

New observations on infanticides among hanuman langurs (*Presbytis entellus*) near Jodhpur (Rajasthan/India)

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Summary. Six eye-witness and five inferred cases of infanticide in two troops of *Presbytis entellus* near Jodhpur, India, are presented. These observations are used to test the hypothesis that infant killing is a male reproductive strategy.

Introduction

It has been asserted several times that adult male replacements in bisexual troops of langurs may be accompanied by infanticides. However, careful reviews (Boggess 1979; Vogel 1979) of the 40–50 reported incidences of infant killings by recently established resident males revealed that the entire procedure of killing has only been observed three times by Mohnot (1971). The majority of reports refer to disappearances of infants during male takeovers or to infants which had been attacked or wounded, although not unambiguously, by males. This led to the controversy of whether langur infanticide should be considered as deviant or even pathological behavior and therefore maladaptive, or whether it should be looked at as being an adaptive male strategy, particularly in terms of gaining reproductive advantage at the expense of the respective former resident male (for review and discussion see Hausfater and Hrdy 1984). This paper presents information about six eye-witness and five suspected cases of infant killings in two carefully studied langur troops near Jodhpur.

Materials and methods

Due to a long-term field study (started by C. Vogel's research team in 1977 and continued by S.M. Mohnot's team since end of 1982) all members of the two bisexual troops Kailana-I (KI) and Bijolai (B) were individually identified as were several members of a third troop, Kailana-II (KII) and several males

belonging to different all male bands. The semi-arid open scrub habitat provides excellent observational conditions. Thus, we are in a position to rely on adequate longitudinal data concerning all significant reproductive parameters necessary to examine infanticidal events in the light of various hypothetical explanations.

Results

Following invasions by males from different bands into the home ranges of the troops KI, KII and B, five adult males were replaced between October 1981 and February 1983 (Table 1). The respective male-male competitions lasted between 6 days and nearly 4 months. Two of these takeovers were definitely noninfanticidal (troop KI by ♂ 20 in November 1981; troop KII by ♂ 10 in February 1982). Neither of these incoming males attacked or harmed offspring of their predecessors present at the time of the takeover or born shortly after (cases 1–6). Three other takeovers, however, were accompanied by infanticidal attacks (troop KI by ♂ 43 in July 1982; troop KI by ♂ 11 from November 1982 until April 1983; troop B by ♂ 38 in January and February 1983):

1. In six cases the infanticide was directly observed; the new leaders (♂♂ 43, 11 and 38) attacked and wounded infants, who died immediately or the following day (cases 9, 12, 13, 16, 17 and 19)¹.

2. One infant disappeared several days after having been injured seriously by ♂ 43 (case 7).

3. Two infants disappeared after having been attacked unsuccessfully by ♂ 11 (cases 10 and 14).

4. Two infants disappeared on the very day the former resident male was ousted (cases 11 and 15).

¹ A photographic documentation of the killing of infant ♂ 6.4 (case 12) has been published by V. Sommer in the magazines *Stern* 29/1983, pp.118–121, and *Bild der Wissenschaft* 10/1984, pp.72–82

Table 1. Fate of infants present during adult male replacements in troops KI, KII and B, October 1981–April 1983

