

COMMENTARY

Behavioral Response of a Chimpanzee Mother Toward her Dead Infant

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The mother–offspring bond is one of the strongest and most essential social bonds. Following is a detailed behavioral report of a female chimpanzee 2 days after her 16-month-old infant died, on the first day that the mother is observed to create distance between her and the corpse. A series of repeated approaches and retreats to and from the body are documented, along with detailed accounts of behaviors directed toward the dead infant by the mother and other group members. The behavior of the mother toward her dead infant not only highlights the maternal contribution to the mother–infant relationship but also elucidates the opportunities chimpanzees have to learn about the sensory cues associated with death, and the implications of death for the social environment. *Am. J. Primatol.* 73:415–421, 2011. © 2011 Wiley-Liss, Inc.

Key words: mother–infant bond; response to death; thanatology; learning; social relationships; *Pan troglodytes*

INTRODUCTION

The mother–offspring bond is arguably the strongest and most essential social bond among mammals. Mothers put themselves at great personal risk to protect their offspring, while the offspring's attachment to the mother forms a crucial template for future social interactions [e.g. Suomi, 1999; Weaver & de Waal, 2003]. Given the central importance of the mother–infant bond to both human and non-human primate sociality, a great deal of research has focused on the typical trajectory of this relationship from parturition to weaning [reviewed in MacKinnon, 2007] as well as the detrimental effects of premature disruption of this relationship through temporary separation [e.g. Harlow, 1986]. However, the maternal response associated with the permanent, premature disruption of this important social bond—through death of the offspring—has rarely been investigated [but see Anderson, 2011 and Fashing et al., 2011; this volume]. By scrutinizing the behavioral pattern of mothers following the death of their infants, researchers are offered insight into the nature of the maternal attachment and the extent of its tenacity in the absence of any reciprocating behaviors by the infant. Moreover, these behavioral details are essential in order to begin to formulate an understanding of how nonhuman primates learn about important changes in their social relationships.

Recent reports have described how chimpanzee mothers carried the bodies of their deceased infants

for days, weeks, or months [Biro et al., 2010; Hosaka et al., 2000; Kooriyama, 2009; Matsuzawa, 1997]. Although these mothers show individual variation in the duration of association with the infants' bodies ranging up to 120 days [Hosaka et al., 2000], reports suggest that mothers gradually transition from extreme attachment to the body immediately following death to a weakened attachment to the body as time passes. Immediately following the death of their infant, chimpanzee mothers have been reported to be protective of the corpse, maintaining constant bodily contact with the body and showing little tolerance of conspecific investigation. Later, mothers transition to allowing others to inspect the body, and in some cases eventually permit others to manipulate and even play with the corpse [Biro et al., 2010; Hosaka et al., 2000].

However, the specific behaviors expressed by the mother during this transitional period have not been

Contract grant sponsors: Gonzaga University; Max Planck Society; VU University Amsterdam.

Additional Supporting Information may be found in the online version of this article.

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Received 10 December 2010; revised 17 December 2010; revision accepted 17 December 2010

DOI 10.1002/ajp.20927

Published online 21 January 2011 in Wiley Online Library (wileyonlinelibrary.com).

carefully examined. Careful recording of behaviors expressed by surviving individuals when faced with naturally occurring deaths is integral to building an understanding of how chimpanzees respond to death [Anderson, 2011]. Following is an objective account of the behavior of a female chimpanzee on the first day that she was observed to stop carrying the body of her deceased infant. The observation took place 2 days after the infant died, on the final day the mother was seen with the body. The behaviors expressed by the mother toward the infant's body are reported, as well as the behaviors expressed by other chimpanzees in the social group who encountered the body. These data provide valuable insight into how a chimpanzee transitions from providing constant care to her infant to separating herself from the infant's body following its death.

