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Cases of maternal cannibalism in wild bonobos (*Pan paniscus*) from two different field sites, Wamba and Kokolopori, Democratic Republic of the Congo

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Abstract Maternal cannibalism, whereby a mother consumes her own offspring, occurs in various animal taxa and is commonly explained by nutritional stress or environmental pressures. It is rare in nonhuman primates and is considered an aberrant behavior only observed under high-stress conditions. It was therefore surprising when, in the first reported case of cannibalism in wild bonobos, a mother consumed part of the dead infant at LuiKotale. Here we report two more cases of maternal cannibalism by wild bonobos at two different study sites, Wamba and Kokolopori. The dead infants' mothers participated in the cannibalism in both cases. At Kokolopori, although the mother did consume part of the carcass, it was held and shared by another dominant female. At Wamba, the mother was a dominant female within the community and was the primary consumer of the carcass. In both cases, cannibalism resembled other meat-eating events, with the dominant female controlling meat consumption. Infanticide was not observed in either case, but its occurrence could not be ruled out. Although rare, the occurrence of maternal

cannibalism at three different study sites suggests that this may represent part of the behavioral repertoire of bonobos, rather than an aberrant behavior.

Keywords Bonobo · Cannibalism · Meat eating · *Pan paniscus* · Thanatology

Introduction

Nonhuman primate mothers often show interest in their dead infants and may carry them for a prolonged period [e.g., ring-tailed lemur (*Lemur catta*): Nakamichi et al. 1996; Japanese macaque (*Macaca fuscata*): Sugiyama et al. 2009; gelada baboon (*Theropithecus gelada*): Fashing et al. 2011; chimpanzee (*Pan troglodytes*): Biro et al. 2010]. Chimpanzee mothers may carry their dead infant for over a week, and even up to 111 days (Matsuzawa 1997; Hosaka et al. 2000; Biro et al. 2010), in cases where the infants likely died of natural causes. But when a chimpanzee infant is killed by infanticide, the carcass is often consumed by the killer and other community members. In these events, the mother has never been observed to consume the infant (e.g., Goodall 1977; Arcadi and Wrangham 1999).

In bonobos, dead infants are often carried by mothers or relatives for several days (Kano 1992; Fowler and Hohmann 2010; T. Sakamaki, personal communication), but prolonged carrying (more than 10 days: Fashing et al. 2011; Anderson 2011) has not yet been reported. Infanticide has also never been reported. Cannibalism, however, has been reported in wild bonobos at LuiKotale (Fowler and Hohmann 2010). After the mother had carried the dead infant for one day, the carcass was consumed by several community members, including its mother. Maternal cannibalism, whereby a mother consumes its own offspring, occurs in various animal

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species, ranging from insect to mammals (e.g., Bartlett 1987; Elwood 1991; Mociño-Deloya et al. 2009). It is rare in primates, and has been attributed to high maternal stress levels (Tartabini 1991; Culot et al. 2011), or is suggested to be an aberrant behavior (Dellatore et al. 2009). In tamarin species (*Saguinus* spp.), two cases of maternal infanticide followed by cannibalism have been observed; in both cases the likelihood of infant survival was low, and the mothers might therefore have killed and consumed the infant to cut their losses and improve their lifetime fitness (Culot et al. 2011). However, in the case of wild bonobos at LuiKotale, the authors did not observe signs of environmental or social stress in the community; nor did they observe infanticide prior to the cannibalism (Fowler and Hohmann 2010). They suggested that maternal cannibalism in bonobos may not necessarily be a result of high stress or an aberrant behavior, or to be preceded by infanticide (Fowler and Hohmann 2010). Here we report two more cases of maternal cannibalism in wild bonobos observed at two different field sites, Wamba and Kokolopori, and discuss the similarities and differences among these three cases.

