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SPECIAL FEATURE: NEWS AND PERSPECTIVES

Responses to Death and Dying: Primates and Other Mammals

Prolonged care and cannibalism of infant corpse by relatives in semi-free-ranging capuchin monkeys

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Abstract

Cannibalism is a quite common behaviour in animals that can have survival value when food is scarce or in the case of overpopulation. Conversely, cannibalism can also increase pathogen transmission and reduce fitness. In primates, some cases of cannibalism are associated with infanticide or are performed by mothers after their newborn has died (filial cannibalism). We report here the first observation of cannibalism, specifically infant cannibalism, in a semi-free-ranging group of brown capuchin monkeys (*Sapajus apella*). The baby was likely stillborn, as parts of the cranial bones were missing and no fresh injuries were visible. After half a day of taking care of the dead infant, the mother ate part of the corpse's skin and the highly nutritional viscera, possibly thereby compensating for the physiological costs of pregnancy. After attentively watching his mother's behaviour, the older brother of the dead newborn similarly ate parts of the corpse. Although we cannot rule out idiosyncrasy and vertical social transmission, it is possible that cannibalism is a normal—albeit rare—part of the behavioural repertoire of capuchin monkeys.

Keywords Cannibalism · Filial cannibalism · Death · Thanatology · Maternal care · *Sapajus apella*

Introduction

Cannibalism is a common behaviour throughout the animal kingdom, having been recorded in more than 1500 species ranging from molluscs to mammals (Polis 1981). Because cannibalism can provide animals with energy and nutrients, it can be advantageous in environments where food is scarce (Snyder et al. 2000). Cannibalism rates generally increase when food availability decreases (e.g., in molluscs, Hughes 1985) or when population density increases (e.g., in rodents, Southwick 1955). However, cannibalism may also increase the risk of pathogen and disease transmission (Rudolf and Antonovics 2007).

In mammals, cannibalism often follows infanticide (Culot et al. 2011), an adaptive reproductive strategy reported in many animal species (e.g., artiodactyls, Bartos and Madlafousek 1994; carnivores, Corbett 1988; perissodactyls, Duncan 1982; chiropterans, Joermann 1988; rodents, Coulon et al. 1995; primates, Ebensperger 1998, Arcadi and Wrangham 1999, Soltis et al. 2000, Harcourt and Stewart 2007, Masi and Bouret 2015). In primates, however, infanticide does not always result in cannibalism; males kill infants not for food, but so that the mothers will resume reproductive cycling sooner (e.g. Soltis et al. 2000). In fact, cannibalism has been documented in only a few wild primate species, including common marmosets (e.g. Bezerra et al. 2007), snub-nosed monkeys (Xiang and Grueter 2007), moustached tamarins (Culot et al. 2011), rhesus macaques (Tian et al.

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2016), chimpanzees (e.g. Watts and Mitani 2000), bonobos (e.g. Tokuyama et al. 2017) and semi-free-ranging orangutans (Dellatore et al. 2009). In chimpanzees, infanticide victims are often at least partly consumed by the killer and other community members (Watts and Mitani 2000), but the mother has never been observed to consume her infant (e.g. Goodall 1977; Arcadi and Wrangham 1999).

The killing and consumption of their own infants by mothers is rare in free-ranging primates compared with other mammal species (Hrdy 1979). However, partial consumption of the infant's body without evidence of prior killing by conspecifics may occur, i.e., "passive cannibalism" (Anderson 2019). Filial passive cannibalism has been observed in captivity and in the wild, in galagos (e.g. Tartabini 1991), tamarins (Culot et al. 2011), Japanese macaques (Watson et al. 2015), Tonkean macaques (De Marco et al. 2018), Taihangshan macaques (Tian et al. 2016), bonobos (e.g. Tokuyama et al. 2017) and orangutans (Dellatore et al. 2009). Filial cannibalism has been interpreted as an aberrant behaviour (Dellatore et al. 2009), arising from stressful conditions (Tartabini 1991; Culot et al. 2011), or as a possible natural part of the repertoire (e.g., bonobos, Tokuyama et al. 2017; Tonkean macaques, De Marco et al. 2018).

