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Carola Borries

Infanticide in seasonally breeding multimale groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal)

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Abstract In the seasonally breeding langur (*Presbytis entellus*) population of Ramnagar, South Nepal, where multimale groups prevail, 25 attacks on 11 infants (including one actual killing) by seven adult males were witnessed in five groups by six observers between 1990 and 1996. Circumstantial evidence also indicates three additional attempts at infanticide and in seven additional cases infanticide was presumed or likely. Infanticide presumably accounted for 30.8–62.5% of infant mortality in the first 2 years of life. Most attackers (91.4%) were residents of the infants' group and had immigrated after the infants had been born (75.0%) or conceived (25.0%). Thus, they were not related to the victims. The interbirth interval was shortened if an infant died either prior to September of its 1st year of life (mean = 1.2 years), or its 2nd year (mean = 2.0) and even its 3rd year (mean = 2.4). All attackers remained in the group at least until the next mating season; high-ranking males maintained their dominance rank and lower-ranking males rose in rank. Since rank and mating success were correlated and rank and reproductive success might be correlated, all attackers had a good chance of siring the next infant of the victims' mothers and could thus have benefited by their action. Infanticide seems to be a male reproductive strategy at Ramnagar. Infanticide has never before been reported among seasonally breeding langurs living at such low densities. This is also the first detailed report of infanticide as a male reproductive strategy in a seasonally breeding primate population.

Key words *Presbytis entellus* · Infanticide · Male-infant relation · Interbirth intervals · Infant mortality

C. Borries
Deutsches Primatenzentrum, Abteilung für Verhaltensforschung/Ökologie, Kellnerweg 4, D-37077 Göttingen, Germany
Tel.: (+) 49 551 3851301; Fax: (+) 49 551 3851228;
e-mail: cborri@www.dpz.gwdg.de

Introduction

In several populations, male Hanuman langurs (*Presbytis entellus*) have been reported to kill infants during adult male replacements (first published by Sugiyama 1965; compilation in Sommer 1994). Five explanatory hypotheses for the occurrence of infanticide were given by Hrdy and Hausfater (1984). Of these, the sexual selection hypothesis (Hrdy 1974, 1979; Newton 1986; Sommer 1994) and the social pathology hypothesis (Dolhinow 1977; Curtin and Dolhinow 1978; Boggess 1979, 1984) are the most pertinent contenders here. Although most biologists now accept that infanticide is adaptive under some conditions, the existence of infanticide among nonhuman primates and the idea that it might be adaptive remains hotly debated in anthropological journals (Bartlett et al. 1993; Sussman et al. 1995; but see Hrdy et al. 1995).

If infanticide is attributable to sexual selection, the following conditions should be fulfilled: (1) the male is not related to the infant, (2) the subsequent interbirth interval of the victim's mother is shortened and (3) the male has access to the female afterward and thus improves his chances of siring her subsequent infant (Hrdy 1974). The idea that sexual selection might be a reasonable explanation has been examined and was supported for Hanuman langurs at Mount Abu (Hrdy 1977), Jodhpur (review in Sommer 1994), and Kanha (Newton 1986, 1987, 1988).

Infanticide among Hanuman langurs has primarily been reported in one-male groups, possibly because having a situation where only one male breeds facilitates the evolution of this trait (Newton 1986, 1988; Newton and Dunbar 1994). Even a recent case reported from the Mundanthurai Wildlife Sanctuary (South India) – where most langur groups are multimale – was observed in the only known one-male group of the population (Ross 1993). Only one publication mentions male infanticide in Hanuman langur multimale groups (at Polonnaruwa:

Ripley 1980). Unfortunately, no further details have been published.

In multimale groups the costs for infanticidal males seem likely to be high, since other resident males might defend the victim, and the benefits seem likely to be low because of the generally lower paternal probability in multimale groups (e.g. Newton and Dunbar 1994; Sommer 1994). However, in other primate species living in multimale groups, males have been observed to kill infants (e.g. *Macaca sylvanus*, Angst and Thommen 1977; *Macaca fascicularis*, Angst and Thommen 1977; de Ruiter et al. 1994; *Macaca mulatta*, Angst and Thommen 1977; Camperio Ciani 1984; *Papio ursinus*, Busse and Hamilton 1981; Collins et al. 1984; *Papio anubis*, Collins et al. 1984; *Colobus badius*, Struhsaker and Leland 1985; *Macaca fuscata*, cited in Hiraiwa-Hasegawa and Hasegawa 1994). The aggressors were extra-group males, recent immigrants, had recently been introduced or were conceived outside the group. Thus, they could not be related to the infants they killed. Most males were of high dominance rank, so their chances of benefiting from infanticide were good. Perhaps in Hanuman langurs infanticide has mostly been reported for one-male groups because extensive data are mainly available from areas with excellent observational conditions where one-male groups happened to live.

Seasonal breeding reduces the likelihood that males will benefit from infanticide since females which lose their infants cannot resume cycling until the following mating season. Hrdy and Hausfater (1984: xxiii) predicted "that sexually selected infanticide will rarely be found among seasonal breeders" but suggested that "infanticide might still confer on males a limited reproductive advantage were it the case that a female who loses her litter in one season is more likely to breed successfully or reproduce a larger litter in the subsequent breeding season." Exactly these conditions, and cases of infanticide, have recently been reported for *Propithecus diadema* (Wright 1995) and for *Lemur catta* (Pereira and Weiss 1991; Hood 1994) and Newton (1986) witnessed infanticide in Hanuman langurs at Kanha, which breed seasonally but live in one-male groups.

Infanticide in seasonally breeding multimale groups of Hanuman langurs has not been reported so far. However, in a non-provisioned langur population living in a natural forest near the village of Ramnagar (South Nepal), several attacks on infants and infanticide by males were observed. Most groups were multimale multifemale and breeding was seasonal. The aim of this paper is to describe the circumstances under which attacks and infanticide occurred and to examine whether the conditions predicted by the sexual selection theory are met, i.e. the attacking males were not related to the infants, the interbirth interval depended on the survival of the preceding infant and attacking males increased their chances to sire the subsequent infant. Non-fatal attacks were included in the analysis to test whether at least the first two conditions for infanticide as an adaptive strategy were fulfilled.

