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SHORT COMMUNICATION

Infanticide following male takeover event in Verreaux's sifaka (*Propithecus verreauxi verreauxi*)

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Abstract Two infanticides occurred after a male takeover in a population of Verreaux's sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, Madagascar. The first infant was found dying from wounds received to the chest and groin after three adult males had immigrated into the group. The second infanticide was directly observed 2 weeks later when one of the immigrant males targeted and attacked the infant after it was separated from its mother. The directed nature of the attack suggests that the infant's death was not a result of generalized aggression during a period of increased group instability. Although the sexual selection argument does not fully explain infanticidal events in seasonally breeding lemurs, such as Verreaux's sifaka, it is clear that transferring males present a measurable threat to infant survival and female reproductive success in this species.

Keywords Infanticide · Verreaux's sifaka · Lemur · Reproductive strategy · Male transfer

Introduction

There is growing evidence to suggest that infanticide occurs in highly seasonally breeding lemurs, contradicting predictions of the sexual selection hypothesis that infanticide is unlikely to occur when the loss of an infant does not shorten the time to onset of the reproductive cycle (Hausfater and Hrdy 1984; Hrdy 1979; van Schaik and Janson 2000). Infanticide has been documented in *Lemur catta* (Hood 1994; Jolly et al. 2000), *Eulemur fulvus rufus* (Jolly et al. 2000), *Propithecus diadema edwardsi* (Erhart and Overdorff 1998; Wright 1995), *P. verreauxi verreauxi* (Lewis et al. 2003), and even *Lepilemur edwardsi* (Rasoloharijaona et al. 2000). These observations present a challenge for interpreting infanticidal behavior within strepsirhines and for understanding the extent to which the evidence supports the sexual selection hypothesis. The following description of infanticide in *P. verreauxi verreauxi* after a male takeover event provides additional evidence that infanticide occurs across a wide spectrum of lemur species despite the fact that they are strictly seasonal breeders.

Methods

The infanticidal events occurred in a population of wild sifaka (*P. verreauxi verreauxi*) at Beza Mahafaly Special Reserve in southwest Madagascar. The 80-ha reserve forest contains about 50 separate sifaka groups, ranging in size from two to 13 individuals, with one to three females per group (Richard et al. 1991). Individuals are identified by unique collars and tags with numbers, and groups are censused monthly, providing updated information on residency patterns. The mating season occurs from January to March, with females displaying estrus within a narrow window of time (0.5–96 h) (Brockman 1999). Behavioral data were collected on eight females with infants, two from each of four groups, during a 5-month field season from mid-July to mid-December 2007. Each group was sampled for 4 days twice a month on alternating weeks using focal

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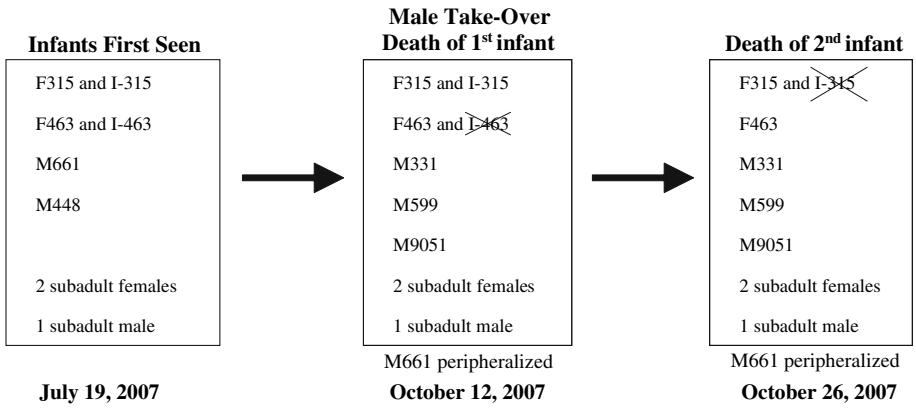

Fig. 1 Group composition of Nenibe (NB) and timeline of male takeover event and infanticides

sampling techniques (Altmann 1974), resulting in 606 total hours of observation.

The events transpired in mid-October within the group Nenibe (NB), which ranges within the high-canopy gallery forest of the eastern part of the reserve. Before the infanticides, the group consisted of nine individuals: two adult females, both with infants; two subadult females; two adult males; and one subadult male who had transferred into the group just prior to the beginning of the study period (Fig. 1). Both infants were first seen by the census team on 19 July, so infants were about 3 months old at the time of the attacks.

Results

I located NB on 12 October at 0727 h, 10 days after the previous sample on this group. Three new males were travelling with the group: M331, M599, and M9051, each previously seen in other separate groups (Fig. 1). Resident males M448 and M661 were missing, and F463 did not have her infant. At 0810 h, F463 retrieved her male infant (I-463) from underbrush on the ground, where he was still alive but had a bleeding puncture wound in the chest and another long gash across the right upper thigh near the groin. F463 stayed with the infant for the next 3 h, occasionally grooming him and picking him up, while the rest of the group moved off. At 1039 h, the infant was no longer vocalizing and did not appear to be moving. F463 left her dead infant at 1055 h to rejoin the rest of the group. In addition to the two major wounds, I-463 also had three wounds on his back, neck, and right knee. Later that afternoon, M661 was seen on the periphery of the group. He was missing large tufts of hair from his head, back, and torso and was panting heavily, but no visible wounds were observed. Given the fresh injuries of I-463 and M661, it is probable that the takeover event was recent—either earlier that morning or during the previous day. However, as I had not seen the group for 10 days, it is not possible to know exactly when the new males moved into the territory. M661 continued to travel on the periphery of the group for the rest of the focal week, although the new-transfer males chased him if he came too close. At the end of the focal week, F315's infant was alive and uninjured.