Troop	Period of male change	New resident male	Infant				Fate	Age at death (I) disappearance (II) attack (III) or takeover (IV)	Observer ^c
			Case	Denotation ^a	Sire ^b	Date of birth			
KI	Oct–Nov 81	♂ 20	1	♂ 8.2	♂ 4	22 Sep 80	Survived; left troop Apr 83	13.8 months (IV)	So
			2	♂ 11.2	♂ 4	15 Dec 80	Survived; left troop June 82	11.0 months (IV)	So
			3	♀ 1.3	♂ 4	20 Dec 80	Survived	10.8 months (IV)	So
			4	♂ 7.4	♂ 4	1 Mar 81 ^d	Survived; left troop June 82	7.5 months (IV)	So
KII	Feb 82	♂ 10	5	♂ inf.	(♂ 63)	Dec 81	Survived	2 months (IV)	So
			6	♀ inf.	(♂ 63)	Jan 82	Survived	1 month (IV)	So
KI	June 82	♂ 43 (infanticidal)	7	♂ 1.4	(♂ 4)	27 Mar 82	Wounded 13 July; disappeared 19 July 82	3.7 months (II)	So
			8	♀ 4.5	(♂ 4)	11 Apr 82	Attacked (?) 12 July 82 survived	3.0 months (III)	So
			9	♂ 11.3	♂ 20	5 Jun 82 ^d	Wounded 9 July; died 10 July 82	1.2 months (I)	So
KI	Sep 82–Jan 83	♂ 11 (infanticidal)	10	♀ 4.5	See above		Attacked 6, 11, 22, 25 Nov 82; disappeared 12 Jan 83; disappeared 13 Jan 83	9.1 months (II)	So Da
			11	♀ 12.1	♂ 20	30 Jul 82	Disappeared 4 Nov 82	3.2 months (II)	So
			12	♂ 6.4	♂ 20	11 Oct 82	Wounded 25 Nov; died 26 Nov 82	1.5 months (I)	So
			13	♀ 11.4	♂ 43	10 Mar 83	Wounded 21 Mar; died 22 Mar 83	0.4 months (I)	Da
			14	♀ 1.5	? ^e	8 Apr 83	Attacked 26 Apr; disappeared 17–25 June 83 ^f	2.6 months (II)	Da Da
B	Jan 83	♂ 38 (infanticidal)	15	♂ 3.5	♂ 22	5 May 82	Disappeared 17 Jan 83	8.4 months (II)	Ag
			16	♂ 1.5	♂ 22	25 Sept 82	Wounded, died 11 Feb 83	4.6 months (I)	Ag
			17	♀ 6.5	♂ 22	29 Oct 82	Wounded, died 9 Feb 83	3.4 months (I)	Ag
			18	♂ 6.1.2	♂ 22	25 Oct 82	Survived	3.3 months (IV)	Ag
			19	♂ 5.4	♂ 22	6 Dec 82	Wounded, died 3 Feb 83	1.9 months (I)	Ag

^a '8.2' means second infant born to ♀ 8 after observations of the German team started in 1977. It does not imply that 8.2 is only the second infant of ♀ 8. However, ♀ 11, ♀ 12 of troop KI and ♀ 6.1 of troop B gave birth to their first offspring after the study started

^b Sire=resident male with whom female copulated about 200 days before birth; Parentheses indicate: no observations around time of insemination

^c Ag Agoramoorthy; Da Dave; So Sommer

^d Calculated on the basis of 200 days gestation period

^e ♀ 1 copulated with ♂ 57, ♂ 51 and ♂ 11

^f Disappeared after having an infected tail portion

Eleven infants apparently became victims of three infanticidal male. Nine of these infants were between 0.4 and 4.6 months of age, the remaining two aged 8.4 months (case 15) and 9.1 months (case 10). Two infants, 3.0 (case 8) and 3.3 months (case 18) old, survived infanticidal takeovers, though one of them was probably attacked unsuccessfully (case 8).

Infanticidal males differ in their behavior towards infants born after the takeover: ♂ 43 did not harm infant ♀ 12.1, born 4 weeks after his takeover of troop KI (this infant disappeared only when ♂ 43 himself was ousted; see case 11). ♂ 11, on the other hand killed infant ♀ 11.4 (case 13), born 2 months after his takeover of troop KI. Another infant, ♀ 1.5 (case 14), born

Table 2. Paternity and interbirth intervals following (presumed) infanticide in troops KI and B, correlated with age of previous infants at the time of death or disappearance (footnotes cf. Table 1)

Victim of infanticide						(Putative) sire ^b of subsequent infant	Interbirth interval (months)
Case	Troop	Denotation	Age (months)	(Putative) sire ^b	(Presumed) killer		
13	KI	♀ 11.4	0.4	♂ 43	♂ 11	Not yet known	
9	KI	♂ 11.3	1.2	♂ 20	♂ 43	♂ 43	9.2 months
12	KI	♂ 6.4	1.5	♂ 20	♂ 11	Female stopped cycling	
19	B	♂ 5.4	1.9	♂ 22	♂ 38	Female died	
14	KI	♀ 1.5	2.6	(♂♂ 57,51 or 11) ^e	(♂ 11)	Not yet known	
11	KI	♀ 12.1	3.2	♂ 20	(♂ 11)	♂ 11	14.8 months
17	B	♀ 6.5	3.4	♂ 22	♂ 38	♂ 38	13.9 months
7	KI	♂ 1.4	3.7	(♂ 4)	(♂ 43)	(♂♂ 57.51 or 11) ^e	12.3 months
16	B	♂ 1.5	4.6	♂ 22	♂ 38	38	12.4 months
15	B	♂ 3.5	8.4	♂ 22	(♂ 38)	Female died	
10	KI	♀ 4.5	9.1	(♂ 4)	(♂ 11)	♂ 11	16.4 months

after 3 months, was attacked and disappeared several weeks later.

