



## Review

## Behavior toward the dying, diseased, or disabled among animals and its relevance to paleopathology

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## ABSTRACT

Compassionate behavior towards dying, diseased, or disabled individuals is often regarded as a uniquely human trait, though recent reports of reactions to death and dying in nonhuman animals highlight the value of adopting a comparative evolutionary approach toward these behaviors. Here, we review recent studies of animal behavior toward the dying, diseased, or disabled which may be of interest to paleopathologists and bioarchaeologists studying compassionate behavior in humans and their extinct ancestors. 'Compassionate' behavior toward the enfeebled and dying has now been reported in several non-primate mammals (e.g., wild African elephants and river otters) and nonhuman primates (primarily captive chimpanzees). In addition, a number of recent reports have documented wide variation in non-human primates' reactions to recently deceased group mates (or offspring) both across species, as well as across individuals belonging to the same social group. We suggest there is considerable potential for collaboration among paleopathologists and primatologists in examining the causes of illness and disability in animals and its impact on their lives.

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'Compassion' toward dying, diseased, or disabled individuals is regarded as being among the 'socio-moral' behaviors that make us human (Counts and Counts, 1991; Keltner et al., 2010). Understanding the origins of compassionate behavior is a growing area of interest in several subfields of evolutionary anthropology, including bioarchaeology and paleopathology (e.g., Hawkey, 1998; Tilley and Oxenham, 2011). Although controversial, the earliest evidence from the fossil record of compassion toward the dying, diseased, or disabled appears 1.8 million years ago (Hublin, 2009; Lordkipanidze et al., 2005). While studying the fossil record is a key avenue for evaluating the evolution and relative uniqueness of human compassion, another promising route is to examine the behavior of nonhuman primates and other animals for evidence of compassionate behavior toward enfeebled family members or group mates. By adopting a comparative evolutionary approach toward compassionate behavior among animals, the timing of the evolution of various behaviors, and the number of times they evolved independently, can be estimated. Although long confined primarily to rare, isolated accounts (e.g., Cowgill, 1972; Nakamichi et al., 1996), the literature on animal behavior toward infirm group mates has expanded rapidly, especially among our closest relatives, chimpanzees, over the past several years. Here, we briefly review the findings from several journals which have recently featured

articles focusing on animal behavior toward the dying, diseased, or disabled which may be of interest to paleopathologists studying compassionate behavior in humans and their ancestors.

Several of the most striking recent examples of compassionate behavior toward the enfeebled and dying come from non-primate mammals, emphasizing the importance of caution in making claims about human or primate exceptionalism. In *Applied Animal Behaviour Science*, Douglas-Hamilton et al. (2006) recently provided a detailed account of the last days of a dying African elephant (*Loxodonta africana*) matriarch at Samburu, Kenya. Struggling to stand upright and left behind by her own fellow group members, the dying female was approached by the matriarch of another group who repeatedly attempted to bring her to her feet using her tusks. Perplexingly, while the 'compassionate' matriarch was clearly stressed, other members of the 'compassionate' matriarch's group exhibited no interest in the dying female. Douglas-Hamilton et al.'s (2006) observations suggest that individual African elephants vary in the extent to which they exhibit compassion toward enfeebled individuals, a pattern also characteristic of humans (Keltner et al., 2010). Another intriguing recent study in *PLoS One* (Davenport, 2010) reported how an elderly river otter (*Pteronura brasiliensis*) matriarch with failing vision and poor mobility was kept alive in a Peruvian oxbow lake for many months through provisioning with pieces of large fish caught by other members of her group. This study represents one of the only documented examples among nonhuman animals of younger individuals transferring food to elderly group members.

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Recent video footage and an accompanying paper in *Current Biology* by Anderson et al. (2010) focusing on observations of captive chimpanzees (*Pan troglodytes*) created a flurry of interest in behavior toward dying individuals in nonhuman primates. In this paper, Anderson et al. (2010) describe the remarkably compassionate care directed toward a dying older female chimpanzee by her group mates, who groomed and caressed her for hours as she lay dying in an indoor enclosure at Blair Drummond Safari Park in Scotland.

Inspired by Anderson et al.'s (2010) paper, a comparative evolutionary discussion of dying and death among primates has since continued in the *American Journal of Primatology* which is fast becoming the journal of choice for publications describing advances in 'primate thanatology'. For example, Fashing et al. (2011) described how, unlike Anderson et al.'s (2010) chimpanzees, members of a wild gelada (*Theropithecus gelada*) group, and the herd in which it was traveling, abandoned two group mates, a sick and dying adult female and her seven-month old dependent infant, when they fell behind. Over the next two days, the female and subsequently her infant both died, without any members of their herd returning to search for them. Similarly, Stewart et al. (2012) reported that among wild chimpanzees at Gombe, Tanzania, a dying female spent her last several days in a mostly solitary state, the authors making no mention of compassionate behaviors having been directed toward the female by others during this period. These field studies raise the possibility that wild primates, including chimpanzees, do not exhibit the same levels of compassion as captive chimpanzees or even, more perplexingly, as wild giant otters and African elephants, animals far less closely related to humans.

Although perhaps less directly related to paleopathology, many of these same journals have also recently featured articles of potential interest to funerary archaeologists and taphonomists focusing on the extremely variable responses of nonhuman primates to the bodies of recently deceased individuals. Reactions by conspecifics to recently dead group mates (or offspring) appear to vary widely across primate species, as well as across individuals belonging to the same social group. Interested readers are encouraged to consult articles in *Current Biology* by Biro et al. (2010), *American Journal of Primatology* by Cronin et al. (2011), and *Anthropological Science* by Sugiyama et al. (2009), the latter representing an excellent example of a long-term study quantifying the rate and length of carrying of infants after death by their mothers. Of course, it is important to note that primates are not alone in their interest in investigating the bodies and even the bones of the dead, as recent papers about African elephants in *Biology Letters* (McComb et al., 2006) and *Neuroscience and Biobehavioral Reviews* (Hart et al., 2008) remind us. Anderson (2011) also published a useful commentary in the *American Journal of Primatology* offering a 'primatological perspective on death' emphasizing unanswered questions relating to awareness of death among primates. Here, we also wish to emphasize the importance of obtaining a comparative evolutionary perspective on primate compassion toward dying, diseased, or disabled individuals focusing on as diverse an array of species and populations as possible. Indeed, recent evidence from paleoanthropology indicates that inferences into the evolution of human behavior based solely on a chimpanzee model are less informative than previously believed (Lovejoy, 2009), suggesting that by adopting a broader, more comparative view of primate adaptations, we may gain greater insights into the evolutionary roots of human behavior.

The recovery of the remains of individuals after death enables identification of any diseases or disabilities afflicting these individuals and which may have contributed to their deaths. Such remains are especially useful when they come from individuals with known life histories from intensive behavioral study (e.g.,

McFarlin et al., 2009, 2011). Several long-term behavioral field studies of primates have begun to more carefully collect and curate dead individuals, entering into collaborations with museums and their scientific personnel in habitat countries. Of course, to avoid disrupting the natural behavior of the study animals, fieldworkers must take care not to recover individuals until they have been abandoned completely, an event which may not take place for several weeks after death among individuals of some species (e.g., Biro et al., 2010; Fashing et al., 2011). Clearly, there is considerable potential for collaboration among paleopathologists and primatologists in examining the causes of illness and disability in study animals and its impact on their lives.

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