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ORIGINAL ARTICLE

Female-committed infanticide followed by juvenile-enacted cannibalism in wild white-faced capuchins

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Abstract

On 5 February 2021, we observed the first instance of female-committed infanticide followed by cannibalism in a long-studied (> 35 years) population of wild white-faced capuchins (*Cebus imitator*) in the Santa Rosa Sector of the Área de Conservación Guanacaste, Costa Rica. The events leading up to and including the infanticide and cannibalism were observed and documented ad libitum, with segments digitally recorded, and a post-mortem necropsy performed. Here we detail our observations and evaluate the events within the framework of leading adaptive explanations. The infanticide may have been proximately motivated by resource competition or group instability. The circumstances of the observed infanticide provided support for the resource competition, adoption avoidance, and social status hypotheses of infanticide, but not for the exploitation hypothesis, as neither the perpetrator nor her kin consumed the deceased infant. The subsequent cannibalism was performed by juveniles who observed the infanticide and may have been stimulated by social facilitation and their prior experience of meat consumption as omnivores. To our knowledge, cannibalism has been documented only once before in *C. imitator*, in an adjacent study group, with the two cases sharing key similarities in the context of occurrence and manner of consumption. These observations add to our growing knowledge of the evolutionary significance of infanticide and its importance as a reproductive strategy in nonhuman primates.

Keywords *Cebus imitator* · Conspecific necrophagy · Social facilitation · Primate thanatology

Introduction

Infanticide is the harming of an infant by non-parents of the same species that directly (e.g., physical aggression) or indirectly (e.g., kidnapping and neglect in care) leads to instant or imminent infant death (Digby 2000; Lukas and Huchard 2019). Infanticide is widespread in mammals (Ebensperger 1998) and is most commonly performed by males in polygynous societies characterized by high male reproductive skew (Harano and Kutsukake 2018; van Schaik and Janson 2000). In primates, infanticide is most commonly performed by males (reviewed in Bartlett et al. 1993; Palombit 2012; van Schaik and Janson 2000). By committing infanticide, a male may increase his fitness, as the female will resume ovarian cycling faster, thereby providing the male with the opportunity to sire offspring with her sooner than if her dependent infant had survived (Sexual Selection Hypothesis of Infanticide: Hrdy 1977, 1979).

Although females in other mammalian clades, such as rodents, are known to more commonly commit infanticide (Brown et al. 2020; Digby 2000), female-committed infanticide appears relatively uncommon in primates and has only been documented in a handful of species—including ring-tailed lemurs (*Lemur catta*: Jolly et al. 2000; Kittler and Dietzel 2016), red lemurs (*Eulemur fulvus rufus*: Jolly et al. 2000), yellow baboons (*Papio cynocephalus*: Shopland and Altmann 1987; Wasser and Starling 1988), chimpanzees (*Pan troglodytes schweinfurthii*: Townsend et al. 2007), saddle-back tamarins (*Saguinus fuscicollis*; Herrera et al. 2000), black-fronted

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titi monkeys (*Callicebus nigrifrons*; Cäsar et al. 2008), and common marmosets (*Callithrix jacchus*: Bezerra et al. 2007; Digby 1995). Females may kill the offspring of others for nutritional gain (exploitation hypothesis of infanticide; Hrdy 1979) and as a means to reduce current or future competitors with their offspring over limited resources, such as food, shelter (resource competition hypothesis of infanticide: Hrdy 1979; Rudran 1973; Sherman 1981), allocare (adoption avoidance hypothesis of infanticide: Ebensperger 1998; Pierotti 1991), or dominance rank (e.g., social status hypothesis; Digby 2000; Hrdy 1976; Lukas and Huchard 2019), thereby increasing their own infant's probability of survival.