Methods

Habitat

The langurs inhabit a semi-evergreen forest dominated by sal trees (*Shorea robusta*) near the village of Ramnagar (Chitwan District, South Nepal; 300 m above sea level; 27°44′N, 84°27′E; Podzuweit 1994). The density of trees is 199 specimens ha^{-1} (Koenig et al. 1997; floristic inventory in Wesche 1997). In the forest, trees are regularly cut, cattle are grazed and every spring the undergrowth is burnt by local people. However, the vegetation is still dense and visibility is poor. The langurs are not hunted by people but are occasionally harassed for fun. Food is not provided and crop-raiding by langurs has not been observed or reported. Known predators are leopards (*Panthera pardus*) and domestic dogs (*Canis familiaris*).

Climate

Three major seasons can be distinguished at Ramnagar: Spring (March and April) is dry and hot, summer monsoon (May to September) is hot (up to 43 °C) and provides 92% of the annual precipitation (yearly mean: 2279 mm) and winter (October to February) is dry and moderate with minimum temperatures of 5 °C in the early morning (Koenig et al. 1997).

The langur population at Ramnagar

The langurs live at a density of about 26 individuals km^{-2}. Females are philopatric (only 2 of more than 100 females immigrated into a neighbouring group during the 6-year study period), whereas males leave their natal group and migrate between bisexual groups. Males enter a new group alone. Within the first few days, immigrant males establish their dominance position. If the α position is gained, the former α male may either be ousted or remain in the group. Thus, male immigration into a multimale group at Ramnagar does not resemble a take-over in a one-male group. Permanent all-male bands are not found and most males are members of bisexual groups. Extra-group males are encountered as solitaries, in pairs or in temporary associations of up to five males. A total of 19 bisexual langur groups were identified, of which 16 were designated by a capital letter. Of the bisexual groups 76.5% were multimale with up to nine adult males per group. The mean group size was 19.6 in June 1992 and decreased to 16.9 in May 1996 (mean: 18.7, based on 12 censuses between 1992 and 1995). Females in each bisexual group were numbered consecutively (e.g. P1, P2, ... A1, A2, ...). Dependent infants received their mother's number and an additional number indicating birth order (e.g. P5.2 is the second known infant of female P5). Male infants were designated by an additional "M" (e.g. MP2.1). All other males were designated "M" and a consecutive number (M1, M2 ...). About 290 individuals are known. The langurs breed seasonally (Koenig et al. 1997): births only occur from January to June (with 47.1% in March). Copulations are regularly seen from May/June to November/December. Conceptions, however, are confined to the period from July to November (with 49.0% in August).

Observation period

Since August 1990 several langur groups have been studied by a total of 21 observers, all of whom could identify all the individuals in their respective study group(s). By 30 April 1996 a total of 37,291 h had been spent in contact with the langurs (all observers). All data refer to and were calculated for the period from August 1990 to April 1996. Additional information on male membership, male dominance rank and sexual behaviour for May to December 1996 was provided by T. Ziegler.

Data collection

My calculations summarize *ad libitum* observations of all 21 observers concerning births, deaths, disappearances, migrations, dominance ranks, and rare events such as attacks on infants. Most of our observations were concentrated on two out of three focal groups (P troop since August 1990; O troop since October 1992) providing long-term data on individual life histories. In addition, every 3rd month, beginning in March 1992, at least the ten best known groups were contacted and their members re-identified and counted, providing cross-sectional data for interbirth intervals, infant survival, and other population parameters.

Definitions and calculations

The following events were distinguished and are arranged in ascending order of probability.

1. *Attempted infanticide assumed* (AIA): no attack on the infant was observed, infant was found wounded but survived, the injury could have been inflicted by the teeth of a male langur (small holes, sharp cuts, a distance of three to four cm between injuries) *and* the infant as well as other group members were afraid of, almost continuously watched, and avoided one or several of the group's males.
2. *Attempted infanticide* (AI): infant experienced non-fatal attack (clearly targeted approach of a male at high speed).
3. *Presumed infanticide* (PI): infant disappeared during the first 2 months after a male immigrated into the group *and* the respective male was seen to chase females and/or infants prior and/or after the presumed event.
4. *Likely infanticide* (LI): infant died or disappeared after it had been wounded, circumstances as in AIA.
5. *Witnessed infanticide* (WI): a male was seen to attack and injure an infant which died from its injuries.

These categories follow Sommer (1994) as closely as possible, with the added category of AIA. Since six infants and five or six males were involved in more than one case, all parameters were calculated three times: (1) once for each infant (n = 18, for the earliest and strongest incident respectively); (2) once for each male-infant pair (n = 24, for the earliest and strongest incident per pair); and (3) once for all events (n = 35). All cases were analysed as if they had been successful.

Infants which disappeared in the first 12 months of life are presumably dead since the shortest lactational period (total n = 23) ever known for Ramnagar langurs is 19 months (mean: 24.9 months; C. Borries and P. Winkler, unpublished work). Interbirth intervals are calculated to the year since the langurs breed seasonally and most data stem from censuses. Male dominance rank was assessed by the outcome of dyadic displacement interactions (Borries et al. 1991).

Results

During the study period, 3 attempted infanticides (assumed), 24 attempted infanticides, 5 presumed infanticides, 2 likely infanticides and 1 witnessed infanticide occurred (n = 35; Table 1). A total of 18 infants from six bisexual groups and 11 adult males were involved.

The males were twice observed wounding an infant and five additional injuries were attributed to males (Table 1). The infants were wounded on the legs (twice), the back (twice), and the arm, face or belly (once each). So far we have never seen adult males wound adult females.

Eyewitnessed events

A total of 25 events (AI plus WI) were directly observed during 37,291 h, leading to a frequency of one eyewitnessed case every 1,554 contact hours. These witnessed events (six observers) involved 11 infants from five bisexual groups as victims and seven adult males as attackers. Five infants were attacked more than once. Infant O20.1 was the target in 11 eyewitnessed cases and two additional attempts of infanticide are assumed (Table 1). A closer look at this infant's fate reveals that the males might have preferred handicapped infants, which are an easy target:

Female infant O20.1 was born on 3 May 1994. Her mother (O20) broke an arm on 5 January 1995 (A. Koenig, personal communication) when O20.1 was 8 months old. Afterward, O20 could hardly follow the group; she dropped in rank and almost stopped carrying her daughter. Usually, infants at the age of 8 months are still regularly carried at Ramnagar. O20.1 became very thin and small compared to her peers. When the first case of attempted infanticide was assumed 4 months later (case 12), she was noticeably smaller than all her peers. The event left her with both legs paralysed (for about 2 weeks) and she never regained full mobility. At the age of 15 months she lost one eye (case 13). Afterward, when O20.1 was obviously handicapped, she was repeatedly attacked (cases 14–24).

