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DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys

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Although the killing of dependent infants by adult males is a widespread phenomenon among primates, its causes and consequences still remain hotly debated. According to the sexual selection hypothesis, infanticidal males will gain a reproductive advantage provided that only unrelated infants are killed and that the males increase their chances of siring the next infants. Alternatively, the social pathology hypothesis interprets infanticide as a result of crowded living conditions and, thus, as not providing any advantage. Based on DNA analyses of wild Hanuman langurs (*Presbytis entellus*) we present the first evidence that male attackers were not related to their infant victims. Furthermore, in all cases the presumed killers were the likely fathers of the subsequent infants. Our data, therefore, strongly support the sexual selection hypothesis interpreting infanticide as an evolved, adaptive male reproductive tactic.

Keywords: infanticide; sexual selection; social pathology; paternity analysis via DNA; subsequent infant; *Presbytis entellus*

1. INTRODUCTION

The killing of infants by adult males in primates was first and most widely documented among Hanuman langur monkeys (*Presbytis entellus*; Sugiyama 1965; Mohnot 1971; Hrdy 1977; Newton 1986; Ross 1993; Borries 1997) and is now known to occur in five of the six primate radiations (Hrdy *et al.* 1995, p. 151) as well as in several non-primate species (Hrdy 1979; Hausfater & Hrdy 1984; Parmigiani & vom Saal 1994). Although a common phenomenon, its causes and consequences still remain hotly debated, particularly in anthropological contexts (Bartlett *et al.* 1993; Sussman *et al.* 1995; but see Hrdy *et al.* 1995).

Five explanatory hypotheses for the occurrence of infanticide were given by Hrdy & Hausfater (1984). Of these, the sexual selection and social pathology hypotheses are the most pertinent contenders here. The sexual selection hypothesis proceeds on the assumption that infanticide results from reproductive competition between males. By killing an infant a male will gain reproductive advantage provided that (i) the male is not related to the infant he kills, (ii) the death of an unweaned infant shortens the subsequent interbirth interval of the mother, and (iii) the killer increases his chances of mating with the mother and siring her next infant (e.g. Hrdy 1974, 1979). According to the social pathology hypothesis, infanticide results from high male aggression caused by unnatural living conditions, such as deforestation or overpopulation and has no adaptive value (Dolhinow 1977; Curtin & Dolhinow 1978; Boggess 1979, 1984). Infants are only accidental victims; males may even kill their own offspring and will not gain reproductive advantage (Bartlett *et al.* 1993; Sussman *et al.* 1995).

Existing evidence favours the sexual selection hypothesis. It has been shown that, primate females, after having lost their dependent infant, resume sexual activity earlier and bear the next infant significantly sooner than females with surviving infants (question (ii); e.g. Altmann *et al.* 1978; Collins *et al.* 1984; Crockett & Sekulic 1984; Leland *et al.* 1984; Sommer 1994; Borries 1997). The two remaining questions could only be investigated indirectly. Infanticidal males were new immigrants (Butynski 1982; Collins *et al.* 1984; Sommer 1994; Borries 1997), sexually immature or not observed to copulate with the mother during the time when the infant was conceived (Collins *et al.* 1984; Struhsaker & Leland 1985). Thus, it seems very unlikely that they killed their own offspring. Furthermore, in most documented cases, infanticidal males remained residents in the group where they committed infanticide and behavioural observations have indicated that they might have sired the subsequent infant and might therefore have benefited by infanticide. They were either observed to mate with the victim's mother (Sugiyama 1965; Crockett & Sekulic 1984; Struhsaker & Leland 1985) and/or were the highest ranking males in a multimale group (Collins *et al.* 1984; Borries 1997) or the only adult male in a one-male group (Sugiyama 1965; Struhsaker 1977; Sommer 1994).

However, as long as the two questions can only be examined indirectly it cannot be determined whether or

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not infanticide is an adaptive male behaviour. Since both predictions aim at genetic relationships (between male–infant victim and male–subsequent infant) DNA data is required but has not been available so far. We are now in a position to examine these relationships for a wild population of Hanuman langurs by DNA profiling. In this population, immigrant males might risk killing their own offspring since, in general, 21% of the infants were sired by resident males from neighbouring groups or extra-group males (total $n = 42$ in five groups; Launhardt 1998; Launhardt *et al.* 1999) and 25–40% of the immigrant males were former residents of neighbouring groups (Borries 1999).

In this investigation we hope to resolve the controversy of whether infanticide by adult males can be an adaptive male reproductive tactic in Hanuman langurs and whether it is in accordance with the sexual selection hypothesis.

2. MATERIAL AND METHODS

With the support of 19 colleagues, we studied 18 wild groups of Hanuman langurs (72% multi-male and 28% one-male groups) in a semi-evergreen forest near the village of Ramnagar, Southern Nepal. In spite of breeding seasonality (births January–June; Koenig *et al.* 1997) the mean interbirth interval of 2.4 years was significantly shorter if the infant was lost prematurely (Borries 1997). During more than 37 000 h spent in contact with the langurs, one infanticide was witnessed (J. Nikolei and K. Thapa, personal communication; cf. Borries 1997), seven cases were likely or assumed (definitions in table 1) and 24 severe though non-fatal attacks by adult males on infants were observed, while three were inferred from wounds (Borries 1997). Non-fatal attacks were included in the analysis because they might have been attempted though unsuccessful infanticides and the males should likewise not have been related to the infant.

