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Infanticide Among Free-ranging Langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): Recent Observations and a Reconsideration of Hypotheses

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ABSTRACT. Considerable disagreement characterizes the debate concerning frequency, causation, and function of infanticide in connection with adult male replacements in bisexual one-male troops of hanuman langurs (*Presbytis entellus*). Detailed observations are presented about two noninfanticidal and three infanticidal male changes including six eye-witness and five presumed cases of infanticide within three langur troops during a long-term study at Jodhpur, Rajasthan, India. The results do not support any explanatory hypotheses focussing on social crowding, regulation of population density, social stress, sexual frustration, incest avoidance, or social bonding, but are in general though not total agreement with the reproductive advantage hypothesis: mainly unrelated infants were killed (one possible exception), the infanticidal male generally sired the subsequent offspring (one exception), and the mean interbirth interval subsequent to infanticide is by 2.1 months shortened. Likewise, several cases of stress induced abortions occurred. It is demonstrated that post-conception estrous behaviour is by no means a female counterstrategy to infanticide in order to confuse males concerning the issue of paternity, since an infanticidal male did not spare the subsequent offspring of mothers who copulated with him during pregnancy and pregnant females did not discriminate between fathers and non-fathers.

Key Words: *Presbytis entellus*; Infanticide; Reproductive strategies.

INTRODUCTION

The grey Indian langur (*Presbytis entellus*) became famous both within and beyond primatological circles (see, e.g., textbooks of WICKLER & SEIBT, 1977; ALCOCK, 1979; BARASH, 1980; TRIVERS, 1985) because adult male replacements in bisexual troops can be accompanied by infanticide. Infant killings have been reported from several study sites in India such as Dharwar (SUGIYAMA, 1965a, b, 1966), Jodhpur (MOHNOT, 1971; MAKWANA, 1979), Mount Abu (HRDY, 1974), Harihar (PARTHASARATHY & RAHAMAN, 1974), and recently from Kanha (NEWTON, 1985, 1986). Infanticide was long considered as a pathology due to abnormally high population density (CURTIN, 1977; CURTIN & DOLHINOW, 1978, 1979). However, HRDY (1974) interpreted langur infanticide as an adaptation: Since ovulatory cycles are blocked as long as females suckle infants, a new resident male reduces his waiting time to inseminate the mother by killing his predecessor's offspring.

However, careful reviews of all published 40 to 50 incidences of infant "killings" in langurs made obvious that primatologists very rarely eyewitnessed the entire infanticidal episodes, whereas the overwhelming majority of reports refer to infants who disappeared during male changes, or infants which indeed had been attacked or wounded, but not unambiguously by males (BOGGESS, 1979; VOGEL, 1979). Moreover, for several other study sites (mainly places with predominantly multi-male troop organization) there are no published reports of killings, e.g., Junbesi (BOGGESS, 1976) and Melemchi (BISHOP, 1975) in Nepal, Orcha, Kaukori (JAY, 1965), Singhur (OPPENHEIMER, 1977) and Rajaji (LAWS & LAWS, 1984) in India, and Wilpattu (MUCKENHIRN, 1972), and Polonnaruwa (RIPLEY, 1967, 1980) in Sri Lanka.

Hence, premature statements such as "infanticide occurs regularly, and under conditions that must now be considered as normal for this species" (HRDY, 1977) gave reason for a long-running and sometimes emotional debate (see SCHUBERT, 1982: "Infanticide by usurper hanuman langur males: A sociobiological myth" and the reply of HRDY, 1982). A comparative cross-species review of infanticide (HAUSFATER & HRDY, 1984) generally supported the explanatory value of the sexual selection hypothesis not only for langurs but also for infanticides in other primates such as redtail, blue, and colobus monkeys (LELAND et al., 1984; see also BUTYNSKI, 1982; STRUHSAKER & LELAND, 1985), howler monkeys (CROCKETT & SEKULIC, 1984) or mountain gorillas (FOSSEY, 1984). Referring to the model of "mixed evolutionary stable strategies" (MAYNARD-SMITH, 1974) and using longitudinal data of the Jodhpur langur population, computer simulations made clear, that only about one-quarter of all adult male replacements should be accompanied by infanticide, no matter whether infant killing is an acquired or genetically determined male reproductive strategy (HAUSFATER et al., 1982; HAUSFATER, 1984).

However, consensus among scientists has not completely shifted (see, e.g., EIBL-EIBESFELDT, 1984; CHALMERS, 1986). Especially BOGGESS (1984) as a leading critic holds strong criteria regarding (1) qualitative data providing acceptable evidence of infanticide and (2) quantitative data which support the predictions of the sexual selection hypothesis or other hypotheses that assign evolutionary value to langur infanticide (e.g., via resource competition).

Based on preliminary records given by VOGEL and LOCH (1984) and SOMMER and MOHNOT (1985) this paper presents detailed qualitative descriptions along with photographic documentation as well as quantitative reproductive data concerning six eyewitness and five suspected cases of infant killing during three infanticidal adult male replacements compared with two noninfanticidal replacements within three carefully studied langur troops near Jodhpur. These data allow a critical evaluation of functional explanations of infant killing in langurs as well as of suspected female counter-strategies.

MATERIAL AND METHODS

Data presented here are from a long-term study of the free ranging langurs of Jodhpur. From January 1977 to January 1981 the investigations were carried out by VOGEL and coworkers (e.g., VOGEL & LOCH, 1984; WINKLER et al., 1984). My own observations cover a 14-month period from October 23, 1981 to December 20, 1982, with four main study periods of about 235 hr each from October 23, 1981 to January 14, 1982, from March 8, 1982 to May 15, 1982, from July 5, 1982 to September 15, 1982, and from September 16, 1982 to December 20, 1982. The analysis presented here is restricted to ad-libitum data. Since December 1982 observations continue by MOHNOT and coworkers. Data referring to periods before October 1981 and after December 1982 were provided by members of both teams.

Jodhpur is located in Rajasthan at the eastern edge of the Great Indian Desert. The climate is characterized by hot summers with maximum temperatures up to 50°C and moderate winters. The scanty rainfall is received mostly during monsoon between July and September, averaging 360 mm (MOHNOT, 1971; WINKLER, 1981).

In and around Jodhpur lives an isolated population of about 1200 langurs (*Presbytis entellus entellus* Dufresne, 1797), in 1980 consisting of 29 bisexual troops comprising 4–35 animals and an unknown number of all-male groups (Winkler et al., 1984). The reproductive social units are organized as one-male troops with a single adult breeding male, each troop occupying its own home range. Extratroop males live in rather nomadic groups of fluctuating size composed of all age classes except infants. They invade home ranges of bisexual troops in an unpredictable pattern, sometimes resulting in rapid or gradual replacement of the adult resident male.

The main study area is located about 6 km west of Jodhpur city in a hilly area covered by reddish sandstone. The area is partly protected and no human settlements are allowed. The vegetation in this open scrub habitat is xerophytic and dominated by *Prosopis juliflora*, *Acacia senegal*, and the latex-bearing *Euphorbia caducifolia*. The langurs are concentrated around two big artificial lakes (called upper and lower Kailana lake) separated by a dam, which serve as water reservoir for the city.

Within that area three bisexual troops named Kailana-I (KI), Kailana-II (KII), and Bijolai (B) live in close proximity with partly overlapping home ranges (Fig. 1; forthcoming publications of Mohnot's team denominate Troops B, KI, and KII as B21, B19, and B20, respectively). The troops are subject to the same ecological conditions. Water is available for the langurs throughout the year. The diet consists of 8–10 plant species as staple foods. As with most other troops of the Jodhpur population, the langurs of Kailana are fed by local people for religious reasons. Artificial feeding averages four times per day in Troops

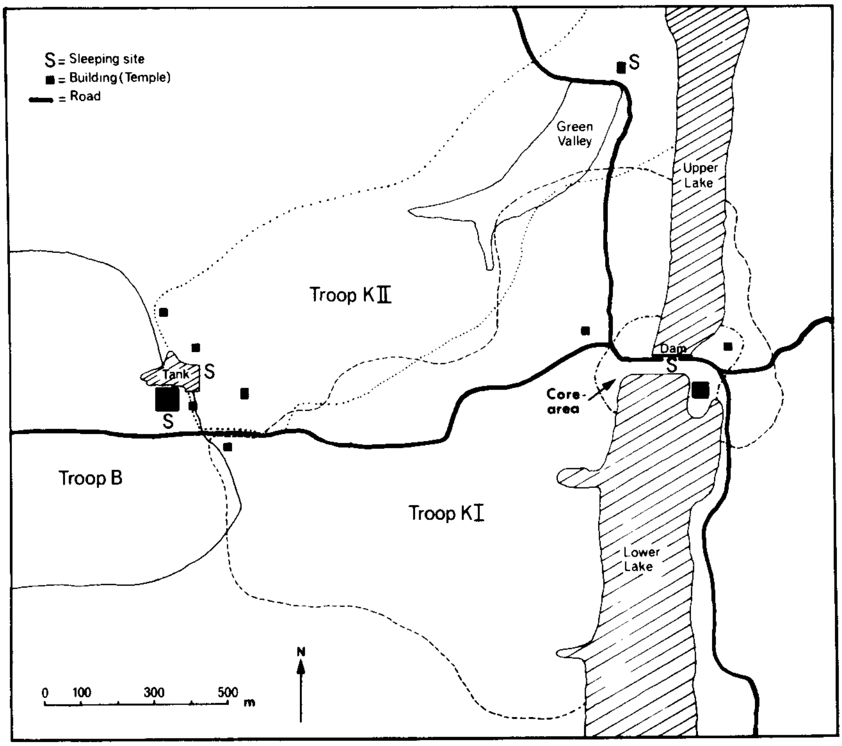

Fig. 1. Home ranges of Troops KI, KII, and B at Jodhpur, Kailana region in 1982.

KI and B and somewhat less in Troop KII. Apart from feral dogs, natural predators are absent. The animals are easy to observe since they are not shy and spend most of the daytime on the ground.

All members of Troops KI and B were known individually as well as several members of Troop KII and different all-male groups (AMG). Adult females were numbered, and their respective infants denominated by the mother's number and a second one, representing the rank within the birth order. For example, "*6.1*" stands for the first *known* infant born to ♀*6* during the study; it does not imply that *6.1* was the first infant born to ♀*6* since all adult females (except ♀*11* and ♀*12* of Troop KI and ♀*6.1* of Troop B) were already parous when the study started. Extratroop males were also labelled by numbers. Since their natal troop is usually not known, these simply refer to the order of their appearance since observations began. Males without conspicuous marks who were reencountered after longer periods were possibly given a second figure.

In Jodhpur langurs, infant-I stage lasts from birth to 5–6 months, when the black natal coat changed completely into white. Infant-II stage lasts until weaning ends at about 12–15 months. In the case of females, juvenile stage lasts up to 3 years of age. Females are considered youngadult from the onset of regular cycling to the birth of the first infant, but not longer than 4 years. Age classification for males is still preliminary: Juvenile stage lasts up to about 4 years, subadult (and later youngadult) stage up to 6 to 7 years. Males leave their natal troop usually as juveniles and join male groups.

The main female reproductive characteristics are the following (SOMMER, 1985; partly completed set of data already used for evaluations of VOGEL & LOCH, 1984; WINKLER et al., 1984): age of menarche 30.6 months ($N = 5$; range 25.2–34.5 months); age of first conception 34.2 months ($N = 4$; range 31.7–39.1 months); cycle length 24.3 days ($N = 47$; range 17–36 days); gestation length 199.9 days ($N = 9$; range 195–202 days); interbirth interval without loss of previous infant 15.3 months ($N = 19$; range 11.2–20.2 months).

Jodhpur langurs have no breeding season and births occur throughout the year. Estrous females solicite males for copulation through head shaking and presentation of the genital region. Mounting of estrous females by other females or immature males is common.

NONINFANTICIDAL VERSUS INFANTICIDAL MALE CHANGES

The three troops of Kailana region experienced five adult male replacements from October 1981 to January 1983. Periods of intense male-male competition including multimale stages and interimresidencies alternated with periods of undisputed tenureship of a single male resident. As a result of the takeovers at least 6 but probably 11 infants were killed by the new male residents ♂*43*, ♂*11*, and ♂*38*, whereas male residents ♂*20* and ♂*10* did not harm infants of their new harems. The fate of infants present during male changes or born shortly thereafter (summarized in Table 1) shall be described in detail.

The balance of our observations includes: (1) In six cases infanticide was directly observed: New male residents attacked and wounded infants, who died during the same or the following day (cases 22, 26, 27, 30, 31, and 33); (2) one infant disappeared several days after it was seriously wounded by a new alpha male (case 20); (3) two infants disappeared after they were attacked unsuccessfully by a new male resident (cases 24 and 28); (4) two infants disappeared the very day that their sire was ousted from the troop (cases 25 and 29); and

(5) several infants remained unharmed (cases 1–4, 6–19, 23, and 32) or died due to reasons other than infanticide (e.g., case 5).

Noninfanticidal Male Change in Troop KI, October–November 1981 (♂*4* to ♂*20*)

Observations in Troop KI were resumed October 23, 1981 after a ten-month break. The troop was then comprised of 20 members (census October 25, 1981): 1 adult male (♂*4* ?; see below); 11 adult females (para ♀*1*, ♀*2*, ♀*3*, ♀*4*, ♀*6*, ♀*7*, ♀*8*, ♀*9*, and ♀*11*; nullipara ♀*12* and ♀*13*; ♀*13* had joined the troop between January and October 1981); 4 juvenile females (♀*6.3*, ♀*4.4*, ♀*2.3*, and ♀*3.2*); 3 infant-II males (♂*8.2*, ♂*11.2*, and ♂*7.4*); 1 infant-II female (♀*1.3*).

The age of nonadults ranged from 8–22 months. No blackcoat infants were present.

It is not clear whether the adult male reencountered was still ♂*4* whose tenureship lasted from end of 1978 through at least January 1981, or an interimresident at the final stage of a longer lasting male competition. In any case, about 15–20 males invaded the home range of Troop KI from October 25, 1981 onwards. The male resident disappeared after five days of agonistic interactions with the invaders. Sixteen days of multimale stage followed during which none of the males involved was able to keep his rivals away from the females. The invaders belonged to the following two rival male groups: (1) AMG 10 included about seven adults (♂*20*, ♂*11*, ♂*10*, ♂*38*, ♂*39*, ♂*40*, and ♂*41*) and eight subadult and juvenile members. ♂*20*, ♂*11*, and ♂*10* were already identified in the 1980 competition for Troop B described by Vogel and Loch (1984: Fig. 2). Together with ♂*38* they played a key role in the future structural developments: (2) AMG 7 consisted of five adult members out of which ♂*37* and ♂*42* were permanently identifiable.

