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Response of Rhesus Macaques (*Macaca mulatta*) to the Body of a Group Member That Died from a Fatal Attack

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Abstract

Among animals that form social bonds, the death of a conspecific may be a significant social event, representing the loss of an ally and resulting in disruptions to the dominance hierarchy. Despite this potential biological importance, we have only limited knowledge of animals' reactions to the death of a group member. This is particularly true of responses to dead adults, as most reports describe the responses of mothers to dead infants. Here, we describe in detail and provide video evidence of the behavioral responses of a group of free-ranging rhesus macaques (*Macaca mulatta*) immediately after the death of a mid-ranking adult male as a result of a fatal attack. High-ranking male members of the group, suspected to have carried out the attack, dragged and bit the dead body, exhibiting a rate of aggression 20 times greater than baseline levels. Lower-ranking individuals approached and inspected the body by looking closely, smelling, and grooming the fur. There was inconclusive evidence that these rhesus macaques found the death of a conspecific stressful: Levels of grooming between group members after the fatal attack were significantly higher than baseline levels, and higher than levels of grooming after nonfatal attacks. However, when grooming levels were adjusted based on the assumption that individuals positioned close to the body, i.e., those visible to researchers, were more likely to be engaged in grooming than those positioned farther away, this difference from baseline was no longer significant. The rate of self-directed behaviors after the fatal attack was also not different from baseline. Many of the behaviors we observed directed toward the body (aggression, inspection) have been previously reported in chimpanzees and geladas, and are similar to reactions sometimes displayed by humans. As such, this report represents a potentially valuable contribution to the nascent field of nonhuman primate thanatology.

Keywords

Cognition; Death; Grooming; Stress; Thanatology

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Introduction

The death of a conspecific for animals that form social bonds may represent the loss of an ally or potential mate, and may result in changes to the dominance hierarchy. These are potentially substantive and disruptive effects, yet we have only limited knowledge of animals' reactions to the death of a known individual (Byrne and Bates 2010). Apart from humans, species with reports on their responses to the death of a conspecific include African elephants (*Loxodonta africana*; Douglas-Hamilton *et al.* 2006; McComb *et al.* 2006), some social insects (Howard and Tschinkel 1976; Visscher 1983), and a handful of primates, e.g., *Pan troglodytes* (Anderson *et al.* 2010; Cronin *et al.* 2011; Stewart *et al.* 2012; Teleki 1973), *Theropithecus gelada* (Fashing *et al.* 2010). Few of these reports describe responses immediately after death because researchers almost never witness fatal events (Teleki 1973) or because bodies of captive animals are often promptly removed by caretakers. Moreover, many previous reports describe responses to dead infants, typically by mothers (Cronin *et al.* 2011; Fashing *et al.* 2010), but not responses to dead adults.

Reports of responses to dead adults may be particularly informative because adults often establish long-term relationships with other group members and their deaths may thus elicit the most widespread and varied responses. For example, some chimpanzees (*Pan troglodytes*) behave agonistically toward bodies of dead adults, e.g., dragging and using bodies in displays, while others exhibit exploratory behaviors toward them, e.g., sniffing, looking closely, and grooming (Anderson *et al.* 2010; Stewart *et al.* 2012; Teleki 1973). These responses may be species specific and may hint at the cognitive faculties of chimpanzees (Stewart *et al.* 2012). How other nonhuman primates respond to the deaths of adults remains largely unknown (Fashing *et al.* 2010). To address this gap, we describe in detail and provide video evidence of the behavioral responses of free-ranging rhesus macaques (*Macaca mulatta*) immediately after the fatal attack of an adult male. Our findings suggest that widespread and varied responses to dead groupmates may be more common than previously thought.