Methods

We observed one case of cannibalism on March 11, 2015, at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo. Long-term bonobo research has been ongoing at Wamba since 1974 (Kano 1992). Habituation of “PE group” community started in October 2010 with bed-to-bed following, and the bonobos were fully identified and habituated at the time of the event. PE group consisted of 25 individuals, including 9 adult females, 5 adult males, and 1 adolescent male. We followed the mother of the dead infant, an old adult female called Hide, intensively. The cannibalism event was recorded (written and filmed) *ad libitum* by NT, KEG, and four field assistants (two in the morning and two in the afternoon).

We observed another case of cannibalism on May 7, 2014, at Kokolopori Bonobo Reserve (KBR), Democratic Republic of the Congo. Work at KBR has focused on conservation efforts, including a monitoring program that began in 2002. Habituation of Ekalakala community started in March 2014 with bed-to-bed following. At the time of the event, the bonobos were semi-habituated, with 12 out of 19 individuals identified. The event was observed by two field assistants. The following day, DLM interviewed them and collected their field notes, which recorded bonobo activity at 15-min intervals. The field assistants were not able to identify all individuals, but were familiar with the two adult females central to this event, Mabel and Liselle.

Results

Case at Wamba

Background

Two adult female bonobos, Hide and Ichi, and their offspring participated in the cannibalism event. Hide was first identified in 2007. Her left leg had already been amputated below the knee, probably by a hunting snare. She was estimated to be 38 years old in 2015, and her son, Hideo, was 4 years old. Hide was a high-status central female. Starting in January 2015, she frequently disappeared from large parties and appeared to be in late pregnancy, judging from her genital swelling and changes in behavior. The other female, Ichi, was 26 years old and accompanied by 11-year-old and 3-year-old sons, Ikura and Isao, respectively. Ichi was also in late pregnancy and gave birth on March 24, 2015. Ichi was lower ranking than Hide, as judged by dominance behaviors such as meat-sharing interactions.

Before cannibalism

Although we usually observed PE group from bed to bed, we lost them from 12:00 on March 9 until 08:40 on March 11. Hide was observed without an infant immediately before we lost PE group, and was observed carrying a dead newborn infant at 08:42 on March 11. Her amputated leg affects her mobility, so she held the carcass between her left thigh and belly (groin pocket: Nishida et al. 1999). The infant was already decomposing, very soft, and emitting a strong rotten odor. Its head was greatly deformed, but no injury was observed on the carcass.

Hide did not exhibit any unusual behavior while carrying the dead infant, except that she persistently swatted flies that gathered around the carcass. She traveled with other party members (see Table 1), and engaged in genito-genital rubbing with another female, Maluta, when feeding on fruit of *Pancovia laurentii*. Other adult members did not show apparent interest in the carcass, whereas three immatures approached it. At 11:38, a female infant, Mazy, approached and licked the carcass. Hide pushed her away. At 12:10, Isao peered at the carcass. Hide grabbed him to drive him away and he screamed. At 12:54, Hideo touched the carcass. Hide blocked him using her right hand. Aside from these protective behaviors, Hide did not show apparent maternal behavior (such as grooming) toward the dead infant.

Table 1 Individuals present during the dead infant carrying and cannibalism event at Wamba

