

Nonhuman Primate Responses to Death



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Introduction

Humans are preoccupied with death. In art and literature, there is a fascination with supernatural beings, specifically those that are immortal or “undead,” such as vampires and zombies (more recently adapted for TV and movies). We celebrate Halloween with depictions of death, and are so obsessed with tragic news stories involving mass deaths, suicides, and disasters that there are dedicated cable networks covering both news and criminal cases, largely focused on murder cases. The awareness and fear of one’s own eventual demise have inspired countless traditions, ranging from religious and spiritual beliefs to mourning and burial rituals. The fear of death has also been posited as an explanation for in-group biases and other cultural prejudices (e.g., terror management theory; Harvell & Nisbette, 2016; Rosenblatt, Greenberg, Solomon, Pyszczynski, & Lyon, 1989). In cases like this in which a trait is widespread across cultures and contexts, biologists begin to consider whether the trait evolved. Although there are many ways to answer this question, one approach is to examine whether other species share the trait. This comparative approach not only sheds light on whether a trait evolved, but may also indicate for what purpose and in what context it did so, which helps us to better understand the trait in humans as well. To what degree, then, do other species share our fascination with death? Given the significance attributed to the inevitability of death in shaping human cognition and behavior, it is surprising that research on how other species, particularly other primates, conceptualize and respond to death is severely lacking.

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Understanding this will not only help us to better understand the question at hand—how other species understand death—but also more generally inform our understanding of the evolution of other behaviors and cognitive abilities.

A systematic study of primate responses to death can paint a fuller picture of the continuity, or lack thereof, between humans and other primates. A fundamental goal of comparative psychology is to isolate the role of particular processes in evolved tendencies, biases, and attributes by comparing multiple species (Eaton et al., 2018). This is of particular importance when attempting to determine which traits are unique to a specific species, most commonly humans. For example, language has long been considered to be a core capacity underpinning much of what appears to be uniquely human cognition, such as abstraction, theory of mind, and metacognition. If researchers are able to show that animals without humanlike language, or even a symbolic communication system, have abstract concepts, metacognition, or theory of mind, then language is not an essential building block for these capacities. Similarly, demonstrating that humans are unique in the way they conceptualize death may help to explain why humans alone engage in practices related to death (e.g., burial rituals and preservation of bodies) as well as organized religion, which also appears to be uniquely human.

In this chapter, we explore what (little) we know about primate conceptions of death. In addition to exploring what this tells us about the evolution of human conceptions of death, we will also consider what other primates' behaviors might reveal about their cognition and social behavior. We begin with a discussion of the cognitive capacities that may be required for a full representation of death and all that it entails. We then review the sparse literature regarding behaviors that result from the death of conspecifics. In addition, we report the results of an informal questionnaire in which we asked our colleagues about their experiences in working with captive primates to gather anecdotal evidence of differences in response to death among various primate groups. We end with a discussion of the challenges in interpreting primate responses to death, which parallel challenges faced in other areas of comparative psychology that require researchers to speculate about the internal workings of other minds.

Cognitive Capacities Required to Understand Death

Before considering how primates respond to death, we first must address the degree to which other species have the capacity to think about death. This is admittedly a black box, in that we can never know with certainty what another species (or, arguably, even another individual) thinks. However, we can understand the parameters of what is feasible based on the capacities species do or do not show (and, conversely, we might learn something about these capacities based on how primates respond to death and dying). Therefore, prior to introducing the evidence of how primates behave around dying or deceased individuals, we summarize a variety of cognitive capacities related to understanding death and dying to properly

place our interpretations of their behaviors into perspective. For each of these, we provide a brief summary of the state of the field and a consideration of why it is important in the context of death and dying.

Are Nonhuman Primates Capable of Abstraction?

An ongoing quest within comparative psychology is to understand the nature of concepts held by other species and, in particular, the extent to which they can reason about unobservables. Unobservables are hypothetical constructs that cannot, in principle, assume physical form and cannot be directly perceived (Vonk and Povinelli 2006). Death is one such construct. Although we can observe the process of dying and the physical remains of the deceased individual, we cannot perceive death itself. The construct of death involves other equally abstract ideas including the absence of life, agency, animacy, and “being.” Humans have conjured the notion of a “soul,” or a sense of self that provides us with an individual identity that continues across time and space. The idea of cessation of this self, including all thoughts and memories, is difficult to imagine and unsettling to most humans (Greenberg, Pyszczynski, Solomon, Simon, & Breus, 1994). Yet, humans can put voice or pen to such reflections, indicating that they understand the absence of existence, the finality of death, and its inevitability.

There is little empirical evidence that nonhumans represent these kinds of constructs. The lack of evidence is in part due to the challenges of studying abstractions. That is, it is premature to conclude that nonhuman primates lack such concepts; it may instead be the case that scientists have not yet broken through the barrier that precludes our access to the internal mental states of other beings. In this case, then, rather than our current understanding of nonhuman primate cognition constraining interpretations of behavior, it may be that a better understanding of observable responses to death can contribute to the larger corpus of data allowing us to make inferences about the internal states and concepts giving rise to such observable behavior.

Inevitability

A humanlike concept of death involves an appreciation of the inevitability of death—no one escapes, no matter how hard he or she tries to do so. Inevitability is a hypothetical, unobservable construct in its own right. Furthermore, understanding the certainty of an event that has not yet happened encompasses additional abstractions like the capacity to imagine the future and to calculate probabilities. The question of whether primates reason about the probability of events has barely been investigated (although see Eckert, Rakoczy, & Call, 2017; Tecwyn, Denison, Messer, & Buchsbaum, 2017), and the work that does exist does not address the prediction of future events never before experienced. As with any abstraction, part

of the challenge is in designing experiments to test the question, and it is likely that many primates can reason about the likelihood of future events based on previous experiences. For example, they may know that food will become scarcer as temperatures drop and day length shortens, or even that conspecifics will disappear if they hear an alarm call. However, the question of whether they anticipate their inevitable cessation of being is equivalent to asking them to imagine something that they have never directly experienced and may not have the capacity to comprehend (for reasons outlined in subsequent sections).

For humans, the certainty of death contributes to the anxiety it provokes. The question of whether other species ponder their eventual demise factors into discussions of animal ethics. One can suffer through the knowledge that one is going to die, but this suffering may be reduced or absent if an organism is unaware of its own death (Benatar, 2017). As such, a better understanding of how nonhumans think about death (if at all) may be critical to evaluating ethical practices in animal husbandry, especially in the food industry. Unfortunately, we are not aware of any empirical work that addresses this question. There are anecdotal reports that Koko, a gorilla that learned sign language, could communicate about death and loss, and even that she was sad upon hearing of the death of a celebrity she once met (Robin Williams; <https://www.koko.org/koko-tribute-robin-williams>), but these claims are unsubstantiated and anecdotal.

Finality/Absence

To properly represent death, an individual must comprehend the finality that comes with it. It is possible to imagine a number of constructs that together comprise the capacity to conceive of death. For example, first one must appreciate that physical objects—including living beings—continue in time and space; that is, they continue to exist when they are not observable (i.e., object permanence). Conversely, one must appreciate that objects can also cease to exist. A first test of this construct is to examine whether nonhumans can appreciate an absence of objects for a given category. This notion can then be extended to incorporate the idea that objects once present are now absent. To imagine death, one must then understand that this absence is permanent at some point. Lastly, one must generalize this idea of the disappearance of objects to understand the cessation of life in a living being.