METHODS

Study Site and Subjects

Observations were conducted at Chimfunshi Wildlife Orphanage Trust (Chimfunshi), a chimpanzee sanctuary located in the Copperbelt region of Northwestern Zambia, approximately 60 km west of Chingola on the southern bank of the Kafue River. Chimfunshi is a member of the Pan African Sanctuary Alliance (PASA) and approximately half of the 100 chimpanzees in the Project Area of Chimfunshi were rescued from illegal trade between 1983 and 2004 and brought to Chimfunshi for rehabilitation and socialization. The other half of the population was mother-reared in social groups at Chimfunshi.

The Project Area consists of four stable social groups living in outdoor enclosures ranging in size from 0.20 km² (47 acres) to 0.77 km² (190 acres) situated in densely vegetated miombo forest. All enclosures have indoor holding areas used for mid-day feeding and visual health inspections, solar-powered electric fencing around the perimeter and an observation deck on the roof of the indoor holding area. Chimpanzees are provisioned in or near the indoor holding area between 11:30 AM and 1:30 PM; they are in their forested enclosures at all other times of the day and overnight. The observations described below took place in Group 2, a stable social group composed of 43 individuals that inhabits a 0.65 km² (160 acre) enclosure. Given the large size of the enclosure, it is not uncommon for chimpanzees to be out of the sight of researchers located at the fence or observation deck.

The deceased infant was female, born on January 26, 2009 to Masya, a wild-born chimpanzee who entered the sanctuary in 1994 at approximately 3 years of age after confiscation from private owners. Masya had successfully reared two previous daughters, one of whom was 5 years old and present in the social group at the time of the infant's death (Mary).

No previous offspring of Masya's were reported to have died.

Data Collection

On May 17, 2010, Masya was seen during the mid-day provisioning with her live infant. On May 18, Masya was seen carrying the dead body of her infant; the cause of death was unknown but there were no visible injuries to the body. Staff reported that the infant had not been healthy since birth and was often coughing. On this day, Masya was sighted on multiple occasions, each time she was in physical contact with the infant's body. When moving, she supported the body with one arm and carried it ventrally. The report below took place on the afternoon of May 19, when Masya was first observed to place the body on the ground in an open, grassy clearing and relinquish physical contact with it. This took place mid-afternoon, when all of the chimpanzees were in their outdoor enclosure.

When the observers saw that Masya had placed the infant's body on the ground, they opportunistically began video recording. Initial video was obtained by a single observer (8 min 20 sec). Minutes later, uninterrupted observation began with at least one camera recording continuously for 63 min 54 sec. The first 45 min of this uninterrupted observation took place while the infant's body was in the clearing, the final minutes took place in a social group. Observer 1 recorded from the observation deck with a Sony HD Handycam and Observer 2 from the ground outside the fence with a Canon miniDV camera. The observers were approximately 12 m from the body in the clearing and 20 m from each other. Data collection adhered with PASA guidelines as well as the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates.

Videos were synchronized for simultaneous dual views using ELAN 3.9 [Brugman & Russel, 2004]. Behavior was coded using a standard ethogram supplemented with behaviors directed toward the body (Table I). The mother (Masya) and older sister (Mary) were treated as focal subjects, and behavior and proximity to the infant were coded every second. Additionally, head direction (dichotomously coded as toward infant or away from infant) was coded continuously for the mother. For all other chimpanzees, behaviors were continuously coded when they were within 9 m of the infant's body (the approximate distance from which chimpanzees were able to see the body from any direction).

Sixty percent of the observation time was coded by a second, independent observer with the mother as focal subject. Interobserver reliability was calculated for head direction (Cohen's $\kappa = 0.65$), all behaviors (Cohen's $\kappa = 0.80$), and the subset of behaviors directed toward the dead infant (Cohen's $\kappa = 0.87$).

