those denied some or all human traits are excluded as 'out-group'. This process holds for human entities (e.g., humans denied human traits are excluded from the circle of moral regard; Bastian, Laham, Wilson, Haslam, & Koval, 2011) as well as nonhuman entities (e.g., anthropomorphism of nature increases the propensity to protect it; Tam, Lee, & Chao, 2013).

In the domain of moral reasoning, anthropomorphism impacts attributions of responsibility to those who have carried out an action that harms others. Entities granted human-like mental capacities such as free will and consciousness are held to be more morally responsible for their actions than entities who are denied such capacities (Phelan and Waytz, 2012; Shapiro, 2006). This concept of moral agency applies in the case of human entities (Giffin and Lombrozo, 2018; Gray et al., 2012; Gray and Wegner, 2009; Robbins and Litton, 2018), as well as in the case of nonhuman entities: attributing more mind to artificial intelligence software correlates positively with perceived intentionality and wrongness of moral violations brought about by the software (Shank and DeSanti, 2018).

Thus, from a functional perspective, anthropomorphism appears to stem from the human needs to understand the surrounding world and to connect socially with others. One key consequence of anthropomorphism is that it shapes moral reasoning about an entity: whether it deserves concern and protection and also whether it is held morally accountable for its actions. As we now make the case, these processes that underlie and flow from anthropomorphism are especially pertinent in the context of human-nonhuman animal interactions.

In the discussion of animal anthropomorphism specifically, it is relevant to distinguish between two types of anthropomorphism. Burghardt (2004) discriminates between *naïve anthropomorphism* and *critical anthropomorphism*. Similarly, de Waal (1999) delineates *anthropocentric anthropomorphism* from *animal-centered anthropomorphism*. For both, the former (i.e., naïve or anthropocentric anthropomorphism) reflects the process of anthropomorphism captured by the social psychological research reviewed above: the casual attribution of human traits to nonhumans. By contrast, the latter (i.e., critical or animal-centered anthropomorphism) sits at the heart of anthropomorphism in science: the assumption of continuity in conscious experience, behavior, and cognition between phylogenetically-closely related species made in the effort to develop testable scientific hypotheses. Bekoff (2000) uses the term *biocentric anthropomorphism* to describe a similar process.

Naïve or anthropocentric anthropomorphism is inculcated from an early age, especially via exposure to anthropomorphized representations of animals. Indeed, animals are pervasively depicted in an anthropomorphized manner in children's books, cartoons, and films (Blanchard, 1982; Geerdts et al., 2016). Deploying the above social psychological theories, it would seem that children's media creators leverage the dynamics of agency and communion: anthropomorphized animals might help bridge gaps of understanding and also might be a conduit

for social connection, respectively. In terms of the former, the effects of such representations are mixed, with some research suggesting that anthropomorphized animals undermine learning about the biological world (Ganea et al., 2014; Waxman et al., 2014), whereas other research documents learning benefits (Bonus and Mares, 2018; Geerdts et al., 2016; McCabe and Nekaris, 2018). In terms of the latter, anthropomorphized animals are used to promote learning about human social dynamics and morality (Mierek, 2010), though such efforts may ultimately fail to produce anticipated prosocial outcomes (Larsen et al., 2018). Related research suggests that anthropomorphized depictions of animals in marketing targeting children are effective because they promote kinship between the child and the product (Veer, 2013), corroborating the view that anthropomorphism serves social ends.

Among adults, anthropomorphism of animals is readily apparent, though it varies as a function of species. Work by Eddy and colleagues (1993) demonstrated increased anthropomorphism of animals with increasing perceived similarity to humans, with primates high in both and invertebrates low in both (see also Harrison & Hall, 2010). Such a pattern is consistent with de Waal's (2016) perspective, given the close phylogenetic distance between non-human primates and humans, particularly the great apes, whose lineage diverged from ours only relatively recently (Prüfer et al., 2012). Given that phylogenetic relatedness also predicts moral concern over the distress of animals (Rae Westbury and Neumann, 2008), it is no surprise that anthropomorphic representations of animals can result in increased concern for animal welfare, a form of moral regard (Butterfield et al., 2012). Urquiza-Haas and Kotrshcal (2015) offered a theoretical model which argues that anthropomorphism of phylogenetically similar species is relatively more automatic and reflexive than that of phylogenetically dissimilar species, which in turn is more reflective.