From November 15, 1981 onwards ♂*20*, highest ranking member of AMG 10 and easily recognizable by the pointed shape of his right earlobe, installed himself as the new resident male. Extratroop males invaded the troop's home range on another 21 occasions up to January 11, 1982 but were without exception chased away by the new alpha ♂*20*. Afterwards the residency of ♂*20* remained undisputed up to June 1982.

During the multimale stage from October 31 to November 14, 1981 no attack by any competing male on any troop member was observed. This is interesting since two rival males (♂*11* and ♂*38*) later turned out to be infanticidal (see below). However, mothers with dependent infants in general avoided close contact with males. Several times during agonistic male-male interactions infants and juveniles obviously became frightened and uttered chattering distress vocalizations while in their mother's lap.

During his entire seven-month long tenureship the new alpha ♂*20* likewise did not display any goal directed aggression towards nonadults (cases 1–4 in Table 1). The three infants ♂*7.5*, ♂*1.4*, and ♀*4.5* born in March through April 1982 (cases 5–7) did not provoke any agonistic behaviour by ♂*20* though they were probably sired by the former resident male. Newborn ♂*7.5* was found dead after nine days without any visible injury. During his first week of life the baby spent only 12.3% of the daytime with his mother compared to a mean of 72.4% of three other babies. Instead, his elder brother ♂*7.4*, who was only partly weaned, continued suckling at mothers breast. Hence ♂*7.5* almost certainly died of starvation.

♂*20* also behaved nonaggressively when he again became interimresident in Troop KI from September 17 to November 4, 1982 (see below). ♂*20* then encountered two babies

Table 1. Fate of infants present during male changes or born shortly after in Troops KI, KII, and B (October 1981–June 1983).

Troop	Period of male change	New resident male	Infant: Case	Infant: Denotation	Infant: Sire[2]	Infant: Date of birth	Infant: Born during/after male change	Infant: Fate	Infant: Age during death (I), disappearance (II), attack (III) or onset of male change (IV)	Observer[12]
KI	Oct.–Nov. '81	♂*20*[1] (non-infanticidal)	1	♂*8.2*	♂4	Sept. 22, '80		Survived; left troop Apr. '83[5]	13.8 months (IV)	V.S.
			2	♂*11.2*	♂4	Dec. 15, '80		Survived; left troop June '82[5]	11.0 months (IV)	V.S.
			3	♀*1.3*	♂3	Dec. 20, '80		Survived; disappeared Apr. 27, '83[6]	10.8 months (IV)	V.S.
			4	♂*7.4*	♂4	Mar. 1, '81[3]		Survived; left troop June '82[5]	7.5 months (IV)	V.S.
			5	♂*7.5*	(♂4)	Mar. 13, '82	×	Died Mar. 22, '82[7]	0.3 months (I)	V.S.
			6	♂*1.4*	(♂4)	Mar. 27, '82	×	Survived (but cf. case 20)		V.S.
			7	♀*4.5*	(♂4)	Apr. 11, '82	×	Survived (but cf. case 21, 24)		V.S.
KII	Feb. '82	♂*10* (non-infanticidal)	8–14	*2*♀♀ inf. II *5*♂♂ inf. II	(♂3 resp. ♂63)	May–Oct. '81		9 infants survived[8] 1 ♂ inf. II died Apr. 9, '82[9] 2 ♂♂ inf. II disappeared[10]	4–9 months (IV)	V.S.
			15	♂inf. I	(♂63)	Dec. '81			2 months (IV)	V.S.
			16	♀inf. I	(♂63)	Jan. '82			1 month (IV)	V.S.
			17	♀inf. I	(♂63)	Apr. '82	×			V.S.
			18	♂inf. I	(♂63)	Apr. '82	×			V.S.
			19	♀inf. I	(♂63)	July '82	×			V.S.
KI	June '82	♂*43*[1] (infanticidal)	20	♂*1.4*	cf. case 6			Wounded July 13; disappeared July 19, '82	3.7 months (II)	V.S.
			21	♀*4.5*	cf. case 7			Attacked (?) July 12, '82; survived (but cf. case 24)	3.0 months (III)	V.S.
			22	♂*11.3*	♂*20*	June 5, '82[4]		Wounded July 9, died July 10, '82	1.2 months (I)	V.S.
			23	♀*12.1*	♂*20*	July 30, '82	×	Survived (but cf. case 25)		V.S.
KI	Sept. '82–Jan. '83	♂*11*[1] (infanticidal)	24	♀*4.5*	cf. case 7			Attacked Nov. 6, 11, 22, 25, '82, Jan. 12, '83; disappeared Jan. 13, '83	9.1 months (II)	V.S. V.K.D.
			25	♀*12.1*	cf. case 23			Disappeared Nov. 4, '82	3.2 months (II)	V.S.
			26	♂*6.4*	♂*20*	Oct. 11, '82		Wounded Nov. 25; died Nov. 26, '82	1.5 months (I)	V.S.
			27	♀*11.4*	♂*43*	Mar. 10, '83	×	Wounded Mar. 21; died Mar. 22, '83	0.4 months (I)	V.K.D.
			28	♀*1.5*	♂*57*, ♂*51* or ♂*11*	Apr. 8, '83	×	Attacked Apr. 26; disappeared June 17–25, '83[11]	2.6 months (II)	V.K.D.
B	Jan. '83	♂*38* (infanticidal)	29	♂*3.5*	(♂22)	May 5, '82		Disappeared Jan. 17, '83	8.4 months (II)	G.A.
			30	♂*1.5*	♂22	Sept. 25, '82		Wounded; died Feb. 11, '83	4.6 months (I)	G.A.
			31	♀*6.5*	♂22	Oct. 29, '82		Wounded; died Feb. 9, '83	3.4 months (I)	G.A.
			32	♂*6.1.2*	♂22	Oct. 25, '82		Survived	3.3 months (IV)	G.A.
			33	♂*5.4*	♂22	Dec. 6, '82		Attacked Jan. 23; wounded, died Feb. 3, '83	1.9 months (I)	G.A.

Table 1.
1) In the preliminary record given by Vogel and Loch (1984) ♂ *20* was denotated as "Zip," ♂ *43* as "Rip" and ♂ *11* as "Fleck"; 2) resident male about 200 days before birth. Parantheses indicate lack of observations around time of conception. Sexual contact of fertile females with male invaders can almost certainly be excluded in cases 1–4, 22, 23, 26, 27, and 29–33. Actual copulations with resident males during conception estrus were observed in cases 22, 23, 26, and 27. In case 28, ♀ *1* copulated with three different males 199 days before birth; 3) calculated on the basis of 24 months interbirth interval between ♂ *7.3* and ♂ *7.5*; 4) calculated on the basis of 200 days gestation period; 5) joined all-male group; 6) the day after sister ♀ *1.5* was attacked (case 28); 7) died due to starvation. Elder brother ♂ *7.4* was only partly weaned and continued suckling after birth of ♂ *7.5*; 8) at least up to December 20, 1982; 9) died due to electrocution; 10) might have joined all-male group; 11) disappeared after having an infection of its tail; 12) V.S.: V. Sommer; V.K.D.: V.K. Dave; G.A.: G. Agoramoorthy. Observer in 1980: H. Loch.

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sired by himself, ♀ *12.1*—born during his absence—and ♂ *6.4*—born during the interim-tenureship itself.

♂ *20* should therefore considered to be a noninfanticidal male even if the classical constellation (encounter of blackcoat infants just at the time of takeover) did not occur.

NONINFANTICIDAL MALE CHANGE IN TROOP KII, FEBRUARY 1982 (♂ *63* TO ♂ *10*)

Extratroop males also repeatedly penetrated into the home range of neighbouring Troop KII, e.g., on October 25, December 13, 22, and 24, 1981. During these months, the troop was under control of ♂ *63*, an extraordinary large male with whitish skin, who took over the troop sometime between January and October 1981. As a result of continued invasions—which were not followed in detail—♂ *10*, a member of AMG 10, took over in February 1982. ♂ *10*, a male with a conspicuous bent tail, held his position up to the middle of 1983.

On February 15, 1982 Troop KII had 25 members: 1 adult male; 13 adult females (12 para, 1 nulliparous); 2 juvenile males; 5 infant-II males; 2 infant-II females; 1 infant-I male; and 1 infant-I female.

♂ *10* exhibited aggression neither towards the nine infants present during his takeover (cases 8–16 in Table 1) nor toward three infants born shortly after and presumably sired by his predecessor (cases 17–19). Nine out of these 12 infants survived at least up to December 20, 1982. One male whitecoat died of electrocution on April 9, 1984. Two male whitecoats disappeared by August 1982. They might have joined a male band; there were no indications that ♂ *10* harmed them.

♂ *10* was occasionally chased by females when he coincidentally approached babies, as well as on July 9, 1982, 10:07, when KII-females watched the fatal attack of ♂ *43* on baby ♂ *11.3* in Troop KI (see below). On August 12, 1982, 19:00, ♂ *10* came close to a blackcoat infant which started screaming since it had climbed too far into the thin outer branches of a *Prosopis* tree. Immediately four females forcefully attacked ♂ *10* who, obviously quite distracted, fell down from the tree. On other occasions mothers with newborns would sit very close to ♂ *10*.

Though ♂ *10* behaved peacefully towards infants of his own troop the following episode is somewhat puzzling:

September 4, 1982, 18:40. During an encounter between Troops KII and B, ♂ *10* looks towards a 1-year-old male of Troop B (♂ *6.4*, ♂ *6.1.1*, or ♂ *3.4*) whose left hand is heavily crushed and bleeding, perhaps due to electrocution. Additionally, the juvenile has lost toes from both feet. ♂ *10* runs after the mutilated juvenile and tries to catch—not only to chase—it. Three females of Troop KII (!) including one female with an elder infant-I at her breast harass ♂*10* who retreats uttering convulsive barks.[1] The injuries of the juvenile later healed.

INFANTICIDAL MALE CHANGE IN TROOP KI, JUNE 1982 (♂*20* TO ♂*43*)

Following a break of observations on Troop KI from May 16 to July 4, 1982, former alpha ♂*20* had disappeared and ♂*43* was found to be the new male resident. Local people who regularly feed monkeys bimonthly, on full- and newmoon, said that the situation had been peaceful in Troop KI on June 8. On June 21 however many males had mixed with the females. Therefore the male change probably took place in the second half of June 1982. Simultaneously juveniles ♂*11.2* and ♂*7.4* had left their natal troop. They joined AMG 10 where they were later almost certainly identified as young members. Since ♂*43* lacked conspicuous marks he could not be recognized as a former member of a known male group. The tenureship of this young male was short but nearly undisturbed up to mid September 1982. Three times two to three male invaders were driven away by ♂*43* (June 19, August 20, and September 6). Encounters with Troop KII occurred almost daily.

After the male change Troop KI had 21 members (census July 5, 1982): 1 adult male (♂*43*); 11 adult females (para ♀*1*, ♀*2*, ♀*3*, ♀*4*, ♀*6*, ♀*7*, ♀*8*, ♀*9*, and ♀*11*; nullipara ♀*12* and ♀*13*); 5 juvenile females (♀*6.3*, ♀*4.4*, ♀*2.3*, ♀*3.2*, and ♀*1.3*); 1 juvenile male (♂*8.2*); 2 infant-I males (♂*1.4* and ♂*11.3*); and 1 infant-I female (♀*4.5*).

The new male resident turned out to be infanticidal: ♂*11.3* was killed by ♂*43* (case 22 in Table 1); ♂*1.4* was seriously wounded and disappeared shortly after (case 20); ♀*4.5* survived but was probably attacked at least once (case 21). Only ♀*12.1*, born about five weeks after the takeover, was not attacked (case 23).

Killing of Infant ♂*11.3* (case 22)

July 9, 1982 (♂*11.3*, 33 days old). At 09:14 Troop KI's resident ♂*43* performs a whooping and jumping display. The females follow him about 200 m northwest into the overlapping area of Troops KI's and KII's home ranges. Reciprocal chasing by ♂*43*, Troop KII's resident ♂*10* and his females follows, associated with teeth grinding, head bobbing, whooping, and jumping display. Females of Troop KI remain in the background, feeding, and looking around. At 09:50, after moving along the border of their home ranges, both parties reach the southern end of the "green valley," which normally belongs to Troop KI's area. ♀*2*, ♀*3*, ♀*7*, and ♀*13* participate in defending this site, whereas mothers ♀*1*, ♀*4*, and ♀*11* with their offspring watch the encounter from behind the "frontline." ♀*1* and ♀*4* sit together about 15 m behind, ♀*11* only 5 m behind under a bush of *Prosopis*.

At 10:07 ♀*2* and ♀*7* lunge towards females of the neighbouring troop, supported by ♀*6*, ♀*12*, and ♀*13*. The resident males do not intervene; both occasionally grind their teeth, but only ♂*43* shows penile erection. Moments after an attack of Troop KI's females on Troop KII, ♂*43* runs towards ♀*11* and her infant. For 2–3 sec the individuals are hidden by *Prosopis* branches. Guttural vocalization is heard from ♀*11*. Meanwhile, ♂*43* must have bitten infant ♂*11.3* just below the neck, inflicting several deep punctures around and in the spine. Immediately, five to seven females, amongst them ♀*4* (with baby?) attack and chase the male about 20 m away onto a hillock. Simultaneously, Troop KII's females chase their resident.[2]

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[1] Equivalent to the sequences of sharp exhalations [e] and inhalations [i] with [e-i-e], [e], [e-i], or [e-i-e-i] patterns described by VOGEL as "low pitched threat-alarm-bark" (1973) or "aggressiv getönter Doppelruf" (1976). Similar male vocalizations during infanticidal attacks were obviously heard at Dharwar ("convulsive threats," SUGIYAMA, 1965b; see also SUGIYAMA et al., 1965), Jodhpur ("deep-throated alarm bark in high pitch, [hiicheeik-heihke]," MOHNOT, 1971) and at Abu ("convulsive threats...a sequence of spasmodic brays," HRDY, 1974).

[2] Counterattacks by females are, even if not particularly mentioned, nearly always accompanied by guttural vocalization as previously described by MOHNOT (1971, "cough and bark") and SUGIYAMA (1965b, "violent cry [gyaaa]").