TABLE I. Infant-Directed Behaviors Performed by the Mother

Infant-directed behavior	Description	Freq	Mean duration (sec)	# events followed by sniffing hand used for behavior	Supplemental video example
Inspect face	Both hands touch dead infant's face with movement of fingers; focal subject's face positioned <10 cm from infant's face	2	16.5 (range 8–25)	2 (100%)	S1: Mother inspects dead infant's face
Touch neck	Part of hand physically contacts dead infant's neck with fingers held still	10	5.4 (range 1–20)	1 (10%)	S2: Mother touches dead infant's neck
Touch face	Part of hand physically contacts dead infant's face with fingers held still	9	5.1 (range 1–16)	4 (44%)	S3: Mother touches dead infant's face
Touch body (other location)	Part of hand physically contacts dead infant's body somewhere other than face or neck with fingers held still (all events were touches to inner thigh)	2	2.5 (range 1–4)	0 (0%)	S4: Mother touches dead infant's inner thigh
Peer	Positions own face <10 cm from dead infant, no physical contact or any other behavior	6	6.7 (range 2–11)	n/a	S5: Mother peers at dead infant
Gaze	Stand close (<1 m) to the dead infant's body while watching the infant, no physical contact or any other behavior	20	7.7 (range 2–29)	n/a	S6: Mother gazes at dead infant
Hand above infant's face	Stand close (<1 m) to the dead infant's body while watching the infant, moving one arm above infant's face without making physical contact	8	2.4 (range 1–5)	0 (0%)	S7: Mother holds hand above dead infant's face
Fly swat	Swift hand/arm movement directed towards flies surrounding the dead infant's body	12	<1	0 (0%)	S8: Mother swats flies over dead infant
Pick up infant	Dead infant's entire body is lifted off the ground	1	4	0 (0%)	S9: Mother picks up dead infant

RESULTS

Behavior of the Mother Upon Initial Physical Separation From the Infant's Body

Video recording began when the mother was opportunistically sighted having laid the infant's body on the ground in a clearing; this is the first time any physical distance was observed between the mother and the corpse. The body remained in this location for over 45 min, during which time the mother repeatedly approached the body and retreated from it, often retreating to the same location 2 m from the body. The proximity of the mother to the infant's body while it was located in the clearing is shown in Figure 1.

During this approach-retreat period, the mother's head was oriented toward the infant for 19 min 48 sec, or 44.1% of the continuous observation period. The mother's head was directed away from the infant for 51.1% and 4.8% could not be scored due to an obstructed view. The longest interval during which the mother's head was not directed toward the body while she was within 9 m was 1 min 19 sec.

The mother displayed a variety of behaviors directed toward the infant's body during her repeated approaches in the clearing (Table I and Supplemental Videos S1–S9). The mother touched the dead infant's body on 23 separate events; 21 of these were directed toward the infant's face ($n = 11$)