Here we report on an observed case of female-committed infanticide, followed by cannibalism, in a well-studied population of wild white-faced capuchin monkeys (*Cebus imitator*) in the Santa Rosa Sector (SSR) of the Área de Conservación Guanacaste, Costa Rica. White-faced capuchins are long-lived (can live well into their 30s in the wild; Perry 2012), highly social primates that reside in multi-male/multi-female groups composed of related adult females (≥6 years), immigrant adult males (≥10 years), and their immature offspring (Jack and Fedigan 2018). Each group has a distinct alpha male, multiple subordinate males of indistinct rank (Schoof and Jack 2013), and a linear female dominance hierarchy in which infants maintain a similar rank as their mothers (Bergstrom and Fedigan 2010). Although all adult males copulate with females and are capable of reproduction, there is high reproductive skew amongst males, with alpha males siring the majority (ca. 60–80%) of group offspring (Jack and Fedigan 2006; Muniz et al. 2010; Wikberg et al. 2014). Male-committed infanticide is common in *C. imitator* following alpha male replacement (Brasington et al. 2017; Schoof et al. 2014). To our knowledge, female-initiated infanticide has not been previously reported in *Cebus*, and this is our first observation of this behavior in 38 years of intensive observation of this population. Here we detail our observations of an infanticide by a female white-faced capuchin and evaluate the event within the framework of the exploitation, resource competition, adoption avoidance, and social status hypotheses of infanticide. We also describe the subsequent cannibalization of the infant by juveniles in the group, compare the context of the occurrence to the only other documented cannibalism in this species (which occurred in one of our adjacent study groups 22 months earlier; Nishikawa et al. 2020), and discuss the potential role of social facilitation.

Description of event

On 5 February 2021, we witnessed a female-committed infanticide followed by juvenile-enacted cannibalism in the GN group in the SSR study population. The events leading up to and including the infanticide and cannibalism were observed and documented by SC, NK, RL, and SM. Individual identifications and behaviors leading up to and throughout the event were recorded ad libitum. Segments of the event were digitally recorded using two camera phones by SC and SM (see Online Resources 1–5). The *C. imitator* study groups at SSR are fully habituated to researchers and have been under near-continuous study since 1983 (see Fedigan and Jack 2001, 2012, for history of the project), with observations of the GN group since 2006. All group members are individually recognizable based on unique markings (scars, facial markings, fur color/patterns) (Table 1). Kinship relationships have been confirmed using microsatellite data from feces (Wikberg et al. 2014).

At 9:20 am, adult subordinate female, GB (pregnant), and adult beta female, LL (an older multiparous female), were heard fighting (conflict vocalizations) for unknown reasons. GB was observed to grab LL's 18-day old infant (LL-21), who was mounted dorsally on her mother, bite the infant, and then drop her to the ground. LL-21 appeared to be paralyzed from the waist down and was bleeding visibly from her left flank. LL-21 was retrieved by her mother and able to grasp to her chest as she traveled for the next hour. After dropping LL-21, GB fled from the immediate area, returning only when LL began traveling with the infant at 9:47. At that time, GB and her maternal half-sister (HI: adult subordinate female) threatened LL and LL-21 from a 10–20 m distance.

At 10:25, adult subordinate male, TD, approached and aggressively supplanted LL as she was foraging on bromeliad fruits. As LL moved away, LL-21 lost grip of her mother and fell to the ground. GB and five individuals (adult alpha female: PT, adult subordinate female: MY; juvenile female: QN; juvenile males: AG, FD, both 4 years old) ran over and began to threaten LL and TD. PT and TD left the scene. GB, MY (maternal first cousin of LL-21), QN (maternal first cousin of GB), AG (maternal first cousin of LL-21), and FD (distantly related to LL-21) surrounded LL-21 on the ground, causing LL to flee. The individuals threatened and touched LL-21 as she cried intermittently. At 10:30, GB bit LL-21 on the left foot, inflicting a wound. Juvenile males, AG and FD, inflicted the second, third, and fourth bites. AG and GB vigilantly glanced at LL between bites, who watched the events quietly from ca. 10 m away. At 10:32, GB bit LL-21 again twice within 10 s. FD leaned down to watch and then bit LL-21 again. GB and FD took turns biting LL-21 as she cried. GB then bit LL-21 again, inflicting a long and what appeared to be a particularly hard bite as LL-21 screamed loudly in response, causing FD and AG to flee to ca. 3 m away. GB continued to bite LL-21 four more times as the others remained vigilant toward the event. FD then rejoined and GB bit LL-21 two more times, the second of which invoked another loud cry from LL-21, causing

