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NEWS AND PERSPECTIVES

Infant carrying by a wild chimpanzee father at Bulindi, Uganda

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Abstract

Although infanticide by wild adult male chimpanzees has been reported from multiple sites, affiliative infant carrying by males is rare. We observed infant carrying by an alpha male chimpanzee at Bulindi (Uganda) on two consecutive mornings and collected faecal samples from the newborn infant female, her mother and all candidate fathers to determine whether the alpha male was the infant's father using a likelihood-based method of paternity assignment. In contrast to previous observations of male care of orphans, in this case the mother was present during observations. Further, unlike reports of male aggression towards infants, the infant was reunited with her mother on the third morning, and survived. Neither mother nor infant presented visible injuries. The alpha male never directed aggression towards the infant. Rather, he displayed attentive behaviours, for example by holding the infant to his chest, supporting her while moving, grooming her, and 'cuddling' and 'rocking' her. Paternity results revealed with a high degree of certainty that the alpha male was the infant's father. There are several alternative explanations for the male's behaviour, but this unusual case also highlights the need for further studies to determine under what circumstances adult male chimpanzees can recognise their own offspring.

Keywords Infant carrying · Paternity · *Pan troglodytes* · Bulindi · Uganda

Introduction

Infant carrying by adult males is rare in mammals, but more common in primates than in other mammalian orders (Kleiman and Malcolm 1981; Clutton-Brock 1991; Dunayer and Berman 2018). The high level of sociality typical of primates has been suggested to facilitate increased affiliative behaviours towards infants (Hrdy 2016). Nevertheless, males of only a few primate species (e.g. marmosets *Callithrix* spp., tamarins *Saguinus* spp., titi monkeys *Callicebus* spp. and owl monkeys *Aotus* spp.) regularly exhibit infant carrying (Fernandez-Duque et al. 2009). For example, titi monkey fathers may carry infants more often than mothers, with infants transported up to 70–90% of the time by fathers (Fragazi et al. 1982). Chimpanzees (*Pan troglodytes*) live in male philopatric, multimale–multifemale 'communities', characterized by a male dominance hierarchy (Goodall 1968; Nishida 1979; Boesch and Boesch-Achermann 2000; Mitani et al. 2010). The community represents the primary breeding unit with only a small proportion of extra-group paternities (Vigilant et al. 2001; Boesch et al. 2006; Inoue et al. 2008; Wroblewski et al. 2009; Newton-Fisher et al. 2010), since males of neighbouring chimpanzee communities are highly territorial and intercommunity interactions can have fatal consequences (Wilson et al. 2014).

Affiliative behaviour towards infants by adult male chimpanzees occurs commonly in the wild and typically involves males playing with and grooming infants (Nishida 1983; Goodall 1986). Extended care towards orphans (both weaned and unweaned) by adult males—including carrying

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orphaned infants—has been reported only from chimpanzees in Taï, Côte d'Ivoire (Boesch et al. 2010). However, infant carrying by wild adult male chimpanzees when the mother is alive appears uncommon and carrying episodes are typically brief (< 3 min; Nishida 1983). Conversely, adult male chimpanzees sometimes take infants by force from females within their community, but they usually kill the infant shortly thereafter (infanticide with or without cannibalism; e.g. Goodall 1977; Takahata 1985; Hamai et al. 1992; Arcadi and Wrangham 1999; Sakamaki et al. 2001; Murray et al. 2007, Nishie and Nakamura 2018).

