

Male-Male Competition and Infanticide Among the Langurs (*Presbytis Entellus*) of Abu, Rajasthan

SARAH BLAFFER HRDY

Peabody Museum Harvard University Cambridge, Mass.

Abstract. Leadership changes accompanied by infanticide are described for two langur troops at Abu, Rajasthan. These events are compared with similar reports from Dharwar and Jodhpur. In each of seven cases, infanticide occurred when males entered the troop from outside it. Females whose infants were killed subsequently exhibited estrous behavior and copulated with the new leader. In three troops at Dharwar and Abu, seventy percent of females who lost infants gave birth within eight months. In these cases, infanticide appears on average to increase the reproductive success of the incoming male. Confronted with a male reproductive strategy disadvantageous for them, females respond to usurping males with various counter-strategies. From a comparison with other mammals, infant-killing by males may be advantageous (1) when there is intense competition for females; and (2) when frequent take-overs potentially curtail the tenure of an incoming leader.

Key Words
Reproductive strategies
Presbytis entellus
Infanticide
Sexual selection
Population density

I. Introduction

Isolated instances of adult males killing infants have been reported for a number of primate species under various conditions, including several caged prosimians [MITCHELL and BRANDT 1972], free-ranging rhesus macaques [CARPENTER 1942], caged crab-eating macaques [THOMPSON 1967], free-ranging Barbary macaques [BURTON 1972], wild chacma baboons [SAAYMAN 1971], caged Hamadryas baboons [ZUCKERMAN 1932], and wild chimpanzees [BYGOTT 1972]. Both the chacma and the chimpanzee incidents involved cannibalism. In addition, there is good evidence that adult males kill infants among wild purple-faced leaf monkeys [RUDRAN 1973 b], and adult male infanticide is suspected among wild howler monkeys [COLLIAS and SOUTHWICK 1952] and among caged squirrel monkeys [BOWDEN *et al.* 1967]. Only among

Hanuman langurs however, has infanticide been reported as frequently occurring under conditions which must now be considered normal for this species because they are both widespread and of long duration [HUGHES 1884].

To date, infanticide has been reported for langurs (*Presbytis entellus*) in the forest areas near Dharwar, Mysore State, South India [SUGIYAMA 1967; YOSHIBA 1968]; the desert regions surrounding Jodhpur, Rajasthan in North-western India [MOHNOT 1971] and at the hill-station of Mt. Abu, Rajasthan. Circumstantial evidence suggests that infanticide also occurs among grey langurs (*P. entellus thersites*) at Polonnaruwa, Sri Lanka [pers. comm. from S. RIPLEY].

The type case of langur infanticide was reported by SUGIYAMA [1965 b] at Dharwar. A band of seven non-troop males invaded the XXXth troop. The single resident adult male was severely wounded while defending his troop and was eventually driven out. Subsequently, one male from among the invaders usurped troop leadership and drove out his former accomplices. A week after the take-over all five infants in the troop, and two months later, a year old juvenile, were bitten to death by this new leader. Other instances of infanticide at Dharwar, Jodhpur and Abu followed a similar pattern.

A number of explanations have been offered as to why usurping males kill infants. These include: (1) Infanticide occurs as the displacement of aggression built up by the 'simultaneous sexual excitement and enragement' of the new leader [MOHNOT 1971: 196]; (2) The male attacks the infant in order to strengthen his 'social bonds' with the females of his new troop [SUGIYAMA 1965b, cited in SPENCER-BOOTH 1970: 126]; (3) Infanticide is a product of high population densities [SUGIYAMA 1967, cited in CROOK 1970 and BYGOTT 1972; RUDRAN 1973 b]; (4) The male attacks in order to avoid a two to three year delay in female sexual receptivity should the mother continue to nurse her infant [SUGIYAMA 1967: 233].