Discussion

Various hypotheses have been raised with respect to the putative function and/or causation of infanticide in langurs (summarized in Hausfater and Vogel 1982). Some authors considered infanticide to be maladaptive or even pathological, e.g. resulting from overpopulation, social stress, general disturbances (for instance Boggess 1979; Curtin and Dolhinov 1979; Ripley 1980). Additional hypotheses focus on resource competition (Rudran 1979) or psychosocial factors, e.g. sexual frustration (Mohnot 1971), dominance assertion (Parthasarathy and Rahaman 1974), and establishing of social bonds (Sugiyama 1965). However, the broadest and most controversial attention was concentrated on Hrdy's (1974, 1977) hypothesis that infanticide might be a highly adaptive male reproductive strategy: Since the death of an unweaned infant commonly results in the abrupt termination of its mother's lactational amenorrhea, an infanticidal male would be able to inseminate the mother sooner by killing her infant. Thereby the infanticidal male would gain a reproductive advantage (at the expense of his predecessor) compared to a non-infanticidal counterpart.

Though the different hypotheses will be discussed extensively in a forthcoming publication, it should be emphasized that the data now avail-

able from the Jodhpur population do not support any of those hypotheses focusing on general disturbance, social stress/resource competition and/or dominance assertion. As a preliminary statement, we even have to exclude a necessary coexistence of these factors as proximate causes with a reproductive strategy as the ultimate cause. In any case, Hrdy's "sexual selection" hypothesis provides several testable predictions, which can be scrutinized here on the bases of reliable longitudinal data.

Three basic prerequisites are necessary to ensure an infanticidal male's reproductive advantage over a given noninfanticidal counterpart (Table 2; cf. Vogel and Loch 1984):

1. *The infanticidal male should not have been the sire of any infant harmed or killed by himself.* This prerequisite is almost certainly proven for cases 9, 11, 12 and 13; it is probably true for cases 7, 8, 15, 16, 17 and 19; however, it is uncertain for case 14 (cf. footnote e of Table 1).

2. *The infanticidal male should actually sire the subsequent offspring of the victim's mother.* This prerequisite is almost certainly proven for the subsequent siblings of the victims of cases 9, 10, 11, 16 and 17. It is, however, refuted for case 7; two mothers of victims died before giving birth to the next infant (cases 15 and 19). In cases 12, 13 and 14 the data are not yet available.

3. *The infanticide should significantly shorten the subsequent interbirth interval (IBI) of the victim's mother.* The mean IBI of the females of troops KI and B, without premature loss of the respective

preceding infant has been calculated by Winkler et al. (1984) as 15.3 months (range 11.2–20.2 months; $n = 19$). All but one of the IBIs subsequent to infanticides or disappearances fall within the normal range of variation (see Table 2). However, the mean value drawn from these data is 13.2 months, clearly less than the average IBI without premature loss of the preceding infant. More important, there is a tendency towards a strong positive correlation between the age of previous infants at the time of death or disappearance and the IBI to the succeeding infant. Thus, the infanticidal strategy provides the new resident male at least with a respectable probability of gaining reproductive advantage by shortening the period of lactational amenorrhea. As a rule, the younger the victim, the more a male has to gain from infanticide. Winkler et al. (1984) calculated the critical age up to which the loss of an infant may accelerate the reproductive process of its mother to be 7.0 months. On the basis of this calculation only two infants (cases 10 and 15) were too old when they disappeared to serve the male's purpose of ceasing their mother's lactational amenorrhea.

Thus, our data are in general, though not total, agreement with the above-mentioned predictions derived from Hrdy's "reproductive advantage" hypothesis.

Computer simulations showed that an infanticidal male will not gain reproductive advantage under all circumstances if compared with a noninfanticidal new resident male (Chapman and Hausfater 1979; Hausfater et al. 1982; Hausfater 1984). The proportion of infanticidal versus noninfanticidal takeovers may therefore reflect the frequency equilibrium of a behavioral polymorphism in the sense of a mixed evolutionarily stable strategy. If so, infanticide is not an "all or none" phenomenon during male takeovers. Because they are not fully predictable, it is difficult to observe infant killings. We do not know yet whether particular males are always infanticidal (e.g. due to their respective genetic constitution) or whether they are all capable of choosing their strategy according to particular circumstances.

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