Recent events at the study site point in the same direction: Female infant O7.1 (born 20 March 1994, so a peer of O20.1) broke her left femur on 31 May 1996 and afterward in June was attacked three times by M85 (T. Ziegler, personal communication). As long as the infant was healthy, no attacks were witnessed. Furthermore, female infant P3.1 (case 4) was attacked after she fell out of a tree about 25–30 m to the ground and female O4.3 (case 28) fell and was unconscious when attacked.

Of the attacked infants 64.0% were alone when attacked (i.e. not in body contact with another langur; n = 16; Table 1), which further indicates that male attackers seem to prefer easy targets. Infants attacked while alone had a mean age of 15.2 months (range: 4.6–20.3 months). The other 36.0% of the infants (n = 9) were on their mother's belly when attacked. Their mean age was 2.9 months (range: 1 day–16 months). In these cases we could not be sure about the males' target. However, occasionally the males' "intention" could be inferred. For example in case 25 the male ran after a mother carrying her infant. He grabbed and pulled the infant hanging under its mother's belly. He did not pull the mother (see also Gust et al. 1995). Since infants younger than 3 months will hardly be encountered alone, a male aiming at them has to attack the caretakers too. Eight out of nine infants attacked while with their mothers were younger than 3 months of age (mean = 1.3 months, range: 1–90 days, n = 8). Only one infant was remarkably older (case 19). This infant was repeatedly attacked by the same male in the course of 3 h (Table 1), leaving almost no doubts about the

Table 1 Infant sex, fate and age as well as male rank, tenure and access to the infant's mother for attempted infanticides assumed, attempted infanticides, presumed infanticides, likely infanticides, and witnessed infanticide (*Case* cases in chronological order, per infant, first three cases for males from neighbouring groups, the strongest or earliest incident per infant in bold italics; *Infant* identity of the infant, male infants begin with "M", *case 2* identity of the infant not clear; *Date* date of event; *Event AIA* attempted infanticide assumed, *AI* attempted infanticide, *PI* presumed infanticide, *LI* likely infanticide, *WI* witnessed infanticide, the strongest or earliest incident per male-infant pair in bold italics, *a* infant alone, *m* infant with mother; *Fate* infant's fate after the event, *S* survived, *I* injured, † died, *D* disappeared; *Age* infant age at the time of event in months; *Male* identity of the male, *M?*, *X-troop* unidentified resident male of X-troop, *M 12?* presumably M 12, males in bold italics when first mentioned; *Rank*^{E} male dominance rank at the time of event, total number of adult males per group in brackets; *Tenure* male tenureship at the time of event in months; *Access* male in the same group as the infant's mother in the next mating season; *Rank*^{M} male dominance rank in the next mating season, total number of adult males per group in brackets; *Witness* (of attempted and witnessed infanticides only) *CB* Carola Borries, *AK* Andreas Koenig, *DP* Doris Podzuweit, *KT* Keshab Thapa, *JN* Julia Nikolei, *KL* Kristin Launhardt; *initials* in bold italics when first mentioned)

Case	Infant	Date	Event	Fate	Age	Male	Rank^{E}	Tenure	Access	Rank^{M}	Witness
1	MU 2.1	11.06.92	***AI***^{m}	S	3	***M ?***, ***X***-Troop	? (2)	0	No	?	***CB***
2	MK	18.06.92	***AI***^{m}	S	3	***M ?***, ***I***-Troop	1 (1)	0	No	?	CB
3	MA 1.2	08.04.94	***AI***^{m}	S	1	***M13***, ***P***-Troop	3 (3)	0	No	3 (3)	***AK***
4	P 3.1	22.11.91	***AI***^{a}	S	9	M 13	2 (5)	4	Yes	2 (3)	***DP***, CB
5	MP 2.1	~15.10.92	***LI***	I, †	7	***M 12*** ?	1 (3)	~10	Yes	1 (3)	–
6	X 2.2	07.–08.93	***PI***	D	3–5	***M 65*** ?	1 (1)	1–2	Yes	1 (1)	–
7	MX 4.1	07.–08.93	***PI***	D	3–5	M 65 ?	1 (1)	1–2	Yes	1 (1)	–
8	O 19.1	~07.11.93	***LI***	I, D	~8	***M 49*** ?	1 (5)	~6	Yes	1 (3)	–
9	O 5.2	08.–21.10.94	***PI***	D	9	***M70?/M69?***	1/2 (5)	1/1	Mother: D	1/2 (5)	–
10	MO 10.2	08.–21.10.94	***PI***	D	5	M70?/M69?	1/2 (5)	1/1	Yes	1/2 (5)	–
11	O 11.1	08.–21.10.94	***PI***	D	5	M70?/M69?	1/2 (5)	1/1	Yes	1/2 (5)	–
12	O 20.1	15.05.95	***AIA***	I, S	13	M 70 ?	1 (5)	2	Yes	1 (6)	–
13	..	14.08.95	AIA	I, S	15	***M 74 ?***	2 (6)	1	Yes	2 (6)	–
14	..	20.08.95	***AI***^{a}	S	16	***M 78***	2 (7)	1	Yes	1 (5)	***KT***
15	..	24.08.95	***AI***^{a}	S	16	M 74	3 (7)	1	Yes	3 (7)	***JN***, ***KL***
16	..	24.08.95	AI^{a}	S	16	M 74	3 (7)	1	Yes	3 (7)	JN, KL
17	..	24.08.95	AI^{a}	S	16	M 74	3 (7)	1	Yes	3 (7)	JN, KL
18	..	24.08.95	AI^{a}	S	16	M 74	3 (7)	1	Yes	3 (7)	JN, KL
19	..	24.08.95	AI^{m}	S	16	M 74	3 (7)	1	Yes	3 (7)	JN, KL
20	..	25.08.95	AI^{a}	S	16	M 74	3 (7)	1	Yes	3 (7)	KT
21	..	25.08.95	AI^{a}	S	16	M 74	3 (7)	1	Yes	3 (7)	KT
22	..	29.10.95	AI^{a}	S	18	M 74	4 (7)	1	Yes	2 (3)	JN, KT
23	..	29.10.95	AI^{a}	S	18	***M 85***	1 (7)	1	Yes	1 (3)	JN, KT
24	..	29.10.95	***WI***^{a}	I, †	18	M 85	1 (7)	1	Yes	1 (3)	JN, KT
25	O 1.2	15.06.95	***AI***^{m}	S	2	M 70	1 (5)	3	Yes	1 (6)	KL
26	..	20.01.96	***AI***^{a}	I, S	10	M 85	1 (4)	4	Yes	1 (3)	KT
27	O 4.3	18.06.95	AIA	I, S	4	M 70 ?	1 (5)	3	Mother: †	1 (6)	–
28	..	05.08.95	***AI***^{a}	S	5	M 70	1 (3)	5	Mother: †	1 (6)	JN
29	O 3.2	05.11.95	***AI***^{a}	S	18	M 85	1 (6)	1	Yes	1 (3)	KL
30	..	03.01.96	***AI***^{a}	S	20	M 74	4 (4)	3	Yes	2 (3)	KT
31	MO 17.1	06.12.95	***AI***^{a}	S	21	M 74	5 (6)	2	Yes	2 (3)	JN
32	O 11.2	26.01.96	***AI***^{m}	S	1	M 74	4 (4)	4	Yes	2 (3)	JN, KT
33	..	01.03.96	***AI***^{m}	S	2	M 85	1 (4)	5	Yes	1 (3)	KT
34	MO 10.3	23.02.96	***AI***^{m}	S	1	M 85	1 (4)	5	Yes	1 (3)	KT
35	..	23.02.96	AI^{m}	S	1	M 85	1 (4)	5	Yes	1 (3)	KT