Several of these explanations, but especially the fourth, can be subsumed under the more general sexual selection hypothesis¹ which will be detailed in section IV-B of this paper. According to this hypothesis, infant-killing is part of a reproductive strategy whereby the usurping male increases his reproductive success at the expense of the former leader (presumably the father of the infant killed), the mother and her infant. As such, infanticide would be an extension of male-male competition, a phenomenon which occurs among a wide variety of birds and mammals [TRIVERS 1972].

¹ As used in this paper, 'sexual selection' refers to CHARLES DARWIN'S 1859 definition: 'a struggle between individuals of one sex, generally males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring...'

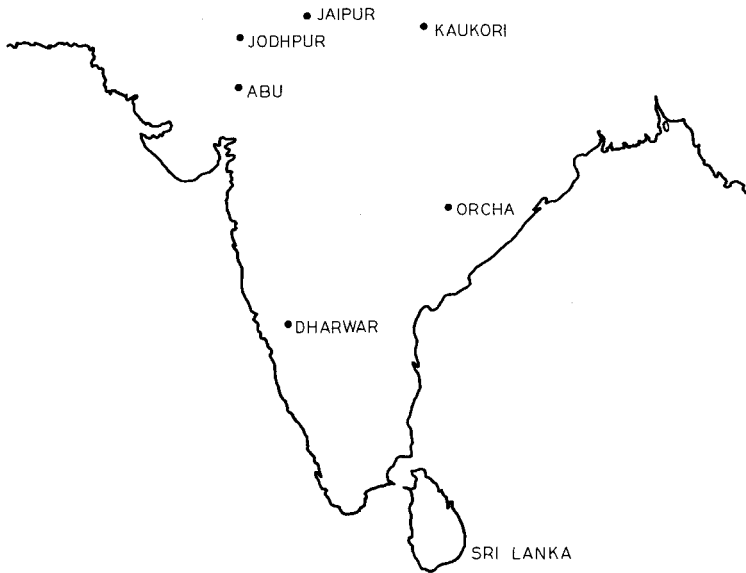


Fig. 1. Map of study sites.

In sections II and III, new information on competition between males, political change, and infanticide among langurs at Abu is presented. A synopsis of these complex events is provided in the summary. In section IV-A, events at Abu are compared with similar occurrences at Dharwar and Jodhpur (as summarized in tables VI and VII); the apparent correlation between high population density and infanticide is also analyzed, and a case is made for the likelihood that infanticide is adaptive rather than pathological male behavior. In section IV-C the divergent interests between males and females and female adaptations to counter infanticide are discussed. Social conditions conducive to infanticide among these langurs, as well as among other groups, including Serengeti lions and the Yanamamö tribe, are outlined in the last section.

II. Langurs of Abu

A. Study site, observation conditions and methodology

The main study site was Abu, a hill-station beside a year-round lake at the top of Mt. Abu (3822 feet above sea level), one of the Aravalli chain in southwestern Rajasthan. Six troops labelled B-2, B-3, B-4, B-5, B-6, and B-9 in and around the town, and a seventh, B-1 at the Chippaberi bus-stop halfway between Abu and the base of the mountain, were

observed for 986 hours from June 29 to September 13, 1971; June 19 to September 12, 1972; February 11 to March 26, 1973, during both wet and dry season conditions.

The 'home ranges', that is, the areas habitually traversed by these troops in the course of their daily life, remained remarkably stable throughout the years of this study. On any given day, a specific troop could be found within the same approximately ninety acre plot outlined in figure 2. Troop members left their home ranges only under exceptional conditions, usually having to do with inter-or intra-troop conflict. Although these ranges appear small on the map (averaging 0.38 km²), actual distances travelled over the hilly terrain might be as much as 3.5 kms. in a single day, though shorter treks were more common.

Within each troop's home range, certain localities are used almost daily for feeding or sleeping whereas other locations are visited more sporadically, once a week or less. Sites of relatively intensive and usually but not necessarily exclusive occupation are designated here as 'core areas' [JOLLY 1972]. Troop B-3 for example spent some part of almost every day foraging in the Bazaar. With the exception of nomadic males, who were not members of any permanently based troop and of two B-6 females who were temporarily travelling as satellite members of troop B-3, no other langurs besides B-3 were ever seen to enter the Bazaar.