Perhaps the most straightforward way to evaluate whether nonhumans appreciate absence at the most basic level is to test their understanding of a true zero concept (Nieder, 2016). Although the number of species tested for such a concept is negligible, Beran (2016) argues that monkeys, like humans, have a concept of zero as part of the analog number line that can be differentiated from other numerosities. This argument stems from recent findings of parietal lobe activation in response to zero (Okuyama, Kuki, & Mushiake, 2015). In this study, Japanese macaques (*Macaca fuscata*) added or subtracted stimuli from an array on a computer screen to match the number presented in a target stimulus. Brain activity was measured as the

monkeys performed the task. These results have been corroborated by studies in other monkey species. For example, Merritt, Rugani, and Brannon (2009) found that rhesus macaques (*Macaca mulatta*) treated empty sets like values along a numerical continuum in both matching and ordering tasks. Evidence of a zero concept has also been reported in a single grey parrot (*Psittacus erithacus*; Pepperberg, 2006; Pepperberg & Gordon, 2005), and in honeybees (Howard, Avarguès-Weber, Garcia, Greentree, & Dyer, 2018), suggesting that it may be an evolutionarily ancient capacity.

Outside the lab, additional behaviors suggest that some animals appreciate when objects cease to exist. For example, animals recognize when a food source has been depleted, as evidenced by discontinuation of searches for food at particular sites. However, an understanding of how nonhumans conceptualize the disappearance of objects is complicated by questions about the extent to which they exhibit object permanence. Many species struggle with the notion that objects continue to exist when they are no longer observable, and it has been suggested that only “more intelligent” species exhibit object permanence (Etienne, 1984). Thus, if an individual dies, and is removed from their group, their conspecifics may not continue to think about that individual. There is some evidence of object permanence in at least great apes (e.g., de Blois, Novak, & Bond, 1998; Jaakkola, 2014), but there is little evidence that they search for individuals that are missing. Some primates have grouping calls that function to minimize or maintain distance and keep the group together, but the extent to which these calls are under conscious control or lead to searches for missing group members is unknown. There is some evidence that primates do recognize when an individual is not returning to the group. For instance, orphaned infants are sometimes adopted (Cäsar & Young, 2008; Dunham & Opere, 2016; Thierry & Anderson, 1986) and group members recognize that a new alpha has assumed control of the group if the former alpha disappears (Pruetz et al., 2017; Scarry & Tujague, 2012). Even then, however, it is difficult to know whether they recognize that the individual has ceased to exist, or simply alter their behavior because the individual is no longer present. And, of course, alphas assume control of a troop after winning an altercation regardless of whether the deposed leader dies or drops in rank. Overall, whereas the evidence indicates little reason to question that nonhuman primates have a concept of absence with respect to physical objects, it is less clear that they can imagine the absence of self or nonexistence as it pertains to the mental lives of individuals.

Sense of Self

Comprehension of what death means for a living thing hinges upon an understanding of the continuation or extension of the self through time. If one exists only in the present, never reflecting on the past or anticipating the future, one is unlikely to represent the self as a being that extends through time with a past that is inextricably tied to the future. Despite the centrality of time in motivating planning, teaching,

and many other potentially uniquely human endeavors, the manner in which time, especially the future, is conceptualized is poorly understood in human children, and even more sparsely researched in nonhumans (Vonk 2016). Most researchers that have tackled this question have done so by examining planning abilities in animals like corvids (Kabadayi & Osvath, 2017) and apes (Bourjade, Call, Pele, Maumy, & Dufour, 2014; Osvath & Persson, 2013), but these studies typically allow for the subjects to form associations between future states and locations or objects, which does not require abstract planning (although it could; Hampton, 2018). In addition, the experiments often fall short of revealing a sense of auto-noetic consciousness or a self that continues in time (e.g., Povinelli, Landry, Theall, Clark, & Castille, 1999; Povinelli & Simon, 1998). Thus, the corpus of data is currently mute on the question of whether animals anticipate themselves existing at some future point of time. Without such a reflection, the concept of death—of ceasing to exist—is less relevant.

In the preceding section, we contemplated whether nonhumans appreciate when *something* ceases to exist. However, a full understanding of death involves understanding when *someone* ceases to exist as well. This distinction would exist only for those that are capable of differentiating between animate and inanimate beings and identify themselves as the former. That is, an organism cannot understand the significance of ceasing to exist without first appreciating the existence of self and others as mental beings. Although an understanding of the mental states of others (i.e., theory of mind; Premack & Woodruff, 1978) is one of the most enthusiastically studied constructs in comparative psychology, the understanding of self has been more limited. The majority of empirical studies on self-concept have utilized Gallup's mirror self-recognition (MSR) paradigm (Anderson & Gallup Jr., 2015). However, this paradigm has been criticized on various grounds, with many researchers questioning the extent to which it reveals anything beyond an appreciation of body awareness (Anderson & Gallup Jr., 2011; de Veer & Van den Bos, 1999; Swartz, 1997). More recently, researchers have used video techniques to investigate whether nonhumans have a sense of self that extends in time (Hirata, Fuwa, & Myowa, 2017), although these tests have also been subjected to scrutiny (Vonk, 2018).

The construct of metacognition, or the ability to think about thoughts, may be more informative regarding self-awareness to the extent that it reflects an individual's understanding of one's own mental states. Research in this area has focused on attempts to reveal that animals know when they are experiencing uncertainty (e.g., Smith, Shields, & Washburn, 2003) or the extent to which they know what they know (e.g., Call & Carpenter, 2001). If animals can indicate that they know when they do (or do not) know information, and selectively work to access information they are lacking, they can be said to have achieved a level of self-awareness. Although the growing body of research on this topic suggests that many animals can make metacognitive judgments, the abilities demonstrated so far do not require consciousness (Kornell, 2009) and, thus, may not be sufficient to infer self-concepts.

Mental Time Travel

Like metacognition, episodic memory may depend on some level of self-awareness. Episodic memory is also relevant to the concept of death, given that it allows individuals to imagine future states. Episodic memory is sometimes defined as the ability to bind what-where-when components of a single event—the memory of which is evoked through cues linked to the event (Clayton, 2017), thus connecting past, present, and future. This construct might be extended to include an awareness that one exists and can shape the future. However, there is a consensus that existing studies of episodic-like memory cannot fully reveal a sense of autothetic self that is similar to that expressed by humans when they write memoirs and reflect on their experiences (Schwartz & Evans, 2001; Shettleworth, 2012). The construct is coined “episodic-like memory” to express this limitation. As such, the current evidence of episodic-like memory in nonhuman primates is not sufficient to argue that primates can comprehend the limitations of their own existence into time.

Theory of Mind

There are distinct theoretical perspectives regarding the relationship between self-awareness and other-awareness, with some suggesting that self-awareness precedes other-awareness, and some suggesting that the latter occurs through simulation and projection (for reviews, see Apperly, 2008; Flavell, 1999). Regardless of how one conceives the relationship, it seems apparent that both abilities rest on the capacity to represent mental states, and simultaneously represent perspectives that may conflict with each other. Thus, the acid test for theory of mind has often been considered the false belief test, which has only recently been applied to nonhumans, with mostly negative results (Andrews, 2018). Although some species, including some nonhuman primates, have provided evidence suggestive of understanding some mental states, such as seeing, they have routinely failed to produce evidence indicative of false belief understanding (e.g., Call and Tomasello 1999; Martcorena, Ruiz, Mukerji, Goddu, & Santos, 2011 although see Buttelmann, Buttelmann, Carpenter, Call, & Tomasello, 2017; Krupenye, Kano, Hirata, Call, & Tomasello, 2016), leaving a high level of disagreement as to whether other species are capable of theory of mind (Burge, 2018; Heyes, 2017; Kano, Krupenye, Hirata, Call, & Tomasello, 2017).