Given the threat of deliberate or inadvertent infanticide, maternal protectiveness could explain the lack of documented cases of infant carrying by adult male chimpanzees. In addition, female chimpanzees usually disperse from their natal communities to join other communities and breed with unrelated males, and in the absence of supportive kin, chimpanzee mothers are typically protective of their infants and reluctant for others to interact with them (Nishida 1983; Goodall 1986). Moreover, chimpanzees are polygynandrous and females typically mate with several males when sexually receptive, making father–offspring recognition difficult and reducing the likelihood that males can target their own offspring for affiliative behaviours. Indeed, most cooperative behaviours described in the literature involve mothers permitting older offspring, or more rarely, non-kin females, to hold and carry infants (Pusey 1990; Nakamura and Hosaka 2015; Stanton et al. 2017). While carrying offspring potentially results in high energetic costs to carriers (Schradin and Anzenberger 2001), researchers recently discovered that female chimpanzees at Ngogo (Uganda) invest in their next offspring sooner through accelerated weaning when infants are handled by others (mostly by older juvenile siblings; Bãdescu et al. 2016).

Notman and Munn (2003) reported the only previous observation of extended infant carrying by a wild adult male chimpanzee, at Budongo (Uganda). In that case, the infant presumably died of starvation and dehydration after being carried for 2 days since it was not returned to its mother. We report another unusual case of infant carrying by an adult male chimpanzee (*Pan troglodytes schweinfurthii*) on two consecutive mornings at Bulindi (Uganda) that we compare with previous observations. Recently, Murray et al. (2016) showed that chimpanzee fathers at Gombe (Tanzania) associated more with their own offspring than with non-kin infants, particularly during early infancy when risk of predation and infanticide is highest. Similarly, Lehmann et al. (2006) reported that fathers at Taï played more often with their own offspring than with unrelated infants. These studies suggest that chimpanzee fathers may be able to recognise their own offspring. Here, we (1) present behavioural observations of infant carrying by the alpha male chimpanzee at Bulindi, and (2) use genetic parentage analyses to confirm that the female was the infant's mother and to test whether the male was the infant's father. Even if the paternity is confirmed there remain several potential explanations for this behaviour, but it would also highlight the importance of conducting further studies to determine under what circumstances adult male chimpanzees can recognise their own offspring.

Materials and methods

Bulindi (1°28′N, 31°28′E) is situated in Hoima District, western Uganda, midway between two main forest blocks separated by ca. 50 km (Budongo and Bugoma Forest Reserves). A genetic survey revealed that 260 or more chimpanzees from at least nine communities inhabit the intervening landscape (McCarthy et al. 2015), which is dominated by subsistence and commercial agriculture (McLennan 2008), and that female-biased dispersal has occurred frequently, at least until recently (McCarthy et al. 2018). The Bulindi chimpanzees are one of these communities. Their home range (ca. 20 km^2) consists of small degraded fragments of riverine forest and *Cyperus papyrus* swamp amid agricultural gardens and villages, and is bisected by a main road (McLennan and Plumptre 2012; McLennan and Asiimwe 2016). In heavily logged areas the understorey is characterised by dense vine tangles and *Lantana camara* thickets, which the chimpanzees use habitually for resting and shade.

At the time of the present observations (May 2016), the Bulindi community included 21 individuals: 2 adult males, 6 adult females (adult, ≥ 12 years), 1 adolescent male, 1 adolescent female (adolescent, 8–11 years), 4 juveniles (juvenile, 4–7 years) and 7 infants (infant, 0–3 years). They were fully habituated to researchers by 2015 (McLennan et al. 2019), but full day follows were not initiated until 2018. At the time of the present observations, the chimpanzees were followed during morning hours only. The behavioural observations reported here were made ad libitum on three consecutive mornings on 16–18 May 2016 by M. Cibot and T. Sabiiti, at distances of 10–40 m. Visual observation time (and total contact time including periods when the chimpanzees were not clearly visible because of dense vegetation) for each morning was 3 h 21 min (3 h 57 min), 2 h 25 min (4 h 45 min) and 2 h 18 min (5 h), respectively.