Temperature and rainfall at Abu can be divided into four seasons: the cold dry months from December to February, when there is little precipitation other than haze; a moderately hot and very dry summer from March to about mid-June; a temperate, wet monsoon arriving some time in June and lasting through August, during which Abu receives more than 95 percent of its annual rainfall; and a temperate post-monsoon season from September to November.

Range usage does vary slightly from season to season, and the boundaries in figure 2 represent cumulative occupation recorded during both wet and dry months. Since we were not present during all possible conditions, ranges could be slightly larger than those shown here.

*During the driest winter months shrubs (especially *Lantana camara* and *Carissa spinarum*) and trees (*Erythrina blakei* and *Bauhinia racemosa*) which provide staple foods for the langurs at other seasons dry up or lose their leaves. At this time of year, the langurs depend on plants that grow year-round (such as anogeuissus trees and the cactus-like *Euphorbia*) and on remnant seeds and pits (of *Eugenia jambolana* and *Mangifera indica*) from the previous season as well as on mature, dry leaves. At Abu however, this season of scarcity is much shorter than the dry season itself; months before the monsoon actually arrives (as early as late February) flush, flowers (on *Erythrina*, *Bauhinia* and *Mangifera* trees) and immature fruit (on *Mangifera* trees), as well as various species of *Ficus* fruit, are available. Though infants are born all through the year, birth peaks in four troops coincided with this dry season, presumably so that the infants can be weaned during the wet season when food is plentiful [see also RUDRAN 1973a]. Winter birth peaks have also been reported by PRAKASH [1962] at nearby Jaipur.*

During the dry season, observation conditions are better than during the wet season when rain, heavy mist, and thick vegetation occasionally make it difficult to follow the monkeys. Because of Hindu beliefs, langurs are protected. Though they are brazen thieves and cause some damage to local vegetable and ornamental gardens, langurs are chased away almost never killed. In addition, all seven troops are fed by pilgrims and local people. As a result, langurs near the town and at the bus-stop are habituated to human proximity. These langurs spend between 30 and 70 percent of the day on the ground, depending on