Ten days later, on 26 October, I initiated focal sampling of the group at 0718 h and found F315 and M331 at 0718 h resting 10 m apart in a tree. M661 was resting in a nearby tree, and the remaining members of NB were out of view. At 0730 h, M331 approached within 2 m of F315 and her female infant (I-315), who was resting on her back. At 0741 h, F315 lunged at M331, cuffing and biting at him. I-315 was dislodged from F315's back and was left out of arm's reach behind her on the tree branch. M331 did not display aggression towards F315. Instead, he circumvented F315, grabbed I-315 with both hands, bit the infant in the neck, and then dropped her onto the tree branch. F315 turned and chased M331 out of the tree and then returned to her infant, who was hanging limply from the branch with a deep puncture wound to the neck. At 0812 h, M661 approached I-315 and briefly groomed her, while F315 lost-called to the rest of group. By 0835 h, F315 and M661 left I-315 and joined the rest of the group. Upon retrieval of the infant's body, I noticed an additional small wound on the back (Supplementary Fig. I).

M331, M599, and M9051 successfully immigrated into the group, ousting M448, who was subsequently seen in November with another group, and peripheralizing M661, who remained on the outskirts of the group for the remainder of the study period. After the takeover event, both F315 and F463 showed aggression towards the immigrant males, often cuffing, lunging, or biting them upon approach, and were rarely seen grooming the new males. Although the study ended before the onset of the next mating season, monthly census data up to September 2008 revealed that M331 remained with the group. M599 and M9051 were not seen with NB during the February

2008 census but returned to the group in March and remained there until at least September. The resident male, M661, finally left the group in February and was later seen with group LL2. F463 was seen with a new infant in August 2008, whereas F315 did not have another infant. At this time, the paternity of F463's new infant is unknown.

Discussion

This is the second documented case of an observed infanticide in this species (Lewis et al. 2003) and provides additional evidence for the occurrence of infanticide in *Propithecus*. The directed nature of the second attack suggests that the infant death was not a result of generalized aggression during a period of group instability (Bartlett et al. 1993). Although F315 was aggressive towards M331, he directed aggression specifically toward the infant and not the mother. In fact, M331 actually avoided F315 and moved around her in order to gain access to the infant. These infanticidal events were very similar to those reported in *P. diadema edwardsi*, where a period of 1 month elapsed between the infanticides of two dependent offspring by an immigrant male (Wright 1995). As documented in the case of *P. diadema edwardsi*, the resident male in this study did not attempt to defend the infant from the immigrant male, most likely due to his peripheralized status. In addition, even though both resident females demonstrated aggression towards the immigrant males, they were unable to prevent the new males from successfully transferring into the group, demonstrating that even though this species exhibits female dominance, immigrant males remain a potential threat to infant survival.

Researchers have proposed several hypotheses to explain infanticidal behavior in strepsirhines: (1) Infanticide may provide a reproductive advantage to immigrant males by enhancing breeding opportunities for the next season, especially in species such as *P. diadema edwardsi* where males and females often exhibit stable breeding relationships for several years (Wright 1995), or in *L. catta* where females often display priority mating with resident males (Pereira and Weiss 1991). Whereas females in this population of *P. verreauxi verreauxi* also display priority mating with resident males, they occasionally mate with peripheral males (Brockman and Whitten 1996), and males sire infants outside of their resident groups (Lawler 2007). (2) Infanticide also may decrease the interbirth interval, as in *P. diadema edwardsi* (Erhart and Overdorff 1998). However, in this population, the loss of an infant does not appear to reduce the interbirth interval. In fact, females with a surviving infant are more likely to have an infant the following year compared with females without an infant (Richard et al. 2002). Although for some primate species the loss of an infant may increase the survival of the subsequent offspring (Hausfater and Hrdy 1984; Hood 1994; Jolly et al. 2000; Pereira and Weiss 1991), this does not appear to be the case in this population (Richard et al. 2002). (3) Finally, infanticide may be a form of intrasexual competition, where the killing of male infants functions to eliminate future rivals (van Schaik and Janson 2000). The victims of infanticide reported here include both sexes, and a larger sample size of infanticidal victims is required to adequately test this hypothesis. Clearly, more research is needed in this population to determine the possible advantages of infanticide to males and the extent to which infanticidal males are the sires of subsequent surviving offspring.

Regardless of whether infanticide serves as a reproductive strategy for males in this species, it is certainly a behavior that occurs with more frequency than originally thought, especially if inferred as well as observed infanticides are included to assess rates of infanticide (van Schaik and Janson 2000). During this same time period, three other infants disappeared from another group, Masiaka Be, as new males attempted to transfer into the group. Attacks on infants were not directly observed, but changing group dynamics and increased aggression among males led us to infer that these disappearances were most likely the result of infanticide. Given that no other infant deaths were reported in the reserve around this time, it is unlikely that the deaths can be attributed to ecological circumstances. Even if the disappearances were not directly attributable to immigrating males, it is probable that the increased aggression and instability observed in the group during this time was indirectly responsible for the loss of these infants. Furthermore, previous research on this population has shown that in the presence of immigrating or peripheral males, some females exhibit sexual receptivity outside of the narrow timing of estrus, suggesting that females in this species may use multiple matings as a strategy to confuse paternity and possibly avoid infanticide (Brockman and Whitten 1996). Taken together, these observations suggest that transferring males provide a measurable threat to infants (e.g. Brockman and Whitten 1999), which has a direct impact on female reproductive strategies and success in this species.

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