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BRIEF REPORT

Infant Mortality After Takeovers in Wild Ethiopian Hamadryas Baboons

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In this work we report the first observational evidence of infanticide in wild hamadryas baboons. The study group inhabits the lowlands of the northern Rift Valley in Ethiopia and has been under observation for over 1,200 hr, on and off, since October 1996. Here we report observations from August and September 2002 of the consequences of two takeovers of known females with black infants. After the first takeover, the respective infant disappeared and was presumed dead within 11 days of the takeover. After the second takeover, the infant incurred repeated severe aggression from its mother's new leader male and eventually died 4 days after the takeover. We interpret these findings as support for the sexual selection hypothesis regarding male infanticide. We suggest that hamadryas leader males usually protect infants born into their units, but may withhold this protection—or even directly attack and kill infants—after takeovers. *Am. J. Primatol.* 60:113–118, 2003. © 2003 Wiley-Liss, Inc.

Key words: hamadryas baboons; infanticide; infant mortality; protection; sexual selection

INTRODUCTION

Infanticide by males has been reported to occur in many wild primates, most notably hanuman langurs (*Semnopithecus entellus*) but also in other colobine monkeys, platyrrhines, guenons, lemurs, and African great apes [e.g., Hausfater and Hrdy, 1984; van Schaik and Janson, 2000; van Schaik, 2000, and references therein]. Circumstantial and/or observational evidence of male infanticide and attempted infanticide has also been reported for several populations of wild baboons (*Papio hamadryas* spp. [Shopland, 1982; Collins et al., 1984; Smuts, 1985; Palombit et al., 1997, 2000; Weingrill, 2000]).

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According to the sexual-selection hypothesis, infanticide is a competitive strategy whereby a male, by killing infants of other males, increases his own relative fitness and brings the infant's mother into reproductive condition sooner than she would have had her infant survived [Hausfater & Hrdy, 1984; van Schaik & Janson, 2000]. The generalized aggression hypothesis, by contrast, proposes that infanticide is not adaptive but is simply an epiphenomenon of periods of intense aggression, such as during group takeovers and intergroup encounters [Bartlett et al., 1993; Sussman et al., 1995]. Both hypotheses predict that infanticide would be likely to occur during aggressive takeovers. The sexual selection hypothesis alone, however, predicts that infanticide would occur most often at times when most infants in the group have presumably been sired by a competitor and most future infants will be sired by the new, infanticidal male. In such cases, infanticidal males would be killing the infants of other males rather than their own and would then gain opportunities to sire offspring with the infants' mothers sooner than they would have otherwise.

In many of the primate taxa in which infanticide has been reported, it appears to be associated with 1) male takeovers, male immigration, or changes in group leadership, where the infanticidal male is a new or newly dominant male; or 2) aggressive intergroup encounters, after which the victim's mother may transfer into the group of the infanticidal male [Hausfater & Hrdy, 1984; Borries et al., 1999; van Schaik & Janson, 2000, and references therein]. Not only do males in these cases appear to be killing the infants of other males, but the infants killed are of a sufficiently young age that their deaths may cause their mothers to return to reproductive condition sooner than they would have otherwise. In many of these cases, the females copulate with infanticidal males during and after male takeovers and infanticidal events [Hausfater and Hrdy, 1984; van Schaik, 2000], and, at least in human langurs, the infanticidal males sire those females' offspring [Borries et al., 1999].

Prior to this study, infanticide in hamadryas baboons (*Papio hamadryas hamadryas*) had been observed only in captivity [Angst & Thommen, 1977; Rijksen, 1981; Gomendio & Colmenares, 1989; Kaumanns et al., 1989; Chalyan & Meishvili, 1990; Zinner et al., 1993], though circumstantial evidence suggested that it occurred in the wild as well [Swedell, 2000b; Kummer et al., 1974]. As a result of Kummer et al.'s [1974] experiments, two mothers with infants were transferred into new one-male units. One infant was missing a day later, and the other was seen dead with large canine-inflicted wounds on its skull and thighs. The only evidence of infanticide in wild, non-experimentally-manipulated hamadryas was reported by Swedell [2000b], who noted that after two takeovers of known females, the only female in each takeover with a black infant had either 1) lost her infant or 2) been the victim of prolonged infant kidnapping, with no protective behavior on the part of her new leader male. However, no direct infanticide or attacks on infants were observed in either study.