Keeping at a distance of about 20 m, females of both troops sit slightly scattered, grooming and looking around. ♀*11* keeps a bit apart together with ♀*3*, who is holding the profusely bleeding and vocalizing baby. At 10:09 ♂*43* climbs down from the hillock and, while grunting, approaches estrous ♀*7*. At 10:17 ♀*11* attacks and chases ♂*43* up a tree. Later, at 10:38, ♂*43* climbs down and joins ♀*2*, who grooms him for 3 min.

The wounded infant ♂*11.3* occasionally vocalizes mildly. Until the following morning it is almost invariably carried by ♀*3*. It is clinging to the belly of ♀*3* only with its forelimbs, whereas its legs and lower portions of the body are hanging, obviously paralyzed by a spinal injury. After the male attack ♀*11* keeps other troop members away from ♀*3* and ♂*11.3* by chasing, slapping, and pushing, whenever they try to inspect the infant or coincidentally come close. This happens for the first time at 10:21 to ♀*2*, at 10:23 to ♀*1*—who is even bitten by ♀*11*—, at 11:52 to ♀*6.3* and ♀*3.2*, and at 11:59 again to ♀*6.3*. The mother ♀*11* herself carries the baby only a few times, at first from 11:20 to 11:21. She sometimes moves apart from the allomother ♀*3*, even going out of sight, at first from 11:37 to 11:50 in order to feed on a tree. Sometimes ♀*3* leaves the motionless infant alone, at first from 11:50 to 12:50, but she remains nearby and retrieves the baby again when it vocalizes or moves parts of the body. ♂*43* is cautiously avoided by allomother ♀*3* as well as by ♀*1* and ♀*4* with their babies.

July 10, 1982. At 06:26 estrous ♀*7* and ♀*8* solicit ♂*43* during artificial feeding. Moments later he comes close to ♀*3* with the wounded infant; ♀*3* likewise displays head shaking though she is not estrous (next menstruation July 13). At 06:28 when ♂*43* approaches allomother ♀*3* again, he is attacked and chased away by ♀*11* and ♀*2*. During the day the troop moves on an usual route. At 16:01 ♂*43* grinds his teeth and approaches ♀*1* with her black coated infant, but the female quickly runs away. The wounded infant of ♀*11* is still carried by ♀*3*. Only once another female (juvenile ♀*2.3*) manages to pick up the unattended baby from 17:56 to 17:57. At 18:30 the baby is seen alive for the last time. Probably it fell into the lake from ♀*3*'s belly, when the female drank at the bank near the dam.

July 11, 1982. At 18:30 the troop returns to the sleeping site at the dam. ♀*7* utters [hiii...]-vocalization and stares apparently excited into the water. As a result, I discover the corpse of the missing infanticide victim and carry it away by the tail. ♀*7* and ♀*3* watch the event. ♀*3* follows for about 100 m until I cover the corpse.

Wounding and Disappearance of Infant ♂*1.4* (case 20)

July 12, 1982 (♂*1.4*, 107/♀*4.5*, 92 days old). At 18:04 under the sleeping trees at the lake dam, ♂*43* without penile erection or vocalization, tries to attack ♀*1* and/or ♀*4*, who sit together with babies on their breasts. ♀*3* and ♀*4* (?) counterattack the male who withdraws, giving a short whoop call. At 18:05 ♂*43* again approaches ♀*1*, who is pressing her infant at the belly, but does not move away. The male passes by slowly.

July 13, 1982. At 17:58 Troop KI consumes peanuts distributed by a religious feeder on the steps of the Shiva temple east of the lake dam. ♀*4* with her baby is feeding apart. ♀*1* feeds about 5 m away from ♂*43*, her infant ♂*1.4* hopping around her. Unexpectedly and without any vocalization, ♂*43* suddenly jumps, grabs the baby, and bites its face, thus chopping off parts of the nose and penetrating both cheeks. He drops the victim only seconds later. Immediately, between five and seven females attack and chase ♂*43* onto the top of the temple. ♀*1*, pressing the wounded baby at her breast, flees about 30 m down towards the lake shore. Most of the troop members follow and start grooming or looking around. Pregnant ♀*6*, who displayed postconception estrous behaviour during the last three days, remains only 15 m away from the temple. Three juvenile females stay close to ♂*43* on the top.

From 18:03 onwards ♀*1* grooms herself beside the profusely bleeding baby, which is quiet and crouches over an increasing puddle of blood (Fig. 2). At 18:12 the juvenile sister ♀*1.3* utters [hii...]-vocalization and approaches the bleeding baby, who tries to avoid mother's grooming. At 18:14 estrous ♀*8* displays head shaking towards ♂*43* and grooms him for 4 min. From 18:20 to 18:30 the troop is fed with bananas. ♀*1* and her infant remain apart, but fruits are thrown towards them. ♂*43*, who usually is one of the first individuals to receive provisioned food, continues teeth grinding, head bobbing, and grunting on the temple top.

From 18:35 to 18:53 ♀*13*, who was estrous up to July 12, associates with the male and grooms him for 2 min. Afterwards, ♂*43* climbs down and feeds. At 18:56 ♂*43* jumps without any vocalization towards ♀*1*, who stays at the troop's periphery with her baby still bleeding. ♀*1* shows no reaction,

Fig. 2. ♂*43* has bitten 3.7-month-old infant ♂*1.4* on its face. The injured baby crouches near mother ♀*1*, whose left breast is smeared with blood due to the escape with her baby (July 13, 1982, 18:03).

but the male stops 15 m before reaching her. At 19:00 ♀*1* collects her baby, which is bowing the head into the neck to avoid contact of its wounded face with mother's breast. From 19:01 to 19:14, ♀*1* and ♀*4* guard their babies close together. There is no more blood trickling from the wound and (surprisingly) the baby is hopping around. At 19:15 the two mothers with their offspring climb on roosting trees at the lake dam.

July 14, 1982. The wounded baby has heavy swellings on the forehead, dried blood is spotted over the whole face and it is unable to suckle. Milk is dropping from the mother's breast, which she licks with her fingers and tongue. Up to July 18, the wound continues healing. Although obviously painful, the infant resumes suckling around July 16, and its locomotion appears quite normal two days later. Mothers ♀*1* and ♀*4* mostly guard their offspring together, often away from the center of the troop and thus avoiding proximity to the infanticidal male.

July 18, 1982. At 11:30 the infant ♂*1.4* is seen for the last time. When observations are continued on *July 19*, 08:15, the baby has disappeared. No extraordinary tensions can be detected amongst male and females. The infant-deprived mother remains between 50 and 200 m behind the wandering troop until noon, restlessly looking around from hillocks. Though a careful search is made, the infant cannot be located.

Survival of Infant ♀*12.1* (case 23) and ♀*4.5* (case 21)

♀*12* gave birth to her first infant ♀*12.1* on July 30, 1982, about five weeks after the male replacement. She mostly avoided ♂*43*, but the male never showed any aggressiveness towards the infant. He also did not try to harm ♀*4.5* anymore.

INFANTICIDAL MALE CHANGE (♂*43* TO ♂*11*) AND PRECEDING INTERIMRESIDENCIES (♂*20*, ♂*46*, ♂*11*) IN TROOP KI, SEPTEMBER 1982–JANUARY 1983

On September 15, 1982 Troop KI was comprised of 20 members: 1 adult male (♂*43*, resident since June 1982); 14 adult females (para ♀*1*, ♀*2*, ♀*3*, ♀*4*, ♀*6*, ♀*7*, ♀*8*, ♀*9*, and ♀*11*; primiparous ♀*12*, nulliparous ♀*13*; youngadults ♀*6.3*, ♀*4.4*, and ♀*2.3* started regular cycling between August 8 and 13, 1982, when menarchal bleeding occurred); 1 juvenile male (♂*8.2*); 2 juvenile females (♀*3.2* and ♀*1.3*); 1 infant-II female (♀*4.5*); 1 infant-I female (♀*12.1*). Additionally, ♂*6.4* was born on October 11, 1982.

Table 2. All-male groups (AMG) invading home range of Troop KI (September 15, 1982–January 12, 1983).

	AMG10		AMG7		Duo		Duo		Solitary		
Age class	*N*	Identified individuals	*N*	Identified individuals	*N*	Identified individuals	*N*	Identified individuals	*N*	Identified individuals	Total
Old	1	♂*3*	1	♂*37*	1	♂30					3
Adult	6	♂*11*, ♂*38*, ♂*49*, ♂*50*, ♂*51*, ♂*54*	2	♂*46*, ♂*42*	1	♂*20*			1	♂*62*	10
Youngadult	3	♂*52*, ♂*53*, ♂*KI4.2*	2	♂*47*, ♂*48*			2	♂*44*, ♂*45*			7
Subadult	9	♂*55*, ♂*56*, ♂*57*, ♂*58*									9
Juvenile	16	♂*59*, ♂*60*, ♂*KI7.4*, ♂*KI11.2*									16
Total	35		5		2		2		1		45

Two young adult males (♂*44* and ♂*45*) invaded the troop's home range on September 15, 1982. Probably due to fights with these males resident ♂*43* suffered deep and gashing cuts in his left shank the next evening. ♂*43* had disappeared by the morning of September 17, 1982. New and long lasting competition for Troop KI began with 45 male participants appearing nearly simultaneously on the "battle field." They belonged to different alliances (Table 2): (1) Duo ♂*44* and ♂*45*: Initiated the change but disappeared by September 18, 1982; (2) Duo ♂*20* and ♂*30*: Former male resident and ex-member of AMG 10, ♂*20*, appeared on September 17, 1982 with a new and subordinate ally, old ♂*30*; (3) AMG 7: Appearing on September 17, 1982, the group consisted of five adult members (as in November 1981) with ♂*46* holding alpha and ♂*37* beta position of the intragroup rank order; (4) AMG 10: Appearing on September 19, 1982, the group size fluctuated during the next months between 28–35 members of all age classes except infants. ♂*11* clearly held alpha position with ♂*38* as beta and ♂*49* as gamma males; and (5) Solitary ♂*62*: Crossed Kailana region on December 6, 1982 from west to east, interacting briefly with other males.

From September 17, 1982 onwards the highest ranking members of the different male congregations managed to establish themselves as interimresidents for periods of between 1–23.5 days until ♂*11* succeeded finally on January 12, 1983. First ♂*20* with his ally ♂*30* took over on September 17. Despite heavy conflicts with the numerous rivals besieging the home range ♂*20* controlled the troop with only short interruptions during the next seven weeks (September 17–October 5; October 8, October 10–11; afternoon of October 19–morning of November 4). ♂*20* also expelled his ally ♂*30* for several periods of up to 24 days. Ultimately ♂*20* had to withdraw when he was wounded on November 4.—Several times AMG 7 or its alpha ♂*46* peripheralized all other rivals (October 9, October 12–morning of October 19, November 7–morning of November 11, afternoon of November 14–November 20, afternoon of December 16–December 20, December 22–24, December 27–30, January 1, 1983–morning of January 9). Following commonly gained victories ♂*46* usually did not tolerate his four allies, but chased them away.—AMG 10 likewise managed to keep other competing male parties away resulting in numerous multimale periods (October 6–7, afternoon of November 6, afternoon of November 11–morning of November 14, November 21–22, December 21, 25, and 31, afternoon of January 9–morning of January 12, 1983). Alpha ♂*11* chased his fellow members only twice away, thus becoming relatively undisturbed

Table 3. Aggressive behaviour of males directed towards members of Troop KI during takeover (September 16–December 20, 1982).*

		Males						
		Adult		Subadult		Juvenile[3]	Total	
Context		♂*11*	Others[1]	♂*55*	Others[2]		events (*N*)	%
During food provision (~5.6 % of observation time)		3	3	1			7	9.1
During other situations (~94.4 % of time)								
Directed towards females not carrying infants		3	2	14	4	2	25	32.5
Directed towards females carrying infants	♀*4*	15	1	3	2	2	23	58.4
	♀*6*	10	3	1	1		15	
	♀*12*			1	1		2	
Directed towards infants alone	♀*4.5*	3					3	
	♂*6.4*					2	2	
Total events (*N*)		34	9	20	8	6	77	
%		44.2	11.7	26.0	10.4	7.8		

*Stalking, harassment, slapping, pulling of fur, chasing, attacks, biting, and fights. 1) ♂*45*, ♂*50*, ♂*53*, and ♂*54*; 2) amongst them ♂*57* and ♂*58*; 3) amongst them ♂*60*.

interimresident (November 23–morning of December 16, December 26), before he finally established himself as a new resident male on the afternoon of January 12, 1983.

Seventy-seven aggressive interactions directed from males towards members of Troop KI were counted from September 16 to December 20, 1982 (Table 3). Fifty-eight point four percent (expected: 20.4 %) of all agonistic behaviour concentrated on lactating mothers or infants alone. Aggression was only observed from members of AMG 10 (with a single exception concerning ♂*45* of AMB 7). Harassment by juvenile males (7.8 %) had a rather playful character though the troop members involved reacted as if frightened. Subadult ♂*55* accounts for 26.0 % of all episodes. He mostly stalked or harassed adult females without infants, and tried to catch, pull, or chase them without attacking seriously. Aggressive behaviour of adult males other than ♂*11* mostly arose during turbulent male-male interactions but never seemed goal-directed. ♂*38* (who later turned out to be infanticidal in Troop B) was never involved. In contrast, alpha ♂*11* of AMG 10 accounts for 44.2 % of all episodes. His attacks were clearly goal directed toward infants. He certainly killed ♂*6.4* (case 26 in Table 1) as well as ♀*11.4* (born after takeover; case 27). ♂*11* is probably responsible for the disappearances of ♀*12.1*, ♀*4.5* (cases 25, 24) and ♀*1.5* (born after takeover; case 28).

Disappearance of Infant ♀*12.1* (case 25)

November 4, 1982 (♀*12.1*, 97 days old). In the morning, ♂*20* occasionally chases AMG 10, obviously trying to guard estrous ♀*8*. During the afternoon the troop is not located until 17:30, when it already has returned to the dam. ♂*20* has vanished. (On the following evening ♂*20* is seen again with a deep wound in his left heel.) AMG 10 is around the troop. Black coat ♀*12.1* has disappeared, too. Circumstances of the following days suggest a violent death of the infant, although no corpse was found and no extraordinary tension between males and females could be detected this evening. However, ♀*6* with her infant hides away from males, and ♀*4* with her infant could not be located at all.