While naïve anthropomorphism can sometimes increase concern for animal welfare, it can also dangerously distort people's perspectives of animal-human closeness, leading to negative consequences for animal welfare and conservation. Research has demonstrated, for instance, that seeing great apes depicted in the movie entertainment industry and other anthropomorphized contexts negatively impacts public attitudes about their endangered conservation status. For example, seeing a chimpanzee placed within a human context led to participants being less likely to consider great apes as endangered and more likely to consider them suitable as pets than when considering or viewing them in naturalistic contexts (Leighty et al., 2015; Ross et al., 2011). In this regard, naïve anthropomorphism can have serious negative implications for people's treatment and understanding of animals, particularly those threatened by environmental destruction in their natural habitats.

Naïve anthropomorphism of animals is common, reinforced from an early age, and varies across phylogeny. It also comes with a risk of undermining support for animal welfare. If it is so common in the general public, to what degree is anthropomorphism of animals common in scientific practice and how does it impact interpretations of behavior that appear to overlap with those observed in our own species? To answer these questions, we turn to the concept of critical anthropomorphism.

3. Anthropomorphism in Comparative Affective Science

Given that researchers are themselves humans, it is no surprise that there exists a natural inclination to anthropomorphize when engaging in comparative science. A major concern is that critical anthropomorphism adopts a top-down approach in which humans are the model species

from which comparisons to other species should be made. Povinelli and colleagues (2000) warn against being held "hostage by a theoretical framework" that uses human experience as the basis of analogy to other species for mental states.

From a biological stance, a more powerful approach would be to objectively identify the environmental pressures shaping the evolution of a given trait and then use those to make bottom-up predictions about which species should expected to display the given trait based on socio-ecology. Such an approach is reflected in Pauen's (2012) description of "third-person" perspectives when making mental state inferences. In Pauen's view, third-person perspectives, in contrast to first- and second-person perspectives, are inherently objective in nature, are driven by theory, and are tested against empirical evidence. Such purely third-person perspectives, however, are difficult to achieve, and indeed identify; Pauen (2012) writes, "it may be difficult to find out whether or not an individual case of mental state ascription in fact involves the second- or the third-person perspective" (pg. 41).

Given the above-noted ubiquity of anthropomorphism, including in science (Asquith, 1984), we argue that it is most useful to consider how and when anthropomorphism influences the scientific process, rather than trying to avoid it altogether. In fact, there may be certain benefits to an anthropomorphic approach. From a philosophical stance, Pauen (2012) argues for the utility of second-person perspectives as an effective way to leverage insights about one's own mental states (i.e., via first-person perspective reflection) to better understand other entities. Focusing on anthropomorphism in comparative science specifically, Bekoff (2000) argues that "anthropomorphism allows other animals' behavior and emotions to be accessible to us" (pg. 867). For closely related species, assuming shared homologies may even be the most parsimonious approach for understanding underlying mechanisms, or in the development of

empirical hypotheses (de Waal, 1999). Such a view extends Burghardt's (2004) proposal of critical anthropomorphism, which involves "not only careful replicable observation, but also knowledge of the natural history, ecology, and sensory and neural systems of animals as well" (pg. 15).

For animals sharing close phylogenetic histories, similar social structures, and behavioral ecologies, anthropomorphism can provide a framework that facilitates identification of larger patterns, a sort of gestalt whole, in a series of discrete or seemingly unrelated behaviors (de Waal, 2016). Given that animals cannot explicitly tell us about their inner experiences, understanding their underlying emotional experiences is inherently challenging. On this view, comparative affective science might use an anthropocentric lens to at least begin to query the affective lives of animals. At the end of the day, what researchers have available to them is observable behavior or, in some limited cases, physiological or neurological markers.