male's intentions. In this case (19) both the mother with the clinging infant and the male pursuing them jumped about 30 m deep into a valley. The likelihood of being injured was higher if the infant was alone (18.8% vs. 0.0%).

With one exception, all infants were defended by other group members. Defensive behaviour included chasing, slapping and loud vocalization. The exception was case 25, when the attacking male ran after the mother who fled, carrying the infant with her (see above), which in itself is a defensive behaviour. If the infant was not on the mother's belly and the mother was still alive, she defended her offspring in 60.0% of the cases (total $n_{\text{infant alone + mother alive}} = 15$). Adult and/or immature females defended in 60.0% of all cases (total $n = 25$). If the mother is included (either carrying the infant or approaching for defence), females were involved as defenders in 88.0% of all cases. Adult males defended in 72.0% of all cases (total $n = 25$). All adult male defenders had been in the group when the respective infants were sired (putative fathers). Other adult males (if present) were never observed to defend. Defensive behaviour, especially by adult males, seems to be rather effective and might be the reason why only one infant was seen to be killed by a male (case 24):

On 29 October 1995, infant O20.1 was attacked three times by two different males (M74 and M85) in the course of 17 min. There were seven adult males present in the group with M49 as the only putative father. 1005 hours: M74 approaches O20.1 who is feeding on the ground. O20.1 starts to scream whereupon M49 chases M74 away. 1007: M74 has returned and *attacks* O20.1 (case 22) whereupon M49 (barking) chases M74 away. 1012: Meanwhile the mother O20 has approached her daughter who is now in a small tree. Other group members have approached, too. M74 approaches O20.1 again and is chased away by M49 and O20. O20 returns quickly and approaches her daughter. 1015: A second male, M85, climbs the small tree where O20.1 and O20 are sitting and approaches them. M49, who is about 20 m away, starts to bark and runs towards the tree. 1016: M85 moves closer to O20.1 and O20, whereupon M49 chases him away. 1017: M85 returns and again climbs the tree, approaching O20 and O20.1. 1020: M85 jumps in the direction of O20.1 (i.e. *attacks*, case 23) but M49, O20, O19 and O17 attack him and all of them – except O20.1 – fall 5–6 m to the ground. Immediately afterward M85 climbs the small tree again and approaches O20.1, but M49 and O17 chase him away. 1021: M85, M49, O20, O19 and O17 all return into the small tree where O20.1 is still sitting. 1022: O19 slaps M85 from below and is threatened away, but she returns immediately and slaps M85 again whereupon at 1023: M85 threatens and slaps O19. M49 (barking) approaches and threatens M85 who returns the threat. 1024: M85 *jumps on* O20.1 (case 24) and, falling 5–6 m to the ground, pulls her with him and carries her away. M49, O20, O19, O17, O8 and O2 jump out of the tree and barking and screaming run after them. 1025: O20.1 is found injured on the ground about 20 m from the small tree. She dies at about 1200 hours (J. Nikolei and K. Thapa, personal communication).

This example also illustrates the repeated and persistent attempts of males to approach infants. Males were also observed stalking infants. Females with dependent infants as well as the infants themselves were generally afraid of unfamiliar males even several months after immigration and tried to avoid them or stayed in the vicinity of familiar males (putative fathers). Also, familiar males stayed in the vicinity of infants if newly immigrant males were present. However, no attempt was made to quantify these behaviours.

Infants involved

Eight male and ten female infants were involved (Table 2). If all cases are considered, female infants were overrepresented (26 out of 35 cases; 74.3% female). At the time of the event the infants were on average 10.0 months old (range: 1 day–21 months, $n = 35$), if repeated events are excluded, the mean infant age drops to 6.8–7.0 months (range: 1 day–21 months, $n = 18$). In all 35 cases the infants were not yet weaned from nipple contact.