Disappearance of Infant ♀*4.5* After Attacks (case 24) and Killing of Infant ♂*6.4* (case 26)

November 5, 1982. In the morning, infant-deprived ♀*12* remains a bit apart from the troop although she is groomed three times by ♀*13*. Similar to a multimale troop structure, six to eight adult to subadult males mix with the females. ♂*11* tries to keep beta ♂*38* and gamma ♂*49* at a distance. Males sometimes stalk females, obviously due to general tension and excitement, but without any serious attempt to attack.

November 6, 1982. (♀*4.5*, 209/♂*6.4*, 26 days old). At 16:55 ♂*11* disturbs an attempt of ♂*38* to mount ♀*11*. At 17:00 ♀*4* with her infant reenters the troop after having remained apart for at least 1 hr. Immediately, ♂*11* tries to attack, but before he can grasp them, mother and infant escape and hide behind an *Euphorbia* bush, while ♀*6.3* pulls the legs of ♂*11*. Infant ♀*4.5* has a small bleeding wound at the surface of left shank just below the knee. The actual wounding had not been observed. When ♂*11* approaches ♀*6* with her black coated infant, they also flee. ♀*11* solicits ♂*11*, and ♀*13* starts grooming him. Afterwards, he is groomed twice by ♀*6.3* and once by ♀*4.4*.

At 17:55 ♂*11* displaces old ♂*3*. When ♂*11* stares conspicuously towards ♀*4* and her infant, they flee, while ♀*6.3* again pulls the legs of ♂*11*, whereupon the male starts feeding on a bush.3) When he moves again, ♀*4* (with the infant on her breast) is obviously frightened and starts running. Apparently confused, at first she runs in the direction of ♂*11*, who does not react. At 18:10 ♂*11* is groomed simultaneously by ♀*13*, ♀*7*, and ♀*8*.

♂*11* is ousted on November 7, 1982 by alpha ♂*46* of AMG 7 who is himself driven away by AMG 10 with its returned alpha ♂*11* on November 11.

November 11, 1982. At 17:30 ♂*11* grunts and displaces ♀*4*, whose infant runs screaming towards her. When they flee, the infant looses its hold on her belly and has to climb on again quickly. ♀*6.3* violently pulls at ♂*11*'s legs and he jumps away with a short whoopcall, after ♀*2* and ♀*8* attack him.

Again ♂*46* installs himself as interimresident from November 14 to 20. After he is driven away by AMG 10, ♂*11* regains leadership for 25 days from November 23 onwards.

November 22, 1982. At 16:00 AMG 10 is scattered near "green valley." ♂*11* and ♂*49* mix with the females. ♀*11* is supported by ♂*11*, when she defends herself against a harassing subadult male. ♀*4* and ♀*6* with their infants keep some distance from ♂*11* and ♂*49*. After having displaced ♂*49*, who is groomed by ♀*13*, ♂*11* himself is groomed by the female for 5 min. ♀*11* joins the pair. ♂*11* is groomed by both the females for another 5 min. The situation seems relaxed.

At 16:15, as soon as ♀*4* appears with her infant, ♂*11* jumps towards them and tries to grasp the infant, but ♀*1*, ♀*9*, ♀*2*, ♀*13*, and three unidentified females attack him and he withdraws. At 16:16 ♂*11* returns, starts grinding teeth and again follows ♀*4* with her infant. They flee, while ♂*11* utters convulsive barks. ♀*11* investigates a small but bleeding scratch wound at the lateral part of the left buttock of infant ♀*4.5*.4) The left thumb of ♀*4* is bleeding, too. At 16:20 ♂*11* suddenly jumps towards ♀*3* and harasses her for about 1.5 min, biting her at least twice without wounding her. ♀*1*, ♀*2*, ♀*6.3* and three other females defend ♀*3* by clapping, pulling, and intercepting ♂*11*; one female solicits ♂*11*, when he pursues ♀*3*. At 16:23 a juvenile male of AMG 10 screams towards ♀*1* and ♀*3*, who chase him away, supported by ♂*11*. At 16:25 ♂*11* runs after ♀*6*, who flees in panic with her infant. ♂*11* does not follow, but he chases while teethgrinding a nearby gathering of about 20 juvenile and subadult males to about 100 m away. After 16:30, while returning to the troop, ♂*11* is groomed by ♀*1*, ♀*4.4*, and ♀*6.3*. Infant ♀*4.5* plays far from its mother among females, coming relatively close to ♂*11* up to about 5 m.

November 25, 1982 (♀*4.5*, 228/♂*6.4*, 45 days old). For the first and only days of ♂*11*'s interimresidency, no other male competitors are seen in the home range. Until 09:30, the troop with ♂*11* in the midst gathers relaxed on a hillock adjoining to the dam at the eastern shore of the upper lake. ♀*1* and ♀*13* groom ♂*11*; ♀*1*, ♀*11*, ♀*2.3*, and ♀*6.3* solicit him successively while he grunts. Infant ♀*4.5* is diarrheic5) and "solicits" ♂*11* four times in the same manner as adult females do whenever he moves. When ♂*11* moves towards ♀*6* and ♀*4*, they twice take their infants and run away. At 09:30 ♀*4* solicits ♂*11*, but the male moves in the opposite direction towards infant ♀*4.5*, who escapes into thin branches of a *Prosopis* tree. ♀*4.5* again solicits ♂*11*, who remains under the tree and utters convulsive barks without having penile erection.

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3) Feeding behaviour of males and females shortly after infanticide or attacks was also observed by Mohnot (1971), Hrdy (1974), and Makwana (1979); see also below.

4) Inspection of a wounded infant by troop members other than its mother is reported only by Makwana (1979) for a juvenile female of Jodhpur's Kaga troops.

He tries to climb the tree, but is unsuccessful because the branches are not strong enough to carry his weight. Mother ♀*4* remains 15 m apart, whereas ♀*2*, ♀*9*, and ♀*4.4* intercept ♂*11*'s movements, but obviously they do not dare to attack him. When ♀*3* and ♀*2.3* join, all five defending females start catfighting with the excited male who displays teethgrinding, convulsive barks, whoopcalls and jumping. During the fight ♀*4.5* climbs down and jumps into the arms of mother ♀*4* who approaches in haste. At 09:35 ♂*11* resumes convulsive barks and teethgrinding, but does not follow the fleeing mother ♀*4* and her little daughter.

At 09:45 puppies of feral dogs squeak between hillocks where most of the troop females sit or feed on *Prosopis* bushes and trees. ♂*11*, attracted by the vocalization, again utters convulsive barks, joins the females and immediately attempts to snatch infant ♀*4.5*, who escapes into thin branches. Twice he unsuccessfully tries to grasp branches that support the screaming infant, while jumping up from the ground. During his third attempt, ♀*4* and ♀*9* hamper him by slapping and pulling his feet. ♂*11* whoops briefly and starts climbing through the scrub. ♀*4* and ♀*9* continue to harass him. In the branches, ♀*4* solicits him from a distance of 0.5 m. After ♀*11* has joined the defending females, ♀*4* manages to take her infant and flees. ♀*4*'s thumb and ball of the left hand is bleeding. At 09:52 ♂*11* remains feeding in the tree, making occasional convulsive barks. At 09:56 ♂*11* follows ♀*4* with the infant on her breast. She flees three times, twice stopping and soliciting the male from a distance of about 15–20 m. Up to 12:00, ♀*4* and ♀*6* with infants remain apart but in sight of the feeding, grooming, and dozing troop at the edge of the "green valley."

When observations are resumed at 15:00, the troop is feeding in a relaxed manner at the same site, while ♀*4* and ♀*6* with their infants still remain apart. At 16:00 Troop KII appears on a hillock, approximately 200 m away. ♂*11* gives convulsive barks. At 16:01 ♀*4*, on a stone wall parallel to the road west of the upper lake, solicits ♂*11*, who turns in the opposite direction towards ♀*4.5* (see 09:37). The infant again flees into thin branches. ♀*2*, ♀*3*, ♀*7*, ♀*9*, and ♀*4.4* move to the place, watching ♂*11*, who gives convulsive barks just under the tree. At 16:03 a car stops for some seconds. After it has moved away, ♀*2*, ♀*3*, ♀*9*, ♀*11*, ♀2.3, and ♀*4.4* start harassing ♂*11*, who tries to escape behind the wall. ♀*4*, so far watching from apart, runs under the tree and flees after her infant jumped into her arms. At 16:06 ♂*11* again follows them twice without having penile erection. Now and two more times, when ♂*11* is just moving, ♀*4* frantically solicits the male before jumping away, while the infant chatters at its mother's breast.

From 16:16 onwards ♂*11* watches Troop KII near its roosting site at the dam of "green valley" and drinks at the lake. At 16:40 the male returns to the troop. ♀*6* withdraws, carrying her infant. ♀*4* solicits him before likewise withdrawing, followed by her infant. At 16:42 ♂*11* follows ♀*4* who solicits him with the chattering infant at her breast. ♂*11* comes nearer to the pair but suddenly stares towards ♀*6* and her infant.

At 16:44 the grunting ♂*11* pursues fleeing mother ♀*6* over the wall. She hides with her infant in an *Euphorbia* bush. When ♂*11* approaches them ♀*6* runs away at full speed, but the male is able to catch up with her after about 25 m though ♀*9* and ♀*6.3* try to block his way. At 16:45 ♂*11* jumps onto the back of ♀*6*, pulls her down to the ground and manages to bite her infant in its left hip. Seconds later, six females—amongst them ♀*3* and ♀*2*—lunge at the spot and attack the male, resulting in a heap of about nine individuals fighting on the ground (Fig. 3a). The mother seizes her infant back out of ♂*11*'s mouth. (Later, the wound is found to continue from a partly torn-off thigh, over split buttocks, to the tail, of which two-thirds are chopped off lengthwise by sharp canine teeth. The long slash was probably caused by the mother pulling the infant from the male's jaws, but it is also possible that the male himself slashed the infant's underbody through his mouth.)[6] ♀*6* with her wounded baby escapes from the struggle (Fig. 3b) and runs about 15 m away whereas ♂*11* is still involved in fierce fights with defending females, mainly ♀*3*, for another 20 sec. Ultimately, ♂*11* escapes with a big jump and a short whoop call (Fig. 3c).

At 16:47 highly excited ♂*11* sits on the ground and gives conclusive barks. About 20 m away, ♀*6* holds her profusely bleeding and whimpering infant at her breast (Fig. 3d), when the elder daughter ♀*6.3* joins her. ♂*11* again tries to catch ♀*6* and pursues the frantically fleeing mother onto the wall top (Fig. 3e), where ♀*6.3* hampers him by pulling his legs, and several other females, amongst them ♀*2*, intercept his run. At 16:50 ♂*11* nevertheless reaches ♀*6* with the bleeding victim in a *Prosopis* tree at the lake dam, 200 m away from his successful attack. Although the male places him-

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5) Similarly, langur mother Pawless of Abu was diarrheic following male attacks on her infant (HRDY, 1974); see also below.

6) Infants at Dharwar (SUGIYAMA, 1966), Jodhpur (MOHNOT, 1971; MAKWANA, 1979), and Abu (HRDY, 1974) suffered similar injuries.

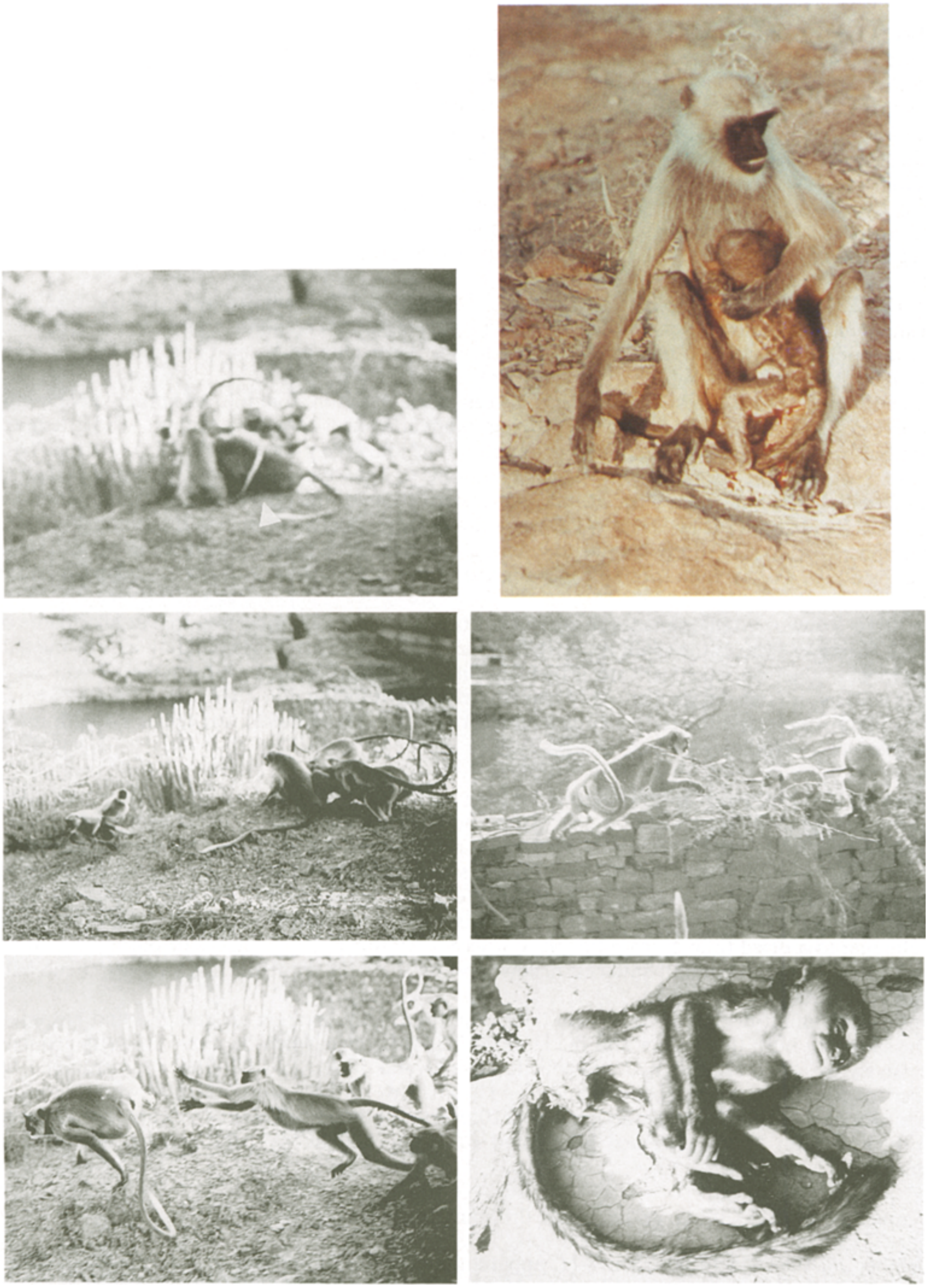

Fig. 3. **a.** ♂*11* (arrow) has pulled down ♀*6* with her 1.5-month-old infant ♂*6.4*. Other females lunge at the spot and attack the male (November 25, 1982, 16:45). **b.** ♀*6* (left) escapes, pressing her baby to her breast. Five to six troopmates catch hold of the male for another 20 sec. **c.** Ultimately ♂*11* (left) escapes with a big jump, the defending ♀*3* (right) jumping after him. **d.** ♀*6* holds her profusely bleeding infant (16:47). **e.** ♂*11* (left) continues pursuing ♀*6* (right; only the black tail of her baby is visible), while the elder daughter ♀*6.3* (middle) tried to intercept ♂*11*'s run (16:48). **f.** ♀*6* abandons her dying baby the next morning. The male's canine has slashed its left thigh, split the buttocks and chopped the tail from the root to nearly the tip (November 26, 1982, 08:05).

self behind them and shakes branches,[7] he ultimately has to come down to the ground, since ♀*2*, ♀*3*, and ♀*6.3* pull him violently by his body and hindlegs.