Stillborn babies and dead infants often elicit maternal care that persists for days, weeks or even months after the death, in both wild and captive primates (e.g. Sugiyama et al. 2009; Anderson 2011; Biro et al. 2010; Cronin et al. 2011; King 2013; De Marco et al. 2018; Watson and Matsuzawa 2018), and in other mammalian groups, aquatic and terrestrial (manatees, e.g. Hartman 1979; sea otters, e.g. Kenyon 1969; seals, e.g. Rosenfeld 1983; cetaceans, e.g. Lodi 1992, Alves et al. 2015; elephants, e.g. Douglas-Hamilton et al. 2006; giraffes, e.g. Muller 2010). Although death-related behaviours such as continuing maternal care were long considered exclusively human (Fashing et al. 2011), more recently have they been related to the cooperative, succouring and protective nature of social mammals (de Waal and Preston 2017; Perez-Manrique and Gomila 2017). These actions have been associated with the hormonal state of the female and/or her emotional attachment to the infant (Biro et al. 2010). Alternatively, such behaviour might reflect lack of understanding by the mother that her offspring is no longer alive (Hrdy 1999). If this knowledge is related to maternal experience, then nulliparous or otherwise inexperienced mothers might be more likely to persist in caring for or carrying dead infants (Biro et al. 2010; Warren and Williamson 2004).

Although cannibalism has never been described in capuchin monkeys, infanticide has been observed in three species (white-faced capuchins, *Cebus capucinus*; Rose 1994, Fedigan 2003, MacKinnon 2002, Manson et al. 2004; wedge-caped capuchins, *Cebus olivaceus*; Valderrama et al. 1990; tufted capuchin monkeys, *Cebus apella*; Izar et al. 2007, Ramírez-Llorens et al. 2008). In wild white-faced capuchins, reported dead infant-directed behaviours include repeated approach/retreat, lick, groom and hold/carry (Perry and Manson 2008), behaviours which lasted no more than 1 day. Here, we describe a case of a short period of continued maternal care followed by cannibalistic behaviour on a presumed stillborn infant by its mother and its older brother, in a semi-free-ranging group of brown capuchin monkeys.

Methods

Observations took place on 3–4 August 2017 at the Primate Centre of Strasbourg University, France. The study group of brown capuchin monkeys (*Sapajus apella*), all captive-born, contained 17 individuals living in a wooded outdoor area of 2332 m^2. They also had free access to an indoor area, in which food (commercial primate pellets) and water were available ad libitum. The individuals involved in the cannibalism events were a 10-year-old alpha female (Willow), her 3-year-old son (Balin), and the 18-year-old alpha male (Popeye), the group leader for more than 5 years. We made these observations during a study on spatial foraging strategies (details in Trapanese et al. 2018, 2019a, b) that lasted from March to October 2017. During this period, we conducted daily focal follows (Altmann 1974) on six individuals including Willow and Popeye, from 09:00 to 12:00 h and from 14:00 to 17:00 h.

Results

Direct observation of cannibalism

The cannibalism events described here were the only ones observed during the 8-month study period, during which one other birth occurred; the infant remained in good health.

Day 1

On 3 August 2017 at 09:00 h, observers G.T. and M.B. saw Willow, clearly pregnant during the previous few days, holding a dead newborn in her arms. As we had left the group at 17:00 h the previous evening, the baby was presumably born during the night or early morning. The baby's skull was incompletely formed: parts of the cranial bones were missing, leaving almost half of the skull cavity visible. Skin was detached from the chin and the mandibles, resulting in what looked like a mask hanging from the skull only by a flap of skin. No fresh wounds were visible; the detached skin appeared dry, with the inner part being dark red (Fig. 1a, b). The rest of the body looked normal. We were unable to determine the baby's sex.