Gomendio and Colmenares [1989] suggested that there is a good reason why infanticide has not been observed in wild hamadryas: it does not occur under natural conditions. According to these authors, a hamadryas takeover is a gradual process, and the new leader male, having previously been a follower male to the unit, is typically already familiar with the unit's females. If infanticide is stimulated proximately by a short period of social upheaval and the unfamiliarity of a new group of females (as in langurs), then the nature of takeovers in hamadryas would not provide a proximate mechanism for infanticide to occur. Ultimately, infanticide in hamadryas may not be adaptive, because leader males and the males who take over their units may be related [Abegglen, 1984] and thus

males may actually gain inclusive fitness by investing in, rather than killing, infants sired by the previous leader male.

Takeovers in wild hamadryas, however, are not always a gradual process and often do not appear to involve males with close kin or social relationships prior to the takeover [Swedell, 2000a]. In such cases, the sexual selection hypothesis would predict that a female's new leader male would benefit from killing her infant or otherwise failing to protect it from harm by outside individuals.

METHODS

The observations reported here are part of an ongoing study of a population of hamadryas baboons inhabiting the lowlands of the northern Rift Valley of East Africa (see Swedell [2002a, b] for details). The study site is the Filoha outpost of the Awash National Park in central Ethiopia. At least five different groups ("bands," cf. Kummer [1968]) of hamadryas baboons range throughout the Filoha area, each showing the characteristic hamadryas social organization and frequent male herding and neck-biting described by Kummer [1968]. The main study group of about 200 individuals was under observation by L. Swedell for a total of 986 hr over 262 days between October 1996 and September 1998, about 25 hr over 16 days in July and August 2000, 35 hr over 19 days in July and August 2001, and about 102 hr over 41 days in June–August 2002. Since September 2002, the group has been under observation by T. Tesfaye for about 15 days each month, 3–10 hr per day. Since 1996, we have observed four takeovers of known females with black infants in which we also observed the consequences of the takeover. Two of these takeovers were reported previously [Swedell, 2000b]. The other two were observed in August and September 2002, and are described in this report.

RESULTS

Takeover #1: 2 August 2002

At the time of the takeover, the one-male unit involved consisted of a leader male and two females, one of which had a 2-month-old female infant. On 1 August, the leader male was seen with fresh wounds on his face. On 2 August, the female with the infant was aggressively taken over by another adult male, who herded and neck-bit her repeatedly and held her in a "possession grip" (a behavior in which a hamadryas male stands over a female, almost completely hiding her from view, and sometimes walks with her underneath him). On 4 August, the female was seen with her infant on her belly, sitting about 1 m from her new leader male. She was next observed on 13 August, at which time she no longer had an infant with her. She also had many new scars and hair was missing on the back of her head, undoubtedly from the repeated neck-bites she had received from her new leader male since the takeover. The female was still with her new leader male and the infant was still missing (and was presumed dead) on 16 August, the last day of observation for that field season.

Takeover #2: 13 September 2002

Prior to the takeover, the female involved was one of four females of a leader male. She gave birth to an infant male on 22 August 2002, and was observed with her original unit through 12 September. On the morning of 13 September, she had been taken over by a new leader male who had one other female. The new leader male's face was bloody, and the previous leader male had a new wound on

his ear. The female had fresh wounds and hair missing from the back of her head (presumably from receiving frequent neck-bites), and her infant had blood on its head and fresh wounds on its face. The female was apparently attempting to stay near her previous one-male unit, but her new leader male repeatedly herded her away from it, neck-biting and mounting her each time she moved more than 1 m away from him, and holding her in a possession grip while she crouched and screamed. At least five times, the new leader male grabbed the female's infant and bit its head and ears while the infant screamed and the mother kecked (see Swedell [2000a] for behavioral definitions). This same pattern of behavior was observed on 14 September as well. On 17 September, the female was observed following her new leader male, carrying her dead infant. She was next seen on 27 September, with a full sexual swelling and without her infant.

