



# Responses to a dead companion in a captive group of tufted capuchins (*Sapajus apella*)

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## Abstract

The observation of specific reactions by animals to dead conspecifics raises questions about their capacity to understand death. We describe the behavior of a captive group of tufted capuchins in the hours following the death of an adult female. The behavior of 12 subjects was recorded over a 5-h period. Most group members displayed exploratory behaviors toward the corpse, peering at it, smelling, touching, lifting or pulling it at least once. Interactions with the corpse were particularly frequent in the first hour, then decreased in the following hours. The relatives of the deceased female were the most involved individuals, and her daughter spent more time near her body than the other members of the group. Rates of interaction with the body were especially high in subadult individuals. Most of the behaviors directed to the body of the deceased individual appeared to be investigative.

**Keywords** Exploration · Social relationship · Thanatology · Epimeletic behavior

## Introduction

The observation of specific reactions to dying or dead conspecifics raises questions about the capacity of non-human primates to understand death (Gonçalves and Carvalho 2019). For example, in wild female baboons (*Papio ursinus*), the loss of a close relative induced a stress-related increase in glucocorticoid levels in the 4 weeks following the death (Engh et al. 2006). In a report describing the events surrounding the natural death of an old female in a captive group of chimpanzees (*Pan troglodytes*), the responses of

group members toward the dying female were in some ways reminiscent of human responses in terms of care, respect, denial, and consolation, leading the authors to ask whether the awareness of mortality is exclusively human (Anderson et al. 2010). By showing interest in the corpse and exploring it, other group members should learn something about its state. The study of these responses can shed light on the motivations of surviving individuals and the extent to which they might experience distress; it may be also possible to consider their awareness regarding the irreversibility, universality, and non-functionality associated with the cessation of life (Speece and Brent 1984; Anderson 2018).

Despite a recent increase in the number of reports describing the behaviors of monkeys and apes towards dead conspecifics, the literature remains quite skewed towards the responses of mothers to their dead babies. This is by far the most frequently documented behavior among non-human primates in both natural and captive settings (Sugiyama et al. 2009; De Marco et al. 2018; Watson and Matsuzawa 2018). The mother–offspring relationship is arguably the closest social bond in primates, and females are commonly observed carrying and grooming their lifeless infant for several days after death. In general, however, other group members display few responses to the corpse partly due to protective

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behavior of the mother, but possibly also because of the absence of a strong relationship with the infant.

The current primate thanatological literature also has a taxonomic bias, being largely dominated by reports in chimpanzees of group members' responses toward dying or dead companions (Anderson 2018). There are fewer descriptions of responses to the death of non-infant individuals in monkeys. It is reported that the corpse of a conspecific can elicit caretaking (*Callithrix jacchus*: Bezzera et al. 2014; *Macaca sylvanus*: Campbell et al. 2016; *Rhinopithecus roxellana*: Yang et al. 2016) or exploratory behaviors (*Macaca mulatta*: Buhl et al. 2012; *Macaca sylvanus*: Campbell et al. 2016), but the limited number of studies available on monkeys precludes informed comparisons between species.

As almost all accounts of responses to death in primates concern unplanned events, a third bias is that descriptions of particularly striking or intriguing events may be more likely to be published than more banal observations. To obtain a representative picture of all reactions to death, we need more records of individuals' behaviors following the death of companions in multiple species. Toward this aim, we collected information on the responses of a group of tufted capuchin monkeys (*Sapajus apella*) in the hours following the death of an adult female. Capuchins are female-bonded New World monkeys which live in multimale, multifemale social groups. In the wild, females form long-term social relationships with stable dominance hierarchies, and most of them remain in their natal groups; males transfer between groups, and correspondingly male–female bonds are generally weaker than female–female bonds (Fragaszy et al. 2004; Perry and Manson 2008). A recent study reported that the death of a group member led to changes in the social network (Engelbert 2018). We observed the interactions of different members of the group with the dead body, and examined the influence of kinship and age-and-sex category on these behaviors.