In addition to directing behaviors toward dead bodies, animals may also interact with the remaining members of their social group in an unusual or noteworthy manner in response to the death of a conspecific. Differences in the behaviors animals direct toward themselves, i.e., self-directed behaviors, such as self-scratching, may also occur. Each of these may provide insight into the physiological responses of animals to dead groupmates. For example, allogrooming (hereafter grooming) may serve to reduce stress levels in primates (Boccia *et al.* 1989; Shutt *et al.* 2007). Elevated grooming levels after the death of a conspecific may therefore indicate that animals find this type of event stressful. Increased stress levels after the death of a groupmate may also be indicated by increased rates of self-directed behaviors (SDBs), which are indicators of stress in nonhuman primates (Schino *et al.* 1996). We predicted that rates of grooming and SDBs in our focal group would be higher after the observed death compared to baseline levels. As the observed death was the result of a fatal attack, increased grooming levels could indicate the death of a group member is stressful or that aggressive events in general are stressful. In an attempt to distinguish between these possibilities, we also compared grooming levels after the fatal attack to grooming levels after nonfatal fights, and predicted grooming levels would be higher in the former compared to the latter case.

Methods

The reported death occurred in a group of *ca.* 300 rhesus macaques living on Cayo Santiago Island, Puerto Rico. Cayo Santiago is a free-ranging field site that occupies 38 acres and is home to >900 rhesus macaques living in six social groups. These macaques are provisioned

daily and have no known predators (Rawlings and Kessler 1986). We have monitored the 58 adult females and 29 adult males in one group (group F) on an almost daily basis since May 2010 as part of a long-term study. As part of our observations, we collect data on subjects using 10-min continuous focal animal samples, with two or three samples collected per individual per week. At the time of the reported death, we had collected a total of 354.5 h of focal animal data, with a mean $\pm$ SD = 4.07 ± 0.39 h of data per subject. During focal animal samples, we recorded the occurrence of all social interactions, along with the identity of the focal individual's social partner. We have determined the dominance ranks of all adults in group F from the direction of submissive interactions (Drews 1993). We recognized all adults as individuals and had information on their ages and pedigrees. Two research assistants who regularly collect behavioral data in this group witnessed the responses of individuals to the body of a dead male group member and recorded their behaviors on video with an iPhone 3GS (Apple). We recorded videos in brief clips ($N = 16$ videos, total video duration: 27 min) to preserve battery life. We recorded video every time contact aggression was directed toward the body. We defined contact aggression to include biting, scratching, grabbing, pushing, or pulling. In addition, we attempted to capture on video all instances an individual groomed or touched the dead body in a nonaggressive manner.

At *ca.* 11:30 h on October 21, 2010, researchers returned after being away from the study group for 45 min and found the body of a recently killed adult male. The dead male, 23T, had blood, lacerations, bruises, and puncture wounds on his face and body. 23T was a mid-ranking 8-yr-old that had immigrated to group F yr before and had sired no offspring on the island as determined from the Cayo Santiago database in which parentage is assigned using microsatellite markers. We observed group members' behaviors until they left the area 1.5 h later and the staff collected the corpse. We had previously witnessed the discovery of dead individuals by rhesus macaques on Cayo Santiago. On these occasions, alarm calls are often produced by the individuals that discover the body, and group members that are not nearby often suddenly stop their current behavior and quickly locomote to the body's location (L. J. N. Brent *unpubl. data*). In the current case, researchers had commenced collecting focal animal samples on their return to the group (45 min after 23T was last seen alive). Five minutes into these observations, the individuals they were observing suddenly ceased the activities they were performing and ran toward the location of the body. Based on this observation, we suggest that the members of group F that were not involved in the fatal attack became aware of the death at this point in time.

Although we did not witness the death, a necropsy performed by a veterinary pathologist determined 23T died as a result of trauma inflicted by adult male macaques, as indicated by the size of the canine puncture wounds. 23T had sustained numerous injuries, including 17 premortem bites to the throat and other areas, a swollen and bruised testicle, bruising and muscle damage to the legs and hindquarters, a damaged kidney, a damaged lung with possible pneumothorax, brain hemorrhage, and pericardial hemorrhage (Fig. 1). One researcher had followed 23T between 10:00 h and 10:10 h that day for a focal animal sample and recorded no unusual behavior during this time. Our longitudinal data also showed no signs that 23T was attempting to increase in dominance because we did not observe 23T directing aggression toward higher-ranking males in the month before the fatal attack. Nor were there signs, such as increased time spent at the periphery of the group, that 23T was attempting to emigrate.