Fresh chimpanzee faecal samples were collected non-invasively from adult female *MD*, her newborn infant *MA* and all candidate fathers during daily observations, with an effort made to collect at least three samples per individual. Faecal samples were collected using the two-step ethanol–silica storage method described in Nsubuga et al. (2004). DNA was purified using the GeneMATRIX Stool DNA Purification Kit (Roboklon) according to the manufacturer's instructions. DNA amplification was performed

using a modification of the two-step multiplex PCR procedure described in Arandjelovic et al. (2009). Extracts were genotyped at 15 autosomal microsatellite loci and amplified in three independent reactions to control for allelic dropout (Arandjelovic et al. 2009).

We determined parentage using the likelihood-based assignment method in CERVUS 3.0.7 software (Kalinowski et al. 2007). First, we confirmed that *MD* was the mother of infant *MA* by conducting a maternity analysis. To do so, we performed 10,000 simulations of parentage, estimating the proportion of sampled mothers at 1 and a genotyping error rate of 0.01. The maternity analysis included the six adult females present at the time of *MA*'s birth, and confirmed *MD* as mother with greater than 99% confidence (LOD score, 8.48; 0 mismatching loci). Next, we performed a trio analysis to test paternity by including *MA* as the offspring with confirmed mother *MD* and four candidate fathers present in the community at the estimated time of conception (August–September 2015, assuming a gestation length of 225 days; Wallis 1997): three adult males (including one young adult male who subsequently died before the observations reported here) and one adolescent male aged 10 or 11 years with fully descended testicles. We performed 10,000 simulations of parentage by estimating the proportion of sampled candidate fathers at 0.80 and a genotyping error rate of 0.01, and subsequent paternity was confirmed with greater than 99% confidence. Genotypes used in these analyses comprised genetic data from newly collected samples as described above, in addition to samples collected previously from chimpanzees in the Bulindi community (McCarthy et al. 2015), and were 97% complete. Population-level data from this earlier study were used to determine allele frequencies used in the parentage analysis.

Fig. 1 *SL* sitting in a tree and holding *MD*'s newborn daughter *MA* to his chest

Fig. 2 *SL* climbing down from the tree, supporting the infant *MA* in his lap with his left hand. *MA*'s hand is visible beneath him

Results

The mother (*MD*) was first seen carrying a newborn infant female (*MA*) on 28 April 2016, having last been seen without an infant on 24 April 2016. Thus, we estimated *MA* was ca. 20 days old on 16 May. The chimpanzees were not observed on the 2 days (14–15 May) preceding the observations presented below. On 16 May 2016, at 08:03, observers located 18 chimpanzees in a stretch of swamp forest. Alpha male *SL* was sitting in a tree holding *MA* to his chest (Fig. 1; Online Resource 1 and 2). *MD* sat less than 2 m from *SL* but did not appear distressed or anxious. She even groomed *SL* and also played with an unrelated juvenile female. *SL* spent his time grooming *MA*, without moving in the tree. When *SL* changed his body posture he supported *MA* with his arm, but she produced small screams and whimpers. In response, *SL* showed silent bared-teeth grins (Parr et al. 2005; Waller and Dunbar 2005), while simultaneously 'cuddling' and 'rocking' *MA* closer to his chest. At 08:30, *MD* began to show behaviours indicating distress. She sat closer to *SL*, showing a bared-teeth expression while emitting low-intensity screams (Parr et al. 2005). *SL* displayed and chased *MD* once. During this sequence, *SL* was piloerect and held *MA* by only one of her arms, and not against his chest. At 08:37, *MD* climbed down from the tree. *SL* continued grooming *MA* until 09:11, when he descended the tree carrying her (Fig. 2) followed by other chimpanzees. From 09:15 until 12:00, when observations ended, the chimpanzees stayed on the ground in a dense *Lantana camara* thicket, which restricted visibility. *SL* was nevertheless observed still in possession of *MA*, while *MD* was observed grooming and playing with her older but still unweaned infant (aged < 3 years).