## Methods

Subjects belonged to a group of 13 tufted capuchins, including Petula, the 17-year-old female who died. They were kept at the Parco Faunistico di Piano dell'Abatino in Rieti, Italy. Adults were at least 8 years old, subadults were 4–7 years old, and juveniles were under 4 years old (Table 1). The group was founded in 2009 with individuals transferred from a group at the Primatology Centre of Strasbourg, France (Dindo et al. 2008). The enclosure at Rieti was approximately 50 m<sup>2</sup> and 4 m high, and was connected to an internal shelter. It was furnished with wooden structures, perches, and ropes. Monkeys were fed with fresh fruit and vegetables every morning, and received a supplement of seeds and commercial monkey pellets in the afternoon.

**Table 1** Sex and age of group members, and maternal relatedness with Petula

Individual	Sex	Age (years)	Relatedness
Rav	Male	16	Non-kin
Pao	Female	17	Non-kin
Ros	Female	16	Sister
Yav	Female	9	Non-kin
Add	Female	7	Non-kin
Cat	Male	6	Nephew
Cid	Female	6	Daughter
Gas	Male	2	Nephew
Gua	Male	2	Non-kin
Gar	Male	2	Son
Han	Male	1	Nephew
Hug	Male	1	Non-kin

Keepers found Petula dead at about 06:30 h on the ground of the outside enclosure. The corpse was immediately removed for inspection. As the body was not yet rigid and the eyes were still shiny, we inferred that Petula's death was recent. She had not shown any signs of illness in the previous days and no physical injuries were noted. We returned the corpse to the outside enclosure at 07:00 h, placing it on the ground. We used a stationary video camera (Sony HD) to record group members' behaviors occurring within the camera's field of view, i.e., within an approximately 1-m radius in all directions around the corpse. Recording was carried out over a 5-h period, after which the corpse was permanently removed from the enclosure.

The video record was used to score the number and duration of behaviors directed toward the corpse. The following brief behaviors were counted as a number of occurrences: peering (closely looking at the face), smelling (smelling at any part of the body), touching (contacting the body with hand), lifting (gripping and moving the head or a limb upwards), pulling (gripping the tail or a limb to drag or try to drag the body), threatening (lunging, staring, or performing an aggressive call or facial display toward the body), and self-smelling (smelling own hand after having touched or groomed the body). Durations of the following behaviors were recorded: proximity (standing within 50 cm of the body), eye grooming (grooming the eye area), body grooming (grooming any part of the body except around the eyes), and fly catching (catching or trying to catch flies on the body).