Time	Individuals observed
8:40–8:59	Females + immatures Hide + Hideo, Ichi + Isao, Maluta + Mazy, Kabo + Kale, Bokuta Males Turkey, Malusu, Ikura
9:00–9:59	Females + immatures Hide + Hideo, Ichi + Isao, Maluta + Mazy, Kabo + Kale, Bokuta, Pao + Pipi + Puka, Marie + Marina Males Turkey, Malusu, Ikura, Daniel, Gai
10:00–10:59	Females + immatures Hide + Hideo, Ichi + Isao, Maluta + Mazy, Bokuta, Pao + Pipi + Puka, Nara + Narisa, Saku + Sachi + Sato Males Malusu, Gai
11:00–11:59	Females + immatures Hide + Hideo, Ichi + Isao, Maluta + Mazy, Bokuta, Kabo + Kale, Pao + Pipi + Puka, Nara + Narisa Males Turkey, Malusu, Ikura, Daniel
12:00–12:59	Females + immatures Hide + Hideo, Ichi + Isao Males
13:00–13:59	Females + immatures Hide + Hideo, Ichi + Isao, Maluta + Mazy, Bokuta Males Turkey, Daniel, Gai
14:00–14:59	Females + immatures Hide + Hideo, Ichi + Isao, Bokuta, Nara + Narisa Males Ikura
15:00–15:59	Females + immatures Hide + Hideo, Ichi + Isao, Bokuta, Kabo + Kale, Saku + Sachi + Sato Males Malusu, Ikura, Gai

**Fig. 1** Hide consuming meat of the dead infant

During and after cannibalism

At 14:04, Hide was sitting on the ground while other members climbed up and fed on *Pancovia laurentii* fruits. She grabbed the carcass in her right hand and suddenly bit off the head and chewed it (Fig. 1). Hideo peered and touched her mouth. At 14:05, she spat out a small piece of meat from her mouth and Hideo ate it. At 14:06, Ichi and Isao approached Hide. Ichi sat within 1 m of Hide but did not perform any begging behavior, such as peering or touching the mouth of the possessor (Goldstone et al. 2016). From 14:09 to 14:14, Isao continually tried to take

the carcass. Hide moved her hand that was holding the carcass to avoid him. Isao occasionally grabbed the carcass and licked his own hand. Hide grabbed Isao's hand and pushed him back three times at 14:10, 14:11, and 14:13. Isao screamed at 14:11. At 14:13, Hideo got a piece of meat from Hide and Ichi grabbed it from him and ate it. Hideo grimaced at Ichi. We did not observe meat-sharing directly between Hide and Ichi.

At 14:14, Hide stopped eating the carcass. She had consumed the carcass's head and most of its torso, but all arms and legs were intact. Ichi lay down ~1 m from Hide. Ikura was lying 2 m from Hide. At 14:23, Hideo climbed ~3 m up a tree with the remainder of the carcass, including three of the arms and legs, and started eating it (Fig. 2). Hide was still holding one detached limb. At 14:38, Hideo finished eating the meat.

At 14:39, the other party members vocalized and started traveling. Hide followed them. She carried the leftover limb between her left leg and body like she had done before. The party continued traveling until they made night nests at 17:18, except for stopping shortly (for less than 10 min) to feed on shoots of *Megaphrynium macrostachyum* and fruit of *Pancovia laurentii*. At 15:39, Hide stopped on the ground, put the remainder of the carcass in her mouth, and ate it.

On March 16, only 5 days after the cannibalism, Hide's genitals reached maximal swelling and she started to copulate. She was observed carrying a newborn infant on January 22, 2016.



Fig. 2 Hideo consuming meat of the dead infant

Case at Kokolopori

Background

Eight adult females, one juvenile female, and two infants participated in the cannibalism. Prior to this event, we had noted that the adult female, Mabel, was pregnant, and on April 28, 2014, she was first observed with a new female infant, whom we named Avril. We observed Avril on 8 of 10 days leading up to her death. An adult female, Liselle, carried the carcass throughout the entire cannibalism event. Although rank order has yet to be established for Ekalakala community, Liselle had demonstrated dominant behaviors (e.g., feeding priority and displacement) during our bed-to-bed follows.