We scored the occurrence of all behaviors directed toward 23T's body that were captured on video clips and made note of any spoken annotations made by researchers therein. Behaviors directed toward the dead body included aggressive; affiliative, e.g. grooming; and exploratory, e.g., smelling, touching, behaviors. We also coded the behaviors of the individuals visible in the videos directed at both themselves, e.g. self- scratching, as well as

each other, e.g. grooming. To examine behaviors after the death of 23T in relation to their occurrence in more typical circumstances, we compared levels of behaviors extracted from video records to baseline levels. We compared levels of aggression, grooming, and self-scratching to baseline levels.

Opportunistically collected video records can pose challenges to quantitative data analyses: the information that can be ascertained is limited to the individuals that appear in the frame of the film, and researchers must take care to avoid videotaping only especially salient or noteworthy events if accurate frequencies of behaviors are to be extracted (Martin and Bateson 1993). We took steps to prevent introducing biases associated with these issues to our data, including videorecording all occurrences of certain behaviors (aggression), and coding data only from specific points in time that we designated *a priori* to reduce the likelihood of over-representing noteworthy events. We describe the specifics of these steps relative to each behavior of interest in the text that follows. In addition, we analyzed only videos recorded 10 min apart to ensure the independence of our data points, and discarded two videos that were <30 s in duration (mean $\pm$ SD duration of clips = 1 min 41 s $\pm$ 77.0 s, range = 14 s–4 min 17 s).

Only the four highest-ranking males (in addition to one adult female) directed aggression toward the body. To determine the rate of aggression by high-ranking males, we treated the dead body as our focal individual and counted the number of times the body was subject to aggressive events by these males. We videorecorded all aggressive events apart for one, which coincided with our arrival as indicated in our spoken annotations. This event was not counted toward the total rate of aggression because it was unclear which individuals were involved. The omission of this one event means that we have slightly under-represented the total rate of aggression directed toward the dead body. We based rates of aggression on the number of bites received by the body because biting was the most visible behavior and could be scored from the videos unambiguously. By counting only biting, we were also able to prevent the rate of aggression from being artificially inflated as would occur if we counted each individual aggressive behaviour, e.g., a bite followed by a grab, as an independent event. In more typical situations, males are found at relatively large spatial distances and do not often act together to direct aggression at another male (outside of coalitionary events, which occur infrequently). This raises the possibility that multimale aggression directed toward the body could have been an artifact of the high density of monkeys observed in the area. To account for this, we therefore counted an aggressive event as a bite directed toward the body by any male, and separated by 30 s in which no bites occurred and in which no males were in the frame of the video or seen interacting with the body in an aggressive manner. All aggressive events involved at least one bite. Therefore, although some bites may have occurred before the camera was turned on, these would have been counted as one aggressive event. We extracted baseline rates of contact aggression from our long-term data. As with data recorded from videos, we defined an independent aggressive event as an event in which contact aggression occurred, and that was separated from other aggressive behaviors by >30 s. We determined the mean baseline rate of contact aggression (events/h) received by mid-ranking males from high-ranking males.

To determine whether grooming was more prevalent after 23T's death, we compared the number of pairs of individuals observed grooming after the death to baseline levels. To determine grooming levels after 23T's death, we counted the number of pairs of individuals involved in grooming at the midway point of each video ($N = 5$). Grooming pairs included pairs composed of all age–sex classes of individuals apart from infants. By counting grooming pairs at the midway point of videos we reduced the likelihood that the video camera was turned on with the intent of capturing an unusually high number of grooming pairs, which could bias our results. We calculated the observed number of grooming pairs

relative to the total number of possible grooming pairs. In this case, we determined the total number of possible grooming pairs from the total number of noninfants visible in the videos at the point in time grooming was recorded. Individuals can give grooming to only one other individual at a time (mutual grooming does not occur in this population), but can receive grooming from multiple partners simultaneously, although based on our observations individuals do not receive grooming from more than three individuals at once. Therefore, at any given moment, the maximum number of possible grooming pairs in a group of size $N = N$. For example, if there are four individuals, A, B and C, D, the maximum number of grooming pairs is four: A gives grooming to B, A receives grooming from C, A receives grooming from D, and B gives grooming to C.