Nonetheless, as described above, this is a double-edged sword; while anthropomorphism may help us identify these experiences, interpreting animal behavior as human-like might impede the ability to see the true abilities, or even the unique capacities, of other species (de Waal, 2016). Moreover, extending first-person perspective ("I") insights to a second-person perspective ("you") inference about the mental states of an animal requires as a starting point that mental states are indeed ascribed to that animal (Pauen, 2012). Anthropomorphism might therefore generate inferential gaps into the mental capacities of other animals. To use a simple example, bats are mammals with eyes. Observable movement behavior of bats could easily be attributed to visual processing. Moreover, their sound production is out of the range of human hearing. Therefore, it would not be unreasonable that we would have assumed that bats, like birds and other mammals, used vision as their primary sense, rather than using sonar to "see"

their world, the latter of which, of course, reflects reality. The anthropocentric misattribution of bats' movement behavior to visual processing could have hindered discovery of this unusual sense. Moreover, because we lack sonar systems, even once we understand that bats use sonar to navigate, it is unlikely that we will ever know what it is like to be a bat (Nagel, 1974).

For affective processes, the challenge is even more acute – we might use a human framework as a starting point, but there is a serious risk of missing or misattributing affective responses that are specific to other species. How do we even know which behaviors might indicate affective experience? Part of solving this puzzle involves understanding which situational cues might generate affective experience. Inferring negative affect is relatively straightforward; we have a good sense of what is aversive (i.e., pain, inability to reach available food), and we have good evidence that these influence cognition and behavior both (Bartolic et al., 1999; Lavric et al., 2003).

Inferring positive affect is more challenging. Indeed, it is as yet unclear what causes positive affect in other species (Smith and Brosnan, 2019). Among humans, the positive affective space is rich with a diversity of emotions (Fredrickson, 2013; Shiota et al., 2014), yet outward nonverbal expression of such states is limited in its relative distinction among these states (Sauter, 2010). Moreover, the quintessential cue presumed to indicate experienced positive affective states in humans, the smile, is in fact displayed in several contexts that are dubiously indicative of positive affective experience (Ansfield, 2007; Bonanno and Keltner, 1997; Fredrickson and Levenson, 1998; Hoque and Picard, 2011; Keltner and Buswell, 1997; Kunz et al., 2013), and sometimes is not displayed in seemingly objectively positive contexts (Crivelli et al., 2015; Fernández-Dols and Ruiz-Belda, 1995; Kraut and Johnston, 1979).

In addition to identifying the most suitable behaviors to infer affective experience of either valence, comparative affective scientists must also overcome inferential biases regarding the complexity of the phenomena at hand. Such biases as they play out in comparative science are explored, and indeed, debated, elsewhere (e.g., Dacey, 2016; Karin-D'arcy, 2005; Zentall, 2018). Put succinctly, most researchers advocate being mindful of parsimony and avoiding assuming complexity. Applying such views to comparative affective science, it is crucial to restrain from presuming that affective processes in humans are complex and to consider the degree to which the most parsimonious explanation may be the best explanation.

To integrate these broad themes regarding the benefits and pitfalls of anthropomorphism in comparative affective science, we will briefly explore three topics relevant to comparative affective science: responses to death (comparative thanatology), inequity aversion, and prosocial behavior.

3.1 Responses to death

The nature of responses to death is of great interest to scientists and philosophers alike, in no small part because such responses provide insight into the evolution of more general cognitive and emotional processes (Brosnan and Vonk, 2019). *Comparative thanatology* is the study of how both human and animal species respond to dying and dead conspecifics (Anderson, 2016; Anderson et al., 2018; Gonçalves and Carvalho, 2019). Animals respond in a diverse number of ways to death in conspecifics, "from exploration, affiliation, caretaking and grief reactions, to avoidance, sexual interest, abusive treatment, and even cannibalism" (Anderson, 2019). Given this large degree of variation, as well as differences in species' socio-emotional and cognitive

capacities, Anderson (2019) argues that existing frameworks, developed within the context of human research, can provide useful starting points for interpreting how and why animals respond to death and what this can tell us about underlying mechanisms. As such, the field of comparative thanatology may be considered anthropocentric in its roots.