If humans are alone in representing others' mental states, it follows that humans alone may have concepts of others as mental beings with distinct mental lives. If so, this might negate the ability of other species to conceive of the death of an animate being. One could argue that a fundamental divide between humans and nonhumans in the capacity to reason about mental states need not preclude nonhumans from conceptualizing death. Although this is true, it would mean that their concept of death is limited to an understanding of cessation of physical animacy and an absence of one's body. This is a restricted concept of death compared to the notion of death that grips

human imagination, although still quite useful for understanding how the human conception of death may have evolved (i.e., as a precursor to the human conception that may help us understand the steps through which it may have evolved).

Animacy/Agency Concepts

The human concept of death is restricted to animate beings. Although humans are prone to animistic thinking, and human children in particular often refer to cars, dolls, and other objects as if they are alive (Lillard, Zeljo, Curenton, & Kaugars, 2000), once adult, we distinguish between the death of, for example, a computer and the death of a pet or a loved one. It is not clear whether nonhumans perceive the death and decay of a conspecific's body any differently than that of a rotting fruit or burned-out tree stump. Furthermore, it is unclear whether they perceive the correspondence between a corpse and the individual that inhabited the body as humans do, or whether corpses are simply treated like strange and novel objects due to alterations in appearance, odor, and self-propelled movement (although see below for an argument that mothers hold on to the corpses of offspring because they cannot tell that they are no longer the same as their living offspring). Although it would be difficult to design an empirical study, future work could clarify the extent to which primates view corpses as synonymous with the living being that once occupied them.

There is evidence that monkeys see self-propulsion as an important component of animacy (Hauser, 1998; Tsutsumi, Ushitani, Tomonaga, & Fujita, 2012), just as infants do (Poulin-Doubois, Lepage, & Ferland, 1996). Additionally, squirrel monkeys can distinguish chasing movements from random movements by geometric objects (Atsumi & Nagasaka, 2015). Furthermore, primates distinguish between stimuli depicting live animals and inanimate objects in categorization tasks (Vonk, Jett, Mosteller, & Galvan, 2013; Vonk & MacDonald, 2002, 2004). However, in our own work, we have not observed that apes respond differently to images of living versus dead individuals when discriminating natural categories (Vonk et al., 2013; Vonk & MacDonald, 2002, 2004). Moreover, it is not necessary to differentiate between animate and inanimate to differentiate photos of animals from photos of foods, plants, manmade objects, or landscapes, so these somewhat artificial tasks may not provide much insight into how primates perceive dead individuals.

A better understanding of how primates conceive of death will inform several related lines of inquiry involving their capacity for abstraction. On the flipside, a better understanding of primate conceptions of various abstractions will inform our understanding of their conception of death. A deeper probing of how other minds view these aspects of their worlds will help us determine the similarities and differences between human and other primate minds, but there are other aspects of human existence that can be informed by studying parallels (or the lack thereof) between human and nonhuman primate minds.

Attachment Bonds

Studies of animals' responses to death may also tell us about the depth of their attachment bonds. This is an argument by analogy with humans, which we do not know for certain is appropriate, but in humans, the strength of a negative reaction to death seems to be proportional to the strength of the bond. This is true for conspecifics (other humans) as well as for heterospecifics, such as pets. Indeed, humans can feel deep loss even about a person they barely knew or never met, but feel bonded with through a cause (e.g., people who mourn the death of a celebrity). Thus, understanding the relationship between degree of attachment and intensity of negative reaction to death for other species can help clarify the extent to which there may be parallels between human and animal grief.

For instance, like us, other species may experience emotions surrounding an individual with whom they have formed an attachment, so understanding their responses to that individual's death provides access to understanding their emotional capacity. Although emotion in animals has been studied for years (Darwin, 1998/1899), the recent resurgence in interest (de Waal, 2011) includes attempts to find other ways to triangulate what is involved in the emotions of animals (see, for example, King, 2013). Relatedly, other species are argued to show prosocial concern for one another in some circumstances (Brosnan et al., 2010; Claidière et al., 2015; Hernandez-Lallement, van Wingerden, Marx, Srejjic, & Kalenscher, 2015; Horn, Scheer, Bugnyar, & Massen, 2016; Horner, Carter, Suchak, & de Waal, 2011; House, Silk, Lambeth, & Schapiro, 2014; Schmelz, Grueneisen, Kabalak, Jost, & Tomasello, 2017), a behavioral outcome argued to be driven by empathy (Bartal, Decety, & Mason, 2011; Campbell & de Waal, 2011; Chen, Panksepp, & Lahvis, 2009; Langford et al., 2006; Yamamoto & Takimoto, 2012). If this is the case, might we expect to find empathetic responses to death? For example, we might find evidence of adults providing additional grooming or support (comfort?) to mothers who recently lost an offspring or adults who recently lost a partner with whom they had a close bond (e.g., a higher than average rate of grooming). Such findings would provide evidence that they not only feel their own loss, but are also able to conceptualize that others feel loss as well, even when they do not personally experience it as such.

Finally, finding group differences in grieving behaviors might indicate something about the groups' cultures (Whiten et al., 1999). Most documented cultural differences have involved instrumental behaviors, such as tool use (Whiten, Horner, & De Waal, 2005) or food acquisition (Byrne, 2007), possibly due to the fact that these are the easiest to test experimentally in the lab (Bonnie, Horner, Whiten, & de Waal, 2006). There is, however, evidence of cultural differences in social behavior (e.g., grooming styles; de Waal & Seres, 1997), and it would be important to document whether there are differences in social relationships as well. As noted, human cultures exhibit a vast array of distinct burial rituals and traditions, so studying primate reactions to death offers an opportunity to explore potential cultural differences further.

Empirical Studies of Primate Responses to Death

Primates are not the only species to respond to a dead conspecific as if there were something awry. Indeed, even insects do so. Worker myrmicine ants rapidly remove deceased group members from the nest, presumably to avoid the spread of potential pathogens (Wilson, Durlach, & Roth, 1958). This system appears to be driven entirely by chemical signals, however. For instance, in the species *Linepithema humile*, individuals who die cease producing two key chemicals, and their absence apparently triggers removal behavior. What most researchers who study death are interested in, however, is not these relatively stereotyped responses that are genetically or chemically controlled, but emotional responses that indicate something akin to grief.

Although the literature is relatively sparse, reported responses to death in primates follow the same general patterns.¹ Subjects who experience the death of a close conspecific are reported to show an increase in exploratory behavior of the corpse, a short-term failure to reduce behaviors not appropriate for a deceased individual (e.g., mothers carrying their babies' corpses after they have died and are, in some cases, substantially decomposed), and changes in their own behavior patterns (e.g., avoiding the area of the death, restless sleep). The alternative to this response appears to be an absence of change in behavior rather than changes of a different sort. Unfortunately, there is no research that we know of on hormonal or neural changes, which would be useful for cross-species comparisons and would provide an additional measure for documenting changes. Nonetheless, the current literature does indicate some patterns that are worth exploring in more detail.

One of the challenges of studying primate responses to death is that there are not many carefully documented examples. Part of this may be due to the fact that, until recently, reactions to conspecifics' deaths were not reported, so it is difficult to determine the extent to which the absence of these reports is due to the lack of behavioral changes versus a lack of experimental effort. Moreover, the opportunity to study reactions to death is a rare occurrence in the course of most studies. Primates, depending on the species, may live as long as five or six decades, and even the longest running field sites are less than four decades old (and many are just a few years old). Moreover, when primates do die, there is no guarantee that the death will be in the presence of either conspecifics or experimenters who can record others' reactions. In captivity, where it is easier to observe subjects' reactions, individuals may be removed at the time of, or very soon after, death. In the wild, subjects may be absent from the group when they die or experimenters may not be present.