Table 1 Details of individuals involved in the infanticide and cannibalism

Monkey ID	Sex and age	Matriline	Relationship to killed infant	Participation in events
LL	Beta female aged ca. 20 years	Minerva	Mother of LL-21	Observed events from ca. 10 m away
LL-21	Infant female aged 2 weeks	Minerva	Self	The subject of infanticide and cannibalism
PT	Alpha female aged 22 years	Minerva	Maternal sister of LL, maternal aunt of LL-21	Threatened TD when aggressive to LL
MY	Subordinate adult female aged 8 years	Minerva	Daughter of PT, niece of LL, maternal first cousin of LL-21	Unclear—present for infanticide and cannibalism but does not appear to harm infant
AG	Large juvenile male aged 4 years	Minerva	Son of PT, maternal nephew of LL, maternal first cousin of LL-21	Aided in infanticide; participated in Cannibalism
GB	Subordinate adult female aged 8 years (nulliparous female—second pregnancy; no live births recorded)	Rosamerta	Distant relation to LL-21	Initiated infanticide
HI	Subordinate adult female aged 10 years	Rosamerta	Distant relation to LL-21, maternal half-sister of GB	Aided GB in threatening LL and LL-21 between the first and second attack by GB
QN	Large juvenile female aged 3 years	Rosamerta	Distant relation to LL-21, maternal first cousin of GB	Unclear—present for infanticide and cannibalism but does not appear to harm infant
FD	Large juvenile male aged 4 years	Maxine	Distant relation to LL-21	Aided in infanticide; initiated cannibalism

the remaining individuals (GB, MY, QN, FD) to retreat from LL-21. At 10:35, FD and AG returned to LL-21 and began to take bites of and consume the tail and right foot of LL-21 for 10 min as LL-21 continued to cry.

At 10:45, LL approached within a meter of LL-21, FD, and AG. FD avoided her submissively by fleeing as she approached, while AG continued to consume LL-21's foot. LL remained vigilant as she watched. A few seconds later, AG fled into a nearby tree, leaving LL alone, and she approached LL-21. While alarm calling quietly and continuously, LL visually inspected, sniffed, licked, and touched LL-21's injuries. She presented to LL-21 multiple times in an attempt to get her to mount her back and she swatted away flies that landed on LL-21's wounds. The rest of the group moved off to forage 10–30 m away. LL attempted to pull LL-21 onto her back, but the infant was too weak to grasp and fell from her mother four times (from heights of ca. 3, 1, 7, and 5 m). After each of the first three falls, LL alarm-called and moved to the ground to retrieve the infant, approaching and retreating repeatedly while investigating LL-21's wounds (touching, gazing, sniffing, and licking) and urgently swatting away the increasing number of flies. After the fourth fall, LL left LL-21 behind on the ground and traveled fast towards the rest of the group while the infant continued to cry. LL-21 convulsed and cried for the next 25 min and died at 12:00, after all video clips were recorded. When it was confirmed that the group was moving away from the area, the body was collected by SC and NK for photographs, necropsy, and sample collection.

Based on our necropsy of the infant LL-21 (led by CC, LMV), we found a main laceration from a bite (initial bite from GB) in the left thoracolumbar region by the 10th and 11th ribs with extensive subcutaneous hemorrhage (Fig. 1 and Online Resource 6). We found a second bite wound in the left thoracolumbar region, distal to the main one, and another on the right side of the thorax close to the vertebral spine (Fig. 2). The bite on LL-21's left flank (initial bite from GB) fractured LL-21's 10th and 11th ribs, punctured the diaphragm and liver, and caused extensive hemorrhage in the left lung lobe and petechial hemorrhage in the right lung lobe (Online Resources 6 and 7). Half of LL-21's tail and the entirety of her right foot, including the ankle joint, were amputated by cannibalism (Fig. 1 and Online Resource 8). The infant also had bite marks on her right and left legs near the knee joints (Fig. 1 and Online Resource 8) (see Online Resources 6 and 7 for photos of internal injuries). Either the initial bite, fall to the ground, or combination thereof, caused paralysis of the legs.

Discussion

In primates, 85% of infanticides occur in association with periods of alpha male instability (van Schaik 2000). Male-committed infanticide in the SSR groups is common following alpha male replacement (AMR), leading to infant mortality rates that are nearly double those during periods of group stability (Brasington et al. 2017). The infanticide