In humans, the concept of death comprises at least four cognitive components: irreversibility, non-functionality, inevitability, and causality (Anderson, 2019). Irreversibility refers to an individual's awareness that death is irreversible; non-functionality reflects understanding of non-sentience following death; inevitability is the awareness that death is inevitable and universal; and causality refers to the understanding of the biological causes of death. A critical question for comparative thanatology, then, is whether animals display behaviors that indicate, or could give rise to, analogous concepts.

Aside from awareness of the inevitability of death, which would be difficult to empirically demonstrate in a nonverbal organism, there is evidence that some animals may exhibit behaviors that would indicate or give rise to the concept of death. For example, in a number of primates as well as other animals, mothers continue to carry, care for, and stimulate their dead offspring for prolonged lengths of time following death (e.g., dingo: Appleby, Smith, & Jones, 2013; giraffe: Bercovitch, 2013; elephant: Payne, 2003; great apes: Biro et al., 2010; Reggente et al., 2016; Sugiyama, Kurita, Matsui, Kimoto, & Shimomura, 2009; Van Lawick-Goodall, 1971). Although this suggests that mothers may not initially be able to detect non-sentience in the corpse, the experience of witnessing an absence of recovery in the corpse is likely to provide mothers (and others) an opportunity to learn about the irreversibility of death (Anderson, 2019).

In a similar manner, numerous animals have been reported to attempt to physically stimulate, manipulate, and revive corpses, sometimes in notably aggressive ways (Anderson et al., 2010; Appleby et al., 2013; Bercovitch, 2013; Biro et al., 2010; Buhl et al., 2012; Douglas-Hamilton et al., 2006; Dudzinski et al., 2003; Kirchhoff et al., 2018; Merte et al., 2009; Payne, 2003; Reggente et al., 2016; Stewart et al., 2012; Sugiyama et al., 2009; Van Lawick-Goodall, 1971; Yang et al., 2016). Making contact with the corpse in this way may provide an individual with a chance to investigate whether there are any remaining signs of agency, thus enabling them to better understand that that the corpse is behaviorally and psychologically non-functional (see Gonçalves and Carvalho, 2019 for a review).

More directly relevant to comparative affective science, comparative thanatology also considers the nature of grief. In humans, grief following death (i.e., bereavement) is characterized by dysphoria and sadness that is initially acute, but can continue for several years (Zisook et al., 1982). However, human grief can also involve positive emotional experience, at least periodically, which might ultimately facilitate coping with the loss (Bonanno et al., 2008). Resonant with recognizing both positive and negative affective components of grief, King (2013) argues that a critical aspect to observing grief-like responses in animals is to consider love-like responses. Notably, theories of human grief hold that it is a process that promotes group cohesion, so is thus socially functional (Averill, 1968; Averill and Nunley, 1988; Bonanno, 2001). Gonçalves and Carvalho (2019) offer a perspective that emphasizes the social functionality of grief-like responses in non-human primates.

A number of studies have reported evidence of grief-like responses in animals that resemble those of human bereavement. For instance, Van Leeuwen and colleagues (2016) reported a case of individuals responding to the death of subadult male chimpanzee at a forested

sanctuary in Zambia. The chimpanzees dragged the corpse out of the forest into an open area near to the fence, where he could be observed and subsequently retrieved by caregivers. More than half of the group gathered quietly around the body to observe and inspect it; some individuals were observed to guard the body, cover it with branches, and even clean its teeth with a piece of grass. Although it is difficult to determine what underlying processes motivated the chimpanzees to respond in this way, the nature of their responses is notably analogous to funeral rituals in many human societies (Bendann, 2013; Robben, 2017).