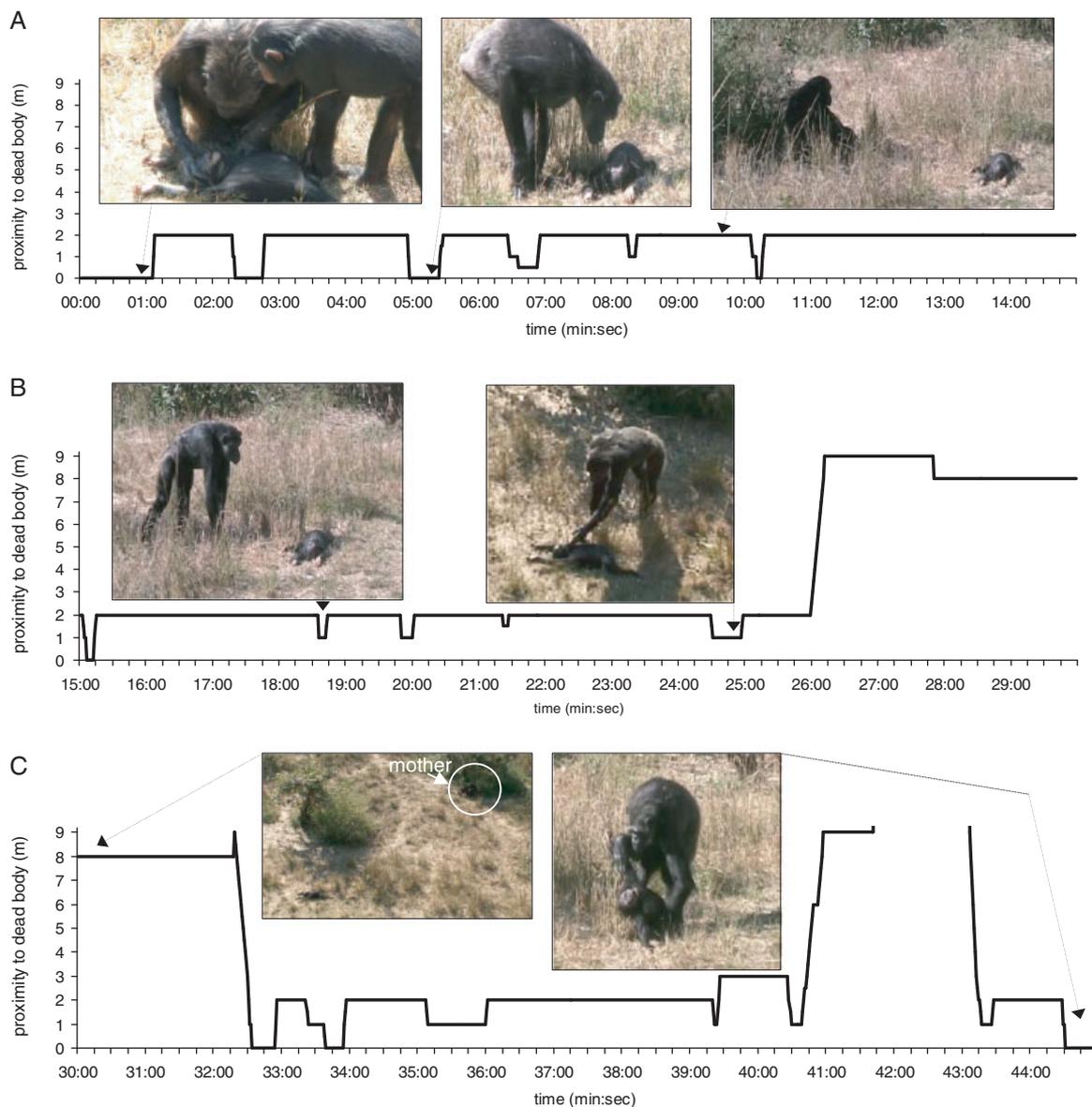


Fig. 1. Proximity of the mother to the dead infant while the infant's body remained in a constant location in the clearing. Distances greater than 9 m are not shown.

or neck ($n = 10$). Additionally, the mother often directed her head toward the infant's face while positioning her head close to the infant's face (peer, <10 cm), or from slightly further away (gaze, within 1 m). During these "peer" and "gaze" events the mother made no observable body movements. Later, the mother picked up the infant and carried it ventrally, supporting it with her right arm to join a group of eight chimpanzees approximately 20 m away. (See supplemental video S10 for continuous sequence of behaviors including gaze, peer, touch neck, touch inner thigh, and pick up infant).

During this time that the infant's body was in the clearing, only two other chimpanzees physically interacted with the body. Vis (δ juvenile/sub-adult) pulled the infant's leg and dragged the body over the ground for approximately 1 m; Masya reacted with a swift body movement toward Vis, which resulted in Vis releasing his grip on the body. Shortly after, Vis approached the body for a second time and slowly poked it four times in the stomach and then sniffed his own hand; there was no visible reaction from Masya.

Mary (♀ juvenile, older sister to dead infant) touched the dead infant's face for 3 sec and subsequently inspected the face for 2 sec. During Mary's interaction with the body, Masya was traveling to a place approximately 8 m from the body. In the midst of Mary's interaction with the body, Masya looked back at the body and then resumed traveling. Mary subsequently approached Masya at the position 8 m from the body and both individuals inspected Mary's hands for 4 sec.

While the infant's body was located in the clearing, 11 individuals were seen near the body (4 m) in addition to the mother: 6 juveniles/sub-adults (2 males) and 5 adults (1 male). Masya only interacted with one of the sub-adults, whom she groomed for 40 sec.