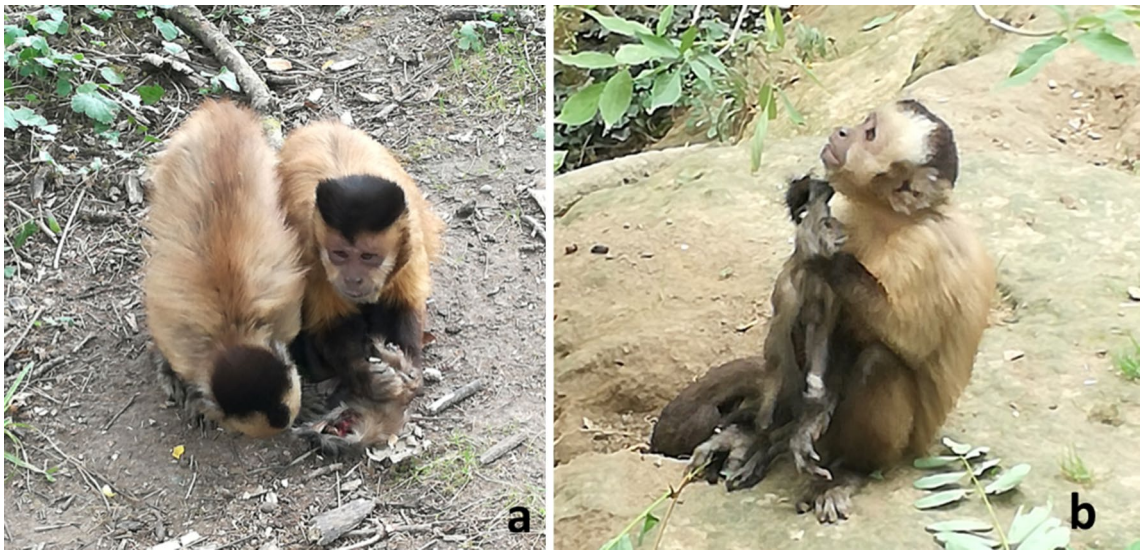

Fig. 1 **a**, **b** The mother of the dead infant (Willow, on the right) holds the corpse in her hands, and the brother Balin (on the left) sits in physical contact with the mother, observing the corpse. The open skull cavity was visible (**a**) because some parts of the cranial bones were missing. **b** The brother holds the corpse with both hands. This picture shows the well-formed face of the dead infant detached from the skull, probably a congenital malformation. No fresh wounds were visible around the head area (photo credits: G. Tonachella)

Throughout the morning, Willow showed intensive interest in and care of the corpse. While moving, she held it tight against her body with one hand, and while resting she held it ventrally. She groomed and licked the corpse's fur frequently. Other individuals in the group showed no notable interest in these events and behaved as usual. Around 11:00 h, a conflict between juveniles broke out approximately 10 m from Willow and her dead infant. The alpha male, Popeye, reacted to the fight by rushing towards the juveniles. This scared Willow, who jumped away from Popeye, causing her to drop the corpse. She immediately retrieved it, shortly after which Popeye approached and sat next to her. He inspected the lower part of the corpse as Willow held its head close to her body, and he gently touched it and pinched the anal region. Immediately thereafter, Popeye approached another baby who was born a few days earlier (31 July); the latter was clinging on the back of his mother, 10 m from Willow. He touched the infant's body, pulled up its tail and touched its anal region for 40–50 s. The baby moved slightly but did not vocalize or wriggle away, while the mother moved 1 m away from Popeye. Then Popeye returned to Willow and again inspected her infant's corpse; this lasted approximately 2 min, although it was unclear whether he only touched the torso or also the anal region again. He then walked away, and we halted observations.

We resumed observations at 14:00 h, and over the next 3 h Willow's behaviour changed. She no longer clutched the corpse tightly against her belly; instead, she held it away from her body and manipulated it more roughly than in the morning. She sometimes held the corpse in awkward positions (i.e., by one arm or by the fur) and dragged it as she moved. She left it on the ground at least five times but retrieved it each time. At around 15:00 h, Willow started to tear at the corpse with her mouth, and with her hands she peeled the ventral skin from the bottom to the middle of the belly. She ate some pieces of skin, and then started to bite into the belly and eat some viscera.

During the afternoon, Popeye approached neither the corpse nor Willow. By contrast, Willow's son Balin was always within about 10 cm or else in physical contact with his mother or the corpse, whereas he had never been within 10 m of them in the morning. All afternoon he watched his mother attentively (Fig. 1a). Balin's younger brother, Conan (2 years old), was never seen close to his mother or older brother.

Day 2

On 4 August at 09:20 h, the cranial and rib cavities of the dead baby were completely opened and empty. The torso appeared empty too, the internal organs missing. Willow was no longer carrying the corpse but was always within 5 m of it. Later that morning she started to move further away from the corpse (up to 10 m) and only occasionally looked at it, whereas Balin approached it and held it (five times). More specifically, he picked up the corpse, held it in both hands, and threw it on the ground several times before retrieving it. He also threw it in the air playfully and jumped on it when it landed. At around 14:00 h, Balin started to eat parts of the trunk and legs, followed by the head. He also bit flaps

of skin and tore them off with his teeth (Fig. 2a). By around 17:00 h, the body was almost divided into two pieces, and Balin was still carrying and biting it (Fig. 2b, c). Again, no other group members showed interest in the corpse, and neither the mother nor the alpha male were seen nearby in the later afternoon. One of the two parts of the corpse was later found abandoned and removed by an animal keeper. The other part of the corpse was not found.