There are additional challenges relating to captivity. There may be fewer reports from captivity, because most captive facilities, including zoos and sanctuaries, are often reluctant to discuss primates' deaths, even in cases of natural deaths. Even

¹Whether this is because they are consistent with one another or because they are consistent with what we know as humans, and therefore project on to what we see in other species, is a different question that we will ignore in this chapter.

when we do have data, there is substantial human involvement in captive settings due to regulations associated with health and well-being. In captive groups, subjects may not have been with the same conspecifics long enough to form close relationships; even in zoos, they can be moved relatively frequently for reasons that are related to the species' well-being (e.g., the Species Survival Plan), and transportation to other facilities, such as sanctuaries, may separate individuals from long-term companions, breaking these close relationships. In addition, veterinary regulations may make it impossible to leave a corpse with the group for them to explore it. Finally, if an animal dies of a long-term illness, at the end they may be separated from their group.

In addition, it is not clear what we should be measuring, so most studies are either descriptive, summarizing all events surrounding the death, or are based on hypotheses focused on what we have come to expect to occur during and after a typical death. The former is problematic because it can be difficult to unpack what is important from the large amount of data, whereas the latter is insidiously dangerous, as it risks missing key elements surrounding the event, and our hypotheses are often biased by what we expect from our experience as humans. Nonetheless, despite these challenges, this is an important area of work to explore further. Below, we synthesize what is known about primate responses to death and what these results tell us about the underlying theory.

Infant Death

The most widely reported phenomenon is how adults, typically mothers, respond to the death of their infants. It is notable, therefore, that there is no published evidence of maternal nurturing of dead infants in prosimians (Santini, 2011; there is also not much evidence of any sort of postmortem behavior in prosimians). However, this oddity may hide a deeper point: postmortem attention is not always possible and, in lemurs, basic anatomy means that mothers cannot carry dead offspring (Nakamichi, Koyama, & Jolly, 1996; Rosenson, 1977). Thus, their lack of postmortem maternal care cannot be described as indicative of lack of attachment without evidence that it is not due to their inability to carry the corpse (Nakamichi et al., 1996; Santini, 2011). Indeed, supporting this hypothesis, Santini (2011) reports a case in which a baby fell off its mother's back and she attempted to stay with it for several hours, but when the group moved on she had to choose whether to stay with the baby or follow the group (and she chose to follow the group). This situation highlights one of the challenges of studying behavioral responses to death (or any behavior): individuals have conflicting needs and the absence of an apparent behavioral response could be due to greater pressure from another need rather than an absence of a response to a conspecific's death.

Unfortunately, there is not much evidence from New World monkeys, making broader generalizations about the primate order premature. In the only formal report we could find that, in an experimental setting, squirrel monkey mothers did carry

corpses of infants, but this depended on context (Kaplan, 1974). Females whose infants were stillborn or died within a day of birth showed maternal responses to all infant bodies they were presented with, whereas mothers whose infants survived longer than 2 weeks were more likely to respond to their own infant's body than those of others. However, this was a somewhat unnatural study, making it difficult to extrapolate, especially in the absence of more data about New World monkeys.

The only report from the wild that we found regards an 8-month-old capuchin (*Cebus capucinus*) male who was orphaned when his mother was killed by a poacher at the long-term study site of Lomas Barbudal in Costa Rica. Perry and Manson (2008) report that he spent the entire day “near her body, cooing and trilling piteously, and nursing futilely from her dead body” (p. 236). What may be more intriguing is his behavior after her death. Despite both being separated from his group that day and being young enough that he should nurse as often as once an hour, he was allo-mothered by the adult females in the group and survived. His behavior changed, however, in ways atypical for his developmental stage; he more than quadrupled the percentage of time he spent alone, dropped to 2% of his former rate of play, and, out of necessity, learned to forage. However, despite being more effective at foraging than other yearlings, he spent twice as much time foraging as he had prior to his mother's death, which concomitantly reduced his social time. Although many of these changes can be explained by necessity, his life was deeply impacted by the death of his mother. Similar effects have also been reported for orphaned chimpanzees (Botero, MacDonald, & Miller, 2012), with two orphaned juvenile chimpanzees spending less time in play and more time exhibiting anxious behaviors compared to four peers that still had their mothers. Whereas the lack of information on New World monkeys is largely due to the relatively lesser experimental effort as compared to Old World monkeys and apes, this example indicates that more information is needed to determine the degree to which patterns seen in apes and Old World monkeys extend across all primates.

Even in Old World monkeys and great apes, the record is spotty and often based on very small sample sizes. The most comprehensive primate study we could find is an analysis of 157 cases of deceased infants being carried by their mothers among a group of Japanese macaques over the first 24 years of study at the Takasakiyama research site in Japan (Sugiyama, Kurita, Matsui, Kimoto, & Shimomura, 2009). Their survey results present a compelling case that bonding is critical in generating post-death carrying behavior, but that there is a trade-off with the infant's age at death. Seventy-four percent of carried infants were live born. Considered from another angle, of the infants carried, only 23% of those that were stillborn were carried, whereas nearly 90% of those that lived only 1 day were carried, so there is a striking increase in carrying behavior based on a fairly short amount of potential bonding time. The greatest likelihood of carrying was for infants that died between 1 and 30 days after birth: about 50% of corpses of babies who died within the first 10 days were carried, and fewer than 5% of corpses of babies who died after 30 days were carried. Deceased babies were carried on average 3.3 days, with a range of 1–17 days. About a third were carried only a single day, and about 80% were carried for no more than 5 days. Together, these data indicate that some bonding with a

living infant is important for postmortem carrying, but also that older infants are rarely carried, despite presumably greater bonding.

Indeed, most studies of responses to death focus on the importance of the relationship between the mother and baby. A report of Yunnan snub-nosed monkeys in China discussed three cases of infant death, one born live and two stillborn (one at term, one preterm). The mother whose baby was born live carried it for 4 days following the death, whereas the mother of the term stillborn carried it for only a day and the mother of the preterm stillborn did not carry it. The authors suggest that duration of relationship strongly impacts infant-carrying behavior (Li, Ren, Li, Zhang, & Li, 2012). However, a long-term relationship is clearly not essential, as mothers will carry stillborn infants, and even try to retrieve the body if others claim it (chimpanzees: Kooriyama, 2009).

Moreover, not only mothers carry infants. In the above examples, non-mothers sometimes interacted with the corpses, and Warren and Williamson (2004) report prolonged carrying of two infant mountain gorilla corpses by both mothers and other females. They propose that the non-mothers gain parenting practice from interacting with the corpses. Indeed, this may not be surprising; in many contexts, females, especially young ones, try to get access to infants, for reasons that are not entirely clear (Small, 1993). We wonder if one reason why non-mothers are so interested in these corpses is that it is easier to get access to deceased infants than live infants. If this is the case, it might suggest that, despite mothers' efforts to retrieve stolen corpses of their infants, they are not as protective of them as they are of their live infants. Trying to quantify the frequency of theft of corpses versus live infants might provide more insight into the mothers' attachment to the corpse relative to the live infant and, in particular, whether her attachment decreases as time passes.