DNA was extracted from langur faeces and samples were stored in 100% ethanol. Five informative microsatellite loci (D16S420, D12S67, SCA1, D17S791 and D4S2366) originally established for humans were amplified by the PCR and were used for paternity exclusions. For details on the percentage of PCR reactions with results that could be scored, the method of scoring fragment lengths, controls run, etc., see Launhardt *et al.* (1998). Whenever a male could be excluded by at least one microsatellite system he was treated as a non-father. If he could not be excluded he was considered as the likely father. The average paternity exclusion probability for all five loci combined was 88.8% (Selvin 1980; Chakraborty *et al.* 1988). The 35 observed or inferred events of infanticide or attacks concerned 24 male–infant pairs (some infants were repeatedly attacked by the same male). Of these, we had a complete set of faecal samples (male, infant and mother) for 16 pairs. In total, samples from 41 sexually mature langur males entered the analysis. The combined paternity exclusion probability was determined for each male–infant pair indicating the probability that the male not excluded from paternity was indeed the father of the respective infant.

3. RESULTS

In all 16 cases with complete DNA samples the male could be excluded as father of the infant he attacked or killed (table 1). Thus, all 14 attacks were performed by unrelated males, as were one likely and one witnessed infanticide. Own infants were never attacked nor killed.

Table 1. *Kin relationship between male langurs and the infants they attacked or killed*

(Numbers indicate male–infant pairs.)

male	paternity analysis excludes the male as father	no DNA sample for male or infant	total
attacked infant[a]	14	2	16
killed infant (presumed[b])	0	5	5
killed infant (likely[c])	1	1	2
killed infant (witnessed)	1	0	1
total	16	8	24

[a] Infant experienced non-fatal attack, i.e. clearly targeted approach of a male at high speed (includes one presumed attack).
[b] Infant disappeared within the first two months after a male immigrated into the group and the male was seen to chase females and/or infants.
[c] Infant died or disappeared after it had been wounded. The injury could have been inflicted by the teeth of a male langur—small holes, sharp cuts, a distance of 3–4 cm between injuries—and the infant as well as other group members were afraid of one or several of the males, i.e. they almost continuously watched and avoided these males; categories according to Borries (1997).

We further examined whether infanticidal males could have sired the subsequent infant of the victim's mother. During the study period eight infants fell victim to infanticide (presumed, likely or witnessed; table 1). In four out of five presumed infanticides, another infant was born subsequently. The DNA analysis revealed that, in all these cases, the presumed killer of the preceding infant was the likely father of the subsequent infant (table 2). In two cases, two males were presumed as killers (males M69 and M70) out of which one male was the likely father of the subsequent infant, whereas the other male was excluded from paternity.

4. DISCUSSION

We examined the genetic relationship between males and the infants they attacked or killed as well as subsequent infants via DNA profiling. We found that male langurs at Ramnagar invariably killed or attacked only infants they had not sired (table 1). Since there was no exception, it is highly likely that attacks on infants were indeed attempted though unsuccessful infanticides, which might have failed due to frequent protective behaviour by males and females (Struhsaker & Leland 1987; Borries 1997; Borries *et al.* 1999).

Infanticidal males seem to benefit from infanticide because, in all four cases investigated, they sired the subsequent offspring of the victim's mother (table 2). Yet the conclusion of 100% reproductive benefit is premature because the sample size was small. However, it was comparatively large and unique, even for a long-term study on reproductive success in wild primates. All four cases were preceded by presumed (not witnessed) infanticides. The mother of the only infant observed to be killed

Table 2. *Kin relationship between presumed killers and the subsequent infants of the victims' mothers*

infant killed (presumably)[a]	presumed killer[a]	subsequent infant[a]	likely father of subsequent infant[a]	paternity exclusion probability
X2.2	M65	X2.3	M65	72.0%[b]
MX4.1	M65	MX4.2	M65	99.9%
MO10.2	M69 or M70	MO10.3	M70[c]	91.0%
O11.1	M69 or M70	O11.2	M70[c]	91.5%

[a] M, male; other letters indicate group names.
[b] Only three out of the five systems were analysed due to the very small amount of DNA in the infant's sample.
[c] M69 was excluded as father.

had, at the end of the study, not yet carried another infant to term. Finally, in two of the four cases, two males were suspected of infanticide, of whom one male sired the subsequent infants. If the other male (M69) had killed these two infants but did not father their subsequent siblings the success rate of infanticidal males would only be 50%. However, male M70 was our main suspect because, on two other occasions, he was observed to attack an infant (Borries 1997, table 1, cases 25 and 28), while male M69 was never observed to attack an infant. However, since both males immigrated into the same group within five days of each other and females as well as infants avoided them, they were both suspects. A larger sample size would definitely help to illuminate this point but will be difficult to obtain. Nevertheless, our findings suggest that a male's chances of gaining reproductive advantage via infanticide are very high.

In summary, empirical data support the hypothesis that infanticide is in accordance with the sexual selection theory and, thus, adaptive in langur monkeys. Both questions were answered in favour of the sexual selection hypothesis.

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