At 16:52 ♂*11*, sitting under the tree, continues giving convulsive barks. The whole troop except ♀*1* watches the scene from a distance of 5 m, gathering on the dam's wall. At 17:00 ♂*11* lunges towards ♀*4* and her infant, sitting about 10 m away. ♀*4* interrupts her escape three times in order to solicit ♂*11* frantically whenever ♀*2*, ♀*3*, and ♀*7* get involved with him in catfights. At 17:05 ♂*11*, grinding teeth and barking, whoops and does a jumping display without having penile erection. During the following 20 min ♀*6*, accompanied by her daughter, has to escape from ♂*11* four times within the branches of several trees. Whenever the mother moves the wounded baby whimpers, its left leg hanging down lame. ♂*11*'s attempts are thwarted twice by ♀*2*, once together with ♀*11*. At 17:27 ♀*6*, ♀*6.3*, and ♂*11* feed on *Prosopis*.

At 17:32 ♂*11* resumes his aggressive barks. ♀*6* emits a vehement [zi-zi-i]-vocalization.[8] The utterances increase when a Red-wattled lapwing (*Vanellus indicus*) responds to the similar frequency of the langur female's vocalization with his [pity-to-do-it]-cry. Obviously, bird and monkey stimulate each other. ♀*2*, ♀*12*, and ♀*4.4* participate in the concert.

After 17:36 ♂*11* moves restlessly under the trees of the dam for 20 min, occasionally giving convulsive barks. Twice he chases fleeing ♀*4* with her infant and once ♀*6* with her infant, who attempted to climb down from the trees. At 17:58, ♀*4* with infant joins ♀*6* on a tree. At 18:02 ♀*6*, carrying her infant, crosses the dam and, obviously attempting to hide, climbs into a round pump shaft of about 2 m diameter and 10 m depth at the southeastern shore of the upper lake. At 18:05, after ♀*3*, ♀*6.3*, and ♀*4* with infant began to follow but draw apart, ♂*11* approaches the pump shaft and places himself behind ♀*6* in the completely dark shaft, though ♀*2* bites him twice in his tail when he climbs down. For 10 min nothing can be heard in the gloomy shaft other than teethgrinding of ♂*11*.

At 18:16 ♀*6* with infant manages to escape out of the shaft and climbs on a tree at lake dam. At 18:17 ♂*11* likewise leaves the shaft. As dusk falls, he climbs the guest house building east of the dam where most of the troop members are at their sleeping site, about 50 m apart from the tree on which ♀*6* sits with her infant. ♀*6.3* solicits ♂*11* immediately after noticing him and utters [hiii...]-vocalization as if she were searching for her little sibling. At 18:30, shortly before darkness, ♀*4* with infant is also seen on the building.

November 26, 1982. At 07:30 ♀*6* is found sitting without her infant on a prominent tree above western shore of the lower lake, a bit apart from the dozing and grooming troop around ♂*11*. Only five nonadults (♀*1.3*, ♀*2.3*, ♀*4.4*, ♀*6.3*, and ♀*3.2*) remain together in trees at the dam. The wounded infant ♂*6.4* is probably carried by one of them, since at 08:00 it falls through the branches to the ground. None of the young females reacts when a feral dog snatches the screaming infant and transports it about 60 m away towards the north. I pursue the dog until he eventually drops the infant, still clinging to a dried branch from the place where it fell down. Beside its 15 hr old injuries at the underbody (Fig. 3f), the infant suffers a new wound on the back from the dog's mouth. (The baby dies around 22:00 at my camp.)

Until 11:00 infant-deprived ♀*6* stays in the troop's periphery, looking around. ♀*4* and her infant do the same but both the mother and the infant solicit ♂*11* once, when he moves. ♂*11* is groomed successively by ♀*1*, ♀*11*, and ♀*13* and solicited by ♀*1* and ♀*11*. At 11:02 after ♀*6.3* groomed her mother for 5 min, ♀*6* grooms her daughter for 11 min. At 11:16 ♀*6.3* grooms ♂*11* who afterwards chases members of the nearby gathering AMG 10. Further attacks on infant ♀*4.5* are not observed. —In the afternoon ♂*11* is groomed by ♀*1* and ♀*6.3*, solicited by ♀*11*, ♀*2.3*, ♀*4.4*, and once by infant ♀*4.5*.

November 27, 1982. At 16:45 ♀*6* licks milk dropping from her breast.

November 28, 1982. At 17:00 when ♂*11*, apparently without any interest in ♀*4.5*, moves under a tree on which the infant is sitting, he is attacked by ♀*9* and ♀*2*, and 30 min later during the same situation by ♀*9*, ♀*3.2*, and ♀*6.3*.

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7) HUGHES (1884, cited in HRDY, 1974) and HRDY (1974) likewise observed males shaking females out of branches.

8) This vocalization was heard only once during the whole study period. The [zi-zi-i]-tritonus is based on exhalation-inhalation-exhalation and hence probably equivalent to male convulsive barks (see footnote 1).

During the following weeks, infant ♀*4.5* repeatedly solicited ♂*11* from a safe distance: on November 27 once, November 28 five times, and November 29 three times. Mother ♀*4* solicited the male on November 28 ten times and on November 29 six times from less than 0.5 m. ♂*11* copulated once with her and her solicitings ceased afterwards. Infant ♀*4.5* was diarrheic at least up to December 1 and even simple movements of ♂*11* elicited its frightened chatterings up to December 7. ♀*4* groomed her little daughter much more frequently than she did before the attacks of ♂*11* started. ♂*11* did not show any more interest in ♀*4.5* for about seven weeks. Nevertheless, he attacked ♀*4.5* on January 12, 1983, the very day when all other male competitors left the home range and ♂*11* thus finally became new male resident. ♀*4.5* disappeared one day later on January 13 at an age of 277 days.

Killing of Infant ♀*11.4* (case 27), Attack on and Disappearance of Infant ♀*1.5* (case 28)

(Observer in Troop KI since December 21, 1982: V. K. DAVE; for details see AGORAMOORTHY & MOHNOT, in prep.)

♂*11* is also the first known resident male langur who definitely killed a baby born long after his takeover (♀*11.4*) and perhaps another one he sired himself (♀*1.5*). ♀*11.4* was born on March 10, 1983, nearly two months after takeover. ♂*11* wounded the baby at an age of 11 days; it died one day later on March 22, 1983. ♀*1.5* was born on April 8, 1983, 199 days after ♀*1* copulated with ♂*57*, ♂*51*, and ♂*11*. ♂*11* attacked the infant on April 26, 1983 at an age of 18 days but it was rescued. (Additionally, juvenile sister ♀*1.3* was not seen after April 27, when she was 28.2 months old.) No further attacks were observed up to June 1983. However, ♀*1.5* disappeared between June 17 and 25, 1983 (after having an infection on its tail).

INFANTICIDAL MALE CHANGE IN TROOP B, JANUARY 1983 (♂*22* TO ♂*38*)

(Observer in Troop B since December 21, 1982: G. AGORAMOORTHY; for details see AGORAMOORTHY & MOHNOT, in prep.)

♂*11*, new alpha of Troop KI, expelled his former allies of AMG 10 finally on January 12, 1983. The more than 30 males then occupied the home range of neighbouring Troop B. ♂*22*, the male resident in Troop B since November 17, 1980 (see VOGEL & LOCH, 1984: Fig. 2), was found dead on January 17, 1983, probably killed by males of AMG 10. ♂*38*, now the highest ranking member of AMG 10, established himself as the new resident male on January 22.

Before the takeover (census January 1, 1983) Troop B was comprised of 20 members: 1 adult male (♂*22*); 8 adult females (para ♀*1*, ♀*2*, ♀*3*, ♀*5*, ♀*6*, ♀*6.1*, ♀*7*, and ♀*9*); 3 juvenile males (♂*7.3*, ♂*3.4*?, ♂*6.1.1*?, and ♂*6.4*?; only two of the three animals marked with "?" were identified but could not be attached to their mothers, the third male had disappeared); 3 juvenile females (♀*2.3*, ♀*1.4*, and ♀*7.4*); 1 infant-II male (♂*3.5*); 3 infant-I males (♂*1.5*, ♂*6.1.2*, and ♂*5.4*); and 1 infant-I female (♀*6.5*).

Between January 17 and February 11, 1983 ♂*38* killed at least three but probably four out of five infants present (cases 29–31, 33 in Table 1). One infant survived (case 32). The three male juveniles aged about 15.5–32 months disappeared between January 12 and 17. They might have joined AMG 10.

The situation in Kailana region stabilized despite repeated visits of AMG 10 and AMG 7. The residency of ♂ *11* in troop KI lasted until end of June 1983, that of ♂ *10* in troop KII until July 1983, and the residency of ♂ *38* in troop B at least to April 1987.

FEMALE COUNTERSTRATEGIES

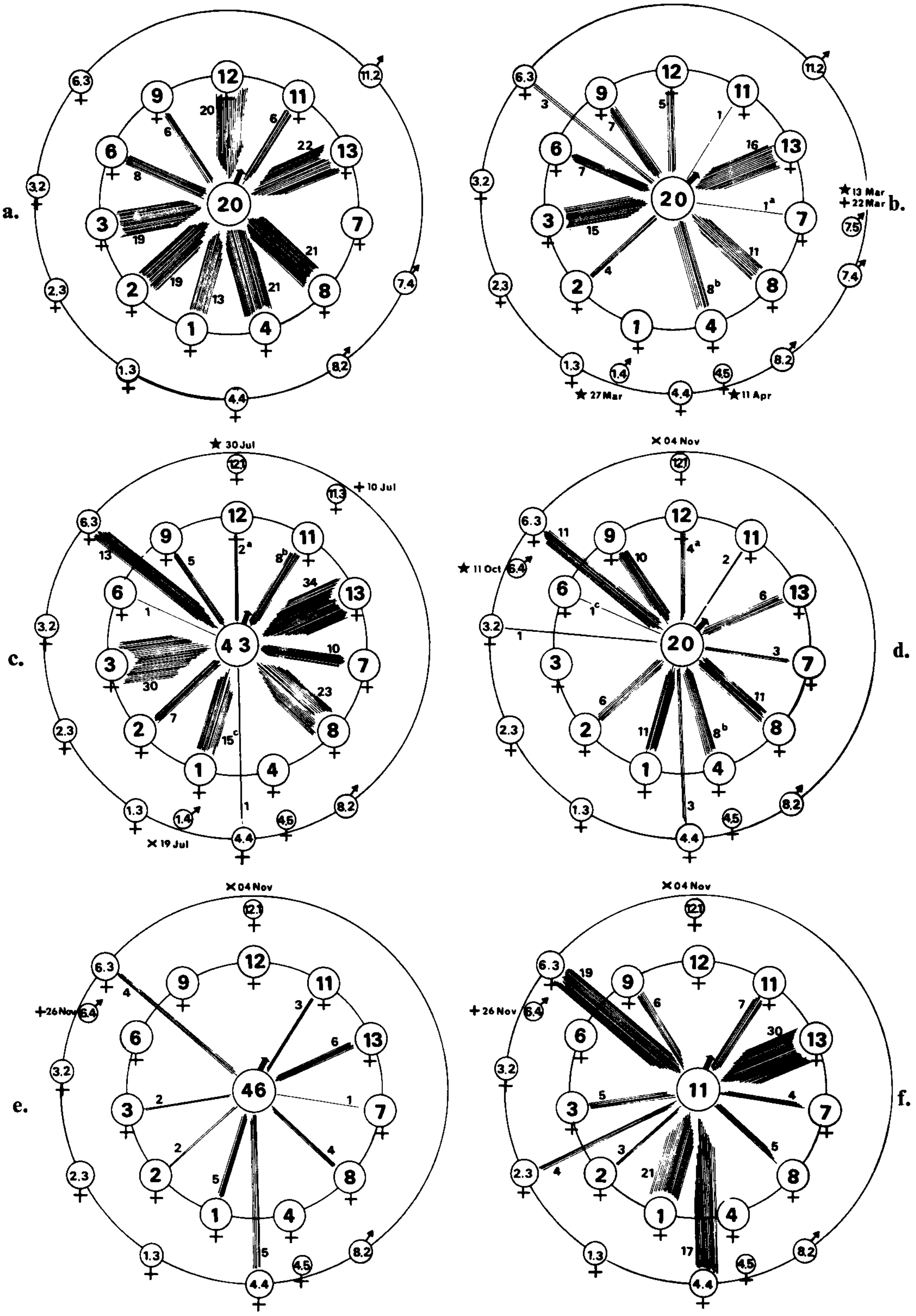
Langur females in principle have several options to forestall infanticide, including offensive long-term strategies as well as defensive short-term tactics. However, the recent data suggest that in fact only short-term actions exist to counter infanticidal males.