Males involved

All males involved were adult at the time of the event. Three males were residents of a neighbouring group (Table 1, cases 1–3). All other males (91.4%) were members of the same group as the infant. Most of these males had recently immigrated and attacked the infants in the first month of their tenure (50%, total $n = 32$; Table 1). Two males immigrated twice into O troop: M74 stayed from 14 August 1995 until 28 August 1995; he re-immigrated on 17 October 1995 and remained at least until December 1996 (T. Ziegler, personal communication). M70 stayed from 29 September 1994 until 2 February 1995 and again from 5 April 1995 until 3 September 1995. The two tenures of these two males were treated as separate tenures. At the time of the event, the mean tenure length was 2.5 months (range: 1 day–10 months) and was higher, if repeated events were excluded (mean: 3.1 months, range: 10 days–10 months; Table 2).

Table 2 Sample size, infant sex ratio, mean infant age as well as mean male tenure and mean male dominance rank at the time of the event

		Attempted Infanticide Assumed	Attempted Infanticide	Presumed Infanticide	Likely Infanticide	Witnessed Infanticide	Total
n	All cases	3	24	5	2	1	35
	Male-infant pairs	1	15	5	2	1	24
	Infants	–	10	5	2	1	18
Infant sex [male/female]	All cases	0/3	6/18	2/3	1/1	0/1	9/26
	Male-infant pairs	0/1	5/10	2/3	1/1	0/1	8/16
	Infants	0/0	5/5	2/3	1/1	0/1	8/10
Infant age [months]	All cases	10.7	10.9	5.0–5.8	7.5	18.0	10.0–10.1
	Male-infant pairs	13.0	8.5	5.0–5.8	7.5	18.0	8.3–8.5
	Infants	–	6.4	5.0–5.8	7.5	18.0	6.8–7.0
Male tenure[a] [months]	All cases	2.0	2.4	1.0–1.4	8.0	1.0	2.47–2.53
	Male-infant pairs	2.0	3.2	1.0–1.4	8.0	1.0	3.0–3.1
	Infants	–	3.4	1.0–1.4	8.0	1.0	3.1–3.2
Male rank[a]	All cases	1.0	2.4	1.0–1.6	1.0	1.0	1.9–2.0
	Male-infant pairs	1.0	2.2	1.0–1.6	1.0	1.0	1.7–1.8
	Infants	–	2.1	1.0–1.6	1.0	1.0	1.5–1.7

[a] Males from neighbouring groups excluded (n all cases = 32; n male infant pairs = 21, n infants = 15); data as in Table 1

Table 3 The effect of immigrant males and infanticide on infants and infant mortality during the first 2 years of life

	Population	Main study groups		
Groups	A B K O P S U X	P	O	P + O
Group years	20	4	3	7
Infants born[a]	52	9	14	23
Infants with new male[b]	37	2	14	16
Infants not affected[c]	19	0	7	7
Attempted infanticide (AI)	10	1	2	3
Presumed infanticide (PI)	5	0	3	3
Likely infanticide (LI)	2	1	1	2
Witnessed infanticide (WI)	1	0	1	1
Infants died	26	4	8	12
PI + LI + WI	8	1	5	6
% Of dead infants	30.8%	25.0%	62.5%	50.0%

[a] Only infants born until 1994 (which would have reached or reached 2 years of age during the study period) if male membership was known since the time of conception
[b] At least one adult male migrated into the infants' natal group after the infants were conceived and before they reached 2 years of age
[c] No incident observed or suspected

In the majority of the cases (75.0%, n = 24; male infant pairs = 15), the males immigrated after the infants were born. In eight cases (nos. 5,25,27,28,32–35; male-infant pairs = 6) the males immigrated before the infants were born, but, after they had been conceived. (Note that conceptional estruses in Hanuman langurs can be identified by the pattern of sexual behaviour, Sommer et al. 1992; C. Borries and P. Winkler, unpublished work.) Thus, all males immigrated after the infants were conceived. As far as can be inferred from behavioural observations, the males were not related to the infants they attacked.

Infant mortality and infanticide

Up to 1994, 52 infants were born (i.e. infants which would have reached or reached 2 years of age – the mean weaning age – during the period analysed; Table 3) in eight bisexual groups. Only those infants were considered for which complete information on male troop membership is available since conception. Out of these, 37 infants (71.2%) had a new adult male in their natal group before they reached the age of 2 years. Of these 37 infants, 21 died 56.8%), including 8 victims of presumed, likely or witnessed infanticide. If these eight cases were excluded, the remaining infant mortality is 35.1%.

The other 15 infants had no new male in the group between conception and the completion of their 2nd year of life. Of these infants five died (33.3%). Thus, infant mortality was higher if there was a new male in the group. The difference is, however, not significant (χ^2 = 1.50, df = 1, P = 0.22, corrected for continuity; Siegel and Castellan 1988).

In total, 26 infants out of 52 died 50.0%) before they completed their 2nd year of life. Likely, presumed or witnessed infanticide accounted for 30.8% of infant mortality (Table 3).

The comparison of P and O troops (Table 3), which had about 20 and 30 group members respectively, suggests the following group size effects: In the smaller P troop, a smaller proportion of the infants experienced male immigration (22.2% versus 100.0%) and the contribution of infanticide to infant mortality was lower (25.0% versus 62.5%).

Infant loss and subsequent interbirth interval

The mean interbirth interval for Ramnagar langurs is 2.4 years (n = 72, range: 1–4 years; C. Borries and P. Winkler, unpublished work). The length of the interbirth interval depended on infant survival. There was a significant positive correlation between the infants' age at death in the first 24 months of life and the subsequent interbirth interval of their mothers (Fig. 1; Spearman rank order correlation; r_s = 0.81, n = 19, P < 0.001; two-tailed, corrected for ties; y = 1.277 + 0.07 x); the younger an infant died, the shorter the subsequent interbirth interval.