Several other examples of grief-like responses in animals appear in the empirical literature. A chimpanzee's death happened in the course of a zoo-based study on sleep patterns, which allowed the experimenters to empirically document substantive changes in conspecific's patterns of sleep, behavior, and use of the enclosure subsequent to the death (Anderson et al., 2010). In a study of baboons, Engh and colleagues (2006) showed that females who had recently lost a close relative during predatory attacks showed significant elevations in their cortisol levels as compared other females who had also observed the attacks but were unrelated to the victim. Such a pattern is consistent with documented links between cortisol and grief in humans (Jacobs et al., 1987; Pfeffer et al., 2009; Richardson et al., 2015).

Taken together, these studies suggest that animals may experience states akin to human grief. Driven by an inherently anthropomorphic view (namely, that other animals may respond to death in similar ways to those observed in humans), comparative thanatology, has made great strides even despite being a nascent field. Additional work is needed, however, to determine the contexts of these behavioral responses and, importantly, what they indicate about the affective processes involved in death responses. We call for objectivity in documenting and reporting responses to death, and for researchers to consider both what evidence would be crucial to

demonstrate in terms of establishing support for the view that animals grieve. The field of comparative thanatology may benefit from thorough documentation of the full range of responses to death, and indeed the contexts in which they arise (see also Gonçalves and Carvalho, 2019). A strong argument can be made for the need to examine responses to death across species, while also recognizing the inherent variability the emerges within a species (King, 2013). In some cases, this may mean recording cases of 'no response' – but such evidence is important when seeking to establish the core comparative question at hand.

Within any field of comparative science, including that of thanatology, we advocate a phylogenetic approach that spans many animal species. Currently, work in this area is predominantly focused on primate species, which will need to broaden. Fortunately, the field is now growing in positive directions, with case reports now coming in from a broader range of species (e.g., Bearzi et al., 2018; Valdes and Laidre, 2019). It is plausible that the emergence of grief-like responses occurs along phylogenetic, or indeed species sociality, lines. We are excited at the prospect of the field of comparative thanatology undertaking such an approach.

3.2 Inequity aversion

Critical anthropomorphism makes the case that informal anecdotal observations and corresponding anthropomorphic interpretations can inspire novel research questions and enable researchers to gain a more contextualized view of animal experience. This is not to say that anthropomorphic interpretation should stand alone, but rather can be used to generate testable hypotheses to determine if, in fact, continuity across species holds.

One such example is relayed by Brosnan, who as a graduate student experienced an alpha male in her group repeatedly trading food found in the group's enclosure with her in an effort to

obtain peanuts. This was notable as some of the foods, such as orange quarters, were generally assumed to be of higher value than peanuts. Why, then, was the alpha male going to such effort to "trade down"? One possibility is that he wanted what everyone else had. To test this empirically, Brosnan designed a study to test how monkeys responded to a food they normally readily ate when a partner received a more preferred food immediately beforehand (Brosnan and de Waal, 2003). Indeed, capuchin monkeys refused to participate for rewards they would normally work for if their partner got something better. In the sixteen years since, Brosnan and others have demonstrated that other primates do this, have begun to document the causes of the sometimes substantial variability seen across individuals, and have found a pattern of presence and absence across species that suggests that it evolved in concert with cooperation tendencies (Brosnan and de Waal, 2014). Evidence for inequity aversion has also been found in non-primates, and also, thus far, generally follows the same pattern linking inequity responses and cooperative tendency (Massen et al., 2012; Range et al., 2009; Wascher and Bugnyar, 2013). Thus, an initial (anthropomorphic) observation led to an empirical study that opened an entire area of research.

