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Corpse-directed play parenting by a sterile adult female chimpanzee

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Abstract

The study of representational play in nonhuman primates, including chimpanzees (*Pan troglodytes*), provides interspecific perspectives on human cognitive development and evolution. A notable form of representational play in chimpanzees is play parenting, wherein parental behavior is directed at inanimate objects. Though observed in captivity, unambiguous examples of play parenting by wild chimpanzees are rare. Here, we report two cases from Ngogo in Kibale National Park, Uganda, in which a wild adult female chimpanzee (*P. t. schweinfurthii*) directed parental behaviors at corpses. Both cases involved the same adult female chimpanzee, aged 20–21 years. The first case was observed on 5 March 2016, and the play object was the corpse of a bushbaby (*Galago thomasi*); in the second case, observed on 6 May 2017, the play object was a recently deceased chimpanzee infant postmortally stolen from the mother. The chimpanzee possessed the first and second play objects for approximately 5.5 h and 1.8 h, respectively. In both cases, she performed a variety of maternal behaviors, including co-nesting, grooming, and dorsally carrying the play objects. In contrast to previous observations of play parenting in captivity, the play parent was a presumably sterile adult female, well beyond the average age of first birth. These observations contribute to the expanding literature on chimpanzee interactions with the corpses of both conspecifics and heterospecifics.

Keywords

Chimpanzee; Representational play; Object manipulation; Play parenting; Bushbaby

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Introduction

Representational play is play behavior in which one element “stands in” for another (Leslie 1987). Given its developmental associations with language (McCune 1995; Orr and Geva 2015) and theory of mind (Lillard 1993; Schwebel et al. 1999), representational play may elucidate the neural structure, development, and evolution of higher cognitive processes (Weisberg 2015; Riede et al. 2018; Pellegrini and Smith 2005). Yet, representational play is not uniquely human; it has also been reported in our closest living relatives, the chimpanzee (*Pan troglodytes*; Jensvold and Fouts 1993) and bonobo (*P. paniscus*; Lyn et al. 2006), as well as rhesus macaques (*Macaca mulatta*; Breuggeman 1973). One notable form of representational play in chimpanzees is play parenting, in which parental behaviors are directed at inanimate objects. Like other forms of symbolic behavior in nonhuman primates (Miles 1983), play parenting has been repeatedly observed in captive chimpanzees (Lyn et al. 2006; Pellegrini and Smith 2005). However, given the extensive human influence on captive chimpanzee behavior (Persson et al. 2018; Tomasello and Call 2004; Lyn et al. 2010), observations of play parenting in captivity may reflect abnormal [e.g., Birkett and Newton-Fisher (2011)] rather than natural behavior. Observations of play parenting in wild populations are therefore critical to determine whether it is a naturally occurring behavior in chimpanzees or exclusive to captive populations.

Despite high rates of object manipulation in this species (Whiten et al. 1999; Koops et al. 2015), unambiguous examples of play parenting in wild chimpanzees are rare (Matsuzawa 1997; Wrangham and Peterson 1997). A compelling argument for play parenting comes from Kanyawara in Kibale National Park, Uganda, where chimpanzees carry and play with sticks (e.g., small logs, bark, vine) for extended periods of time with no discernible immediate purpose (e.g., tool-assisted foraging) (Kahlenberg and Wrangham 2010). It is suggested that stick carrying is analogous to doll play in humans, in that sticks represent infant chimpanzees to those that carry and play with them. This interpretation is largely based on a female bias in stick carrying, just as doll play in human infants and children is female biased (Jadva et al. 2010; Serbin et al. 2001; Golombok et al. 2008). This sex bias is consistent with captive studies of social play in several primate species, in which immature males and females exhibit different preferences by play type (e.g., *Cebus apella*; Paukner and Suomi 2008) and toy type (e.g., *Macaca mulatta*; Hassett et al. 2008). Furthermore, this sex bias cannot be explained by overall rates of object manipulation, as cumulative frequency of stick manipulation by immature chimpanzees is male-biased (Koops et al. 2015).

Other potential cases of play parenting concern interactions between chimpanzees and heterospecifics, some of which comprise behaviors characteristic of parental care. For example, at Bossou, Guinea, chimpanzees have been observed playing with both living and deceased heterospecifics (Hockings et al. 2012), including hyraxes (*Dendrohyrax dorsalis*) (Hirata and Mizuno 2011). However, these episodes involve diverse behaviors ranging from aggressive (e.g., striking and plucking the play object) to affiliative (e.g., grooming the play object), and are not explicitly defined by the authors as play parenting (Hockings et al. 2012; Hirata et al. 2001).