If mothers start carrying a corpse, what factors affect when they stop? One possibility is that mothers (and other group members) are simply confused, and initially do not understand that the corpse is lifeless. After all, initially it *looks* like the baby, even though it does not move or vocalize. If primates do not understand the concept of death, the combination of familiar olfactory and visual cues, even in the absence of familiar behavioral and vocal cues, may lead the mother to treat the corpse as her infant until further information can be gathered (Hrdy, 1999; Santini, 2011). The slow decomposition in extreme environments (i.e., very cold, very dry) may elongate this process in some species. Chimpanzees in Bossou, New Guinea, regularly carry and groom their infants for extended periods (19–68 days), which may be facilitated by the fact that the babies' corpses appear to mummify (Matsuzawa, 1997; despite the smell of decay; Biro et al., 2010). Fashing et al. (2011) report a high rate of carrying in gelada over extended periods, and suggest that this is due to an extreme environment that promotes mummification of the babies. Finally, the attachment bond between mothers and infants may be difficult to break (Li et al., 2012), potentially due to a combination of emotional attachment and an endocrine system that takes time to catch up with the mother's new reality (Biro et al., 2010; Kaplan, 1974).

One possibility that we have not seen reference to in the literature is that females may be loath to give up the baby if they are getting extra attention because of its presence. Babies are widely sought after in primate societies, and low-ranking females may in particular benefit by the extra attention they receive for having an offspring (this is primarily a benefit, but can be a problem when it results in kidnapping of low-ranking mothers' babies; reviewed in Small, 1993). It may be that these mothers are particularly likely to continue to carry the corpse because the benefits remain even after the baby has died. If this is the case, we predict that individuals who get more benefits from having babies will be more likely to carry the corpses, and for longer. This would include lower ranking individuals, but also individuals who receive a higher-than-average amount of grooming or other social support from females who wish to access their infant.

Care of Dying and Dead Adults

There is less evidence of subjects' responses to dead and dying adults than to infants. In this case, some of the best evidence comes from captivity. One of the best documented examples is from a small zoo group at Blair Drummond Safari Park in England (Anderson, Gillies, & Lock, 2010). The alpha female of a group of four adult chimpanzees, Pansy, died after an illness, and the caregivers documented how the others' behavior changed in the time surrounding her death. Conveniently for the report, the authors had been performing a nighttime sleep study prior to her death and therefore had good before-death and after-death data on subjects' baseline behavior. They note that Pansy's adult daughter slept with her the night she died despite having never been seen sleeping in that particular location on the sleeping platform in the 29 previous nights of the study, and the daughter went to sleep more than 90 min later than any of her previously recorded times. In addition, the three surviving adults' postural changes during the night rose from a range of 0–14 over the 29 nights of the study to 11, 15, and 42 times the night of Pansy's death. Curiously, none of the other adults groomed Pansy after death, which is in contrast to most of the reported literature on infant deaths. However, the other female groomed the male far more than was typical in any previous night, and the male, who had displayed only three times on all previous evenings combined, displayed three times that night, each time ending by attacking Pansy's corpse. The authors report that the surviving chimpanzees were "profoundly subdued" (p. R350) for the subsequent 2 days. Once the night area was opened up, the male refused to enter it, the chimpanzees slept in their day area the first night, and for five nights subsequent to the death, no chimpanzee nested on the platform on which the female had died, despite someone nesting there each of the previous 29 nights of the study. Pansy's daughter was the first to resume sleeping there. Although only anecdotal due to the small sample, the fact that there is quantitative before and after data demonstrates that the surviving chimpanzees changed their behavior both the night of the death and for at least several days subsequent to it.

Other reports also indicate a high degree of curiosity or agitation following the death of a non-infant. A study of the death of a 9-year-old male in a sanctuary group showed that, subsequent to his death, others were extremely interested in the corpse, gathering around and grooming, with some display behavior (van Leeuwen, Mulenga, Bodamer, & Cronin, 2016). Similar to the case with infants, the authors suggest that the degree of social bonding influenced responses, as the most attention was given by a male with whom the deceased male had formed a close bond after his mother's death. This is supported by evidence from Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), who form one-male units. Yang, Anderson, and Li (2016) report on the death of an older female in which the members of the one-male unit and, in particular, the male, paid close attention to the female in the last hours of her life, including grooming her and keeping others away. The male stayed with her briefly after she died, and appeared to hesitate in following the rest of his unit away from her corpse. They report far more interest from the members of the unit than from other units, which they interpret as a result of their closer social bond.

Indeed, if the social bonding hypothesis is true, one would expect that offspring would be particularly affected by the death of a parent, which appears to be the case. Goodall (1990) reports an instance in which a fully weaned chimpanzee offspring, Flint, quit eating and died subsequent to his mother's (Flo's) death. There also appears to be recognition that individuals who lose a mother may require extra care and assistance. There are several documented cases of adults, usually siblings, assuming additional care of a younger—but weaned—chimpanzee orphan, allowing it to share a night nest, sharing food, and otherwise providing additional grooming and support (Hobaiter, Schel, Langergraber, & Zuberbühler, 2014; Thierry & Anderson, 1986). Reports of adoption appear in monkeys as well as apes (e.g., rhesus monkey; Berman, 1982; chacma baboons, Hamilton, Busse, & Smith, 1982).

Whereas most reports of infants' response to the death of their mothers come from the wild, Whilde and Marples (2011) report on the case of a captive 3-year-old female orangutan that lost her mother. In this case as well, the orangutan appeared to be adopted by another adult female, without human intervention. Fortuitously, these authors also had observed the infant's behavior before and after her mother's death. Consistent with other reports, the infant decreased time spent resting and increased time spent in other activities like climbing and object manipulation. These authors point to a literature involving the behavior of infants that are separated from their mothers, which would make an interesting comparison if enough data could be amassed. Another captive report documents a 3-year-old orphaned bonobo that apparently survived in the absence of an adoption bond (de de Lathouwers & van Elsacker, 2007). She showed an increase in initiating grooming toward other group members following her mother's death, but also received more aggression from the group. The authors acknowledge the obvious developmental confound in comparing pre- and post-observations, but document that these behaviors differed from those of typical bonobos of the same age. With further examples, it might be possible to determine which behavioral changes are a direct response to the death of a mother, rather than other factors.

In what appear to be even more atypical cases, care will be provided even in the absence of the mother's death. In one case, unrelated females provided care to a young male separated from his mother for 6 days until they were reunited (Uehara & Nyundo, 1983), and in another a grandmother adopted an infant for unknown reasons (Wroblewski, 2008). These are important observations as they suggest that postmortem care is a continuation of behavior that exists even in the absence of a death.