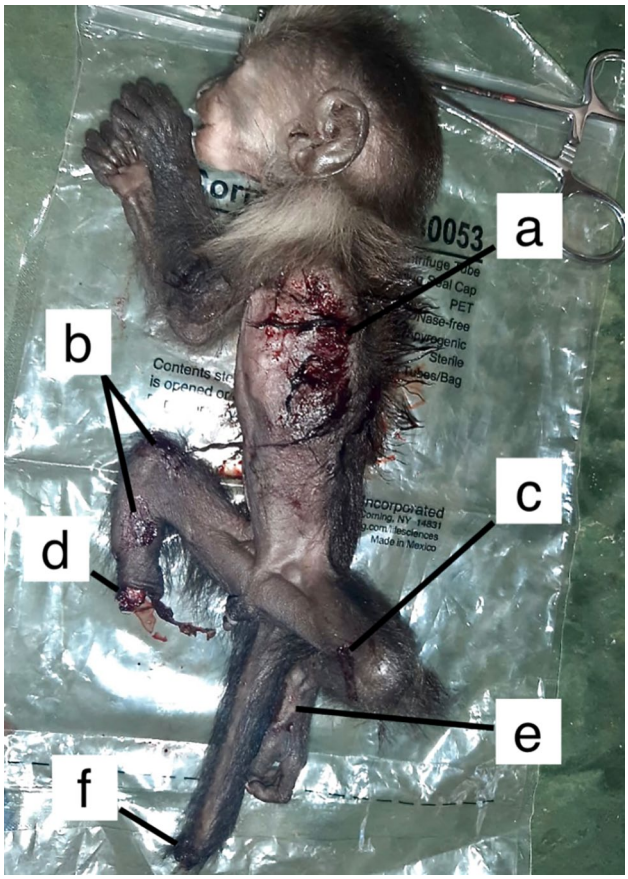

Fig. 1 Wounds on LL-21 following the infanticide and cannibalism events: (**a**) the initial bite inflicted by GB in the left thoracolumbar region by the 10th and 11th ribs, (**b**) bite marks on the right leg near the knee joint, (**c**) bite marks on the left leg near the knee joint, (**d**) wound from cannibalism of the entirety of the right foot and ankle joint, (**e**) bite marks on the left foot, (**f**) wound from cannibalism of half the tail

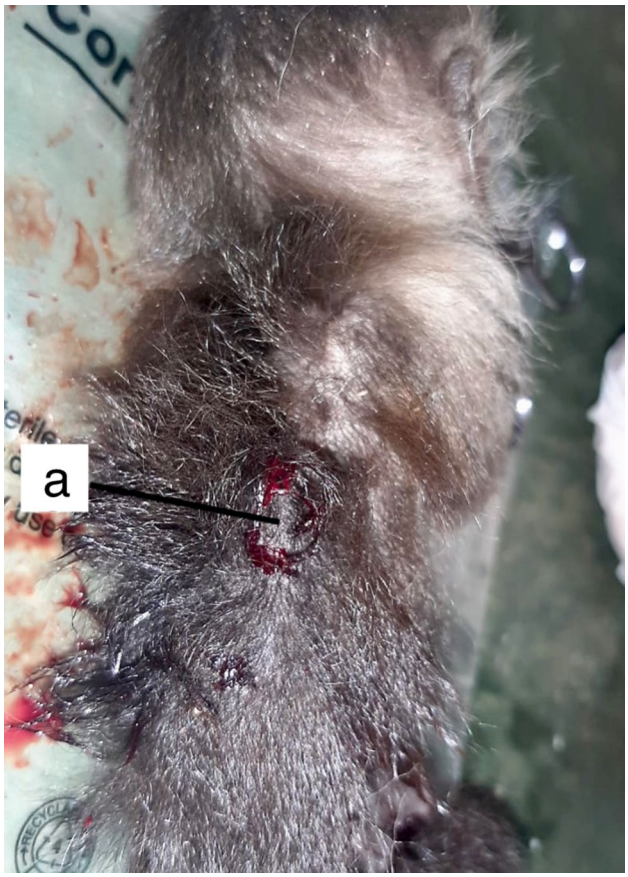

Fig. 2 Wounds on LL-21 following the infanticide and cannibalism events: (**a**) bite on the right side of the thorax adjacent to the vertebral spine

reported here may have been linked to group instability, as GN experienced an alpha male replacement in September 2021 (6 months prior to the case reported here), with the former alpha (EC) remaining on as a peripheral group member following the rise of DD, an extragroup male, to alpha status. However, all of the AMR-related infanticides observed to date have been perpetrated by the new alpha, rather than other group members, and never by females (Brasington et al. 2017; Fedigan 2003).

Female-initiated infanticide occurs more often in communally breeding species, those with high maternal investment, and in species with temporal birth peaks that occur when resources for offspring are limited (reviewed in Lukas and Huchard 2019). Although infanticide by females has not been reported in *C. imitator* before, it is possible that until now it has gone unwitnessed by observers. Indeed, many primate species were initially thought not to exhibit infanticide, but with increasing length of intensive study, these rarer behaviors have now been observed (Lukas and Huchard 2019). However, we have now documented many cases of male-committed infanticide in the SSR population since our studies began in 1983, and this is the first time we have observed an infanticide by a female (Fedigan et al. 2021). Additionally, while Dr. Susan Perry has observed similar patterns of males committing infanticide for this species at her nearby study site of Lomas Barbudal, Costa Rica, she has also never observed a single case of females committing infanticide since beginning her study in 1990 (personal communication, July 2021). As one of the most intensively studied species (nearly 70 combined years of observation at just two study sites), it seems unlikely that female white-faced capuchins kill group infants with any regularity.