Here, we report two cases of corpse-directed play parenting by a wild adult female chimpanzee (*P. t. schweinfurthii*) of the Ngogo community in Kibale National Park, Uganda. We describe (1) the constitutive play parenting behaviors, and (2) ways in which this incident both resembles and deviates from patterns of play parenting observed at other study sites.

Materials and methods

The Ngogo study site, with an area of approximately 35 km² and an altitude of 1400 m above sea level, lies in the middle of the 795-km² Kibale National Park (0°29' 89"N, 30°25' 51"E) and consists primarily of moist evergreen forest. Further description of the study site is provided by Ghiglieri (1984) and Struhsaker (1997). The Ngogo chimpanzee community has been continuously and systematically studied since 1995 and is the largest wild chimpanzee community ever described; at the time of the observations reported here, the community consisted of approximately 206 individuals including 35 adult males and 61 adult females (Wood et al. 2017). The Ngogo chimpanzees have experienced minimal anthropogenic disturbance: they have never been provisioned, and human exposure is limited to research personnel. To the best of our knowledge, corpse-directed play parenting has not been previously observed at Ngogo (Mitani, pers. comm.).

The reported play parenting behavior was exhibited by Lucy, an adult natal female chimpanzee. At the time of observations, Lucy was 20–21 years old and nulliparous. As average age at first birth for natal female chimpanzees is 13.72 years (Walker et al. 2018; Nakamura 2015), she is likely sterile. Otherwise, Lucy is a typical adult female; she is socially integrated, appears in good physical health, and develops sexual swellings that attract substantial mating interest (Negrey and Langergraber, unpublished data).

Results

Case 1

On 5 March 2016, Lucy was first observed by JDN at 9:32 in a party of 12 chimpanzees comprising four adult females (including Lucy), two adult males, one adolescent female, two adolescent males, and three infants. As she finished feeding arboreally on the ripe fruit of *Morus mesozygia*, Lucy held an object between her abdomen and thigh that could not be identified by JDN. Within 30 s of being observed, Lucy built an arboreal day nest and rested. Although Lucy remained with the party throughout the day, she was not closely observed again for more than 4 h.

At approximately 10:20, the party traveled to a separate *M. mesozygia* tree 200 m to the northeast, in which they fed for approximately 45 min. After feeding, the party moved to the ground and rested for approximately 2 h. Lucy, like most individuals at this time, was not visible due to thick vegetation. The party began traveling northeast at approximately 13:05, intermittently resting on the ground and feeding on sapling leaves and pith.

By 14:05, the party had traveled 360 m northeast to a fruiting *Ficus natalensis*, where they were joined by another adult female and her two offspring. Approximately 10 min later,

Lucy climbed into the tree, at which point the object she was carrying, a bushbaby (*Galago thomasi*) corpse, became easily visible to JDN. Lucy was followed into the *F. natalensis* by other members of the party; however, no attempts were made to steal the corpse. As she fed on ripe fruit, Lucy held the bushbaby between her abdomen and thigh, sporadically touching the corpse with her hand for no discernible reason. While traveling in the tree, she carried the bushbaby in her mouth (Online Resource 1).

After Lucy fed for approximately 20 min, the party left the tree and traveled northeast, during which time Lucy was not visible. They rested 10 min later, at which point Lucy positioned the bushbaby on her thigh. An infant female, Amina, stared for prolonged periods at the bushbaby, but did not beg, and no meat consumption or sharing occurred. Despite Amina's interest, Lucy nonaggressively prohibited her from touching the bushbaby (i.e., placed her arm between the bushbaby and infant). After inspecting the bushbaby, Lucy briefly extended the corpse toward Amina before intermittently grooming it (Online Resource 2).

When Lucy continued traveling northeast, she placed the bushbaby on her mid-to-upper back. Although the bushbaby repeatedly slipped off, Lucy repositioned it and continued traveling (Online Resource 3). Lucy was last observed at 15:01, when JDN encountered Cape buffalo (*Syncerus caffer caffer*) approximately 514 m northeast of the *F. natalensis* and was unable to continue the follow. When she was found the following day, 6 March 2016, at 9:19, she no longer carried the corpse.

In total, Lucy possessed the corpse for 5 h 29 min, during which she traveled approximately 1.07 km.

Case 2

On 6 May 2017, at 12:45, Lucy was resting in a party with three other adult females (Kidman, Cate, and Shire) and their dependent offspring below a *F. mucuso* tree in which they had been feeding most of the morning. At this time, they were joined by a fifth adult female, Bronte, who was carrying the body of her 5-month-old infant. The infant had died of unknown causes within the previous 2 days; when the body was eventually recovered (see below), no external wounds or signs of illness were apparent. Bronte immediately entered the tree and began to feed while Lucy and the three other females rested below.