This example is particularly relevant to comparative affective science for several reasons. There are (at least) two non-mutually exclusive ways in which this reaction could come about. Individuals might cognitively assess their rewards, comparing them to those of others, and then make a decision about how to respond. Alternately, individuals may experience an affective response to serially receiving less than a partner. This latter view is an emerging theory in human research; for instance, there is debate about whether humans' reactions to inequity are driven by spite or frustration (McAuliffe et al., 2014). Relatedly, Yamagishi and colleagues (2009) have argued that humans' rejections of unfair offers are an "emotional commitment device," based on

emotions such as anger or disgust. One reasonable hypothesis, based on this, is that responses to inequity, including those of other species, are driven by affective responses (thus truly constituting 'inequity aversion'). Understanding the differences and similarities in inequity aversion across species could help us to better understand how and for what purpose inequity aversion evolved, and indeed provide insight into the affective and/or emotional processes at play.

3.3. Prosocial Behavior

Research on prosocial behavior in animals underscores another important lesson for anthropomorphism in comparative science. Put straightforwardly, we do not know if animals even understand the tasks we provide in the same way that we do, much less interpret the goal or purpose in the same way (Brosnan, 2018). Achieving alignment between intended dynamics of a task and animals' experience of those tasks is essential for drawing accurate conclusions regarding the comparative nature of the process at hand. Here we consider how anthropomorphic assumptions about the purpose or the goal of the task can lead to errant conclusions.

To set the scene, it is worth noting that prosocial behavior in humans is, at least in some contexts, driven by affective processes. Engaging in prosocial behavior elicits positive states (Aknin et al., 2012; Ferguson et al., 2012). In turn, positive affective states (i.e., 'positive mood') promote prosocial behavior (Carlson et al., 1988), as do a wide range of discrete emotions, including compassion (e.g., Condon, Desbordes, Miller, & DeSteno, 2013), gratitude (Ma et al., 2017), awe (e.g., Piff, Dietze, Feinberg, Stancato, & Keltner, 2015), moral elevation (e.g., Erickson et al., 2017; Schnall, Roper, & Fessler, 2010), and guilt (e.g., O'Malley & Andrews, 1983). Anticipated emotions, or how an individual expects to feel if they were or were not to

engage in a prosocial action, also motive prosocial behavior (Johnston and Krettenauer, 2011; Lindsey et al., 2007; van der Schalk et al., 2015, 2012).

As is clear, a primary driver of research on human prosocial behavior is answering the question of *when* and *why* it occurs. In animals, before querying the affective processes relating to prosocial behavior, it is important first to answer the more fundamental question of *whether* animals display prosocial behavior. Namely, research on prosocial behavior in animals aims to determine whether subjects make decisions that benefit their partners at no cost to themselves (Cronin, 2012; Sosnowski and Brosnan, 2019).

It is relatively straightforward to identify naturalistic contexts or create research contexts in which the motives for human prosocial action are clear. This objective is less easily met for animals. Early studies on prosocial behavior in animals exposed subjects to a choice between two trays, one of which rewarded only them and one of which rewarded both them and their partner with the same food. Such a task is analogous to tasks used with humans (Fehr et al., 2008; House et al., 2013) – and a sense-check from the anthropocentric lens reveals that the task seems reasonable: choose to benefit the self or choose to benefit the self and the other.

Despite passing comprehension controls designed to ensure that they understood the design, in none of these studies did subjects show evidence of prosocial (or even spiteful) behavior. Instead, they were indifferent (Jensen et al., 2006; Silk et al., 2005). These findings were perplexing, given that observational studies showed evidence of what appeared to be prosocial behavior and/or motivation. Moreover, subsequent studies using a different paradigm requiring a choice between two tokens found evidence of prosocial behavior (de Waal, Leimgruber, & Greenberg, 2008; Horner, Carter, Suchak, & de Waal, 2011; Massen, Luyten, Spruijt, & Sterck, 2011; cf. Amici, Visalberghi, & Call, 2014).