Unfortunately, we did not observe the events immediately preceding the grabbing and biting of LL-21 (the infant victim) by adult female GB (infanticide perpetrator). Although we can only speculate on the proximate cause of the infanticide, it was unlikely related to direct nutritional gain (*exploitation hypothesis of infanticide*; Hrdy 1979), as GB did not partake in the consumption of LL-21, and the individuals

that did were unrelated to her. It is possible the initial altercation was motivated by access to food resources, although we did not observe whether GB and LL were eating at the time of the event or what prompted the attack. At the time of the event, GB and LL (mother of attacked infant) were located near fruiting patches of *Manilkara chicle* and *Karwinskia caldronii* trees—important providers of fruit in the early dry season—within which other group members were foraging. SSR is a highly seasonal tropical dry forest located at the limits of *C. imitator*'s physiological range (Orkin et al. 2020). Food and water scarcity during the dry season months of December through April produce nutritional and energetic stress for mothers that can impact their physical condition (Bergstrom 2015; Bergstrom et al. 2018). Given that the nutritional and energetic demands of females are greatest when pregnant and lactating (Bergstrom et al. 2018), it is likely that intragroup female competition for food is heightened in the dry season to meet physiological requirements. However, while it is possible that the infanticide was initially proximately motivated by feeding competition, GB's continued return to and biting of the infant went well beyond any original altercation between the two females.

A number of adaptive explanations have been proposed to explain the occurrence of female-committed infanticide (Digby 2000; Lukas and Huchard 2019), as it may result in increased fitness for the perpetrator and her offspring (current or future) at the expense another female's fitness (Fedigan et al. 2021). It is possible the infanticide reported here will lead to increased access to limited resources for GB and her future offspring, which would lend support to the *resource competition hypothesis* (Hrdy 1979; Rudran 1973; Sherman 1981). At the time of the event, GB was three months pregnant with her first infant (she had at least one other pregnancy, but no live births recorded), and eliminating the offspring of a higher-ranking female could reduce future resource competition for her future lower-ranking offspring. In *C. imitator,* the greatest competition between females on behalf of their offspring is for resources (Bergstrom and Fedigan 2010), which may include competition for allocare and social status (Lukas and Huchard 2019). Thus, the *adoption avoidance hypothesis*, which suggests infanticide functions to reduce or avoid providing care for unrelated young (e.g., Ebensperger 1998; Pierotti 1991), is also supported by this case of infanticide. *Cebus imitator* females provide allocare by nursing, carrying, grooming, and defending each other's infants (Sargeant 2014). A greater helper-to-infant ratio in the group means that infants receive more care, which may contribute to better infant survival (Bales et al. 2000). Thus, if an infant dies, the helper-to-infant ratio increases, allowing additional care to be allocated to the remaining infants (Lukas and Huchard 2019). Of particular relevance in this case, allonursing in *C. imitator* is not equally distributed between ranks; low-ranking females allonurse more often than higher-ranking females (Perry 1996). Thus, with LL's rank as beta female and GB's low rank, GB would have been expected to allonurse at a higher rate than LL. By eliminating the competition imposed by an intragroup infant, GB may have reduced demands of allonursing and thereby expanded her infant's (born 04/01/2021) access to milk and solid food (Hrdy 1979).

In *C. imitator*, female offspring take a similar rank as their mother (Bergstrom and Fedigan 2010). Three matrilines are present in the GN group. The Minerva matriline (LL's family), is the largest and highest-ranking matriline in the group and includes the alpha (PT) and beta (LL) females. The infanticidal female, GB, of the Rosamerta matriline, is one of the lowest-ranked adult females in the group. Thus, GB would not be expected to secure a better rank for her unborn infant by killing LL-21, but she may help eliminate future rivals to her infant by suppressing the reproduction of other females in the group (Beehner and Lu 2013). In social breeders that are female philopatric and rank nepotistic, killing an infant of another matriline may weaken it over the long term, thus limiting its strength within the group (Lukas and Huchard 2019). By killing LL-21, GB may have contributed to limiting the power of the Minerva matriline in favor of her own, thus providing some support for the *social status hypothesis of infanticide* (Digby 2000; Hrdy 1976; Lukas and Huchard 2019).