Killing in Primates

One area that is typically neglected in discussions of animals' responses to death, which focus on natural deaths, is that individuals do sometimes kill conspecifics. A fuller representation of primates' concept of death requires understanding both why individuals sometimes kill conspecifics and whether responses to a violent death differ from those to a natural death. For instance, in infanticide, a non-maternal adult kills a newborn infant. This is widespread across the animal kingdom (Hiraiwa-Hasegawa, 1988; Janson & van Schaik, 2000). The predominant situation involves a newly high-ranking or immigrant adult male killing a newborn (e.g., Teichroeb, Wikberg, Bădescu, Macdonald, & Sicotte, 2012). Because the mother will come back into estrous sooner without a baby nursing, the hypothesized function of this is to promote the male's reproductive output by giving him additional opportunities to mate before he, too, is overthrown (e.g., Beehner & Bergman, 2008; Yao et al., 2016; although see Alvarez et al., 2015; Bartlett, Sussman, & Cheverud, 1993). Much research focuses on the mothers' reactions, which are to try to avoid the event. For example, across animal species, females have evolved several strategies (e.g., pseudoestrus, early weaning; Beehner & Bergman, 2008) to protect either very early pregnancies or babies that are nearly old enough to survive on their own, and may also spontaneously abort if the pregnancy is further along, as well as strategies such as promiscuous mating to avoid infanticidal males and copulation calls to solicit male mate guarding (Pradhan, Engelhardt, van Schaik, & Maestripieri, 2006). At least one study has shown that cooperation between putative fathers and mothers might reduce the threat of infanticide in sooty mangabeys (Fruteau, Range, & Noë, 2010). Although they behaviorally attempt to avoid infanticide, females typically will not invest too much, presumably due to the high cost of an altercation with a potentially much larger male and the fact that they can try again with another offspring soon. Do females tend to carry these infants? If not, why not? Is it that they fail to bond to an infant that they anticipated would be attacked, or that carrying the baby would exacerbate the male's aggression? In some cases following infanticide, infants are cannibalized (e.g., Culot et al., 2011), so does this account for any reduced carrying? Understanding maternal responses to infanticide will be useful in providing data on an alternative to natural death, which will be informative in determining the degree to which maternal responses generalize across contexts.

Adults will also kill other adults. One of the best documented examples of within-group adult lethal aggression is a long-running power struggle among three

dominant males in the group at the Arnhem Zoo, the Netherlands, documented in the book *Chimpanzee Politics* (de Waal, 1982). Jeroen, the long-time alpha male, was eventually superseded by two younger males, Luit and Nikki. Individually, Nikki was the strongest of the three, but Luit and Jeroen formed an alliance, lasting years, that allowed Luit to be the alpha and Jeroen to be the “power behind the throne,” who was allowed to mate and maintain substantial power in return for supporting Luit as the alpha. Eventually, the alliance crumbled and Nikki became alpha almost instantly. One night, while no humans were there to observe, the males got in a fight that killed Nikki. The keepers found the males in the morning together, with the other two males tending to a dying Nikki. De Waal notes that, despite the antagonistic relationship, and the fact that these males had just dealt a mortal wound to Nikki, the males’ actions in tending him appeared to indicate that they cared for him. Although this anecdote does not tell us anything about their understanding of death (e.g., Did they realize that he was going to die? Was that their intention?), it does indicate the strength of even adult male chimpanzees’ bonds with one another, and suggests a complexity to their relationships.

Finally, males also engage in aggressive, sometimes lethal, interactions between groups. This is typically in the context of territorial defense, although females separated from their group may also fall victim to lethal attack, sufficiently often that females prefer to remain in the center of their territories and avoid areas with frequent intergroup encounters. In the last few decades, it has also become clear that chimpanzees will systematically annihilate the members of other groups in order to take over their territory and females. The first documentation of this occurred at Gombe following a split of the Kasakela group into two separate groups. Several years later, the Kasakela group began to systematically kill males in the new Kahama group, despite the fact that they were mostly known individuals, including close kin. Within another few years, the Kasakela group had annihilated the Kahama group, and there was once more a single group (Goodall, 1986). In this case, we know of no evidence that the males in the Kasakela group experienced anything like remorse over the deaths of their former group mates and kin, but this and subsequent reports from other field sites reveal the frequency of lethal aggression in these apes (Mitani, Watts, & Amsler, 2006; Nishida, Haraiwa-Hasegawa, & Takahata, 1985; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006; Wilson et al., 2014). Any understanding of primates’ responses to death will be incomplete without understanding not just their responses to individuals that die of natural causes, but also death in the context of individual or group conflicts.

How Do We Think Primates Respond to Death?

The above results focus on what we see from observing primates, but there are two issues. First, for various reasons (e.g., poor observation conditions, lack of controlled observation protocol), in most situations in which primates die, the reactions of their group mates are not recorded. Second, as we have mentioned, much of what we have access to is implicitly biased by what we expect, and in most cases what we

expect is a sadness that mirrors our own. In the case of long-lived, intelligent animals, including primates, researchers form a bond with the animals, whether they are observing them in the field or working with them daily in a captive setting. As a result, the *researchers* mourn when individuals die, and it is frankly hard to separate our feelings from those of the animals we are assessing.² As a result of these two issues, we thought it would be informative to present an informal summary of how those people who work with nonhuman primates think primates are reacting as an initial attempt to gather more information for hypothesis testing.

To do this, in the fall of 2018 we contacted colleagues who work with nonhuman primates to ask for their recollections of primates reacting to the death of conspecifics. We asked a series of questions that respondents could answer anonymously via the Internet.³ We asked about their history working with primates and for descriptions regarding any death event they had experienced. We asked whether the animals in question were housed socially and whether the group showed any changes from typical behavior in the period immediately preceding and following the individual's death. We asked whether the group members had access to the body of the individual after death. We avoided asking leading questions such as whether the respondents would describe the primates as exhibiting grief; rather, we asked whether respondents noticed any effects of the death on other members of the group, and how they responded to the body (if applicable). Note that this is an informal query of our colleagues, without random sampling methods. The purpose is simply to provide some insight into primatologists' experiences.

Thirty-eight of our colleagues replied. Of these, 47% currently work with primates. The most highly represented context was the zoological setting (82%), whereas 40% of the sample had worked with primates in a laboratory setting and 37% had worked with primates in a sanctuary (as is evident, many worked in more than one context). Most of our respondents worked as primary caretakers for the primates (82%), but 50% had worked as researchers as well. All respondents had worked with primates for at least 1 year, with 53% having worked with primates for over a decade. The majority of the sample (84%) had experienced at least one death of a primate in their care. Our small sample was also biased toward observations of captive primates, especially chimpanzees, and the most detailed description of responses to death came from respondents reporting on chimpanzee behavior.

Nonetheless, some interesting patterns were apparent in the responses. The clearest expressions of grief appeared in cases of strong social bonds, as is present in the literature when females lost offspring or pair-bonded species lost their mates.

²The mourning by researchers is such that many primate centers, including those where we have worked, have traditions that mark the passing of any individual, ranging from making footprints of the deceased individual for each staff member to keep to planting of apple trees or leaving a permanent marker in a memorial area. One of us heard a researcher we work with tell a science writer that losing an ape you had a relationship with was somewhere between losing a beloved family dog and your child.

³We thank all of our colleagues who shared their thoughts with us.

Considering the former, our respondents observed carrying of an infant's corpse in a group of hamadryas baboons, a species for which this has not been reported in the literature. One respondent also indicated that the mother continued to "mope" even after she stopped carrying the corpse. Considering the latter, a male tamarin was described as being distressed and frequently crying in the weeks following the death of his mate, and another was described as experiencing malaise after the death of a sibling. Little is known about lesser apes (i.e., gibbons, siamangs), but as with the callitrichids and owl monkeys they show long-term pair bonding and a monogamous mating structure. One respondent reported that a male gibbon engaged in copious singing, both alarm and mating calls, following the death of his partner, but another reported the case of a murder of a female gibbon by a male partner, reminding us of the variability in primate social behavior. It is of course unclear whether these events really inspired the most intense reactions, or whether respondents projected their own feelings onto situations in which they themselves would experience the greatest degree of loss. However, it is interesting to note that these contexts mirror the literature (although, again, it is not clear whether this is because these are the most common contexts for grief-like behavior, or because these are the contexts in which researchers expect to see grief).