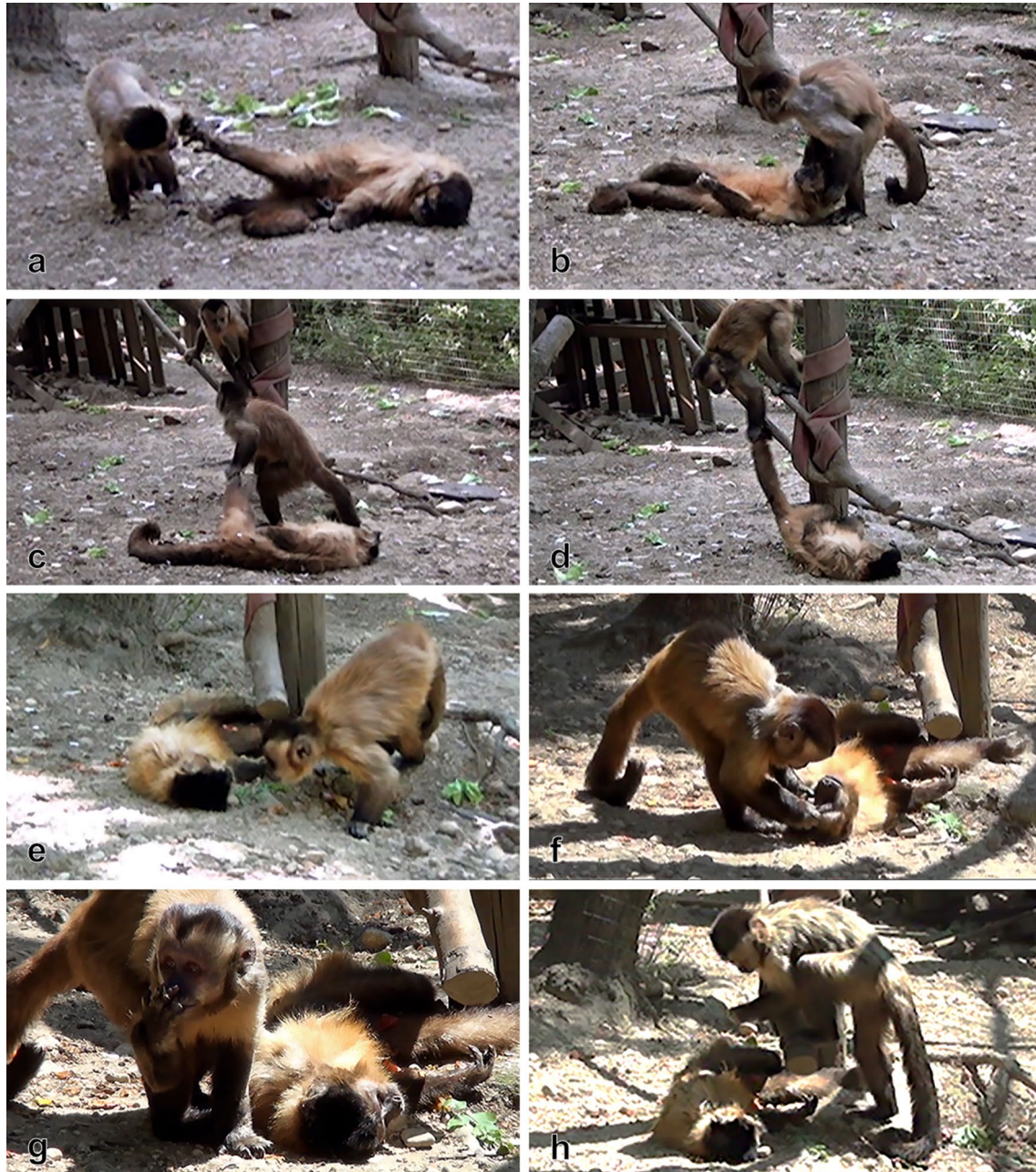
We conducted statistical analyses for two variables: the total number of interactions, and the duration of proximity per subject. We used Wilcoxon matched-pairs tests (exact procedure) to compare behaviors over three time periods (1st hour, 2nd/3rd hours, 4th/5th hours). We used Mann–Whitney tests (exact procedure) to investigate the effects of age,

sex, and kinship on behaviors. Tests were performed with the IBM SPSS Statistics software (version 22). All tests were two-tailed, except for the kinship tests, which were one-tailed. The significance level was set at 0.05.

## Results

### Descriptive data

Most group members approached the corpse, peered at the face and smelled the corpse at least once during the first hour (Supplementary material, Tables S1 and S2). About 1 min after recording started, two subadults, Cat, and Petula's daughter, Cid, lifted one of Petula's legs (Fig. 1a). At nearly



**Fig. 1** a–h Still images from videotape: **a** Cid lifts a limb; **b** Cat lifts the head; **c** Cat pulls limb and drags the corpse; **d** Cat pulls the tail; **e** Add peers at the face; **f** Cat grooms the eye area; **g** Cat smells his hand; **h** Cid catches flies

3 min, Cat lifted Petula's head (Fig. 1b). Thereafter, Cat and Cid occasionally lifted a limb or the head (Table S1). Forty-two minutes after the corpse was reintroduced, Cat dragged it for a few centimeters by pulling on a leg several times (Fig. 1c); he then made two unsuccessful attempts to pull it up by the tail onto a perch (Fig. 1d). After a couple of minutes, a juvenile (Gas) approached Petula's body and stared at it, before lunging at it while emitting brief aggressive calls and facial threats; this entire sequence lasted under 5 s. Grooming bouts were brief and infrequent: only Cat and Cid groomed the corpse, for a few second each time, paying particular attention to the eye area (Table S2). Cid occasionally smelled her hand after having touched or groomed the corpse (Table S1).