Behaviors Toward the Dead Infant After the Mother Carried the Body to a Social Group

After the interactions described above, Masya picked up her dead infant and carried it over to a social group approximately 20 m from where the body had been located in the clearing (Supplemental Video S11). The group consisted of Zsabu (δ adult, alpha), Pippa (♀ adult), Noel (♀ adult), [mother of] Nina (♀ sub-adult), Little Jane (♀ adult), [mother of] Little Jenkins (δ infant), Little Judy (♀ adult) and Mary (♀ juvenile, older sister to dead infant).

Masya placed the body in the group and then sat 0.5 m from the body and started grooming Pippa or Zsabu (while Zsabu groomed Pippa). Mary approached the body first, together with Nina and Little Jamie (δ juvenile), who followed Masya to the group. Mary inspected the dead infant's face, then repositioned to 2.5 m away from the body and inspected her own hand. Little Jamie lifted the dead

infant's leg and then sniffed his own hand. Nina watched the body, and the others interacting with the body, from within 0.5 m. Noel approached and watched the body from within 0.5 m. Zsabu and Pippa directed their heads toward the body, Masya stopped grooming and started to inspect the infant's face with both hands. Pippa repositioned and started peering at the body while sniffing her hands and swatting flies near the body for 8 sec, then she left. Zsabu subsequently started to follow Pippa, and stepped over the body. While doing this, he paused, poked the infant's hand, touched the anogenital region, sniffed his own hand, then left.

Noel and Nina stayed close to the body, as did Masya. Noel and Nina touched the body and sniffed their own hands; Noel touched the anogenital region and Nina touched the face. Nina stroked the dead infant's belly from the lower right to the neck area and stayed close to the body for 4 min. Noel started grooming the body (occasionally using grass or straw tools), whereas Nina watched. Masya stayed within 0.5 m distance, occasionally touching the dead infant briefly while watching Noel. Trixie (♀ adult) approached the body with her daughter Tilly (♀ sub-adult) and watched Noel groom the body from within 1 m for approximately 6 min. Trixie once peered at the body, as did her son Taylor (δ sub-adult), who approached the body once and subsequently stayed approximately 1.5 m from the body. Mary returned to the body after having spent 6 min at 3 m distance, and watched it for 4 min while also looking at Noel's grooming actions. She further inspected the grass/straw that Noel used to groom the dead infant with and occasionally sniffed her own hands.

Noel left the group after having groomed the body for over 6 min; Nina departed 2 min later, after having rested for over 8 min at 2 m from the body. After Noel left the group, Masya touched the lips and inspected the face of her dead infant several times, while being watched from within 0.5 m by Trixie and Tilly. Tilly peered at the body once and stayed within 1 m of the body for the next 9 min. While in the social group (18 min and 25 sec total), Masya stayed within 1 m of the body of her dead infant. Apart from grooming Pippa or Zsabu for less than 15 sec, silently displacing Trixie for 2 sec and exploring an object for less than 10 sec, she did not show any behavior other than resting and physical behavior directed toward her infant (touching, inspecting). Masya directed her head toward the infant 75% of the time that she was in the social group. After all individuals left, only Tilly and Masya stayed behind with the dead infant; at this time the video recording ceased. Minutes later, Masya retrieved the body and carried it out of sight. As of the following morning, Masya was observed without the body.

DISCUSSION

Reported above are the behaviors of a female chimpanzee when she was first observed to place

physical distance between herself and her recently deceased infant. These observations occur during a unique period when the mother transitioned from maintaining close, constant proximity to her deceased infant to initiating physical distance from the dead body. Many primate mothers carry the bodies of their infants after they have died, eventually ceasing this behavior and resuming typical reproductive and maternal behaviors. However, this transitional process to physical separation from the dead body has not been described in detail, and can shed considerable light on both the magnitude of the mother–infant bond and the potential for chimpanzees to learn about death.