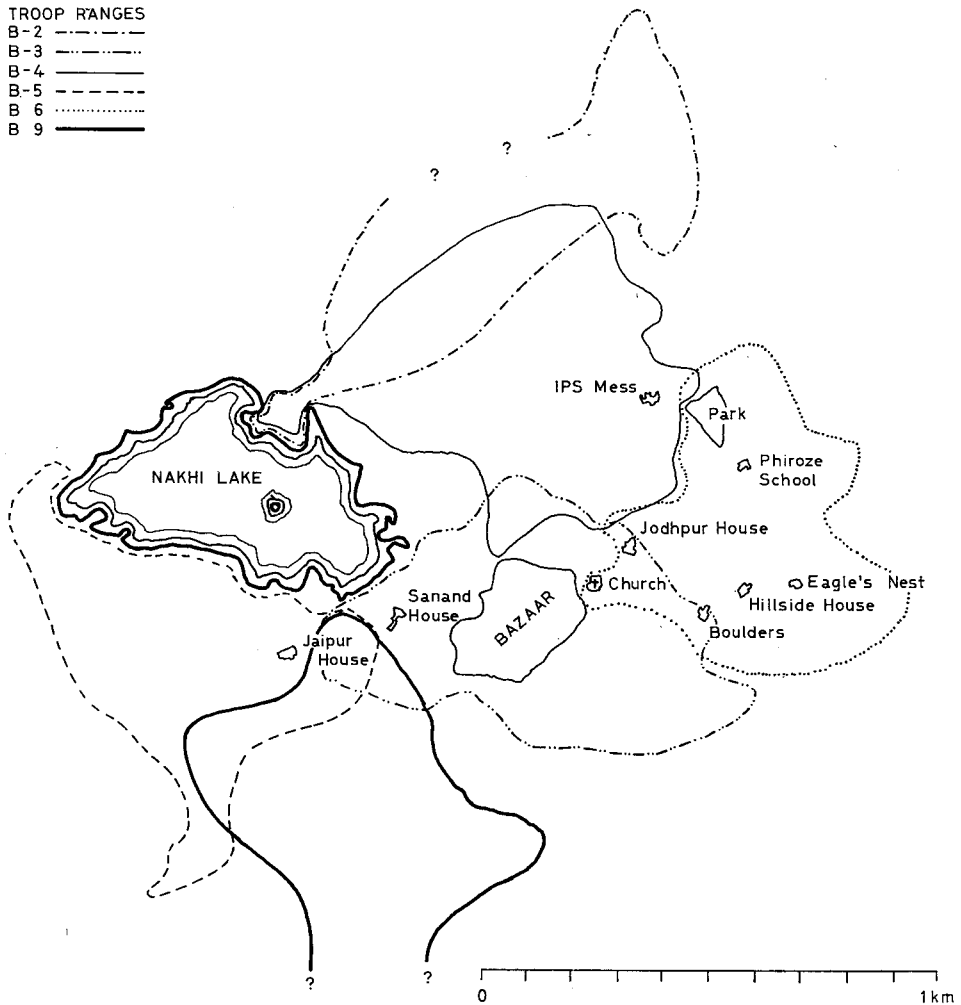


Fig. 2. Home ranges.

feeding conditions and harassment by dogs and men. When on the ground, langurs can be observed from within three to twenty feet. Binoculars were used when the langurs were on rooftops or in trees or in order to keep track of more than one troop at a time. Except for roadside surveys between Abu and the base of the mountain, all observations were made on foot.

Despite relatively good observation conditions, the continuity of my records for any one troop is interrupted by (1) six to twelve months gaps during my absences from Abu; and (2) gaps of several days when I sacrificed information from one troop in order to follow

another. These drawbacks were in part offset by the fact that the langurs of Abu live in or near a town of 8,000 people. Unusual occurrences (such as leadership change or infant-killing) were sometimes witnessed by local people. Where reports from reliable informants coincided with what I knew about troop locations and changes in troop compositions, they were accepted by me as facts and are cited here as personal communications. The main advantage of this policy of intermittent observations was that strategies and their long-term outcomes could be detected.

B. Identification of individuals

In the course of the study, more than 200 langurs were encountered at close range, but only about seventy of these were individually known. These recognizable individuals could be divided into two classes: *marker individuals* composed of twenty-five permanently distinctive animals (eleven males and fourteen females) who could be recognized regardless of context, and *acquaintances*, composed of some forty-five individuals who were identifiable within a given troop or geographic context.

Of the marker individuals, four adult males and two adult females could be recognized by the pattern of a ragged ear; two adult males, two adult females, one juvenile male and one subadult female had a broken or truncated tail; one adult female and one subadult female were missing forearms and two adult females had slightly deformed paws; four adult females and one juvenile male had cataracts or some chronic eye infection; four adult males had permanently disfigured faces, and one very old female had an unmistakable facial expression, even though she had no specific blemish.

In addition, a number of animals had temporary blemishes or else some uncommon feature which was useful in making day-to-day identifications. Among the thirty-five adult males that I most frequently encountered, for example, 80 percent had some injury or scar. Many of these injuries were probably inflicted in fights. Although only one serious wound was seen inflicted in a fight between males, three other males were seen with fresh wounds at times when intra-male conflict was going on. Injuries from agents other than langurs were never witnessed.

Though females had a lower incidence of injuries, and in other respects were harder to identify than males, more females than males were seen with skin and eye infections. During the dry season, mange was relatively common, and patches of hairlessness served temporarily in identifying individuals. Temporary identification was also facilitated by squirting the animals with colored stains.