It is possible that the individuals in the close vicinity of the body, i.e., in the frame of the videos, were more likely to engage in grooming than the individuals positioned farther away. Although this would be an interesting observation in itself, it could artificially inflate our reported grooming levels after 23T's death. We therefore also calculated "adjusted" grooming levels using the number of pairs of individuals in the videos observed grooming relative to the total number of possible pairs in the group as a whole, i.e., 194 pairs of noninfants. However, rather than assume that none of the individuals outside the frames of the videos were engaged in grooming, which would probably be an underestimate, we instead assumed that the individuals outside the frames of the videos had the same likelihood of being engaged in grooming as baseline levels, i.e., 4.7% of individuals.

We calculated baseline grooming levels from data collected during scan samples of the group after the fatal attack and during the same time of day as the attack. We allowed 1 mo, i.e., 30 d, to pass after the fatal attack occurred before conducting scan samples to allow time for group dynamics to stabilize, and conducted scans until the end of our study period (52 d after the fatal attack). We counted the number of (noninfant) grooming pairs during scans. Scans lasted no longer than 15 min, with up to four scans conducted per day, separated by 30 min ($N = 11$ scans). We defined baseline grooming levels as the number of pairs of individuals observed grooming during scan samples divided by the number of possible pairs. We calculated the number of possible pairs for the entire group of 194 noninfant individuals. As previously, for a group of 194 the maximum number of possible pairs engaged in grooming at any given moment was 194.

We also conducted scan samples of the group after major, but nonfatal, fights after the fatal attack. We defined major fights as instances involving three or more adults and either contact aggression and/or high-intensity noncontact aggression, e.g., chases. We collected scans after major fights ($N = 15$) *ad libitum* throughout the day using the same protocol as scans used to determine baseline grooming levels. The number of grooming pairs after major fights was divided by the total number of possible pairs in the group. We compared all grooming levels using two-tailed Mann–Whitney U tests.

We calculated the number of SDBs (self-scratching) per individual observed in each video relative to the duration of the video (h; $N = 5$). Only one of the video clips from which we scored SDBs contained aggression directed toward the body, thus reducing the likelihood that we have inflated SDB rates by targeting videos that may represent peaks in stressful events. We compared rates of SDBs after the death of 23T to the mean individual rate of SDBs (events/h) extracted from our long-term focal animal data. Because we could only sometimes identify the monkeys observed in the videos as individuals, we could not use a matched-paired analysis to compare individual SDB rates after 23T's death to baseline rates and we compare these values in a qualitative manner only.

This research complied with protocols approved by the Institutional Animal Care and Use Committee of the University of Puerto Rico (protocol no. A6850108) and adhered to the legal requirements of the United States of America.

Results

When we arrived at the location of the dead body, we recorded *ca.* 100 group F individuals (of *ca.* 300 total individuals) seated within a 6 m radius of the body. The majority of these individuals were orientated toward the body and appeared to be looking in its direction (Fig. 2a). Others were involved in grooming, self-grooming, or were looking at the ground and using their hands to brush the dirt and leaves back and forth in a stereotypic manner.

The four highest-ranking adult males were biting, grabbing, and dragging the body while giving pant-threats (Fig. 2b, and Video S1). These males directed three independent aggressive events at the body (1.5 aggressive events/h). This value was >20 times higher than the baseline rate of aggression directed by high-ranking to mid-ranking males observed over the course of the long-term study (0.07 aggressive events/h; Fig. 3a).

The second highest-ranking female also directed aggression (biting, dragging) toward the body on three occasions, immediately followed by solicited copulations with the α male (Fig. 2c and Video S1). This was highly unusual because this was not the mating season and females are not normally sexually receptive during this time of year (Hadidian and Bernstein 1979).

Initial frequent attempts by lower-ranking individuals to approach the body were prevented by aggression from high-ranking males. At *ca.* 50 min after observation onset, the high-ranking individuals moved away from the immediate area and lower-ranking individuals approached the body (Fig. 2d). These individuals were observed circling and looking closely at the face and body, as well as smelling the body and the fur that had been ripped out that was on the ground. One adult female and one subadult male groomed the body (Video S1).

A significantly greater number of pairs of individuals were involved in grooming in the period immediately after the death of 23T vs baseline (Mann–Whitney two-tailed test: $U=46$, $P=0.04$; Fig. 3b). Grooming levels were also significantly greater after 23T's death vs during periods after nonfatal fights ($U=75$, $P=0.001$; Fig. 3b). However, we did not observe the difference from baseline when we adjusted the proportion of individuals involved in grooming after 23T's death based on the assumption that individuals in the vicinity of body were more likely to be engaged in grooming than individuals positioned farther away (Fig. 3b).