When first observed to place the dead infant's body on the ground, the mother repeatedly visited the body to inspect it and then returned to a resting location nearby. As determined by her head direction, she regularly maintained visual contact with the body when not in immediate proximity with it. During her repeated visits to the body, she directed the majority of her attention to the infant's face and neck. The mother's motivation to selectively attend to the infant's face may not be specific to this situation, as a bias in attention to the face may be characteristic of maternal behavior toward living infants as well given the general attraction of infant facial features [Lorenz, 1971]. However, the face and neck of the dead infant would indicate differences in the infant's condition. For example, the face alone could indicate that the infant does not adjust eye gaze, inhale, exhale, nor show any changes in facial musculature as it did previously.

After touching the body, the mother (as well as other individuals) sometimes brought her hand toward her face. This behavior presumably would have provided olfactory and potentially gustatory information about the infant's body that differed from information obtained during regular contact while the infant was alive. On other occasions, however, the mother touched the face or neck for multiple seconds without subsequently bringing her hand toward her face, and at other times looked at the body from a close distance without touching it. These behaviors would supply tactile and visual information about the current state of the body. Thus, the mother was at least in the position to obtain sensory information about the dead infant that would have differed drastically from information obtained through the same senses when the infant was alive. The behaviors expressed by the mother are consistent with the suggestion that the mother was actively gathering this novel sensory information about the dead infant. Conceivably, this information could be remembered the next time she encountered the same set of cues, and the implications of death—that the individual is removed from

one's social environment—could theoretically be learned by chimpanzees.

When the mother joined the social group with her dead infant, she tolerated investigation by others and continued to visually monitor the infant while others inspected it. Tolerance of conspecific investigation toward dead infants has been reported in chimpanzees as well as in geladas [Biro et al., 2010; Fashing et al., 2011]. Juveniles and sub-adults approached first, and one adult female who spent the most time in contact with the body used a tool to groom it while others watched and inspected the tool after use. The same adult female used a similar technique to groom the dead body of a 9-year-old male one day prior [van Leeuwen et al., in preparation]. Importantly, during this time the mother remained within 1 m and spent the majority of her time visually monitoring the interactions with the body, potentially gaining additional information about the unresponsive state of her infant.

Albeit obvious, it is important to stress that after the infant's death, any association between the mother and infant's body is maintained solely by the mother. Clearly all infant-directed behaviors occurred in the absence of any soliciting cues from the infant or reciprocation of behavior. Maintenance of proximity and visual monitoring, shown repeatedly by the mother in this observational window, have recently been suggested as reliable measures of bondedness in primates [Dunbar & Schultz, 2010]. Minimally, these observations indicate that in chimpanzees the sustained maternal contribution to the mother–infant relationship is not dependent upon infant behavior, as may be true in other species as well [Connor & Norris, 1982; Douglas-Hamilton et al., 2006; Fashing et al., 2011; Hubbs, 1953; Nakamichi et al., 1996; Sugiyama et al., 2009; Warren & Williamson, 2004]. In combination with existing literature demonstrating that maternal behavior persists independent of hormonal contributions [Broad et al., 2006; Nelson & Panksepp, 1998], these findings further emphasize the extremely reliable yet flexible contribution by the mother to the mother–offspring relationship.

The behaviors expressed by this female chimpanzee when she first endures physical separation from her dead infant provide valuable insight into how chimpanzees respond to the premature severing of the mother–infant bond, the maternal contribution to this bond, and the possible ways in which chimpanzees gather information about the state of responsiveness of individuals around them (hence learning about “death”). With additional opportunistic, objective accounts of the reactions of chimpanzees to deceased offspring, a better understanding of chimpanzee behavior and cognition associated with death of individuals with whom they shared a close social bond may be obtained.

ACKNOWLEDGMENTS

The authors thank the Zambia Wildlife Authority and the Chimfunshi staff who provide care for the chimpanzees. A special thank you (twatotela) to Patrick Chambatu, Felix Chinyama, John Kayuya, Joseph Kasongo, Albert Mulembo and Patrick Mwika whose chimpanzee expertise was integral to this report. Thank you to Tatyana Humle for valuable feedback and to Makiko Sadakata and the Technical Group of the MPI in Nijmegen. This research complied with animal care regulations of PASA and internal guidelines of CWOT and adhered to the American Society of Primatologists principles for the ethical treatment of primates.

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