MALE AVOIDANCE AND GROOMING BOYCOTT

Females with infants of Troop KI reacted to new males in the same manner as reported for mothers at Mount Abu (HRDY, 1974): by avoiding them. Mothers often guarded their infants together at the troops periphery, cautiously gathering them up as soon as males approached. Langur mothers might even leave their troops with their infants in order to avoid potentially aggressive males. However, unlike Abu mothers of Troop KI did so only rarely and for short times (90–150 min; ♀ *4* together with ♀ *12* on September 17 and 19, 1982, ♀ *4* alone on September 18, October 9, November 6 and 26, 1982; see above). MOORE (1983) reports for Abu that two mothers joined a male group for at least two weeks after a probably infanticidal male took over their troop. Likewise, two mothers of Troop KII (one with a black-coat, one with a white-coat infant) were seen at least on two occasions (February 5 and 16, 1982) amongst the male group invading their home ranges. (For whatever reason they might have sought the proximity of the future—noninfanticidal—male resident ♂ *10*.) Similarly, 14 females of Troop K including all lactating mothers remained with the old male resident ♂ *2* in the course of a male invasion between October and December, 1977, whereas eight females without infants joined the invaders around future resident ♂ *3*, thus founding the new Troop KII (WINKLER et al., 1984). In Kanha, an infanticidal male group consorted with females without infants whilst the infant-bearing females and troop resident likewise kept away (NEWTON, 1985).

Following the takeovers described above, mothers with dependent infants generally distinguished clearly between obviously harmless and dangerous males (based on a total of

Fig. 4. Allogrooming of resident males and interimresidents by members of bisexual Troop KI. The resident male or interimresident is shown in the center. Adult females are on the inner circle, arranged clockwise in decreasing rank order with ♀ *12* ranking highest and ♀ *9* ranking lowest (key date May 1982). Immatures are on the outermost circle; infants-II and juveniles are represented by smaller circles, youngadults by larger circles. Neonates and dependent infants-I are shown between the inner and outermost circles, behind their mothers; births (asterisks), deaths (+), and disappearances (×) are marked. (Juveniles ♂ *7.4* and ♂ *11.2* left their troop in June 1982.) Every line represents one allogrooming episode directed towards adult males. Figures 4a, b, and c are based on 220 hr of observation each, Figures 4d, e, and f on 230 hr in total. **a.** Resident male ♂ *20*; 155 episodes from October 30, 1981 to January 14, 1982. **b.** Resident male ♂ *20*; 78 episodes from March 8 to May 1, 1982. [a]: April 12; [b]: March 13, 15, 18, 19, 24, 29, 31, April 8. **c.** Resident male ♂ *43*; 149 episodes from July 8 to September 1, 1982. [a]: July 11, 21; [b]: August 1, 10, 18, 23, 25, 26, 28; [c]: July 31, August 1, 5, 12, 16, 21, 22, 23, 28. **d.** Interimresident ♂ *20*; 77 episodes during 37 days between September 17 and November 4, 1982. [a]: with baby; September 19, October 3, 20, 21; [b]: without baby; September 30, October 21, 22, 24, 26, November 1, 2; [c]: without baby: October 22. **e.** Interimresident ♂ *46*; 32 episodes during 24 days between October 9 and December 20, 1982. **f.** Interimresident (later resident male) ♀ *11*; 121 episodes during 34 days between October 6 and December 16, 1982.


a.
b.
c.
d.
e.
f.
★ 13 Mar
+ 22 Mar
★ 27 Mar
★ 11 Apr
★ 30 Jul
+ 10 Jul
× 19 Jul
× 04 Nov
★ 11 Oct
+ 26 Nov
20
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46
11
6.3
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12.1
11.3
6.4

203 episodes of tolerance or avoidance of an adult male's proximity). Infanticidal ♂*43* was 3 times more frequently avoided than tolerated and infanticidal ♂*11* 4.4 times more. Noninfanticidal ♂*46* was as often avoided as was his spatial proximity tolerated. ♂*20* to the contrary was frequently tolerated, especially during his comeback as interimresident when two infants fathered by him were present and he already had "proved" to be harmless towards alien newborns. Only in case of ♂*20* did mothers allow their babies to hop around his reach, touch his legs and arms or cling to the male's body; he kept still as if not noticing it (♂*1.4* once, ♀*12.1* three times, ♂*6.4* once). All three mothers sought out his proximity and "protection" when male invaders besieged the troop.

Avoidance as a prophylactic tactic is most impressively illustrated through a grooming boycott by lactating females towards new resident males (Fig. 4; these results are likewise important for valuation of the "social bonding hypothesis" as a presumed proximate cause for infanticide, see below):

Tenureship of Noninfanticidal ♂*20* (Figs. 4a, b)

During the first two months of his residency, ♂*20* is groomed more or less frequently by all adult females except ♀*7*, the mother of the youngest infant ♂*7.4* (7.5 months on November 15, 1981). Three infants sired by his predecessor are born during the last two months of ♂*20*'s tenureship. Mothers of these three then boycott ♂*20*: ♀*1* and ♀*4* stop grooming after the births of ♂*1.4* and ♀*4.5*; ♀*7* only starts grooming after her newborn ♂*7.5* has died.

Tenureship of Infanticidal ♂*43* (Fig. 4c)

Lactating ♀*4* boycotts the male. ♀*1* and ♀*11* do not groom him until after their infants are—one probably, one definitely—killed by ♂*43*. ♀*12* stops grooming him after the birth of her first infant ♀*12.1*. All other adult females including two youngadults approaching menarche (♀*6.3* and ♀*4.4*) groom the male.

Interimresidency of Noninfanticidal ♂*20* (Fig. 4d)

Interestingly, ♂*20* is groomed by all lactating females during the seven weeks of his comeback. ♀*4* grooms him eight times when her 5.5-month-old daughter ♀*4.5* plays or moves somewhere else. Likewise, ♂*20* is groomed once by ♀*6* when her newborn ♂*6.4* (fathered by him) is held by another female. ♀*12* even grooms the male while holding her baby ♀*12.1*, sired by ♂*20* but born during his absence.

Interimresidency of Noninfanticidal ♂*46* (Fig. 4e)

♂*46* is not groomed by any lactating female, though not exhibiting any aggressiveness.

Interimresidency of Infanticidal ♂*11* (Fig. 4f)

♂*11* is boycotted by all three lactating females. Unlike the case of infanticidal ♂*43*, infant-deprived mothers (♀*12* and ♀*6*) did not resume grooming ♂*11* for at least several weeks after their infants were—one possibly, one definitely—killed by him.

All in all, grooming frequencies in Troop KI reflect quite precisely the respective reproductive status of females as well as kinship relations of adult males with infants: (1) Females start grooming of adult males around onset of menarche; (2) all nonlactating females groom adult males; (3) lactating females carrying infant-I never groom nonfathers; and (4) lactating females groom males who fathered their respective infants.

However, in contrast to the above, it must be mentioned that mothers sometimes behaved quite incautiously. They allowed even infanticidal males to come so close to their infants that a sudden jump would have been sufficient to grasp the hopping infant from the ground or from mother's breast. Likewise, mothers did not always watch allomothers who carried their babies near to alien males. In some cases just following a previous attack, mothers seemed to be quite shaken and distracted and did not flee when aggressive males approached them (e.g., ♀*1* on July 12 18:05, on July 13 18:56; ♀*4* on November 6, 1982, 17:55; see above). Similar, a mother at Abu just after an assault descended into the midst of builders quarrying stones, though langurs usually avoid such noisy places (HRDY, 1974). However, most incautious mothers simply seemed to have "forgotten" the dangerousness of alien males.

HRDY (1974) assumes that incautiousness of a mother might have been the straightforward reason that male attacks succeeded. On the other hand, incautiousness of Troop KI females only once led to a fatal attack (when ♂*43* grabbed the relatively unattended ♂*1.4* on July 13, 1982, 17:58). Male attacks might therefore to a certain extend be stimulated or reinforced by the act of flight. Males might identify their targets by the fact that they are usually running away.

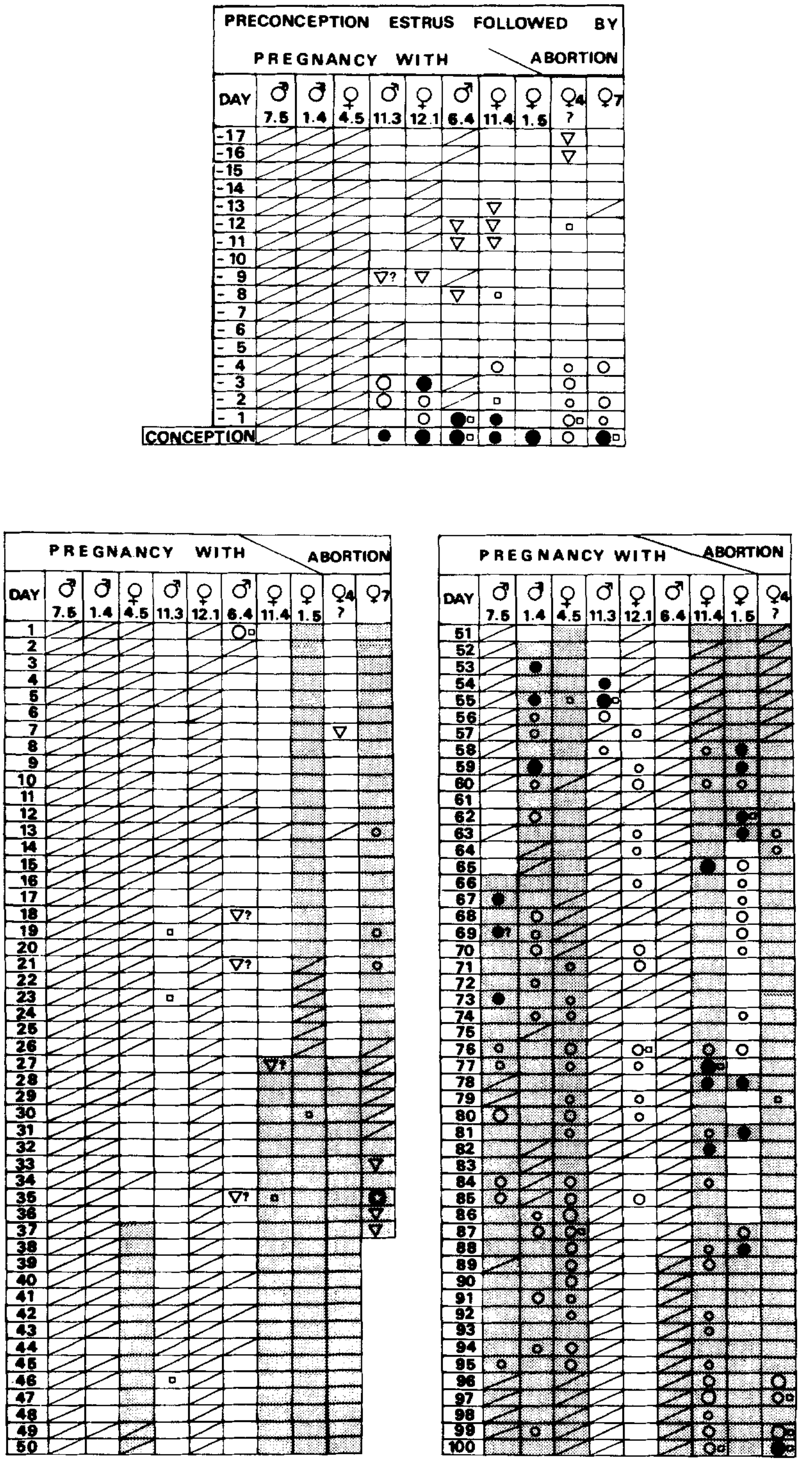
COOPERATIVE DEFENSE OF INFANTS

In almost every instance of actual male attack infants of Troop KI were defended not only by their mothers but also by other troop members (see above), as previously reported from other sites (SUGIYAMA, 1965b; MOHNOT, 1971; HRDY, 1974; MAKWANA, 1979). All members of Troop KI except infants, juvenile ♀*1.3*, adult ♀*12*, and old ♀*6* defended at least once another mother's offspring against ♂*43* or ♂*11*. Including mothers, in eight cases five to seven females cooperated, in five cases three females, in four cases two females, and in seven cases single nonmothers defended infants.

Defending females not only intercepted the run of aggressive males but pulled their legs or fur, bit their tails etc. Counterattacked males normally withdrew without resistance. In Troop KI (on July 9, 1982, 10:17) as well as at Abu (HRDY, 1974) they were even chased up a tree. Only once did a highly excited male attacker bite—not hurt—a defending female (on November 22, 1982, 16:20). At Abu a male turned to threaten but did not even bite female defenders (HRDY, 1974). This seems plausible since a strong counterselection should act against males who injure or kill their own mates.

Half-sisters exhibited strong nepotistic tendencies. ♀*6.3* vehemently defended her little brother ♂*6.4* but rarely tried to help ♀*4.5*. On the other hand, ♀*4.4* defended her little sister ♀*4.5*, but not ♂*6.4*. Three nonmothers (♀*2*, ♀*3*, and ♀*9*) participated particularly frequently in defense of other mother's offspring. Their genetic relationship to the respective infants is unknown.

As suggested by HRDY (1974) for females of Abu, there were also slight indications of reciprocity: ♀*4* at least once defended ♂*11.3* (on July 9, 1982, 10:07) and probably once ♂*1.4* (on July 12, 1982, 18:04). Later, ♀*11* (on November 25, 1982, 16:03) and ♀*1* (indirectly, see on November 22, 1982, 16:20) defended ♀*4.5* but did not defend ♂*6.4*. On the other hand, ♀*1* and ♀*6* showed no reciprocal support when their babies were hurt (on July 13, 1982, 17:58; on November 25, 1982, 16:52).