On 17 May 2016, observers located the entire community at 07:15. *SL* was again carrying *MA*. He moved very carefully with the infant, supporting her with his arm when

moving arboreally. *SL* spent most of his time grooming *MA*, who seemed healthy (Online Resource 3) and was strong enough to grasp *SL*'s hair. However, she was not observed trying to suckle. She was not heard crying and no injury was noted on her. Unlike the day before, *MD* was not observed very close to *SL* and showed no behaviours indicating distress. No injuries were evident, although her left breast was swollen (i.e. turgescent breast tissue, reddish, almost double sized compared to the right breast). At 09:40, the chimpanzees entered a dense swamp in which observers were unable to approach them closely or distinguish individuals reliably.

At 07:00 on 18 May 2016, *SL* was found alone eating a cultivated jackfruit (*Artocarpus heterophyllus*). He was no longer carrying *MA*. At 07:50, *MD* was seen carrying *MA* on her belly and her older infant on her back. At 08:10, she was observed breast-feeding *MA* while *SL* rested ca. 10 m away in the same tree. *MA* appeared uninjured. At 09:18, the chimpanzees entered a dense *Lantana* thicket. They were not visible again for the rest of the morning. In the following days, *MD* was always observed carrying her infant. *SL* and *MD* often maintained close spatial proximity, for example building day nests and resting close to each other. As of February 2019 no further attempt by *SL* to carry *MA* (or other infants) has been observed, and *MA* remains in good health. A complete description of the behavioural observations is available in Online Resource 4.

Among the four candidate fathers, *SL* was assigned as father of *MA* with greater than 99% confidence (log-likelihood ratio (LOD) score = 13.30 and 0 trio loci mismatching with *MA*). The remaining three candidate fathers had negative LOD scores ranging from − 13.50 to − 19.11 and 5–6 trio loci mismatching with *MA*, indicating a very low likelihood of parentage.

Discussion

This study reports a case of a wild chimpanzee infant being carried by an adult male on a minimum of two consecutive mornings and released back to the mother, uninjured and healthy. In Taï National Park, West Africa, several cases of infant adoptions by adult males after the mother had died have been described (Boesch et al. 2010). In East Africa, only one observation has been reported of extended infant carrying by a male chimpanzee in Budongo Forest, located 25 km north of Bulindi (Notman and Munn 2003). In that case, a high-ranking adult male carried a newborn male infant over 2 days, without exhibiting aggressive behaviour towards him. It was unclear if the mother was still alive or from another community since no female within the male's community appeared anxious, distressed or interested in the infant, which might indicate that she was the mother. Across the 2 days, during which the male nested overnight with the infant, the infant tried to suckle and often screamed, suggesting that he was experiencing pain or distress. Finally, the infant died after 2 days and the adult male carried the body during at least one additional morning; whether he subsequently cannibalized the corpse was unknown. Here, the mother's (*MD*) behaviour on the first morning suggests that she wanted her infant back, at least during initial observations. She stayed near *SL* and showed facial expressions and soft screams indicating distress. Nevertheless, the mother did not show any visible injuries, and even if she demonstrated some initial distress, she quickly became calm again. Three hours after observations began, *MD* appeared relaxed, playing with her older infant, without showing much interest in *SL* holding *MA*. This observation is inconsistent with previous reports of infants snatched by adult males, which often resulted in infanticide. In these cases, mothers (whether from the same or a different community as the attacking males) appeared anxious or distressed, screamed, bit, and chased the males who took their infants, and often sustained wounds suggesting that they had fought in an attempt to retrieve their infants from the males (e.g. Goodall 1977; Hamai et al. 1992; Arcadi and Wrangham 1999; Kutsukake and Matsusaka 2002; Murray et al. 2007).