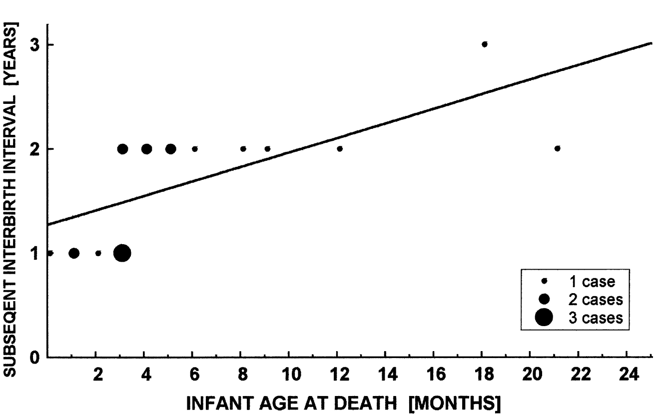

Fig. 1 Correlation between infant age at death and the subsequent interbirth interval of its mother

Interbirth intervals of 1 year were only achieved if the infants were lost prior to September of the same year they were born. The analysis of interbirth intervals in relation to premature infant loss has to take this seasonal aspect into account. In Fig. 2 mean interbirth intervals are given for females which lost their infant before September of the first mating season after it was born (1.2 years, range: 1–2 years), before September of the second mating season (2.0 years, no range), before September of the third mating season (2.4 years, range: 2–3 years), and finally the interbirth interval if the infant *survived* the third mating season following its birth (2.8 years, range: 2–4 years). Thus, the interbirth interval depended significantly on the fate of the preceding infant [Kruskal and Wallis H (3, n = 59) = 30.98, P < 0.001]. Multiple comparisons between treatments (Siegel and Castellan 1988) revealed a significant difference if the infant did not survive the *first* mating season and if it survived the *third* mating season ($30.3 \gg 16.2$, $\alpha = 0.05$; compare the first and the last column in Fig. 2). Interbirth intervals tended to be shorter if the infant died prior to the first mating season *post-partum* than if it died prior to the third mating season, but this effect was not significant ($17.1 > 16.1$, $\alpha = 0.10$). In general, if an unweaned infant died prior to its mother's next conception, the subsequent interbirth interval was significantly shorter than if the infant survived (C. Borries and P. Winkler, unpublished work). These findings can explain why males attacked infants in September or even later in the year: Although the mothers cannot conceive in the same year, the likelihood of conception in the following year is increased (Fig. 2).

If the infants survived at least up to their second mating season post-partum, 43.5% of the females nevertheless had a subsequent interbirth interval of only 2 years. 47.8% of the females had a 3-year interval and 8.7% a 4-year interval. Thus, on average only 56.5% of the infants surviving up to the second mating season post-partum seem to prevent their mothers from conceiving again. In consequence, the males should only attempt to kill infants which are still suckling if their mothers showed no sexual behaviour. Out of the 18 mothers (Table 1) there are sufficient data on sexual behaviour for 13 mothers (P and O troop only): 61.5% showed no sexual behaviour prior to the event, 30.8% invited for copulation during 1 or 2 (scattered) days, but no ejaculatory copulations were observed. Thus, 92.3% of the mothers showed almost no sexual behaviour. Only one mother (7.7%) resumed cycling 3 months before her infant was attacked (case 32), but she did not carry an infant to term in the following birth season. It is likely that she did not conceive.

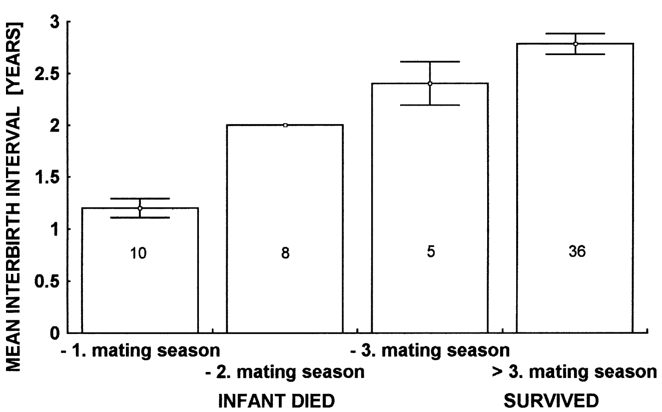

Fig. 2 Mean interbirth interval (±SE) in relation to infant mortality or survival (*first three columns* infants *died* before September of the first, second, or third mating season post-partum; *last column* the infants *survived* the third mating season; *number* of infants is indicated on bar)

Male access to the victim's mother

According to the sexual selection theory, it is only advantageous to kill an infant if the actor increases his chances of siring the next infant of the victim's mother. He should have sexual access to her, even if he has to wait until the next mating season. A simple measure for sexual access is assumed here. If, in the mating season following the event, the male was member of the mother's group, he had sexual access. The deadline (September each year) was the same as for infant survival and interbirth intervals (see above):

In 29 out of the 35 cases (82.9%; Table 1) the males had access to the victim's mother in the mating season following the event, with the exceptions of cases 1–3 (8.6%), where the males belonged to a neighbouring group, and cases 9, 27 and 28 (8.6%), because the females died/disappeared. Thus, if the males were members of the same group as the females at the time of the event and if the females survived, all males had access in the following mating season.

Sexual behaviour and conception of the victims' mothers

If the infant died or disappeared (PI, LI, WI; n = 8; Table 1), 62.5% of the mothers (cases 5, 8, 10, 11, 24) were seen to copulate with the attackers in the mating season following the event. One mother disappeared together with her infant. For the two remaining females (cases 6 and 7), no data on sexual behaviour are available. However, they gave birth in the following year and it is highly likely that the presumed attacker sired these two infants since he was the only adult male in the group. Thus, it can be assumed that all males mated with the victims' mothers (if they survived).

In total, five of the eight mothers produced a subsequent infant. Their mean interbirth interval was 1.8 years (n = 5, range: 1–3 years), 1 year shorter than the mean interval for infants surviving the third mating season (2.8 years, Fig. 2). One female disappeared (see above) and two died before they could carry another infant to term. If the infants died prior to their first mating season post-partum, the subsequent interbirth interval was 1 year ($n = 2$), if they died later, it was 2.3 years ($n = 3$, range: 2–3 years).

Male dominance and mating success

Male dominance rank and mating success were significantly correlated (Fig. 3; Spearman rank order correlation for copulations with ejaculation: $r_s = 0.98$, $P < 0.001$, for copulatory attempts: $r_s = 0.86$, $P = 0.014$; for both parameters combined: $r_s = 0.93$, $P = 0.003$). The α and the β males copulated by far the most frequently.