Over time however, the bulk of known langurs could only be recognized relative to other individuals or to some geographic location which they

frequented. Relatively useful indices included: Age (based on tooth wear; skin desiccation; or in the case of infants, coloration as described in SUGIYAMA 1965a); rough assessments of parity (based on pendulousness of nipples); rank; preferred associates (especially in the case of infants, juveniles, and their presumed mothers); and subtle physical differences such as shape of the tail-tip, coloration, 'freckles', facial expression, and ear shape.

C. Troop dynamics

As reported for other locations, langurs at Abu live either in stable bisexual troops, as solitary or paired males, or in nomadic all-male bands, containing between three and sixty or more adult, subadult and juvenile males. Occasionally, adult females and their progeny travelled for short periods of time without adult males. Whereas most troops studied by JAY [1965] in North and Central India, by RIPLEY [1967] at Polonnaruwa, Sri Lanka, and surveyed by SUGIYAMA [1964] near Raipur in Central India, contained more than one adult male, at Dharwar, Jodhpur, and Abu, a one-male pattern prevailed. Only one troop was encountered at Abu that had more than one permanently resident adult male. This was the B-3 troop, which in 1971 had an older adult male accompanied by two younger adult males who were subordinate to him in terms of access to both food and estrous females.

It has been suggested by SUGIYAMA [1967] that troops with more than one resident male (excluding temporary invasions by male bands) may result from stable leadership in which a single male is able to control a troop long enough (that is five to seven years) for his own sons, who are tolerated by him, to mature [i.e., the age-graded-male troop described by EISENBERG *et al.* 1972].

In such cases, the number of adult males reflects population conditions and historical factors rather than innate differences between langurs in different areas. For example, where langur population densities are high (e.g., at Dharwar and Abu – discussed in section IV-A) there are large numbers of non-troop males and numerous contacts between these extra-troop males and bisexual troops. To the extent that the numbers of non-troop males and the frequency of contact is correlated with the likelihood that such males will take over a troop (as described in the Introduction) environmental factors such as population density may be related to the prevalence of one-male harems.

As observed at Abu, the political organization and composition of a langur troop is constantly changing. The following hypothetical scenario of the life-cycle of a langur troop is illustrated by troop compositions recorded at Abu between 1971 and 1973. In the INITIAL STAGE, an extra-troop male usurps

control over a bisexual troop. He evicts all other adult and subadult males and kills unweaned infants. For example, around April of 1972 a male named 'Shifty' took over the B-3 troop, ousting three adult males and one juvenile male. Subsequently, a second juvenile male also left the troop. Five infants disappeared at the time of this change. These events are summarized in table I. By 1973, four new infants had been born, one subadult female had become pregnant, and three juvenile females had begun to cycle. With such increases in the ranks of child-bearing females, the troop enters a GROWTH STAGE. The remarkably fertile B-9 troop illustrates this stage. In June of 1971, the troop consisted of a single adult male and eight females, every one of which was associated with an infant between eight months and one year old. In March of 1973, four females carried newborn infants while the remaining three were in the last weeks of pregnancy; the eighth female had disappeared. Between 1971 and 1973, another troop, B-4, grew from twenty-four individuals to over forty.

This growth process may continue through a MATURE STAGE, when after five years or more, all age-grades are represented. Troop B-3 in 1971 (table I), and another troop, B-5 in 1972 (see table II) may have been on the verge of

Table I: Changes in the Composition of Troop B-3 between 1971 and 1973

	Adult male	Adult female	Infant	Juvenile m. f.	Subadult m. f.	Total
August 1971	3	8	5	2 2	0 2	22
June 1972 (Shifty)	1	8	0	1 1	0 3	14
February 1973 (Shifty)	1	9	4	0 0	0 3	17

Table II: Composition of Troop B-5 in 1972 and 1973

	Adult male	Adult female	Infant	Juvenile m. f.	Subadult m. f.	Total
June-September 1972 (Splittear)	1	8	5	3 3	2 1	23
February-March 1973 (Splittear)	1	9	3	6 3	1 0	23

such a pattern, though in both troops the age-graded pattern was interrupted. When I re-encountered B-5 in 1973, the oldest subadult male, aged four to five years old, and two younger juvenile-to-subadult males, were no longer with the troop.