At 13:38, Lucy climbed into the tree, approached Bronte, and grabbed the dead infant. Lucy then arboreally traveled 10 m to another tree, carrying the infant ventrally; Bronte screamed and followed Lucy for 2–3 m before stopping. Lucy sat down on a large limb about 7 m from Bronte, held the dead infant in her lap, then groomed the corpse for 10 min. At 13:45, Lucy lightly slapped the stomach of the corpse five times in rapid succession, then resumed grooming. At 13:46, Lucy again slapped the corpse several times, with greater force. At 13:47, Cate's infant climbed into the tree and approached Lucy (Fig. 1), who groomed her until Cate climbed into the tree at 13:50. At this time, Lucy approached Bronte; Bronte groomed Lucy while Lucy groomed the dead infant. At 13:52, Bronte and Lucy went to rest in different parts of the tree, during which time Lucy continued to groom the corpse. At 14:01, she briefly shook the corpse, slapped it once, and then resumed grooming. At 14:05,

Bronte came to the ground to eat leaves. Lucy stayed in the tree grooming the corpse until 14:13, at which point she and Cate descended to join Bronte, Kidman, Shire, and their dependent offspring.

From 14:15 to 14:26, the party traveled on the ground to the southwest, moving about 300 m. Lucy carried the corpse dorsally; however, it fell off every 5–10 m, interrupting her travel. At 14:26, Lucy climbed a tree and made a nest while three of the other four adult females continued traveling southwest. Cate remained on the ground below Lucy's nest, resting. Lucy groomed the corpse in the nest until 14:36, when she left the nest, still carrying the corpse but remaining in the tree. Then a party of five adult males, two adolescent males, and another adult female arrived. When an adolescent male, Gus, climbed into the tree, Lucy descended and began traveling to the southwest. At 15:21, after traveling approximately 100 m with the corpse on her back, she again met adult females Kidman and Bronte. Kidman had since been joined by her adolescent son, Elton, and another adolescent male, Nelson. Lucy sat next to Kidman and groomed the corpse while Kidman watched.

At 15:22, Lucy, Kidman, and Bronte resumed traveling to the southwest. Lucy held the corpse with one hand to her chest while traveling. Once, she dragged the corpse along the ground for 2 m. At 15:24, she dropped the corpse and traveled 5 m before returning to retrieve it. At 15:26, she again dropped the corpse and continued traveling, but this time, she did not return. Bronte stopped and sat next to the corpse for 1 min, swatting at flies. At 15:27, Bronte began traveling southwest while carrying the corpse ventrally. At 15:30, she found Kidman, Elton, and Nelson feeding in another large *F. muscuso* tree. Bronte carried the corpse into the tree and held it ventrally while feeding, before dropping it at 15:45. Bronte was never observed grooming the corpse and did not attempt to retrieve it again. Observer KEL left the chimpanzees at 16:15, transporting the corpse to camp for the collection of tissue samples.

Discussion

This report provides evidence of representational play by a wild female chimpanzee. Lucy's interactions with corpses included several maternal behaviors, supporting the existence of play parenting in wild chimpanzees. First, Lucy rested with the corpses in her day nests, a behavior typical of females with young infants (Goodall 1962). Second, Lucy groomed the corpses. While grooming characterizes all affiliative dyadic relationships (Langergraber et al. 2007, 2009, 2013), mothers groom young infants at especially high frequencies (Yerkes and Tomilin 1935). Third, Lucy dorsally carried the corpses. From approximately 5 months of age an infant rides on its mother's back and may continue to do so throughout infancy (Clarke 1977). However, while Lucy's behavior is largely compatible with mother–infant interactions, it cannot be described as exclusively maternal. For instance, in Case 1, Lucy sometimes carried the corpse in her mouth while traveling, and in Case 2, she briefly slapped and dragged the corpse. Therefore, Lucy's interactions with the corpses are indeed illustrative of, but not restricted to, play parenting.

While corpse-directed play parenting is uncommon, chimpanzee interactions with corpses have been well documented. Physical interaction with heterospecific corpses has been

observed at multiple study sites (Muller et al. 1995; Carvalho et al. 2010; Hirata et al. 2001), including Ngogo (Langergraber, unpublished data). Some of the reported behaviors evoke play parenting while others indicate curiosity or confusion (e.g., probing, slapping). At Bulindi, Uganda, Cibot et al. (2017) report an adolescent male inspecting the feathers of a guineafowl corpse and a juvenile male grooming a hyrax corpse. As previously indicated, juvenile and adolescent chimpanzees at Bossou have been observed capturing—without consuming—hyraxes; in one case, the hyrax was treated like a doll by an adolescent female who groomed, nested, and carried it on her shoulder (Hirata et al. 2001; Hirata and Mizuno 2011). Hockings et al. (2012) report 16 instances of contact interactions between chimpanzees and heterospecifics at Bossou between 1997 and 2009; nesting was observed in four of these cases, and grooming was observed in two cases. Strikingly, Hockings et al. (2012) also report that a 7-year-old male dorsally carried a fledgling bird, although this behavior was brief and not accompanied by other affiliative or parental behavior.