Further approaches and peering at the face of the corpse occurred over the next 4 h (Fig. 1e). Petula's daughter (Cid), in particular, spent long periods near the body (Table S2); she and Cat occasionally touched the corpse and lifted the head or a limb (Tables S1 and S2). Grooming bouts remained brief and infrequent (Table S2; Fig. 1f). Some individuals (Add, Cat, Cid) sometimes smelled their hand after touching or grooming the corpse (Table S1; Fig. 1g). The juvenile Gas approached and directed a brief visual threat at the corpse (Table S1). Individuals spent increasing amounts of time catching and eating the growing number of flies on the corpse (Table S2; Fig. 1h).

### Quantitative data

The mean number of interactions with the dead body was significantly higher during the 1st hour compared with the other two time periods; it was also higher in the 2nd/3rd

hours than in the 4th/5th hours (Fig. 2). Comparisons of durations spent in proximity to the body showed no significant difference between periods (Fig. 2).

Petula's relatives spent significantly more time in proximity to her dead body than non-relatives, but no significant difference was found in the number of interactions with it (Fig. 3). There was no significant difference between males and females in either proximity or interactions (Fig. 3). Subadults showed significantly more behaviors toward the body than juveniles; the same comparison with adults did not reach statistical significance (Fig. 3). Although the trends were similar, comparison of time spent in proximity to the body did not yield significant differences between age categories (Fig. 3).

### Discussion

This study reports how captive tufted capuchins reacted to the dead body of an adult female member of their group. Most responses occurred within an hour of the body being returned to the enclosure. Although frequency of interactions with the corpse decreased in the hours that followed, time spent in proximity to the corpse did not. Of course, the limited space within the enclosure may have influenced the surviving monkeys' behavior with regard to the corpse. Further points to note are that we were not present at the moment of death, and that the corpse was temporarily removed from the enclosure. However, it is likely that death occurred at the end of the night, shortly before being noticed by the keepers.