During cannibalism

At approximately 06:00 on May 7, 2014, two field assistants arrived at Ekalakala's bed site. The party at that time included three adult males, eight adult females, one juvenile female, and three infants (Table 2). Liselle was in the

canopy with her own infant on her back and, in her hand, she was carrying a dead infant by the neck. Mabel was not accompanied by her infant. No injury was observed on Mabel. When Liselle descended to the ground at ~07:00, along with Mabel, six other adult females, one juvenile female, and two other infants, the field assistants observed that the dead infant had been eaten around the eyes. All 11 individuals including Mabel, the putative mother, consumed the carcass. They all reached in and grabbed pieces of the carcass, tearing the skin from the meat. An adult male displayed by branch-dragging in a circle around the group, but this male was not observed to consume any of the meat. Liselle continued to hold the dead infant throughout the morning, and the same individuals (Liselle, Mabel and six other adult females, one juvenile female, and two other infants) continued to intermittently consume the carcass, in combination with other plant foods (e.g., *Scorodophloeus zenkeri*, *Brachystegia laulentii*, *Artabotrys* sp., *Sterculia bequaertii*, *Hibiscus* sp., *Treculia africana*). At approximately 13:00, Liselle discarded the bones.

Discussion

Three cases of cannibalism by wild bonobos have now been observed at three different field sites, and the mothers of the dead infants participated in meat consumption in all cases (Fowler and Hohmann 2010; this study). Although rare, these cases show that cannibalism of dead infants and notably *maternal* cannibalism are part of the behavioral repertoire of bonobos, not an aberrant behavior.

Cannibalism is well documented in chimpanzees (e.g., Watts and Mitani 2000). The behavior is associated with infanticide, which is infrequent but has been observed in multiple long-term chimpanzee field sites (Arcadi and Wrangham 1999). Infanticide has never been reported in bonobos, and it is unlikely that infanticide occurred before the cannibalism events at LuiKotale and at Wamba. At LuiKotale, no agonistic interaction was observed before the infant's death, and there was no injury on the carcass (Fowler and Hohmann 2010). At Wamba, the infant might have been stillborn considering the deformity of the head, soft bones, and degree of decomposition. The cause of death at Kokolopori is difficult to determine because we do not know whether the infant was alive when the dominant female gained possession. Kidnapping by females sometimes occurs in wild bonobos, and if the mother was subordinate to the kidnapper, it would have been difficult for the mother to retrieve her infant, which may have been fatal to the infant (Hohmann and Fruth 2003; Tokuyama 2015).

In all three cannibalism cases, dominant females controlled meat consumption. At LuiKotale, the carcass was

Table 2 Individuals present during the cannibalism event at Kokolopori

Time		Individuals observed
6:00–6:59	Females + immatures	Liselle, Mabel, 6 females, and 4 immatures
	Males	3 males
7:00–7:59	Females + immatures	Liselle, Mabel, 6 females, and 4 immatures
	Males	4 males
8:00–8:59	Females + immatures	Liselle, Mabel, 6 females, and 4 immatures
	Males	4 males
9:00–9:59	Females + immatures	Liselle, Mabel, 6 females, and 4 immatures
	Males	4 males
10:00–10:59	Females + immatures	Liselle, Mabel, 5 females, and 3 immatures
	Males	3 males
11:00–11:59	Females + immatures	Liselle, Mabel, 6 females, and 3 immatures
	Males	3 males
12:00–12:59	Females + immatures	Liselle, Mabel, 5 females, and 4 immatures
	Males	3 males
13:00–13:59	Females + immatures	Liselle, Mabel, 5 females, and 4 immatures
	Males	4 males

removed from a subordinate mother by a dominant female who started to consume it (Fowler and Hohmann 2010). At Kokolopori, the carcass was held by an apparently dominant female and shared with other community members. The case at Wamba was somewhat different in that the mother was the dominant female in the community. She started the cannibalism and shared meat only with her son. It is therefore not always the case that cannibalism starts only when a higher ranking female uses force to gain possession of another female's infant, as Fowler and Hohmann (2010) suggested—the mother of the infant can also initiate cannibalism.