In summary, while it is difficult to discern the exact proximate motivation for this attack (e.g., generalized aggression in a foraging context; Bartlett et al. 1993), the action has the potential to improve the fitness of GB. By eliminating the infant of a higher-ranking female, GB's offspring may experience less competition for her mother's milk and care and may be granted expanded access to future food resources and a higher social rank. Thus, this infanticide event lends support to the resource competition, adoption avoidance, and social status hypotheses of infanticide. By protecting her unborn infant against infanticide in the case of social instability among group males, GB may also gain inclusive fitness benefits through future reproductive success of her infant.

To our knowledge, cannibalism has been documented in *C. imitator* only once before, in one of our adjacent study groups 22 months earlier (Nishikawa et al. 2020). There were many similarities between the two observed cases of cannibalism, including that they were performed by juvenile males following an infanticide inflicted by an intragroup adult (adult male in the first incident), the infants were less than three weeks old (11 days in the previous observation; 18 days here), the back legs were paralyzed from a fall (or bite) prior to consumption, only part of the body was consumed, consumption began at the feet and tail, and the face and head of the infant were left intact; an approach that is very different from the consumption of non-conspecific prey observed in this species (Nishikawa

et al. 2020). In the previous observation, the consumer was not involved in the infanticide and was distantly related to the victim (Nishikawa et al. 2020). In the case described here, the two juveniles joined in the final stages of the infanticide. Juvenile male FD was distantly related to LL-21, while juvenile male AG was LL-21's maternal first cousin. In both cases of cannibalism, the mother of the infant did not try to interfere but stayed close by and watched vigilantly. Once the mother approached, in both cases, she emitted alarm calls and presented herself to the infant to mount dorsally. In each incident, no other group members attempted to approach and consume the infant, a response that differs markedly from the food interest, fought-over access, and complete consumption of flesh that occurs when small vertebrates are caught as prey (Fedigan 1990; Nishikawa et al. 2020).

Many primates are more experimental in action and flexible in behavior during the juvenile life stage, a period when novel behaviors are more likely to develop (Cambefort 1981; Kappeler 1987; Kawai 1965; Nishida et al. 2009; Perry 2020). The juveniles observed here may have been stimulated to take bites of and consume LL-21 first through social facilitation and contagion by watching GB inflict repeated bites to LL-21, then may have been motivated by their prior knowledge of meat consumption as omnivores (Fedigan 1990) to instigate cannibalism. The two juvenile participants were natal males; thus the behavior was not learned from the case in our adjacent study group. This suggests either a spontaneous occurrence of a novel behavior in two adjacent groups or that the behavior is more common than we realize and is locally spread as a socially learned behavior.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10329-021-00949-z.

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References

Bales K, Dietz J, Baker A et al (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. Folia Primatol 71:27–38. https://doi.org/10.1159/000021728

Bartlett TQ, Sussman RW, Cheverud JM (1993) Infant killing in primates: a review of observed cases with specific reference to the sexual selection hypothesis. Am Anthropol 95:958–990. https://doi.org/10.1525/aa.1993.95.4.02a00090

Beehner JC, Lu A (2013) Reproductive suppression in female primates: a review. Evolut Anthropol Iss News Rev 22:226–238. https://doi.org/10.1002/evan.21369

Bergstrom M, Fedigan L (2010) Dominance among female white-faced capuchin monkeys (Cebus capucinus): Hierarchical linearity, nepotism, strength and stability. Behaviour 147:899–931. https://doi.org/10.1163/000579510X497283

Bergstrom ML, Melin AD, Myers MS, Fedigan LM (2018) Dietary profile, food composition, and nutritional intake of female white-faced capuchins. In: Kalbitzer U, Jack KM (eds) Primate life histories, sex roles, and adaptability: essays in honour of Linda M. Fedigan. Springer International Publishing, Cham, pp 213–243

Bergstrom ML (2015) Seasonal effects on the nutrition and energetic condition of female white-faced capuchin monkeys (Unpublished Doctoral Thesis). University of Calgary, Calgary, AB

Bezerra BM, Souto ADS, Schiel N (2007) Infanticide and cannibalism in a free-ranging plurally breeding group of common marmosets (Callithrix jacchus). Am J Primatol Official J Am Soc Primatol 69:945–952. https://doi.org/10.1002/ajp.20394