Provided that they are not driven out, males growing up in a troop would ease into possession of it, as may have occurred in JAY's study group at Kaukori (1965:242). In areas with large numbers of non-troop males, a TAKE-OVER would be more likely, and the cycle would resume again.

Only in the case of troops B-3 and B-6 was it possible to reconstruct transitional events with any degree of confidence. This reconstruction, compiled from (1) direct observation; (2) the reports of local witnesses; and (3) observed changes in troop compositions, is presented below.

III. Reconstruction of Political Changes in Troops B-3 and B-6

A. Shifty takes over B-6 (1971)

In July 1971, troop B-6 consisted of a single adult male (Mug), five adult females, their six infants (including one pair of twins), an older three-legged female named Pawless, a juvenile male (Sancho) who may have been Pawless' son, and a very old female named Sol (see table III). When re-contacted on August 5, a new leader, a permanently identifiable male with a portion of his left ear missing, had taken over control of the troop. All six infants and one adult female were missing. Between August 4 and August 16, three of the mothers (Bilgay, Itch, Oedipa) came into estrus and copulated with the new male, Shifty Leftless (see fig. 3). During this period, neither Pawless nor Sol (who did not have infants at this time) came into estrus. Both females, but especially Pawless, harassed the new male. Pawless would charge repeatedly at Shifty; occasionally other females would join her, and three or more females might be seen chasing Shifty.

Shortly after I first noticed the presence of the new male, I learned from local inhabitants² that an adult male langur had killed two infants, one near the Phiroze School and one near Rajendra Road, which runs past Boulders. These sites were both located in areas used intensively, and in the case of the Phiroze, exclusively, by B-6 (see fig. 2). This information was in accord with observed changes in troop composition and with the behavior of the

² I am grateful to Mrs. PHIROZE MERWANJI and to an unidentified police cadet for these observations.

Table III. B-6 Troop Compositions between 1971 and 1973

	Adult male	Adult female	Infant	Juvenile	Subadult
July 1971:	1. Mug	1. Bilgay 2. Itch 3. Oedipa 4. Harrietta 5. No-name 6. Pawless 7. Sol	1. 2. 3. 4. 5. 6.		1. Sancho
August 1971: Changes: Mug replaced by Shifty; six infants killed; one adult female gone; Sancho peripheralized.	1. Shifty	1. Bilgay ¹ 2. Itch 3. Oedipa 4. Harrietta 5. Pawless 6. Sol			1. Sancho (occasionally present)
June 1972: Changes: Four infants born; two oldest (Virginia and Harry) possibly sired by Mug; the two youngest probably sired by Shifty.	1. Shifty alternates with Mug	1. Bilgay ¹ 2. Itch 3. Oedipa 4. Harrietta 5. Pawless 6. Sol	1. Mira (ca. 3 months) 2. Scratch (ca. 3-4 months) 3. Virginia (ca. 7-8 months) 4. Harry (6-7 months)		
February 1973: Changes: Five males joined Mug; three infants disappeared, and one born.	1. Mug ¹ 2. Righty 3. Kali 4. No-No Man 5. Bluebeard 6. Pequeno alternate with Shifty	1. Bilgay ¹ (pregnant) 2. Itch 3. Oedipa 4. Harrietta 5. Pawless 6. Sol			1. Harry 1. Pawla (ca. 3-4 months)

¹ Ranked according to access to preferred foods, positions, etc.

females, as well as consistent with similar accounts from Dharwar and Jodhpur [SUGIYAMA 1967; MOHNOT 1971]. The concurrence of these diverse clues led me to assume that the new male had killed at least two, and very probably all six infants.