More recent research indicates that subjects may not have understood the original design as intended. A follow-up study using the same design and population as Silk et al. (2005) initially replicated the finding that subjects showed no evidence of prosocial behavior. However, when subjects were given the opportunity to be the recipient of a *different* chimpanzee, who was trained to make prosocial choices, they then were more likely to choose prosocially for their original partner, suggesting that they may not have originally understood the purpose or goal of the task (Claidière et al., 2015). In another study, when access to the choice apparatus depended upon a partner "unlocking" it via costly behavior (i.e., the partner had to give up food), subjects made more prosocial choices (Schmelz et al., 2017). If there was no cost for the partner to unlock the apparatus, or the experimenter unlocked it, subjects were indifferent. The authors interpreted these findings as evidence that the subjects choose prosocially when there was a reason to do so, namely, to help the partner who paid a cost to help them.

The lesson here is clear: proceeding with an anthropocentric view of tasks risks false negative results – if a task reflecting our understanding of a process fails to provide evidence for that process in animals, we may erroneously conclude that animals don't possess the capacity for that process, when in reality they just didn't see the task the same way we did (Brosnan, 2018; de Waal, 2016). Of course, researchers are already cognizant of this, and work hard to provide comprehension controls to verify subjects' understanding of the set up. However, as above, there are cases in which researchers do all of this and fail to identify sources of misunderstanding.

We point here to one factor that may decrease anthropocentric errors in task design: researcher familiarity with the species of study. In primate social cognition, there is greater evidence of complex behavior in long-term studies, for instance at long term field sites or in studies from long-term captive colonies. This is not surprising under the view that researchers at

these sites are both more familiar with their subjects and are seeing them in a more natural context, where the animals clearly understand the ramifications of their decisions. This emphasizes the need to combine information from multiple domains when undertaking comparative science, and to make sure that whenever possible, experiments are informed by knowledge of the contexts in which a behavior emerges in natural contexts (Janson and Brosnan, 2013). In so doing, the field may reap the benefits of critical anthropomorphism, but avoid the pitfalls of anthropocentric task design.

4. Conclusion: Anthropomorphize Mindfully

In our review of anthropomorphism in the context of empirical study into responses to death, inequity aversion, and prosocial behavior, we hope to have identified the potential benefits and pitfalls of anthropomorphism in comparative affective science, and indeed other comparative sciences. As we have discussed, although anthropomorphism can benefit the process of theory generation (as we saw with inequity aversion) and drive inquiry into new domains (as we saw with the emerging field of comparative thanatology), it can also lead researchers to make erroneous conclusions, and thus compromise the conclusions made. We advocate an approach wherein researchers anthropomorphize mindfully – aware of the complexities of it while reaping its benefits. While some have made the case that purely objective, non-anthropomorphic approaches are most desirable (Wynne, 2006, 2004), with the above-reviewed evidence in hand, we agree with others who point out that it is near impossible to discern pure objectivity nor is it clear that purely objective approaches are indeed the most desirable (Pauen, 2012).

In this article, we primarily focused on anthropomorphism as it plays out in psychological and behavioural approaches to comparative affective science. It is worth noting that

neuroscientific approaches offer intriguing and complementary perspectives. For example, Ferrari (2014) argues that embodied simulation, supported by mirror neuron systems, supports complex processes that involve mental state attribution, such as empathy and moral judgment, and, further, that such a system can has evolutionary roots identifiable in nonhuman primates. The impact of such neurologically-driven processes on mental state attribution in terms of anthropomorphism remains to be seen, but is a fruitful path for future inquiry. More broadly, as the methodologies and techniques available to neuroscientists broaden, so too does the ability to examine the brain basis for many of the processes discussed in this article (see also Miller et al., 2019).

Regardless of its benefits or its pitfalls, it is clear that anthropomorphism is a natural bias for human researchers – a bias to see the world through our own human eyes is difficult to avoid entirely. Such a bias has parallels to the cultural bias that researchers bring to the study of human adults (Henrich et al., 2010) and children (Nielsen et al., 2017). We applaud recent efforts to address such biases in human research and suggest that comparative scientists might productively learn from such efforts. Comparative affective science, and comparative science more generally, will be better for not only the awareness of anthropomorphic biases but also effective and active engagement with them.

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