Most males that attacked infants were high-ranking (Table 1), but some males held the third, fourth or even fifth rank position. If male dominance and mating success are correlated, the question arises of why low-ranking males attacked infants at all. Whether or not males could benefit from attacks or infanticide does not depend on their dominance rank when they attacked but on their rank position during the mating season following the event. All attacking males then held either the α, β or γ position (Fig. 4). If the sample is reduced to the 15 infants involved (black columns, Fig. 4), the respective males were either the α or the β males in their group. Assuming a positive correlation between mating success and reproductive success, all attackers had a good chance of siring the next infant of the victim's mother.

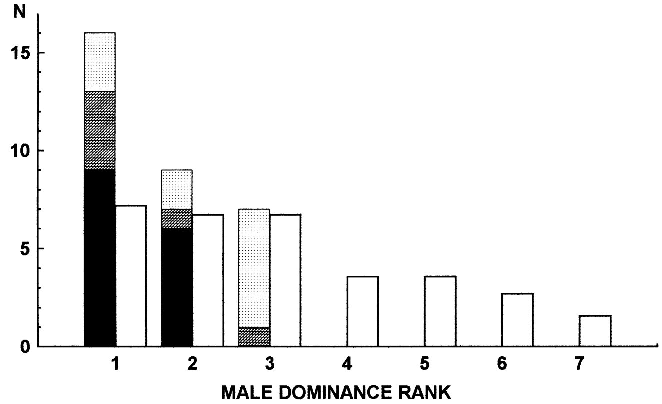

Fig. 4 Male dominance rank in the mating season following the event (*black columns* 15 infants; *striped* + *black columns* 21 male-infant pairs; *dotted columns* + *striped* + *black columns* all 32 cases; *white columns* expected values, based on all adult males in the group for all 32 events; data as in Table 1)

Discussion

Infanticide a rare event?

We witnessed 25 attacks (AI and WI) during 37,291 h in contact with the langurs. In other words, 1 attack was seen every 1,554 h. Only one infant was actually killed in the presence of observers during those 37,291 h. Thus, the likelihood of witnessing an attack or infanticide seems to be low. But this likelihood generally depends on several factors. Besides "luck" and the amount of contact time, the observational conditions, the degree of habituation, group cohesiveness (and thus feeding habits, habitat structure and group size), and the actual frequency of infanticide in particular should be important. This actual frequency is not necessarily represented adequately by the observed frequency. In Ramnagar, for example, the observational conditions are poor and the langurs spend less than 20% of the day on the ground (average for 1 year = 17.7%, Podzuweit 1994), thereby reducing observability. Furthermore, the members of a group can be dispersed over more than 3 ha (C. Borries, unpublished work; mean: 1.1 ha for a group of 21 members, Podzuweit 1994). Consequently, the observed frequency of attacks and infanticide cannot be compared directly to that of other study sites with better observational conditions. That we witnessed attacks and infanticide, in contrast to other studies with comparable observational conditions, is probably due to our long observation period and the large amount of contact time.

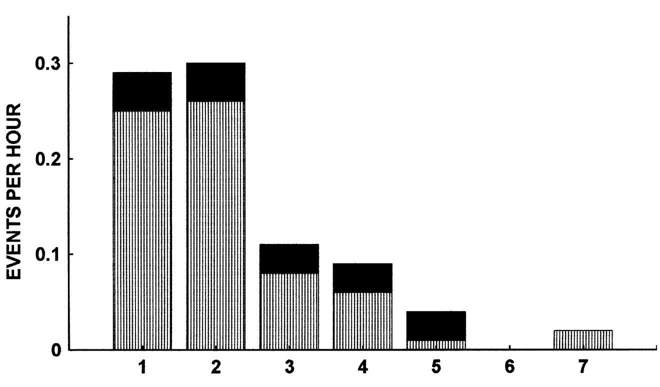

Fig. 3 Male mating success in relation to dominance rank (for P troop males during the mating season in 1991; 708 h of observation; data D. Podzuweit and C. Borries; *Black bars* copulations with ejaculation; *striped bars* copulatory attempts with or without intromission)

Infanticide has not been observed in the following Hanuman langur populations: Orcha and Kaukori (Jay 1965), Gir forest (Kurup 1970; Rahaman 1973), Wilpattu (Muckenhirn 1972), Bhimtal (Vogel 1973), Melemchi (Bishop 1975), Simla and Hatto (Sugiyama 1976), Junbesi and Ringmo (Boggess 1976, 1979), and Rajaji (Laws and vonder Haar Laws 1984). However, the likelihood of witnessing infanticide was small in these studies since none lasted for 2 or more consecutive years and they involved single or few observers.

The actual frequency of infanticide should depend on the number of unweaned infants and thus on group size, on male migration rate (influenced by group size) and to some extent even on the rank acquired by immigrant males. Also, the frequency of infanticide is likely to be lower in multimale groups because the chances to benefit from infanticide are smaller (Newton and Dunbar 1994).

At Ramnagar, the majority of observed attacks did not result in the death or disappearance of the victim, presumably because of counterattacks by other group members, especially adult males (see also Podzuweit et al. 1992) whose efforts might have been more successful than defense by females in one-male groups.

Is infanticide important?

It has been argued that infanticide is so rare, especially in relation to predation, that it cannot be an important cause of death among primates (e.g. Sussman et al. 1995). However, during the same study period only one case of predation was observed at Ramnagar (A. Koenig, personal communication). The chances of witnessing infanticide or predation were therefore identical. Infanticide was presumed or likely in seven additional cases while circumstantial evidence suggests that during the same period five additional cases of predation occurred (by dogs and leopards, C. Borries, unpublished work). Thus, the frequency of infanticide seems to be higher than the rate of predation, though these frequencies cannot be compared directly (e.g. they may be influenced in different ways by the presence of observers).