The mean $\pm$ SD rate of SDBs after the death of 23T was 11.11 ± 10.55 per individual per hour. This value fell within the range of variation exhibited for mean individual rates of SDBs extracted from focal animal samples (19.37 ± 9.03).

Discussion

We have described the immediate responses of a group of free-ranging rhesus macaques to the death of an adult male group member. Documented behaviors included aggressive grabbing and biting by the highest-ranking individuals, visual orientation and exploratory behaviors such as smelling and touching by lower-ranking individuals, and elevated levels of grooming between group members in view of the dead body. Grooming levels were not elevated when adjusted based on the assumption that individuals in view of the body could have been engaged in higher rates of grooming than those positioned further away. Rates of SDBs were also not different from baseline levels.

Given the aggressive behaviors witnessed, necropsy results, and brief window of time in which the fatal attack occurred, we suggest the high-ranking group F males were responsible for the fatal attack. Intragroup lethal attacks are considered rare in noncaptive primates, apart from humans and chimpanzees (Gros-Louis *et al.* 2003; Valero *et al.* 2006). Although we hesitate to speculate how or why the fatal attack occurred because we did not witness the attack itself, we suggest that aggressive behaviors directed at the dead body could have been the result of a continued release of adrenaline from the initial attack in the case of the males, and could represent a case of agonistic social contagion in the case of the males and the one high-ranking female (Hatfield *et al.* 1994). Aggression toward dead adult conspecifics has been reported in some observations of chimpanzees (Anderson *et al.* 2010; Stewart *et al.* 2012, but not Teleki 1973) and has been suggested to represent manifested frustration caused by failed attempts to rouse the dead individual (Anderson *et al.* 2010; Stewart *et al.* 2012) or as curiosity caused by the individual's lack of responsiveness (Stewart *et al.* 2012). These explanations may also be applied to the aggressive behaviors exhibited by rhesus macaques in this case. However, we suggest that a lack of responsiveness on the part of 23T may be a more parsimonious way to explain the postmortem aggression (Semple *et al.* 2010), and could be the root cause of the fatal attack to begin with; if 23T incurred an injury in the course of an agonistic encounter that prevented him from displaying typical submissive gestures or from fleeing the area, e.g., a brain hemorrhage, this could have resulted in an escalation of aggression from high-ranking males, which could have ultimately resulted in fatality.

Researchers have previously documented mating in the vicinity of a dead group member. Teleki (1973) reported copulations between an adult female chimpanzee and several adult males in the immediate area around a dead adult male. However, because this female chimpanzee was in estrus and thus receptive to copulation, we cannot determine whether these copulations were in response to the dead body or would have occurred regardless of the circumstances. Rhesus macaques are seasonal breeders (Hadidian and Bernstein 1979). Because the death we report took place outside of the mating season, our observations of copulation between the second highest ranking female and α male are highly unusual. Moreover, we can tentatively attribute these copulations as responses to the dead body and/or the female's aggressive interactions with it.

Provisioning can increase the amount of time individuals remain in a given area. Our focal subjects were fed a few hours before the reported death and were presumably not highly motivated to leave the area around the body to forage. This group was also the highest ranking on the island at the time and was therefore unlikely to be displaced by another group. Nevertheless, despite an absence of factors limiting the amount of time they could remain in the area, our subjects spent only 1.5 h near the body. This is considerably less time than the 3 h wild chimpanzees remained near a dead adult group member (Teleki 1973). Although these findings may indicate differing levels of interest in dead conspecifics between these two species, further observations of a similar nature are required before any such generalizations are drawn.

Visual orientation toward the dead body, as well as exploratory behaviors such as smelling and touching, may have served to gather visual, olfactory, and tactile information about the state of 23T (Cronin *et al.* 2011). Researchers have previously observed visual orientation and exploratory behaviors toward dead conspecifics in chimpanzees, which they attributed to the considerable breadth of curiosity in this large-brained primate (Cronin *et al.* 2011; Stewart *et al.* 2012; Teleki 1973). Our observations of similar behaviors by rhesus macaques toward a dead adult male, along with reports of concerted interest by female geladas (*Theropithecus gelada*) toward the dead infants of other females (Fashing *et al.* 2010), suggest that exploratory behaviors in response to atypical social events that may be deemed

to be of a “curious” nature may be generalized to other highly social nonhuman primate species.