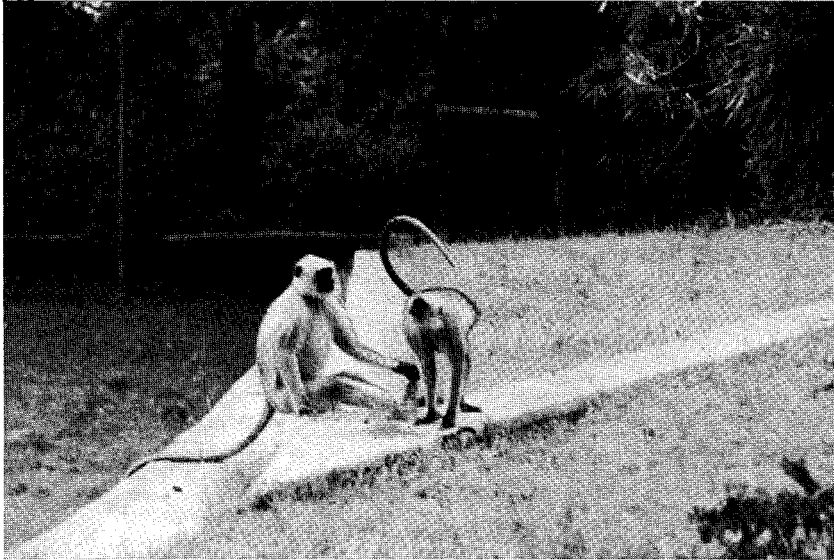


Fig. 3. Harrietta solicits Shifty Leftless in August 1971, shortly after she lost her infant.

In the first weeks after I re-contacted the troop, Pawless stayed at the periphery of the troop with Sancho, only entering the center in order to initiate harassment of Shifty. By August 21, however, Pawless herself came into estrus and left Sancho on the outskirts of the troop while she joined Shifty in a consort relationship. Their copulations were subject to violent harassment from two of the former mothers, especially Harrietta. On one occasion when Harrietta interrupted a copulation Shifty dismounted to chase her only to be repulsed and then chased by every female in the troop except Pawless. On August 25 when Harrietta was in estrus, her copulations were similarly harassed by other females.

As far as I know, Shifty was the only male that copulated with these females after the take-over. Nevertheless, B-6 was not under constant observation, and other males were sometimes in the vicinity of the troop. On August 20, an estrous Harrietta twice approached the leader of a neighboring troop (B-4) only to be chased and headed off each time by Shifty. On August 27, Mug attempted to re-enter his former troop, and in fact chased Shifty some distance before Shifty turned on him and chased Mug.

Eventually, however, Mug was able to re-visit his former troop, after Shifty left B-6 for the larger B-3 troop. This switch is discussed below.

B. Shifty takes over troop B-3 (1972)

Around March-April of 1972, during my absence from Abu, the presence of a new male in troop B-3 was detected and the killing of two B-3 infants by a male was observed by an amateur ornithologist whose rooftop was used by B-3 as an overnight roosting site (Sanand House).³ When I re-contacted B-3 on June 25, 1972, I was able to definitely identify the new male as Shifty (see fig. 4). Three infants (born late in July and in August of 1971) were missing, as were two older juvenile males, and three adult males and one adult female (see table I, and the description of this troop in the section on troop dynamics). On July 1, I encountered the second-ranking of the former B-3 males sitting in a tree near Sanand House nursing a deep unhealed wound in his left deltoid.

Shortly after my return, between July 5 and July 16, six B-3 females came into estrus and copulated with Shifty. Seven months later, in February of 1973, two of these females were accompanied by 3-4 month old infants, two carried newborns, and one was in the last weeks of pregnancy. Using six to seven months as the probable gestation period (discussed in table VII: footnote 1) and counting backwards, it seems that two of the B-3 females conceived in the period from April to May and were already pregnant during the copulations that I witnessed. In the case of two other females, what I saw may have been the second or third cycling since the death of their infants, and they may have conceived on this occasion. The fifth female probably conceived a month or two later.