PRECONCEPTION ESTRUS FOLLOWED BY
PREGNANCY WITH
ABORTION
DAY
♂ 7.5
♂ 1.4
♀ 4.5
♂ 11.3
♀ 12.1
♂ 6.4
♀ 11.4
♀ 1.5
♀4 ?
♀7
CONCEPTION
PREGNANCY WITH
ABORTION
DAY
PREGNANCY WITH
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DAY

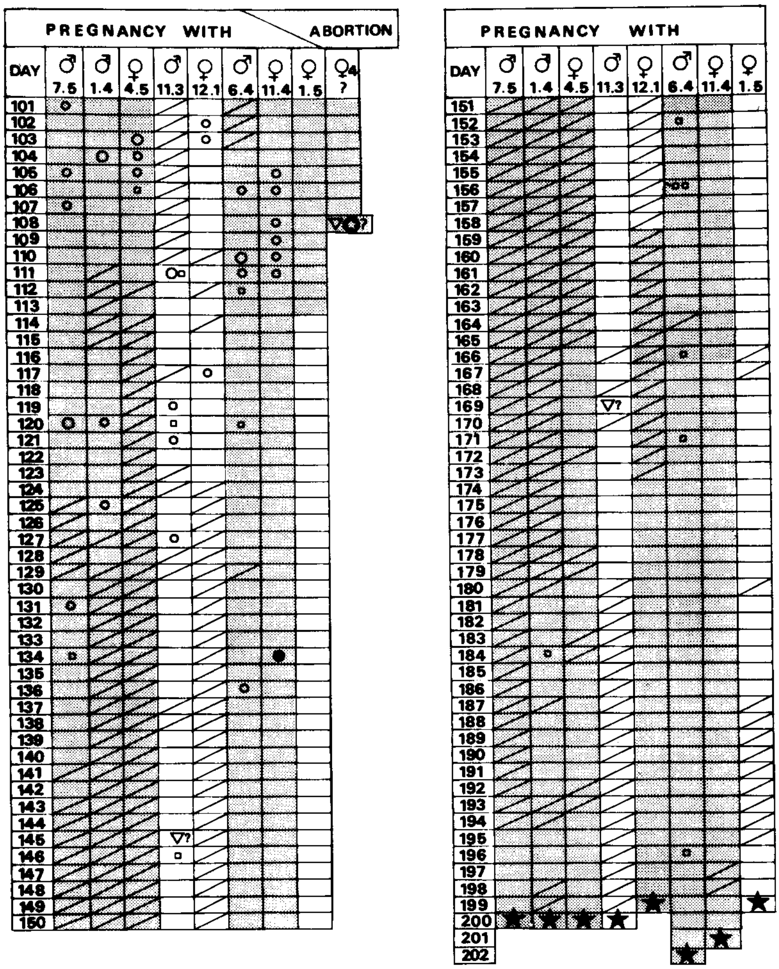

Fig. 5. Estrous behaviour (pre- and postconception) displayed towards fathers and nonfathers during ten pregnancies in Troop KI. Dates of conception/birth: ♂*7.5*, August 25, 1981[1)]/March 13, 1982; ♂*1.4*, September 8, 1981[1)]/March 27, 1982; ♀*4.5*, September 23, 1981[1)]/April 11, 1982; ♂*11.3*, November 17, 1981/June 5, 1982[1)]; ♀*12.1*, January 12, 1982/July 30, 1982; ♂*6.4*, March 23, 1982/October 11, 1982; ♀*11.4*, August 21, 1982/March 10, 1983; ♀*1.5*, September 21, 1982/April 8, 1983; ♀*4*, August 21, 1982/December 7, 1982 (abortion?); ♀*7*, September 16, 1982/October 21, 1982 (abortion). ([1)] Estimated on the basis of 200 days gestation period.)—♂*4*, presumed sire of ♂*7.5*, ♂*1.4*, ♀*4.5*, disappeared October 30, 1981; ♂*20*, sire of ♂*11.3*, ♀*12.1*, ♂*6.4*, left troop around mid of June 1982 (key date June 20); ♂*43*, sire of ♀*11.4* and presumed abortive pregnancy of ♀*4*, disappeared on September 17, 1982; ♂*44*, sire of abortive pregnancy of ♀*7*, remained in the troop's periphery and disappeared two days after insemination. It is assumed that ♂*11* is the sire of ♀*1.5*, though two more males copulated with ♀*1* around conception; ♂*11* was new resident male from January 12, 1983 (day 113) onwards and more or less undisturbed interimresident between November 23 and December 16, 1982 (day 63–86). (Data provided by V. K. DAVE for ♀*1.5*, day 91–200 and ♀*11.4*, day 22–201).—▽: Bleeding; ▽?: slight or supposed bleeding; oOO: 1, 2–4, ≥5 invitings for copulation; ● copulation(s) observed; □ mounting by other females or infants-II—juvenile males; ★ birth; ⭘ abortion; ▭ sire left troop; male invaders or new resident male present; ▨ no data.

As reported for other sites female cooperation in Troop KI could only delay but not finally prevent infanticide by repeatedly attacking males. Infants were at the most temporarily rescued (♀*4.5*) or males dropped their victims after they, however, seriously wounded them (♂*11.3*, ♂*1.4*, and ♂*6.4*).

"PSEUDO"-ESTRUS OF PREGNANT FEMALES?

HRDY (1974, 1977) suggested that postconception estrus behaviour (so called "pseudo"-estrus) could forestall infanticide: If pregnant females copulate with male invaders or new resident males, these males might tolerate their subsequent offspring since they may "think" themselves to be the sire by evaluating past consort relationships. In order to test this hypothesis, ten pregnancies (including two abortions) of females in Troop KI have been analyzed (Fig. 5). According to expectation, menstruations preceded copulations leading to conception. For some females, placental bleedings were detectable between days 7–35 of pregnancy. Surprisingly, the synoptic diagramm reveals in nearly all cases a regular pattern of postconception estrous behaviour: day 1–52: no solicitations; day 53–88: distinct and extended estrous behaviour with frequent copulations; day 89–136: less frequent soliciting, no copulations; day 137-term: no solicitations.

Importantly, females did not discriminate between sires of their subsequent infants and male invaders or new resident males. For example, pregnant ♀*11* and ♀*12* displayed estrous behaviour towards ♂*20* though he was the sire of their subsequent infants ♂*11.3* and ♀*12.1*. On the other hand, pregnant ♀*11* solicited ♂*11* 27 times and he copulated with her on the 82nd day of pregnancy (November 11, 1982) but nevertheless killed her subsequent offspring ♀*11.4* (sired by ♂*43*). Moreover, ♂*11* ignored at least 15 solicitations by pregnant ♀*1*. When he later attacked (and probably killed) ♀*1.5*, he might have acted against his own progeny, since he (and two other males) had copulated with ♀*1* on the probable day of conception.

Hence, HRDY's hypothesis of an infant-protective function of postconception estrous behaviour draws no support from the Jodhpur data: (1) An infanticidal male did not spare the subsequent offspring of mothers who frequently solicited or even copulated with him during pregnancy. (2) Pregnant females did not discriminate between fathers and nonfathers. Estrous behaviour during pregnancy seems to reflect hormonal influences rather than some sort of deliberate decision in response to social conditions.

Nevertheless, female solicitation might function as simple appeasement during intense conflict situations (see, reports of July 10, 1982, 06:26; November 6, 1982, 17:00; November 22, 1982, 16:20), even by infant females (♀*4.5*, November 14–19, 1982; HRDY, 1977; see below).

POSTPONEMENT OF MATING AFTER INFANTICIDE?

Calculations by HAUSFATER (1984) made clear that noninfanticidal males would produce more offspring than infanticidal if females whose infants were harmed postponed mating for three months. However, such a female counterstrategy obviously does not exist (probably for reasons of intrasexuell competition amongst females), since in nearly all described cases of (inferred) infanticide infant-deprived females resumed estrus within periods of 1 to about

Table 4. Resumption of estrus, subsequent conception, and birth in six cases of witnessed or presumed infanticide in Troop KI (1982–1983).

Case (see Table 1)	Victim	(Presumed) killer	Death or disappearance	Subsequent estrus of mother	Days elapsed between loss and estrus	Males solicited or (if underlined) copulated with	Next conception	Males solicited or (if underlined) copulated with	Next birth	Inter-birth interval (months)
22	♂*11.3*	♂*43*	July 10, '82	July 22–25, '82	12	♂*43*	Aug. 21, '82	♂*43*	Mar. 10, '83	9.2
20	♂*1.4*	(♂*43*)	July 19, '82	Aug. 4–8, '82²⁾	(16)¹⁾	♂*43*	Sept. 21, '82	♂*57*, ♂*51*, ♂*11*	Apr. 8, '83	12.3
23	♀*12.1*	(♂*11*)	Nov. 4, '82	Nov. 17–21, '82	13	♂*48*, ♂*37*, ♂*47* ♂*42*, ♂*46*, ♂*38*, ♂*49*³⁾	Apr. 6, '83	(♂*11* resident)	Oct. 23, '83	14.8
26	♂*6.4*	♂*11*	Nov. 26, '82	Dec. 30, '82–Jan. 1, '83	34	♂*37*, ♂*48*⁴⁾	Female stopped cycling in mid of 1983			
24	♀*4.5*	♂*11*	Jan. 13, '83	Jan. 23, '83	(10)¹⁾	(♂*11* resident)	Feb. 4, '83	(♂*11* resident)	Aug. 23, '83	16.4
27	♀*11.4*	♂*11*	Mar. 22, '83	Apr. 8, '83	17	♂*11*				
5	♂*7.4*	—⁵⁾	Mar. 22, '82	Apr. 2–8, '82	11	♂*20*	Sept. 16, '82	♂*43*, ♂*44*	Abortion (Oct. 21, '82)	

1) Female had already resumed cycling before loss of infant; 2) ♀*1* solicited ♂*43* already from July 15–17, '82 after his attack on ♂*1.4* on July 13, '82; 3) ♀*12* copulated with ♂*11* on Jan. 12, '83; 4) *6* ♀copulated with ♂*11* on Feb. 6, 83; 5) only for comparison: Infant died due to starvation.

33 days (HRDY, 1974). Females of Troop KI came into estrus 10–34 days after death or disappearance of their infants (Table 4). *All* females copulated with the (presumed) killer of their infants, if not during the first estrus after loss (with males other than the infanticidal still being present), then during following estrus periods (cases 23, 24, and 26).

INFANT COUNTERSTRATEGIES

Black coat infants have little options to actively defend themselves except clinging to their mother's breast. However, 7.5-month-old ♀*4.5* several times successfully escaped into thin branches where to the heavy male aggressor ♂*11* could not follow. Interestingly, the infant started soliciting the male after onset of the attacks from November 25, 1982 onwards. At Abu, two 10–13-month-old females likewise displayed presentation and head-shaking following male attacks (HRDY, 1977). Similarly, a 5.5-month-old red howler monkey frequently approached and interacted with a newly dominant male (CROCKETT & SEKULIC, 1984). Such prepubescent behaviour seems to reflect a demonstration of maternal independence which might reduce the chance of being killed.

TESTING HYPOTHESES CONCERNING INFANTICIDE

Various hypotheses have been raised with respect to the putative proximate causation and/or ultimate functions of langur infanticide (see reviews in HAUSFATER & VOGEL, 1982; HRDY, 1979) which shall be checked on the basis of the present observations.

SOCIAL PATHOLOGY HYPOTHESIS

CURTIN (1977), CURTIN and DOLHINOW (1978, 1979), and BOGGESS (1979) consider langur infanticide as maladaptive behaviour resulting from overcrowding: Habitat destruction and food provisioning especially in Dharwar, Abu, and Jodhpur are thought to lead to atypical one-male troop structures, high levels of aggression and a general breakdown of social relationships during male takeovers; infants, as the most vulnerable age class, suffer a disproportionally high frequency of wounds, some of which lead to death.

The hypothesis can be rejected for several reasons. First, maladaptive behaviour is not reported from troops kept in captivity, as at the Berkeley colony, where population density is effectively high and food provisioning abundant (HAUSFATER & VOGEL, 1982). SUGIYAMA (1984a) pointed out that there was only slight deforestation and no provisioning when he observed infanticide at Dharwar in 1961–1963. The one-male troop organization did not change even after the langur density at this site decreased to 54.5% between 1961–1976 (SUGIYAMA & PARTHASARATHY, 1979). More important, takeover-associated infanticide recently occurred in the undisturbed forest habitat of the Kanha Tiger Reserve (NEWTON, 1985, 1986).

The Kailana area at Jodhpur is partly protected and human settlements are not allowed. The troops have ample space to retreat from human visitors or feeders. This is not to deny that aggression increases during food provisioning (HRDY, 1977; SOMMER, 1985). A male in fact made two serious attempts to attack infants during artificial feeding (see above July 10, 1982, 06:26; July 13, 1982, 17:58). However, other attacks occurred during periods of tranquility (see the below section "SEXUAL FRUSTRATION AND REDIRECTED AGGRESSION HYPO-

THESIS"). Hence, instead of social stress do attacks during provisioning simply reflect the favourable occasion for a male with infanticidal motivations to come close to an infant.

VOGEL and LOCH (1984) do not exclude that infants were hurt coincidentally as a result of mass chases during a male change in Troop B in 1980. However, attacks, woundings, or killings observed in connection with the takeovers in 1982–1983 were by no means coincidental or mere hyproducts of intense conflict situations due to "enforced proximity" (BOGGESS, 1979, 1984), but the result of clearly goal-directed and sometimes repeated infanticidal intentions of males (see November 25, 1982, 09:37, 16:01). There was no indication of a "general breakdown" of social relations during takeovers, since complex interactional systems as infant transfer or female-male grooming followed patterns similar to undisturbed tenures of single adult males (see Fig. 4).

POPULATION REGULATION HYPOTHESIS

Several authors (SUGIYAMA, 1965b; RIPLEY, 1980; RUDRAN, 1973, for *P. senex senex*) considered infanticide to be a mechanism for decreasing recruitment to an expanding population which maintains the population in balance with its resources.

General objections against the hypothesis derive from the fact that it relies on the contested concept of group selection. It further fails to explain why a population only needs regulation in connection with adult male replacements. Moreover, the most economic regulation would be to eliminate juvenile and young adult females on the threshold of their reproductive career or females could cease to breed (see TRIVERS, 1985). The primary difficulty in testing models developed in connection with the hypothesis (SUGIYAMA, 1984b) is to determine the carrying capacity of a given habitat. Even density scores of different habitats are usually not comparable since they base on different parameters (VOGEL, 1977).

Nevertheless, it can be demonstrated for the Kailana region of Jodhpur, that infanticide is not a function of increasing population density as the hypothesis suggests. Troop B experienced infanticide in 1969 just *after* its size of 82 members had decreased rapidly to only 11 animals as a result of mass dying (MOHNOT, 1971). From 1981 through 1983 the size of TROOP KI fluctuated only slightly between 19 and 22 members. However, both infanticidal and noninfanticidal takeovers occurred. Besides, infanticide has not been reported from the multimale troops of Rajaji with approximately 80 langurs/km^2 whereas Jodhpur with one-male troops and all-male groups has an estimated density of (at the most) 18 animals/km^2 (see Table 12 in BOGGESS, 1980). The cause of infanticide is therefore with great probability based on the structure of the reproductive unit itself.

An indirect connection between population density and the rate of infanticide cannot be ruled out: Attacks on residing males and hence the frequency of adult male replacements perhaps depend on the number of males living outside bisexual troops (e.g., YOSHIBA, 1968; HRDY, 1974).