Brasington LF, Wikberg EC, Kawamura S et al (2017) Infant mortality in white-faced capuchins: the impact of alpha male replacements. Am J Primatol 79:e22725. https://doi.org/10.1002/ajp.22725

Brown AK, Pioon MO, Holekamp KE, Strauss ED (2020) Infanticide by females is a leading source of juvenile mortality in a large social carnivore. bioRxiv. https://doi.org/10.1101/2020.05.02.074237

Cambefort JP (1981) A comparative study of culturally transmitted patterns of feeding habits in the chacma baboon Papio ursinus and the vervet monkey Cercopithecus aethiops. Folia Primatol 36:243–263. https://doi.org/10.1159/000156000

Cäsar C, Franco E, Soares G, Young R (2008) Observed case of maternal infanticide in a wild group of black-fronted titi monkeys (Callicebus nigrifrons). Primates J Primatol 49:143–145. https://doi.org/10.1007/s10329-007-0067-9

Digby L (1995) Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (Callithrix jacchus). Behav Ecol Sociobiol 37:51–61. https://doi.org/10.1007/BF00173899

Digby L (2000) Infanticide by female mammals: implications for the evolution of social systems. In: van Schaik CP, Janson CH (eds) Infanticide by Males and its Implications. Cambridge University Press, Cambridge, pp 423–446

Ebensperger LA (1998) Strategies and counterstrategies to infanticide in mammals. Biol Rev 73:321–346. https://doi.org/10.1111/j.1469-185X.1998.tb00034.x

Fedigan L (1990) Vertebrate predation in cebus capucinus : meat eating in a neotropical monkey. Folia Primatol Internat J Primatol 54:196–205. https://doi.org/10.1159/000156444

Fedigan LM (2003) Impact of Male Takeovers on Infant Deaths, Births and Conceptions in Cebus capucinus at Santa Rosa, Costa Rica. Int J Primatol 24:723–741. https://doi.org/10.1023/A:1024620620454

Fedigan LM, Jack K (2001) Neotropical primates in a regenerating Costa Rican dry forest: a comparison of howler and capuchin population patterns. Int J Primatol 22:689–713. https://doi.org/10.1023/A:1012092115012

Fedigan LM, Jack KM (2012) Tracking neotropical monkeys in Santa Rosa: lessons from a regenerating Costa Rican dry forest. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin, pp 165–184

Fedigan LM, Hogan JD, Campos FA et al (2021) Costs of male infanticide for female capuchins: when does an adaptive male