Responses to conspecific corpses vary greatly across individuals and contexts [Reviewed in Gonçalves and Carvalho (2019)]. Female chimpanzees are well known to carry the bodies of their deceased infants; this behavior may continue for weeks or even months following an infant's death (Biro et al. 2010; Cronin et al. 2011). Other reports of chimpanzee interactions with dead conspecifics indicate alarm, confusion, and/or curiosity. At Gombe Stream National Park, Tanzania, Teleki (1973) describes a variety of behaviors from casual inspections of the corpse to displays and physical embraces with other chimpanzees present. A more recent report from Gombe describes various behaviors directed at the corpse of an adult female including inspection (e.g., sniffing) and aggressive displays in which the corpse was used as a prop (Stewart et al. 2012). At the Chimfunshi Wildlife Orphanage in Zambia, the corpse of a 9-year-old male chimpanzee prompted displays, grooming, and cleaning of the corpse's teeth (van Leeuwen et al. 2016). Together, these reports suggest that chimpanzee responses to conspecific corpses may vary by the identity of the responder and their relationship to the deceased.

Prior cases of play parenting with both heterospecifics and non-animal objects were notable in that the play objects were not consumed (Hirata et al. 2001; Kahlenberg and Wrangham 2010). Consistent with these reports, neither Lucy nor other chimpanzees consumed any parts of the corpses. While chimpanzees are prolific hunters (Boesch and Boesch 1989; Watts and Mitani 2002, 2015), and bushbabies are commonly preyed upon by chimpanzees in West Africa (Pruetz and Bertolani 2007; Pruetz et al. 2015), the disinterest in the bushbaby as meat is consistent with other episodes of heterospecific play (Cibot et al. 2017; Hirata et al. 2001). Importantly, scavenging of meat by chimpanzees is considerably less common than hunting. At Ngogo, Watts (2008) observed only four cases of scavenging over an 11-year period. As we did not observe Lucy kill the bushbaby, she may have recovered it after death; if so, her apparent disinterest in consuming it accords with the rarity of scavenging by wild chimpanzees. Similarly, Lucy's disinterest in cannibalizing the infant chimpanzee corpse is consistent with prior observations. Although cannibalism is common in cases of infanticide (Hitonaru and Michio 2018; Watts and Mitani 2000) and may even accompany the killing of adult conspecifics (Pruetz et al. 2017), consumption of conspecific corpses following non-violent death is uncommon (Biro et al. 2010; Cronin et al. 2011).

Therefore, our observations confirm that both heterospecific and conspecific corpses treated as play objects are rarely, if ever, regarded as food.

The observations in this report are notable in that the play parent was an adult. As with play in chimpanzees in general (Pellegrini et al. 2007), stick play at Kanyawara is most common in immatures (Kahlenberg and Wrangham 2010), as is heterospecific play at Bossou (Hirata and Mizuno 2011; Hockings et al. 2012). Play parenting by an adult appears especially rare. For instance, only six stick-carrying events (in 14 years of observation) at Kanyawara involved adult chimpanzees; in each case, the observation occurred prior to first birth (Kahlenberg and Wrangham 2010). While Lucy was nulliparous, she was 6–7 years past the average age of first birth (i.e., 13.72 years) in wild non-dispersing female chimpanzees (Walker et al. 2018). Lucy's behavior therefore suggests that play parenting may continue in the prolonged absence of offspring.

Finally, our report provides further, tentative support for a female bias in play parenting, recalling the female bias in stick carrying at Kanyawara (Kahlenberg and Wrangham 2010). This sex bias reflects behavioral correlates of chimpanzees' polygynandrous mating systems, in which paternity is uncertain and parental behavior is nearly exclusive to females, with notable exceptions (Cibot et al. 2019). If early differences in play (Lonsdorf et al. 2014) and object manipulation (Koops et al. 2015) reflect sex differences in adult behavior, a female bias in play parenting is expected. Only with further reports of play parenting by wild chimpanzees will we fully understand its demographic, developmental, and cognitive correlates.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.
Lucy holds the corpse of a recently deceased infant chimpanzee