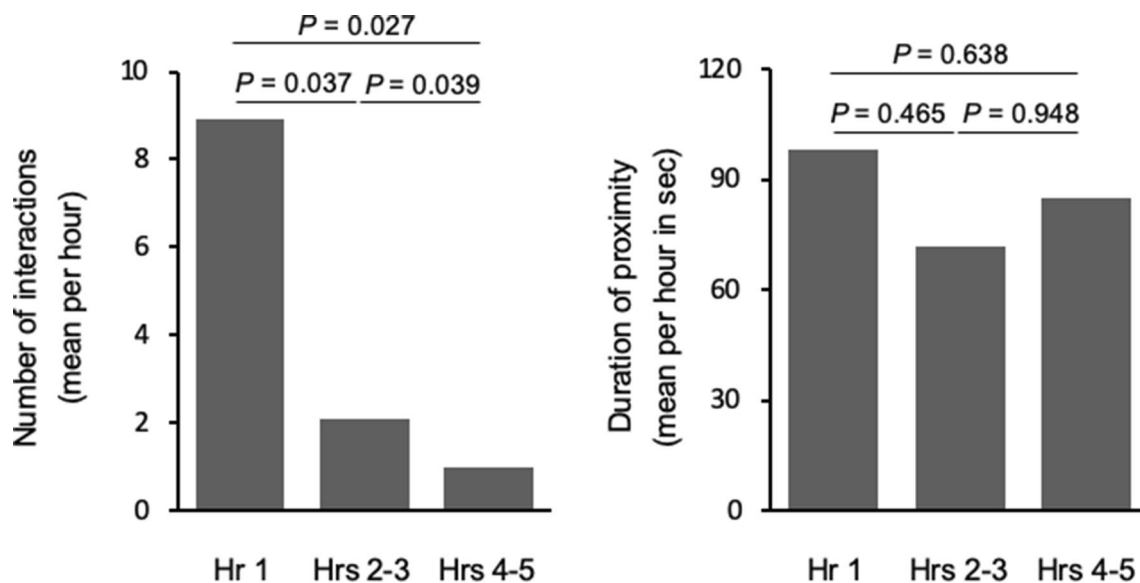
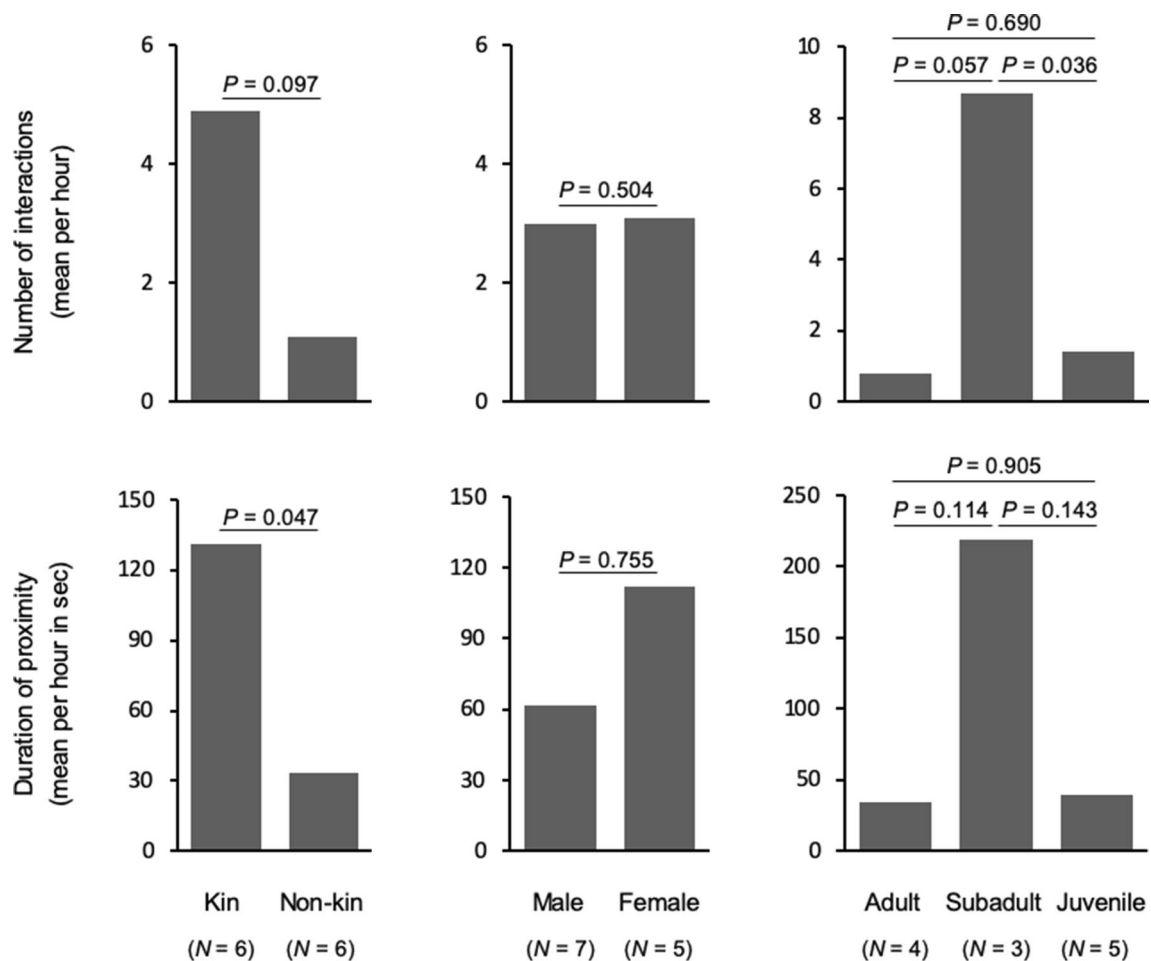


Fig. 2 Change over time in the behaviors of group members and their proximity to the corpse (Wilcoxon tests,  $N = 12$ )



**Fig. 3** Effect of age, sex, and kinship on group members' behaviors and proximity to the corpse (Mann–Whitney tests)

As expected, the social relationship with the deceased influenced individuals' responses toward the corpse. Petula's relatives, especially her subadult daughter, spent more time near her body than did the other group members. This should be viewed in relation to the strong connection linking mother and daughter in female-bonded species. The importance of social bonds and attachment processes in responses to death has been recognized in chimpanzees (Teleki 1973; Stewart et al. 2012; van Leeuwen et al. 2016) and monkeys (Gonçalves and Carvalho 2019). Reports of mothers caring for their dead infants reveal the strength of mother–offspring bonds. Here, the reaction of the daughter to her mother's corpse similarly reveals the strength of the bond between mother and offspring.