That mothers participate in the cannibalism of their infants is a notable behavior, which may be explained nutritionally. Maternal cannibalism in other animal species is usually associated with maternal infanticide (e.g., Elwood 1991; Culot et al. 2011). The most widely accepted interpretation of maternal infanticide and maternal cannibalism is that the mother commits infanticide when the infant has a low likelihood of survival, and she then consumes it to improve her chances of reproduction in the future (Klug and Bonsall 2007). In bonobos as well, it is likely that mothers gain a nutritional benefit by consuming the meat of their dead infant. While we could not quantify the nutritional benefit of the dead infant at Wamba, the mother resumed her estrous cycle only 5 days after she cannibalized her dead infant, and gave birth about 10 months after the event. The duration of pregnancy is 7–8 months in bonobos (Heistermann et al. 1996). It seems that she became fertile shortly after her potential miscarriage, and perhaps this was facilitated by consuming the carcass. However, consuming dead infants poses a risk of disease transmission (Rudolf and Antonovics 2007),

particularly when the infant died of natural causes and when the carcass is rotting. Avoiding such a risk might be one of the reasons why (maternal) cannibalism is rare, despite the potential nutritional benefit.

Besides the nutritional benefits of cannibalism, we should not ignore the very real questions surrounding whether animals are able to understand the concept of “death,” and whether the mother and community members recognize the corpse as her dead offspring or their dead conspecific. It is common to carry an infant after death in nonhuman primates, and the behavior is considered to represent strong social bonding between mothers and infants (e.g., Biro et al. 2010). Chimpanzee mothers regularly carry their dead infant for 1–7 days, but can carry it for much longer, with the longest reported time being 111 days (Matsuzawa 1997; Hosaka et al. 2000; Biro et al. 2010). During this time, they perform maternal behaviors, such as grooming the carcass (Hosaka et al. 2000; Biro et al. 2010). Other community members tolerate the carcass and may touch, groom, play with, and even carry it (Hosaka et al. 2000; Biro et al. 2010).

Although prolonged carrying has not been reported for bonobos, possibly because carcasses decompose rapidly in their hot and humid habitat, bonobo mothers can also carry their infants for 1–3 days after death (Kano 1992; Fowler and Hohmann 2010; this study; T. Sakamaki, personal communication). Kano (1992) observed a dead infant carried and groomed by her mother and older brother. Similarly, in two of three maternal cannibalism cases in bonobos, dead infants were carried by their mother for 1–3 days (at LuiKotale: Fowler and Hohmann 2010; and at Wamba: this study). At LuiKotale, the mother and the older sister groomed the dead infant just before the cannibalism

event started (Fowler and Hohmann 2010). At Wamba, the mother behaved protectively when other infants approached the carcass.

These behaviors may point toward “maternal persistence” (Sugiyama et al. 2009), where the mother continues to care for her infant even after its death. But then suddenly, the infant becomes a food item for both the mother and other community members. As stated previously, maternal cannibalism in other animal species typically occurs immediately after maternal infanticide, not after natural deaths and carrying (e.g., Culot et al. 2011). The dramatic change of a mother’s behavior towards her dead infant from maternal to cannibalistic has only been observed in wild bonobos (Fowler and Hohmann 2010; this study) and in one rehabilitated orangutan (Dellatore et al. 2009). However, in the case of the orangutan, the authors concluded that maternal cannibalism was aberrant behavior caused by the mother’s high stress resulting from ex-captive experiences and the presence of tourists. For bonobos, we still do not know the physiological or emotional changes which may provoke this drastic behavioral change.

To date, three cases of cannibalism in wild bonobos have been observed at three different field sites, and in all cases (1) the subject was a dead infant whose cause of death was likely not infanticide, (2) the mother of the infant participated in consuming the carcass, and (3) the meat consumption was controlled by a dominant female. Bonobos are the only great ape species known to engage in maternal cannibalism under wild conditions, and they treat it like meat-sharing, which brings up the question of how bonobos consider the death of conspecifics.

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Compliance with ethical standards

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

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