The motive for *SL*'s carrying and attentive behaviour toward the infant remains unclear. In the Budongo case, Notman and Munn (2003) suggested that the male was motivated initially by infanticide but may have aborted his goal when he became fixated on the infant. We have previously described fixated behaviour shown by juvenile and adolescent chimpanzees at Bulindi after capturing small animals (guineafowl and hyrax). In these observations, chimpanzees upended the dead bodies, sometimes holding them by one leg and rotating the bodies, and touching and smelling them intently, but without consumption (Cibot et al. 2017). Even if *SL* was fixated on the infant, his behaviour was always attentive (keeping her close to his chest, supporting her with his arm, and 'rocking' her when she emitted soft vocalisations), which seems to rule out the possibility that *SL*'s behaviour was motivated initially by infanticide. In addition, *MA* never seemed in particular distress or discomfort, and appeared in good health throughout observations (i.e. she appeared alert and had sufficient strength to cling to *SL*, and did not try to suckle while he carried her). Unfortunately, our research team did not follow the chimpanzees all day; thus, it remains unclear if *SL* kept the infant continuously throughout the afternoon and night during this period. However, it is hard to believe that *MA* could have stayed physically strong without crying or trying to suckle during the two mornings of observation, without hypothesising that *SL* potentially returned the infant to *MD* during some moments of the day or overnight.

Explanations for the observed behaviour could be either non-adaptive (i.e. it did not benefit *SL, MD* or *MA* in any

way and may be a by-product of selection for other facets of sociality in chimpanzees) or it could have been adaptive. Indeed, we could also suggest that *SL*, by showing attentive behaviours towards *MD*'s infant, might profit by courting her favour, therefore gaining future reproductive benefits by being allowed to mate more often with her in future (van Schaik and Paul 1996). This strategy has already been described in other animal species, notably in birds and fish (e.g. Rohwer et al. 1999). A recent study showed that chimpanzee females in Budongo Forest preferentially associate with a potential 'protector male' when infanticide risk is high (i.e. during early infancy; Lowe et al. 2018). Thus, *MD* could have allowed *SL*'s behaviour at a time when her infant was at an increased risk of infanticide by other males or females. Finally, it is conceivable that *MD* was facing two difficulties at the time of the study. First, she could have been suffering from her turgescent left breast tissue (i.e. engorgement, mastitis or infection). Nevertheless, the swelling of the breast could also have resulted from reduced breast-feeding since her infant was being held by *SL*. Secondly, having two unweaned infants at the same time could have been an extra burden for *MD*. Indeed, we should note the very young age of her older infant, who was less than 3 years old at the time of the incident; the average inter-birth interval at the majority of chimpanzee study sites is greater than 5 years (Emery Thompson 2013). For these reasons, *MD* might have been more tolerant of *SL* carrying *MA*. A previous study described a mother chimpanzee at Mahale (Tanzania) allowing an adolescent daughter to often carry her infant, which was disabled and required additional care (Matsumoto et al. 2016).

Our paternity results revealed that *SL* is *MA*'s father with a high degree of certainty. *SL* is typically highly possessive of maximally swollen females including *MD*, preventing other males from mating by mate guarding receptive females, or taking them on consortship away from other males (unpublished data). *SL*'s ability to monopolise receptive females successfully is facilitated by the relatively small number of male competitors present; at the time of *MA*'s conception only three adult males and one subadult male were present in the Bulindi community. Additionally, opportunities for females at Bulindi to mate with extra-group males (as occurs at other sites at a null or low frequency; e.g. Vigilant et al. 2001; Inoue et al. 2008) are negligible because the chimpanzees' range does not overlap with neighbouring communities (minimum distance to nearest community is ca. 8 km across a human-dominated landscape). This situation may increase the ability of males in small communities like Bulindi to control their reproductive success, and therefore we speculate that *SL* had good reason to recognise the infant as his own. Only two studies have previously suggested that chimpanzee fathers may be able to recognise their own offspring (Lehmann et al. 2006; Murray et al. 2016). However, further research is needed to provide more conclusive evidence that male chimpanzees can identify their own offspring and, if so, under what circumstances they can be certain of paternity.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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