DISCUSSION

Since October 1996, we have observed the consequences of four takeovers of known females with black infants. After the first takeover [Swedell, 2000b], a black infant disappeared, and its mother developed a sexual swelling and copulated with the new leader male within 11 days. After the second takeover [Swedell, 2000b], a black infant was kidnapped by a subadult male for over an hour and a half, and despite the female's obvious distress, the new leader male made no attempt to retrieve the infant. The third takeover (described above) was followed by the disappearance of a black infant within 2 weeks, and the fourth (also described above) was followed by severe aggression toward a female's infant and the subsequent death of the infant.

While we do not yet have enough observations of either infant mortality or takeovers in wild hamadryas baboons to adequately test the competing hypotheses for the occurrence of male infanticide, we interpret the above cases as preliminary support for the sexual selection hypothesis for the following reasons. First, in all three cases of likely infant mortality, it is highly probable that the new leader male was *not* the father of the infant that died. While we have no genetic data to indicate whether the new leader male was a close relative of the deposed leader male, we have no observations prior to the takeover that would suggest such a relationship (as proposed by Gomendio and Colmenares [1989], as discussed above). Second, in two of these cases, the infants' mothers developed sexual swellings within 2 weeks of the takeover, after the infants died. This suggests a possible acceleration in each female's ovulatory cycle in response to the death of her infant and/or the takeover itself, which may have given the new leader males a chance to sire offspring with those females sooner than they would have otherwise. A return to reproductive condition within a similar time frame after takeovers has been reported for captive hamadryas females as well [Colmenares & Gomendio, 1988; Zinner & Deschner, 2000]. Alternatively, these sexual swellings may have been failed (and belated) attempts by the females to *prevent* infanticide, as has been suggested to occur among hamadryas females in captivity [Zinner & Deschner, 2000].

While the above factors do not preclude an interpretation of these events as a simple byproduct of the generalized aggression that surrounds takeovers [cf. Bartlett et al., 1993], we do not agree with such an interpretation for hamadryas baboons. Hamadryas leader males frequently engage in aggressive interactions involving chases, threats, and physical fights with other males. While we have seen fresh wounds on leader males (and other males) after such episodes, we have never seen infants wounded or killed at these times. Likewise, hamadryas leader

males routinely herd their females by aggressively neck-biting them. While such behavior increases in frequency and intensity after takeovers, it is a common element of life for hamadryas females during non-takeover periods as well, and we have never observed an infant harmed during such episodes. Furthermore, takeover #2 involved aggression that was unambiguously directed at the infant itself, not just the mother, suggesting that the infant's death was not simply an indirect result of aggression directed toward the mother.

Regardless of how one interprets infanticide from the male perspective, the above observations suggest that hamadryas infants are at an increased risk of death after takeovers. This may be due to direct infanticide, or to kidnapping leading to starvation or dehydration. Kidnapping may be more dangerous for hamadryas infants than for infants of other baboon subspecies due to the hot, dry climate of hamadryas habitats (including the Filoha region), which would lead to an increased risk of dehydration if infants are separated from their mothers for long periods. Leader males often retrieve infants from non-leader males, who interact frequently with infants and juveniles [Swedell, 2000a], and in most such cases males are probably protecting their own offspring. When paternity is uncertain or unlikely, however, leader males may withhold this protection and "let" the infant die. This can be considered to be an indirect form of infanticide, as the high frequency with which non-leader males interact with young infants probably necessitates protection of infants by leader males simply in order to keep them alive.

Sigg et al. [1982] pointed out that infant survival is higher in hamadryas than in other baboons, and suggested that hamadryas society provides a safer environment for infants and juveniles than the multi-male, multi-female social system of other baboons. This suggests that a leader male plays a large role in protecting the infants in his unit, and that his presence alone may largely account for the higher rates of infant survival—and the rarity of observations of infanticide—in hamadryas compared to other baboons.

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