reproductive strategy become costly for females and detrimental to population viability? Am J Phys Anthropol. https://doi.org/10.1002/ajpa.24354
Harano T, Kutsukake N (2018) The evolution of male infanticide in relation to sexual selection in mammalian carnivores. Evol Ecol 32:1–8. https://doi.org/10.1007/s10682-017-9925-0
Herrera ERT, Knogge C, Heymann EW (2000) Infanticide in a group of wild saddle-back tamarins, Saguinus fuscicollis. Am J Primatol Official J Am Soc Primatol 50:153–157. https://doi.org/10.1002/(SICI)1098-2345(200002)50:2%3c153::AID-AJP5%3e3.0.CO;2-%23
Hrdy SB (1977) Infanticide as a Primate Reproductive Strategy. Am Sci 65:40–49
Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13–40. https://doi.org/10.1016/0162-3095(79)90004-9
Hrdy SB, Hrdy DB (1976) Hierarchical relations among female hanuman langurs (primates: colobinae, Presbytis entellus). Science 193:913–915. https://doi.org/10.1126/science.193.4256.913
Hrdy SB (1976) Care and Exploitation of Nonhuman Primate Infants by Conspecifics Other Than the Mother. In: Rosenblatt JS, Hinde RA, Shaw E, Beer CBT-A in the S of B (eds). Academic Press, pp 101–158
Jack K, Fedigan L (2018) Alpha Male Capuchins (Cebus capucinus imitator) as Keystone Individuals: Essays in Honour of Linda M. Fedigan. pp 91–115.
Jack KM, Fedigan LM (2006) Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (Cebus capucinus). In: new perspectives in the study of mesoamerican primates. Springer, London, pp 367–386
Jolly A, Caless S, Cavigelli S et al (2000) Infant killing, wounding and predation in Eulemur and Lemur. Int J Primatol 21:21–40. https://doi.org/10.1023/A:1005467411880
Kappeler PM (1987) The acquisition process of a novel behavior pattern in a group of ring-tailed lemurs (Lemur catta). Primates 28:225–228. https://doi.org/10.1007/BF02382571
Kawai M (1965) Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. Primates 6:1–30. https://doi.org/10.1007/BF01794457
Kittler K, Dietzel S (2016) Female infanticide and female-directed lethal targeted aggression in a group of ring-tailed lemurs (Lemur catta). Primate Biol 3:41–46. https://doi.org/10.5194/pb-3-41-2016
Lukas D, Huchard E (2019) The evolution of infanticide by females in mammals. Philos Trans R Soc Lond B Biol Sci 374:20180075. https://doi.org/10.1098/rstb.2018.0075
Muniz L, Perry S, Manson JH et al (2010) Male dominance and reproductive success in wild white-faced capuchins (Cebus capucinus) at Lomas Barbudal, Costa Rica. Am J Primatol 72:1118–1130. https://doi.org/10.1002/ajp.20876
Nishida T, Matsusaka T, McGrew WC (2009) Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. Primates 50:23–36. https://doi.org/10.1007/s10329-008-0109-y
Nishikawa M, Ferrero N, Cheves S et al (2020) Infant cannibalism in wild white-faced capuchin monkeys. Ecol Evolut 10:12679–12684. https://doi.org/10.1002/ece3.6901
Orkin JD, Montague MJ, Tejada-Martinez D et al (2020) Selection and local adaptation in capuchin monkeys revealed through fluorescence-activated cell sorting of feces (fecalFACS). bioRxiv. https://doi.org/10.1101/366112
Palombit RA (2012) Infanticide: male strategies and female counter-strategies. In: Mitani JC, Call J, Kappeler PM et al (eds) The evolution of primate societies. University of Chicago Press, Chicago, pp 432–468
Perry S (1996) Female-female social relationships in wild white-faced capuchin monkeys Cebus capucinus. Am J Primatol 40:167–182. https://doi.org/10.1002/(SICI)1098-2345(1996)40:2%3c167::AID-AJP4%3e3.0.CO;2-w
Perry S (2012) The behavior of wild white-faced capuchins: demography, life history, social relationships, and communication. Adv Study Behavr 44:135–181. https://doi.org/10.1016/B978-0-12-394288-3.00004-6
Perry S (2020) Behavioural variation and learning across the lifespan in wild white-faced capuchin monkeys. Philosophical Trans Royal Soc B: Biol Sci 375:20190494. https://doi.org/10.1098/rstb.2019.0494
Pierotti R (1991) Infanticide versus adoption: an intergenerational conflict. Am Nat 138:1140–1158
Rudran R (1973) Adult male replacement in one-male troops of purple-faced langurs (Presbytis senex senex) and its effect on population structure. Folia Primatol 19:166–192. https://doi.org/10.1159/000155537
Sargeant E (2014) Infant Handling and Allonursing in White-Faced Capuchins (Cebus capucinus) (Unpublished Master's Thesis). University of Calgary, Calgary, AB.
Schoof VAM, Jack KM (2013) The association of intergroup encounters, dominance status, and fecal androgen and glucocorticoid profiles in wild male white-faced capuchins (Cebus capucinus). Am J Primatol 75:107–115. https://doi.org/10.1002/ajp.22089
Schoof V, Wikberg E, Jack K et al (2014) Infanticides during periods of social stability: kinship, resumption of ovarian cycling, and mating access in white-faced capuchins (Cebus capucinus). Neotropical Primates 21:192–196. https://doi.org/10.1896/044.021.0206
Sherman PW (1981) Reproductive competition and infanticide in Belding's ground squirrels and other animals. In: Alexander RD, Tinkle DW (eds) Natural selection and social behavior. Chiron Press, Chiron, New York, pp 311–331
Shopland JM, Altmann J (1987) Fatal intragroup kidnapping in yellow baboons. Am J Primatol 13:61–65. https://doi.org/10.1002/ajp.1350130108
Townsend SW, Slocombe KE, Thompson ME, Zuberbühler K (2007) Female-led infanticide in wild chimpanzees. Curr Biol 17:R355–R356. https://doi.org/10.1016/j.cub.2007.03.020
van Schaik CP, Janson CH (2000) Infanticide by males and its implications. Cambridge University Press, Cambridge
Wasser SK, Starling AK (1988) Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. Am J Primatol 16:97–121. https://doi.org/10.1002/ajp.1350160202
Wikberg EC, Jack KM, Fedigan LM, et al (2014) Male reproductive success in white-faced capuchins. In: 霊長類研究 Supplement 第30回日本霊長類学会大会. 日本霊長類学会, p 41. https://doi.org/10.14907/primate.30.0_41_1