Considering adults, the loss of alpha individuals led to changes in behavior and group structure, which were described more often than expressions of grief. In many cases, there were changes in behavior, but it was not clear that they were due to grief. Changes in dominance hierarchy, appetite, and activity levels were reported in capuchins. In Old World monkeys, such as macaques, responses were described as ranging from indifferent to chaotic. However, respondents also indicated that the loss of a drill, who collapsed while on exhibit in a mixed-species display with another drill and several silverback gorillas, sparked copious vocalizing from the gorillas, which was described as angry and fearful. The caretakers also reported changes in food consumption and greater willingness to shift between habitats following the death. Members of both species appeared agitated for weeks following the death, and the gorillas continued to appear anxious and were less compliant for weeks following the removal of the remaining drill from the zoo (he was sent to live with other drills at another zoo). Thus, the remaining primates may not have known whether the transferred male had been relocated or also had died. Reports of antipathy following the death of a group member were most likely to come from prosimians (lemurs) and macaques. There were very few observations with these species, but given the dearth of reports from lemurs in the wild captive reports may be important for understanding this taxon.

There were also contexts in which behaviors potentially related to grief were reported. Observers noted that a young spider monkey appeared to struggle with understanding that an older monkey was no longer present in an adjacent enclosure where he would travel after meals to socialize. That is, his behavior did not immediately change to reflect the absence of his social partner and may have reflected either an inability to process that the older monkey was gone or the kind of grief-based behavior one sees in humans when they visit places where they spent time with deceased loved ones. In olive baboons, the impressions of the

response to the death of an adult female were mixed; a male was reported to miss the female for a period of about 2 weeks, whereas no changes were observed in a multi-female group.

Finally, we received the most detailed descriptions in the great apes (including orangutan, gorilla, and chimpanzee groups). Respondents reported that orangutans exhibited some distress and grieved for several days following the deaths of group members. Grief was described as lethargy, loss of appetite, and despondence. The deaths of dominant females were also described as leading to increased fighting between the remaining female group members. The only gorilla observation we received is restricted to the mention of “some gorillas seeming upset” after a young female died accidentally. Only with chimpanzees did we receive descriptions of individuals investigating the body after death. Chimpanzees were described as being quite aggressive with bodies—poking them with sticks and, in one case, mutilating the face. Others described chimpanzees as being fearful of bodies—making rapid touches and quickly withdrawing, while also screaming. Chimpanzees were also described as whimpering following the death of infants and close associates. They were also described as undergoing a period of quiet that could last anywhere from days to more than 1 month. A chimpanzee mother that lost an infant carried the dead infant. She exchanged the body for a highly valued reinforcer after a few days. Deaths of alpha males resulted in significant shifts in the social structure of groups, sometimes leading to dissolution of the group. Groups were reported to be “subdued” following the death of a group member and less engaged with typical activities such as feeding and keeper enrichment. Again, it is unclear whether chimpanzees show the most grief-related behavioral changes, or whether humans are more likely to expect them in chimpanzees and so overreport compared to other species.

Challenges in Interpretation

It is hardly surprising that deaths of important group members would result in changes in behavior within social groups or pairings. At a minimum, there is a change in group membership, and it may involve a stressful event (fight, fall) or an atypical stimulus (dead body). What is challenging is whether to attribute changes to emotional responses to the loss or whether these behaviors are normal responses to openings in social hierarchies, opportunities to mate, or just change in normal activity. These changes in behavior may be due to any number of factors that do not require inferences about mental distress and grief. Thus, like much of the cognitive work reviewed above, observing only behavior is informative about what animals do, but can tell researchers relatively little about the mental experiences of the surviving members of a group. Below we outline some of the challenges facing anyone who wishes to undertake systematic study of this topic.

Bias in Reporting

Perhaps the most pervasive problem (with anthropomorphic interpretations, discussed below, as a close second) is the bias in the research effort on this question. In many cases, we simply do not have the data that we need to determine how primates respond to death. We routinely miss the moment of death, because animals die when no researcher is around, including at night, or, in captive settings, because the animal is removed prior to the moment of death. This leads to a very small sample. There is also an existing bias in the distribution of studies overall, with the most research effort invested in apes, followed by Old World monkeys (often limited to just a few species, such as macaques), followed by New World monkeys. Finally, as discussed above, most cases involve individuals in very close relationships, such as mother and offspring or mated partners. Is this a bias because close relationships elicit the strongest responses, or a bias because that is the context in which we tend to look for such responses? We cannot answer this question.

Another bias is that we do not know what to look for, so we end up looking for analogues to human emotion and behavior (e.g., lack of appetite, disturbed sleep, lethargy) and may be missing other expressions of grief in nonhumans. Looking for the sorts of responses we expect in humans is a reasonable place to start, thanks to our close phylogenetic relationships; indeed, most humans can identify an angry chimpanzee, because their responses look like ours, including screaming, running, banging, and throwing things (if you do not have children yourself, then spend a little time on a playground for a great display of this sort of anger response). However, naïve humans are not very good at identifying a happy chimpanzee, because they assume that a smile indicates contentment, whereas in chimpanzees a smile (silent bared teeth display) indicates fear, particularly in a social context (Preuschoft & van Hooff, 1995; indeed, humans are poor at correctly interpreting the cues of animal emotional responses, in general; Maréchal, Levy, Meints, & Majolo, 2017). Whereas this may be the precursor to the human smile, it is a similar expression used in a *very* different context. So the big question with primate responses to death is what are they more like? Chimpanzee anger or chimpanzee “smiles”? If primates’ responses are not similar to ours, we have another problem in that we must determine what we should be looking for.

Lack of Controlled Studies

A second difficulty is that the gold standard of evidence, carefully controlled studies, is all but impossible in this context. Even if it were ethically possible to conduct such studies (which, to be clear, it is not), it would be difficult to mirror a natural context of death in such an unnatural situation. As a result, all of the observations of primate death vary on numerous factors and an enormous sample size will be needed

to reveal consistent reactions and to determine whether and how specific contexts influence primates' reactions.

Related to this, one definite gap in our knowledge is how primates' responses to death vary from their responses to other situations in which individuals are removed from the group. Again, the gold standard to assess whether they perceive these two situations as meaningfully distinct is a careful comparison of reactions in contexts of removal versus death, but this is not ethically possible. As a result, we are left with the few instances in which primates disappear outside of the context of death. It is unlikely that two equivalent cases will occur within the same social group during the same period of time, thus introducing a plethora of confounds into any comparison that one would make. In cases such as infant death, in which there is no natural situation in which disappearance does not also mean death,⁴ we could potentially assess responses in cases of natural death versus infanticide to see if differences occur.

Finally, there may be differences in behavior in captive versus wild settings, but it is not obvious in what direction these differences will go. Would you expect to see more responses in captive settings because, freed from the constraints of finding food and shelter and avoiding predators, the primates have more time and energy available to mourn? How is mourning influenced by the less natural social bonds? Do the smaller groups and reduced social flexibility make the death more stressful, or does it lead to less strong bonds and, therefore, less response to death? In a wild context, are responses to death more or less extreme (when compared to captive settings)? Deaths are likely more frequent (it is a much more challenging environment and there is no access to veterinary care) and it is a more natural context where primates have many other pressing concerns and threats to survival that they do not encounter in captivity, but again it is not clear how that would influence mourning.

Anthropomorphism

Anthropomorphism looms large over the study of primates' emotional responses in any context, and their response to death is particularly salient. When we observe animals behaving as humans do, it is tempting to attribute to them the same inner states, including thoughts, intentions, and feelings. For example, the media and the public were captivated in fall 2018 by the story of an orca, J-35, that carried her dead calf for more than 2 weeks. Her actions were attributed to grief, and even scientists proclaimed the observation to be evidence that mother orcas felt the same kind of emotional bond to their infants that humans experience, despite the fact that there was no clear evidence of this (see above alternate explanations).