Discussion

This is the first report of passive cannibalism on a dead newborn in capuchin monkeys, specifically by the mother and then an older brother. Since parts of the cranial bones were missing but no blood or fresh wounds were visible (Fig. 1a, b), we hypothesize that the baby was stillborn, possibly due to mero-anencephaly, a well-known congenital malformation causing stillbirths in humans (Shewmon 1988; Sekhon 2017). We do not consider the observed cannibalism to be caused by stressful conditions, for the following reasons: (a) the study group lived in a large enclosure (2332 m^2) with luxuriant natural vegetation and ad libitum food and water; (b) the mother of the dead infant was the alpha female, with easy access to all resources; (c) no particular tensions were observed in the group during the months preceding this observation; and (d) at around the same time, another baby was born, and it remained in good health. Furthermore, cases of filial cannibalism have been described in wild primate populations, and thus captivity is not the primary cause of the phenomenon (e.g. Tokuyama et al. 2017; Dellatore et al. 2009).

For half a day the mother displayed protectiveness and care of the corpse similar to that provided to healthy offspring. This recalls observations in wild capuchins where maternal care and carrying of the dead infant lasted 1 day (Izar et al. 2007). Although maternal infanticide in primates is rare (but see Cäsar et al. 2008), sometimes-prolonged care and carrying is common (reviewed in Watson and Matsuzawa 2018; Anderson 2019), even though holding a lifeless corpse hinders locomotion and can negatively affect foraging and predator avoidance (Gonçalves and Carvalho 2019). Fashing et al. (2011) suggested that maternal caretaking of dead infants is costlier in terms of predation risk and energy expenditure (e.g., retrieving a corpse that has fallen to the ground) in arboreal species, such as capuchin monkeys, compared with terrestrial species. Indeed, maternal caretaking of dead babies is sometimes notably prolonged in more terrestrial monkeys such as Japanese macaques (Sugiyama et al. 2009; Watson et al. 2015).

A change from maternal care to cannibalizing dead primate infants has been observed both in the wild (Fowler and Hohmann 2010; Tokuyama et al. 2017; Dellatore et al. 2009; Tian et al. 2016) and in captivity (e.g. De Marco et al. 2018; Watson et al. 2015; Tartabini 1991). Maternal inexperience (primiparity) and very early death of the infant were proposed as reasons for prolonged maternal care (1 month) in Tonkean macaques (De Marco et al. 2018). However, in Japanese macaques, the propensity for carrying dead infants did not differ significantly between young, primiparous mothers (6–7 years old) and older, multiparous ones (10–25 years old; Sugiyama et al. 2009). In the case described here, as the infant was likely stillborn and it was the female's third offspring, inexperience does not account for post-mortem carrying and care.