In any case, the frequency provides almost no information about the effect of infanticide on infant mortality. Assuming that all disappearances strongly suspected to have been infanticide (Table 1) were indeed infanticides, we can attribute at least 30.8% of infant mortality to infanticide. If a new male immigrated, the proportion rose to 38.1% (8 out of 21). In the large focal group, 62.5% of infant mortality was attributed to infanticide. The effect of infanticide on infant mortality might be even higher, since the cause of death is not known for most infants. At 30.8%–62.5% or more, infanticide is a major cause of infant mortality at Ramnagar. The proportion matches well with data for langur one-male groups in Jodhpur, where 22% of all dead infants died by infanticide (V. Sommer, personal communication, eyewitnessed deaths only). For langurs at Kanha, 20% of infant mortality in the first year of life were attributed to infanticide (Newton 1987). In red howler monkeys (*Alouatta seniculus*, Crockett and Rudran 1987) at least 44% of infant mortality involved observed, very probable and probable infanticide in the 1st year of life. Struhsaker and Leland (1985) estimated that in *Colobus badius tephrosceles* 10–30% of infant mortality during the first 14 months of life was due to infanticide. At Tana river (*Colobus badius rufomitratus*) the mean death rate for infants/small juveniles was 3.1 times higher than the average after a new adult male entered the group (Marsh 1979).

Male-infant relationship

As far as can be inferred from behavioural observations, none of the presumed attackers was related to his infant target. Most males (75.0%) immigrated into the group after the infant was born and none of them had been in the group when the infants were conceived. Thus, the likelihood of incoming males killing their own kin was zero, which is in accordance with other investigations (e.g. Hrdy 1979; Struhsaker and Leland 1987; Sommer 1994).

During the first 209 days (mean gestation period at Ramnagar, C. Borries and P. Winkler, unpublished work) of their residency, immigrant males will not be related to any infant in the group. Due to seasonal breeding this initial period can be even longer, depending on the month of immigration, because only infants born after the male has spent his first mating season in the group can be his kin. As has been suggested earlier (Sugiyama 1965; Hrdy 1974), males may possibly be able to infer from their past sexual relationship with the mother whether they could be or were definitely not related to her infant. The fact that only putative fathers (i.e. males that had been in the group when the infants were conceived) were seen to defend infants supports this suggestion. In a captive group of sooty mangabeys (*Cercocebus torquatus*), the α male attacked an infant born during his absence from the group (Gust et al. 1995). Their absence or presence during birth was, however, not decisive for langur males at Ramnagar.

Infant loss, subsequent interbirth intervals and seasonal breeding

A crucial point for all considerations about infanticide is the effect of premature loss on the subsequent interbirth interval of the mother, especially when breeding is seasonal. At Ramnagar, there is a positive and significant correlation between the infant's age at death and the subsequent interbirth interval (Fig. 1): the younger the infant died the shorter the interval. The premature loss of an infant reducing the subsequent interbirth interval of the mother has been shown for several primate populations (e.g. Altmann et al. 1978; Leland et al. 1984; Sommer 1994). This effect is unexpected for seasonally breeding groups, in which females can and will produce an infant every year (Hrdy 1979). However, data for free-ranging seasonal breeders show that reproductive failure in one year can increase a female's chances of success in the following year (Newton 1987; Pereira and Weiss 1991). This effect was even stronger in Ramnagar langurs where seasonal breeding occurs together with a long interbirth interval (mean: 2.4 years), leaving ample time for males to act. The interval between parturition and the next conception will depend on the female's reproductive capacity, which in turn depends on the ecological conditions (Koenig et al. 1997; C. Borries and P. Winkler, unpublished work) and may vary tremendously between individuals as well as between populations. At Ramnagar, males may attack and kill infants as long as the infant is not weaned and its mother does not copulate, so the infants can be comparatively old

(Table 2). The longest nursing period known so far lasted for 33 months (C. Borries and P. Winkler, unpublished work).

Male benefit

Males that attempt to attack infants spend time and energy in persistent following, stalking and unsuccessful attacks as well as in concentration on an infant and its social surroundings. They take additional risks because they might get hurt by defenders. Most attackers had a high dominance rank (Table 1) which might reduce their risks. The fact that low-ranking males also attacked infants, however, indicates that these males also took any opportunity available. That injured, handicapped infants and infants encountered alone were the preferred targets further indicates that attacking males attempted to reduce their risks and to increase the likelihood of success.

All attackers at Ramnagar that immigrated into the infants' group remained group members until the next mating season at least. Thus, if the mother survived, they had – although shared – access to her. High-ranking attackers kept their dominance rank and low-ranking males had often increased their rank position in the following mating season. Since rank and mating success were positively correlated (Fig. 3), all males had or would have had a good chance to sire the subsequent infants, assuming that mating success and reproductive success are correlated. We hope to test this correlation (via DNA analyses) in the near future.

All males which presumably/likely killed an infant were seen to copulate with the mother afterwards or (as the only male in the group) are assumed to have sired the next infant. Thus, sexual access was definitely gained and the subsequent interbirth interval was shortened.

Attacks on infants during inter-group encounters

Attacks on infants and infanticide by males during inter-group encounters have mainly been reported for primate species where females migrate (*Pan troglodytes*, Bygott 1972; Goodall 1977; *Gorilla gorilla beringei*, Harcourt et al. 1976; *Presbytis thomasi*, Sterck 1997; but see Shopland 1982 for *Papio cynocephalus*). The males may aim to encourage the females to join their own group. Since langur females at Ramnagar are generally philopatric, the question arises why resident males of neighbouring groups attacked infants. Although at 12.0% ($n = 3$) of the observed attacks (i.e. 8.6% of all 35 cases) the frequency is low, the males should benefit, at least theoretically. Since resident males were seen to copulate with females of neighbouring groups, they may perhaps take any opportunity to increase the number of potentially fertile females in these groups. All three attacks were non-fatal, so we do not know what would have happened had they been successful. For example, the males might have immigrated. More than 30% of the adult (non-natal) males at Ramnagar emigrated from a bisexual group to immigrate into a neighbouring group (C. Borries, unpublished work). At present, the possibility that the three observed attacks were not merely the consequence of between-group aggression aimed at slow group members, i.e. females carrying infants, cannot be excluded. But having witnessed two of the three attacks in question, I am not satisfied with this explanation. The attacks included long and intensive chasing, and the mothers were screaming with fear and defecating, which is normally not seen during inter-group encounters.

Conclusions

The data presented for Ramnagar langurs suggest that infanticide is a male reproductive strategy, since all predictions derived from the sexual selection theory are fulfilled: The male attackers were not related to the infants, the mothers' subsequent interbirth intervals were shortened, and all males had a good chance of siring the mothers' subsequent infants. Infanticide seems to be an important cause of infant mortality and occurs even though the langur groups are multimale, live at a low density, and breed seasonally.

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