The death of a groupmate has been previously associated with increased stress hormone levels in female baboons (*Papio hamadryas cynocephalus*; Engh *et al.* 2006). These baboons broadened their networks of grooming relationships after the death of a social partner, possibly to compensate for their loss, and to return stress levels to baseline (Engh *et al.* 2006). Rates of self-directed behaviors, which are considered indicators of stress in nonhuman primates (Schino *et al.* 1996), did not differ after 23T's death from baseline levels in this group of rhesus macaques. However, we observed many individuals stereotypically brushing the dirt and leaves back and forth. This behavior could also be considered an indicator of anxiety, in effect, akin to grooming the ground. We do not record this behavior in the course of our regular data collection, but we have observed it on occasion. Indeed, because we consider this behavior to be rare, it appeared to occur at higher rates after the death of 23T than normal, although it is difficult to draw conclusions from this observation without quantitative data.

We also found some evidence of elevated grooming levels after the death of a groupmate. Although levels of aggression associated with a fatality are likely to be greater, and potentially more stressful, than those associated with nonfatal attacks, we nonetheless suggest that elevated grooming levels may indicate these macaques found the death of 23T stressful. If this were the case, it may hint at the existence of some understanding that the consequences of death differ from those of nonfatal aggressive encounters. We suggest that in addition to recording the behaviors of individuals toward dead bodies (Stewart *et al.* 2012), future reports of this type should similarly include descriptions of the behaviors of group members toward one another as a source of potentially important information on their physiological and emotional states.

Animal responses to the death of a conspecific may differ based on context (Anderson 2011). Descriptions of responses to dead conspecifics in circumstances not previously documented can therefore illuminate aspects of animals' understanding of this phenomenon that would not otherwise be noted. Our observations of the responses of rhesus macaques immediately after the fatal attack of an adult male group member provide preliminary evidence that members of this species may act aggressively toward a dead body and may attempt to gather sensory information about the dead individual, similar to reactions sometimes displayed by humans in response to the death of another person (Irwin *et al.* 1987).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Fig. 1.

Results of the necropsy of an adult male rhesus macaque, suspected to have died from a fatal intragroup attack. **(a)** Body before necropsy. **(b)** Multiple puncture wounds on the throat, but no vascular damage was observed. **(c)** Swollen bruised testicle (skin pulled back during necropsy). Testicle to the right was normal. Note also bruising and muscle damage on legs and hindquarters (arrows). **(d)** Top arrow indicates damaged lung and possible pneumothorax. Middle arrow indicates damaged kidney; dark purple color was a result of pooled blood. Kidney to the right was normal. Bottom arrow points to brain with hemorrhaging. **(e)** Summary of location and type of injuries.

Fig. 2.

Responses by rhesus macaques to the death of an adult male group member, 23T. **(a)** Group members groomed each other (circled pairs) and looked toward the dead body (arrow). **(b)** Third highest-ranking male bit and dragged the body (arrow). **(c)** Second highest-ranking female bit and dragged the body (arrow) and copulated with the α male (circled pair). **(d)** Group members approached, smelled, closely inspected, and groomed the body (arrow).

Fig. 3.

Behaviors of rhesus macaques after the death of an adult male group member vs baseline levels. **(a)** Rate of aggression received by the dead body from high-ranking males (three aggressive events recorded during 1.5 total h observed) vs the mean baseline rate ($\pm$ SE) of aggression received by mid-ranking males from high-ranking males during the study period. **(b)** Mean ($\pm$ SE) number of pairs of group members (adult and juvenile) observed grooming during videos after the death of 23T vs the baseline mean number of grooming pairs and vs the mean number of grooming pairs observed after nonfatal fights. We reported the number of grooming pairs after 23T's death relative to the number of possible pairs of individuals that were visible in the videos (after death), and also adjusted (after death adj) based on the assumption that individuals in close proximity to the body were more likely to be engaged in grooming than individuals positioned farther away.