Age also affected individual responses. Subadults interacted more with the dead body than juveniles, and they also tended to react more than adults. We know from the study group's history that the juveniles had no prior experience of the death of a conspecific, whereas older individuals had multiple such experiences. Capuchin monkeys are neophobic both in captivity and in the wild (Visalberghi and Fragaszy

1995; Visalberghi et al. 2003), and their neophobic response decreases with repeated exposures to new stimuli (Visalberghi et al. 1998), which could account for the low response levels of juveniles to the corpse. Greater interest in dead companions by subadults has also been reported in chimpanzees (Teleki 1973; Stewart et al. 2012).

Most of the capuchins displayed investigative behaviors: out of 12 individuals, 11 approached Petula's body, and ten inspected it, peering, smelling, touching, lifting or pulling it at least once. Some also smelled their hand after touching the corpse, a relatively rare behavior in usual situations. Peering, smelling, touching, and lifting could all provide information about the current state of Petula. Comparable responses toward dead individuals have been reported in other species (Teleki 1973; Anderson et al. 2010; Li et al. 2012; Stewart et al. 2012; Campbell et al. 2016; van Leeuwen et al. 2016; Yang et al. 2016), and could reflect a “wait and see” strategy that allows individuals to assess the state of a conspecific before leaving it (Campbell et al. 2016).

The most remarkable behavior that we recorded was when a subadult male pulled and dragged the corpse over a short

distance. This male was Petula's nephew, and the son of the highest-ranking female in the group. His social status may help explain his particular interest in the corpse, and his freedom to contact it. Pulling the corpse might be a reaction of anger due to frustration at its lack of responsiveness, or an attempt to test for reactions. Threat responses may be interpreted in the same way, although only two sequences were recorded, the first occurring immediately after the corpse had been dragged a few centimeters. Moreover, these behaviors were intermingled with sequences of non-agonistic behaviors, which lends support to the idea that threats express a feeling of frustration caused by a lack of response. Although admittedly speculative, the same interpretations have been proposed in chimpanzees, where males might drag or hit dead females (Anderson et al. 2010; Stewart et al. 2012). It should also be noted that getting angry at the failure of the conspecific to respond can actually be interpreted as a lack of awareness of death.

We saw few affiliative behaviors directed toward Petula's body, and these were mainly by her relatives. Grooming episodes were brief and infrequent, and were notably directed to the eye area. Several authors have reported special interest in the face and eyes of dead individuals (Boesch and Boesch-Achermann 2000; Fashing et al. 2010; Cronin et al. 2011; Buhl et al. 2012; Yang et al. 2016; Pruett et al. 2017; De Marco et al. 2018; Watson and Matsuzawa 2018). Examining this sensitive area may be especially informative regarding the individual's physical condition (Cronin et al. 2011). Other authors have recorded close affiliative contacts such as embraces with the deceased, or protective behavior (e.g., Bezzera et al. 2014; van Leeuwen et al. 2016; Watson and Matsuzawa 2018; Yang et al. 2016), but no behaviors of this kind were observed in our study. While waving flies away from a corpse is sometimes described as caretaking (Rajpurohit 1997; Boesch and Boesch-Achermann 2000; Biro et al. 2010; Cronin et al. 2011), the capuchin monkeys opportunistically consumed the flies they caught on the corpse.

We did not record any signs of distress in the capuchins: no distress vocalizations occurred, and there was no prolonged contact with the dead body. Instead, the capuchin monkeys' responses to the death of a group member appeared mainly investigative, and they were influenced by social relationships with the deceased individual. Although we have no evidence for death awareness in this species (see Anderson 2018; Gonçalves and Carvalho 2019), this does not mean that they did not know anything about the state of their companion. Future research should continue to investigate whether nonhuman species can distinguish between the living and the dead, and what cues they might use to do so.

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