This problem is not specific to the study of emotional responses. It is dubbed the "Argument by Analogy" (Povinelli, Bering, & Giambrone, 2000), and is, not

⁴In captivity, infants may be removed to a nursery in contexts in which maternal care or adoption is impossible, but these occur primarily in contexts in which death was likely, making this a poor control condition.

surprisingly, most common in species that are closely related to us, those that occupy an important role in our lives, such as pets, or those that are considered particularly charismatic species, such as cetaceans and elephants. We are less likely to attribute grief to the insect that is observed removing the corpse of a conspecific from the colony. One of the reasons it is so insidious is that it is based on a sound scientific principle; when two closely related species share a trait, a reasonable *starting hypothesis*, in the absence of information to the contrary, is that they do so due to homology, or common descent. The problem is when this is the *only* hypothesis, and/or this hypothesis cannot be properly tested. Indeed, it leads to two (opposing) problems; it can lead to the over-attribution of human characteristics to other species (that is, anthropomorphism) or to our missing something interesting about the other species because we never look for it, assuming that it is impossible that the species in question are capable of something so complex (de Waal, 2016). Indeed, researchers' long-standing focus on primates led us to miss sophisticated abilities in other species (e.g., corvids' impressive abilities at planning, problem-solving, causal reasoning, and relational learning; Emery & Clayton, 2004; but see also Vonk, 2015), and the degree of neglect of less social species, such as felines and ursids, makes it difficult to evaluate the extent to which a homology with humans and a socially complex lifestyle are critical to the emergence of complex behaviors such as abstraction, empathy, and social bonding (Eaton et al., 2018).

A related problem is that we tend to gravitate toward the most sensationalistic accounts, which in this case means the ones that make other species look smartest, or most like us. An example of this is the story noted above, of J-35 carrying her deceased calf for more than 2 weeks. Not only was it at the top of the news cycle for nearly 2 weeks, but it was accompanied by stunning photos and videos of her struggle to keep her calf from sinking (in addition, there was a lead-up of the scientists' desperate struggle to locate and treat the sick calf). If J-35 had been seen swimming away from a newly deceased calf, it would not have made the news. Of course, why J-35 did this is a fascinating and important question, but the humanlike aspect of holding on to one's offspring at all costs kept the dialogue around it anything but objective. Although it may have been a good story to get people interested in orcas and, more broadly, conservation, it was not useful for advancing scientific understanding (Bruck, 2018). One challenge is how to balance these aims, keeping the public interested and engaged without reporting the science in a dry and uninspiring way.

This is also a problem in the scientific literature. There is the so-called file drawer problem in which negative (often boring or commonplace) results languish unpublished, leading to the perception of a greater frequency of "interesting" or "positive" results than is true in reality. For example, J-35 could, like many of the primate studies we have discussed, be written up as a case study and published as a note. It would almost certainly be accepted. But no journal would publish a "case study" of a female walking (swimming) away from her infant when it died. How many times has this occurred without documentation? Conversely, how many times has a researcher witnessed a much less charismatic species interacting with a dead conspecific, without it crossing their mind that this could be an example of grief? This may be particularly true in cases in which we are more familiar with the

mechanisms surrounding how living individuals interact with the dead (e.g., the case of pheromones controlling ants' removal of the bodies of dead colony members; Choe, Millar, & Rust, 2009; Howard & Tschinkel, 1976). We have no way of knowing the answers to these questions, so we do not even know the size of the bias problem in the literature.

Conclusions and Future Directions

The recent surge of interest in how nonhuman primates respond to death has begun to yield intriguing results. Early evidence indicates that primates do change their behavior surrounding the death event, and that responses are stronger in the case of a mother losing an infant or any individual losing a conspecific with whom they have a close bond (e.g., mated pairs, members of a one-male unit, presumably friends). There are numerous emerging theories on why these individuals show these responses, ranging from hypotheses about the underlying emotion (e.g., grief, empathy) to the physiological mechanisms that may underpin them (e.g., hormonal changes; note that these explanations are often not mutually incompatible, but address different levels of explanation). There are many unanswered questions, however, with the largest being what exactly it is to which these primates are reacting. Is it the loss? Is it the changes inherent in a group when one member dies? Is it the oddity of an inanimate being? Or the sudden absence of a key individual? Without knowing this, it is difficult to speculate on what these reactions tell us about primates' conceptions of death.

In this chapter, we have attempted to outline some important open questions related to this issue. We have focused on whether nonhuman primates have some of the cognitive abilities related to grief. Indeed, not only does this help us better understand primates' responses to death, but also better understanding primates' responses to death will conversely shed light on the degree to which primates exhibit some of these cognitive mechanisms. Although we highlight numerous areas in which biases in the literature and our own perception may be hindering our ability to address this question, we found this search through the literature both informative and interesting, and see great potential for the field.

We close with a few recommendations for next directions. First, whereas the case studies are important for helping us better understand the behaviors surrounding a death, we suspect that they are biased in the direction of situations in which something interesting (from a human perspective) happened. We encourage researchers to keep records of *any* death, no matter what occurs afterwards, and either publish summaries or make the results available in a database accessible by researchers interested in the question. It will be hard to advance the field until we know whether these spectacular examples are commonplace or represent a divergence from the normal response.

Specifically, we think that this is an excellent candidate topic for a broad-scale collaborative effort. Deaths are relatively rare, especially those for which experimenters are able to record data. Moreover, it will be important to understand

this across species to understand both the distribution of any responses and how ecology and context influence responses. Finally, experimental manipulations are essentially impossible, meaning that opportunistically gathered data will need to suffice. Ideally, there will be a central repository where researchers, caregivers, and veterinarians can record observations of other individuals' reactions to a primate's death. In this way, we can gain a broad perspective on primates' reactions to death with, hopefully, less uncertainty than is present in the current literature.

We also encourage researchers to more explicitly consider how responses to death differ—or not—from other situations. For example, do responses in the first 24–48 h after a death look similar to or different from responses after an individual disappears for other reasons (i.e., emigrates)? Although it is difficult to compare a mother's response to her infant dying to her response to a subadult male emigrating, due to the differences in behavior between an infant and subadult and the mother's different relationship with older offspring, if we had a database we would eventually be able to compare the mothers' responses to subadult sons emigrating versus subadult sons being killed. As mentioned earlier, it would also be useful to look at responses to infants who die of natural causes versus infants who are victims of infanticide, to see if reaction differs in different contexts. Finally, how do changes in the social group compare when an alpha male is unexpectedly killed or dies versus when he is deposed? For instance, is there a more rapid ascent from another male in one case as compared to the other?

We hope that it is clear that, despite the numerous difficulties and constraints we have highlighted, there is much potential to investigate this understudied but fascinating topic, and we can do so in a manner that parallels our scientific approach to other challenging topics. Decades ago, researchers scoffed at the idea of exploring consciousness in nonhumans, and today there is a growing body of work indicating the foundations of metacognition and self-awareness in other species. A systematic undertaking will entail a large-scale collaborative effort among field and lab researchers working with a variety of different species and who are willing to document behaviors in an inclusive fashion without becoming beholden to anthropomorphic expectations. What sparse data do exist provide promise that there is enough continuity in behavior and emotional response to eventually tease apart important differences in how various primates conceptualize death (through exploring contexts and relationships) and use this information to better understand both primates' responses to death and what this tells us about their underlying cognitive ability.

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