RESOURCE COMPETITION HYPOTHESIS

RUDRAN (1973, for *P. senex senex*; 1979, for *Alouatta seniculus*) suggests that infanticide on average increases access to resources (such as food or water) for the killer and his descendants.

The hypothesis predicts a selection of males as well as adult females against vulnerable potential competitors. It fails to explain why (1) only males acted as killers, and (2) they did not preferably kill weaned juveniles who lack constant protection of their mothers but have a proportionally greater impact on the resources than have dependent babies (see STRUHSAKER & LELAND, 1985). In principle, the hypothesis is not mutually exclusive with other adaptive explanations, but, as for the population regulation hypothesis, the necessary quantitative data lack for any given habitat. The environmental conditions in the Kailana region seemed, as a general statement, favourable from the first ecological study in 1977–1978 (WINKLER, 1981) through 1982 (SOMMER, 1985).

INCEST AVOIDANCE HYPOTHESIS

Again based on the concept of group selection, infanticide is considered to destroy inbred offspring produced during long tenureships (ITANI, 1972, 1982) and to preserve genetic polymorphism essential for an ecological generalist such as *P. entellus* (RIPLEY, 1980).

However, the prerequisites of these assumptions are not given. Infants killed in Troops KI and B have certainly not been "classical" incestuous products of males with maturing daughters. In a broad sense, the hypothesis could be attributed to the deaths of infants sired by males who already produced several offspring within the same troop, i.e., ♂*1.4* and ♀*4.5* probably sired by ♂*4*, or the infants killed in Troop B sired by ♂*22*. However, any "detrimental" inbreeding can be excluded for infants ♂*6.4*, ♂*11.3*, ♀*11.4*, and ♀*12.1*, since they represent the first crop of the breeding of ♂*20* and ♂*43*, respectively. These infants have been killed though they contributed positively to their natal troop's genetic polymorphism.

SEXUAL FRUSTRATION AND REDIRECTED AGGRESSION HYPOTHESIS

SUGIYAMA (1965a, b, 1984b) emphasized that "suppressed sexual urge" of nontroop males may "explode" against females in the course of a takeover. This is in accordance with MOHNOT (1971) who considers simultaneous "sexual excitement" and "enragement" as the proximate factors releasing themselves in infanticide.

However, male-male competition during takeovers is not necessarily correlated with sexual frustration of males, since during the male change in Troop KI from September 1982 onwards 15 out of 19 adult males involved managed to copulate. More important, sexual frustration can almost certainly be excluded as a factor eliciting the infanticidal behaviour of ♂*43* and ♂*11*. ♂*43* had already gained sole leadership when he killed ♂*11.3* and wounded ♂*1.4*. During 13 out of 15 days preceding the disappearance of the latter infant on July 19, 1982, ♂*43* was solicited 77 times and copulated 28 times with seven different females of Troop KI. Shortly before his deadly attack on ♂*1.3* on July 9, 1982, 10:07, he copulated with ♀*8* at 08:33. After ♂*11* appeared on September 19, 1982 until November 25, 1982 when ♀*12.1* had disappeared, ♀*4.5* was attacked and ♂*6.4* killed, ten different females solicited ♂*11* 38 times; he copulated five times. Particularly, ♂*11* ignored 16 solicits by ♀*4* on November 25, 1982 and used these occasions at 09:30 and 16:01 to attack her infant who remained apart from its mother. This observation is sufficient to reject the hypothesis of sexual frustration since ♀*4* was in fact ready to copulate with ♂*11* as she did on November 29, 1982, 09:46. From January 1983 onwards, ♂*11* had all females alone at his disposal and in spite of numerous copulations he killed ♀*11.4* in March 1983. Penile erections as exhibited by male *YA-1* preceding infanticides in Troop B in 1969 (Mohnot, 1971) were observed only once on July 9, 1982, 10:07, before ♂*43* attacked ♂*11.3*.

The assumption that "rage" might cause infanticide through a mechanism of redirected aggression deserves more serious consideration. On several occasions attacks, woundings, killings, or disappearances of infants in Troop KI were preceded by displacements or chasings amongst males (November 6, 1982, 17:00, 17:55; November 22, 1982, 16:15, 16:25; probably also on November 4, 1982) or aggressive intertroop encounters (July 9, 1982, 10:07). However, assuming that aggression resulting from past agonistic interactions cannot be "stored up" for longer periods, redirected aggression can be excluded as a proximate cause of all other assaults on infants, which e.g., arose during foraging (July 10, 1982, 16:01), return to sleeping site (July 12, 1982, 18:04) or following relaxed situations like extended grooming sessions (November 22, 1982, 16:15; November 25, 1982, 09:30). Moreover, the hypothesis fails to explain why infant-carrying females or infants are singled out and why a male's rage is not released on troop members at random.

Dominance Assertion Hypothesis

A new male is assumed to assert dominance over all troop members and solidify his position by attacking recalcitrant females and killing infants, since females witnessing "over-demonstratively" executed infanticide no longer dare to "challenge" the male (Parthasarathy & Rahaman, 1974).

However, females of Troop KI who witnessed male attacks on infants did not cease to counter attack males. Even single and not yet fully adult females fought with highly aggressive males in order to defend infants (e.g., ♀*6.3* on November 6, 1982, 17:00, 17:55, November 25, 1982, 16:47; ♀*2* on November 25, 1982, 17:05, 18:05). Only once did a male bite—but not hurt—a defending female (November 22, 1982, 16:20). In nearly all other cases counter-attacked males withdrew without resistance and without any attempt to "punish" the females engaging with them. Besides, if a male attempts to solidify the alpha position the primary objects of aggression should be the females themselves and not their infants (see Schubert, 1982). Between established male residents and members of Troop KI 70 dyadic displacement interactions were counted during 711 hr of observation from November 1981 to September 1982. The noninfanticidal resident ♂*20* was as successful in displacing troop members (1 episode/18.4 hrs) than was his successor ♂*43* after committing infanticides (1 episode/16.7 hrs); ♂*20* was even less frequently displaced by females (1 episode/29.8 hrs) than was ♂*43* (1 episode/16.7 hrs). Hence, the hypothesis draws no support.

Social Bonding Hypothesis

Since the death of an unweaned infant speeds the mother's return to estrus, infanticide is considered—not primarily from a reproductive standpoint—to provide an opportunity for the new resident male to consort with females and establish the necessary bonds to solidify his leadership (Sugiyama, 1965b, 1966; likewise suggested for infanticide among *Papio hamadryas* in captivity by Rijksen, 1981; Kaumanns, cited in Angst & Thommen, 1977).

There can be no doubt that female langurs "without infants may be relatively easily to interact with...but females with dependent infants may go to great lengths to avoid close contact with new, alien males" (Boggess, 1979). However, infanticide in Troop KI did not necessarily accelerate the process of social bonding between a new resident male and his females: (1) Two mothers (♀*1* and ♀*4*) had already resumed—perhaps anovulatory—estrus before her infants (♂*1.4* and ♀*4.5*) were attacked. It appears to be highly unreasonable to continue to stalk and attack the infant of mothers who already repeatedly and even successfully had invited the male to mate (see footnote 2 in Table 4 for ♂*43*/♀*1*; November 25, 09:30, 16:01, November 29, 1982 for ♂*11*/♀*4*). (2) New male residents may attain social integration without either committing infanticide or aggressing against females (see LELAND et al., 1984). The noninfanticidal new resident ♂*20* obviously abbreviated the grooming boycott of lactating females through "harmless" behaviour: He was groomed by ♀*4* though he had not sired her infant. As a father, ♂*20* was frequently groomed by mothers ♀*12* and ♀*6* (Fig. 4d).

The hypothesis assumes that new males kill infants *because* lactating females avoid them. However, this argument confuses cause and effect as implicated by the findings in Troop KI: Lactating females avoid new males *because* they are likely to kill their infants. Though infanticide might accelerate the process of bonding this should not be considered as the primary reason for infant killings.

REPRODUCTIVE ADVANTAGE HYPOTHESIS

Since the death of an unweaned infant results in the termination of it's mothers amenorrhea, a new resident male reduces his waiting time to insemination of the female by committing infanticide and will gain a reproductive advantage compared to a noninfanticidal counterpart (HRDY, 1974, 1977).

HRDY's hypothesis provides several testable predictions: (1) *An infanticidal male should not have sired any infant attacked or killed by himself.* Calculations on the issue of paternity (Table 1) are in general accordance with this prediction. However, one male (♂*11*) might have killed an infant sired by himself (case 28). The prediction fits well with the fact that killings have not yet been reported from multi-male sites with a more or less open breeding system and a consequently great uncertainty concerning the paternity of a given newborn. (2) *An infanticidal male should sire the subsequent offspring of the victim's mother.* As far as data are available up to now this prediction is almost certainly fulfilled in cases 22, 23, and 24 concerning Troop KI as well as in cases 30 and 31 concerning Troop B. Two females of Troop B (cases 29 and 33) died, and one old female of Troop KI (case 26) ceased cycling. In case 20 the infanticidal male (♂*43*) was ousted before renewed insemination of the victim's mother had taken place (for Troop KI see Table 4, for Troop B see Table 2 in SOMMER & MOHNOT, 1985). (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 preceding infant is 15.3 months (range 11.2–20.2 months; $N = 19$; WINKLER et al., 1984). All but one of the IBIs subsequent to infanticide fall within the normal range of variation: case 20, 12.3 months; case 21, 16.4 months; case 22, 9.2 months; case 25, 14.8 months; case 30, 12.4 months; case 31, 13.9 months (see Tables 2 & 4 in SOMMER & MOHNOT, 1985). The mean value from these data is 13.2 months, hence 2.1 months shorter than the average IBI without premature loss of the preceding infant. There is a positive correlation between the age of the previous infant at the time of loss and the IBI to the subsequent infant. 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. According to this, only two infants (cases 24 and 29) were too old when they disappeared to serve the male's purpose of shortening their mother's lactational amenorrhea. Thus, the infanticidal strategy provides the new resident male with at least a respectable probability of gaining a reproductive advantage by shortening the amenorrhea. As a rule, the younger the victim, the more a male has to gain from killing infants.

Hence, our data are in general though not total agreement with predictions derived from the reproductive advantage hypothesis.

According to mathematical simulations using reproductive parameters of the Jodhpur population (Hausfater et al., 1982; Hausfater, 1984) only one-quarter of all replacements are expected to be infanticidal (which fits quite well with our long-term data!). However, these calculations only work under the assumption that infants born *after* takeovers are not killed. This seems to be true in general (see, e.g., case 23 in Table 1), but there are at least two exceptions: ♂ *11* killed ♀ *11.4* born two months after his takeover of Troop KI (case 27) and ♀ *1.5*, born after three months, was attacked and disappeared several weeks later (case 28). Though these findings remain exceptional up to now, they meet well with two additional predictions of the reproductive advantage hypothesis: (4) *In addition to killing infants present during male replacements, it should be even more advantageous for a new male resident to kill those infants born after a takeover until one gestation length has passed because of the otherwise extremely prolonged waiting time until first insemination of the mother.* (5) *New resident males will shorten their waiting time most effectfully if they are able to induce abortions in females pregnant by their predecessors.*

Induced Abortions in Langurs?

Abortions as a result of confrontation with alien males are known to occur, e.g., in rodents (Bruce, 1960; Labov, 1984; vom Saal, 1984), wild horses (Berger, 1983), lions (Packer & Pusey, 1984), and baboons (Pereira, 1983). Stress-induced abortions are known to occur in langur females trapped for captivity (Ramaswami, 1975). Amongst free ranging langurs abortions might theoretically be part of the reproductive strategies of both sexes: In connection with adult male replacements *females* might prefer to abort than to invest in a fetus likely to be killed by new resident males. New *males* might harass and attack females (or their infants) to induce abortions in pregnant troop members. We now have evidences that such strategies in fact exist (pers. obs. for cases a and b; Mohnot et al., 1986, pers. comm. for cases c, d, and e): (1) ♀ *7* of Troop KI was estrous from September 12–16, 1982 when resident ♂ *43* was ousted and the four-months-long male-male competition began. On the evening of September 16, 1982, ♀ *7* copulated six times and became pregnant by invader ♂ *44* (see Fig. 5), who disappeared two days later. On October 21, 1982, 15:20 (during the interimresidency of ♂ *20*) a 35-day-old embryo protruded out of the genital region of ♀ *7* and was finally lost around 16:15. ♀ *7* resumed estrus 17 days later on November 7, 1982. (2) A second case of *presumed* abortion concerns ♀ *4*, an individual whose menstrual bleeding was always clearly visible. ♀ *4* gave birth to ♀ *4.5* on April 11, 1982 and resumed estrus on April 21–22, 1982. ♀ *4* probably became pregnant again by ♂ *43* on August 21, 1982, 132 days after birth (the interval between birth of 4.3 and conception of 4.4 was likewise only 140 days), since no distinct estruses or menstruations could be observed during the following 95 days (see Fig. 5). The bleeding ultimately observed on December 7, 1982 hence is interpreted as result of a nonobserved abortion of an approximately 108 day old fetus. (3) ♀ *2* aborted an about 4.5-month-old male two days after ♂*38* took over Troop B on January 22, 1983. The female resumed estrus after 34 days and gave birth to a subsequent infant almost certainly sired by ♂*38* 365 days post abortion. (4) ♀*7* of Troop KI again aborted an 175 days old fetus seven days after a renewed takeover in 1985; she resumed estrus 10 days later. (5) ♀*7* of Troop KII aborted an about 50 days old fetus nine days after an adult male replacement. The female resumed estrus 8 days later and was immediately inseminated by the new male, since her subsequent infant was born 216 days after abortion.

In case (1) ♀*7* aborted during the interimresidency of the noninfanticidal ♂*20*. (If she in fact aborted "in expectation" of possible future infanticide, she did well, since the birth would have taken place at the beginning of April 1983 when ♂*11* still attacked and killed infants born after his takeover!) Case (2) was preceded by repeated male attacks on ♀*4*'s semiindependent infant ♀*4.5* (see above). Actual male attacks on the pregnant females themselves were only observed in case (3). However, in cases (3), (4), and (5), the new residents were "highly punitive and aggressive towards females and their siblings" (MOHNOT et al., 1986) and turned out to be infanticidal (AGORAMOORTHY, 1986; in prep.).

The probability of stress-induced abortion might hence be the cause for repeated and even unsuccessful male attacks on females (as, e.g., described by HRDY, 1977) or on elder infant whose mothers are likely to be pregnant again.

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