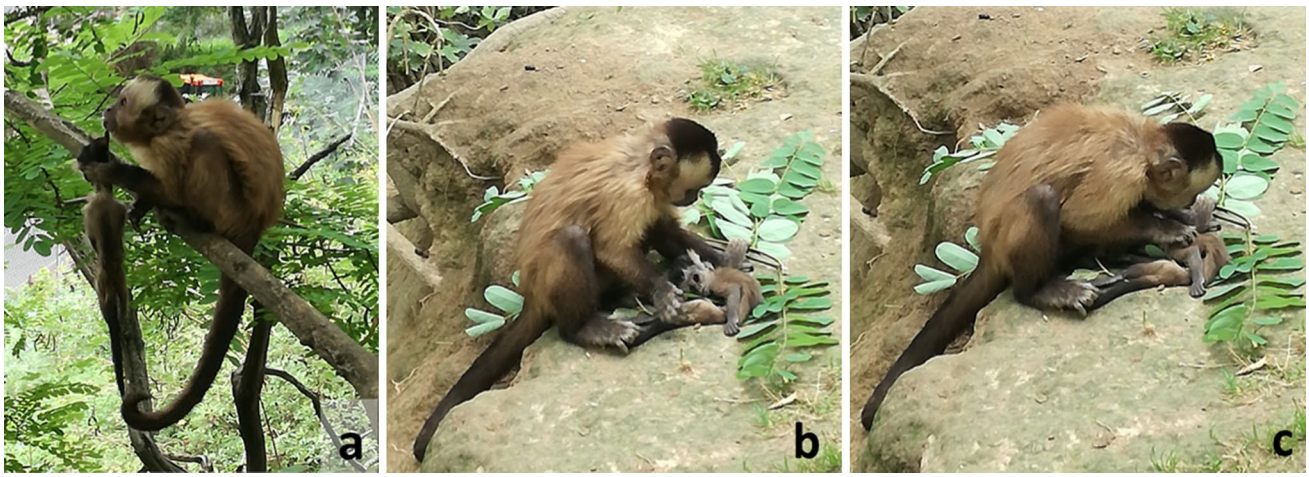

Fig. 2 **a**–**c** Sequences of cannibalistic behaviour by the dead infant's brother. **a** Balin carried the corpse, grabbed and ate part of it, and then dropped it. He always went to pick it up. **b** The facial skin resembled a detached mask. **c** Balin continued eating the corpse on the ground (photo credits: G. Tonachella)

Some hormone levels (e.g., steroids, oxytocin) are particularly high during the second half of pregnancy, playing a role in maternal motivation (Saltzman and Maestripieri 2011; Bercovitch 2019). If cannibalism always occurred at the end of maternal care and carrying of a dead infant, immediately before discarding the corpse, this would be consistent with a gradual weakening of the mother–infant bond and decreasing hormone levels (Saltzman and Maestripieri 2011). These physiological changes could also contribute to the behavioural change from treating the corpse as if it were alive to treating it as an object/food (Watson and Matsuzawa 2018). However, in primates, continued care/carrying and cannibalism may overlap (Watson and Matsuzawa 2018), which might help to compensate for the energy spent in carrying; in some cases, the corpse may be carried until complete mummification (Sugiyama et al. 2009; De Marco et al. 2018). A plausible alternative hypothesis for cannibalistic behaviour after a short period of maternal care (e.g., a few hours) is that it allows mothers to compensate for the costs of pregnancy (Wourms 1977; Elgar and Crespi 1992), and it might hasten the resumption of reproductive cycles (Osawa 2002). Our observation supports this hypothesis: just after she stopped caring for the corpse, the mother fed on the viscera, which are rich in proteins, vitamins and minerals (Walens and Wagner 1971). The female was in oestrus and courting the alpha male on 21 August, just 18 days after giving birth.

Interestingly, filial cannibalism was followed by fraternal cannibalism after the corpse was abandoned by the mother. The oldest brother of the dead infant ate parts of the corpse after he had seen his mother do this. He also carried and manipulated the corpse, sometimes dragging and biting it in ways similar to typical playful behaviour of juvenile capuchins. Even though adults may rarely interact with corpses, infants and juveniles often express interest in them, including play (Hosaka et al. 2000; Biro et al. 2010; Gonçalves and Carvalho 2019; Masi 2019). A female orangutan shared portions of her infant's corpse with an older daughter (e.g. Dellatore et al. 2009), and in other primates, dead infants have been partly eaten by older siblings (e.g., bushbabies, Tartabini 1991; bonobos, Tokuyama et al. 2017). We suggest that in primates, filial cannibalism may emerge through vertical social transmission (including social facilitation, as in orangutans), as related individuals are more likely to tolerate close proximity to each other.

It is noteworthy that the alpha male approached to inspect the dead infant only once, after it fell from the mother's hands. Conceivably, only then did he notice the infant's total lack of responsiveness. Just after inspecting the corpse's anal region, he did something similar with a healthy infant of similar age. Generally, physical contact with the corpse is directed towards the head or face (e.g. Anderson et al. 2010; Gonçalves and Carvalho 2019), but inspection of the anal region was recently reported in eastern gorillas (Porter et al. 2019: video of a silverback's reaction to an extra-group dead silverback). This area may be particularly important for detecting cues about vitality or death, possibly temperature or odour-related (e.g., putrescine).

In conclusion, our observations suggest that, although rare, cannibalism may be part of the behavioural repertoire of capuchin monkeys. Although reactions to dead infants are doubtless influenced by primate mothers' hormonal status, the precise proximal and ultimate causes of these phenomena need further investigation, to help distinguish between idiosyncratic and rare but species-typical death-related behaviours.

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