Based on: (1) Observed demographic changes; (2) NIRMAL KUMAR DHADLAL's report; and (3) the location of the events that he described, I concluded that around April, Shifty had left B-6 for B-3, that he had evicted the three resident males, and that Shifty was responsible for the deaths of the missing infants.

C. Contest for control of B-6 (1972-1973)

Even after Shifty took over B-3, he attempted to retain exclusive access to B-6; throughout the monsoon season of 1972, Shifty and Mug vied for troop control. Whenever B-6 approached their common boundary with B-3, if Shifty and his new B-3 troop were in the vicinity, Shifty would leave B-3 and temporarily join B-6. Occasionally, Shifty would leave B-3 and travel some distance (as much as one km.) to check on B-6. On two such occasions, Shifty whooped several times prior to his actual arrival. This apparently

³ I am grateful to NIRMAL KUMAR DHADLAL for these and other observations.



Fig. 4. Shifty with the B-3 troop in 1972.

investigative call was never answered by Mug; rather, it served as a warning to Mug who promptly left the vicinity of B-6. On five occasions, Mug faded away before Shifty actually showed himself. On three other occasions however, Shifty arrived unannounced and Mug decamped with Shifty in pursuit.

On these occasions, Shifty spent an average of about two hours with B-6. The short duration of his stays may have been due to the dearth of estrous females in that troop. On August 5, 1972, when Pawless was in estrous, Mug was chased out twice (once at 09:30 and again at 17:30) and on that day, Shifty spent a total of eight hours with B-6, mostly in consort with Pawless.

When B-3 was in close proximity to B-6, Shifty might also stay longer, but at such times it was often impossible to say which troop he was actually with. As far as I know, Shifty always returned to B-3 before nightfall. On five occasions in 1972 and 1973 however, after such encounters B-6 spent the night in trees or on a rooftop adjacent to B-3's sleeping site.

As many as three days might pass before Mug returned to B-6. On one occasion however, when B-6 had moved out of the vicinity of the B-3 troop, Mug returned less than an hour after Shifty had left. Another time, Mug apparently misjudged the advisability of return. He loped down a road towards B-6 only to whirl and run away again at full speed when he was still

some thirty yards from the troop: Shifty and B-3 were on a hilltop only a short distance away.

The struggle for control of B-6 was still ongoing when I returned in the dry season months of February and March 1973. At that time, Mug was accompanied by five adult males that I had never seen before. Whether they were with the B-6 females or apart from them, Mug remained individually dominant to each of the other males in terms of access to position and to naturally occurring food items (such as germinated mango pits) as well as to artificially provisioned food items (see table IV). It is not known however if Mug's dominant position meant that he also controlled access to ovulating females. During 98 hours of observation when the males were with the females, Mug was never seen mounting a female. On only one occasion did he even display special interest in a soliciting female. On March 20, when Sol was in estrus, Mug was seen in consort with her in a dense thicket out of view from other males and out of my sight as well. Given the circumstances, undetected copulations could have occurred.

Even though Harrietta, Oedipa and Itch all displayed estrous behavior (they presented to males and shook their heads) during this period, as far as I could determine, Sol was the only B-6 female who was actually cycling. This assessment is based on: (1) detection of menstrual blood⁴; (2) intensity of estrous solicitations; and (3) increased aggressiveness which typically accompanies estrous behavior. Sol's menstruation was visible on February 12. On February 19, and again from March 17 to 20th she vigorously solicited males. On these occasions she was mounted by Bluebeard (once); Kali (twice); and Righty (four times); and as mentioned above, she was in consort with Mug on the afternoon of March 20th. Since B-6 was only observed briefly (between 30 minutes and two hours) on March 18, 19, 21 and 22 the above list undoubtedly is incomplete. Throughout the three years of this study, Sol's cycles had been fairly regular, though she had never been seen with an infant or noticeably pregnant. Judging from her worn teeth and her generally debilitated physical condition (i.e., boniness), Sol was one of two very old females at Abu; neither of these had infants. It is possible that she was either barren or that the period between births was an extended one.

Though Mug did not respond to the solicitations of any female except Sol, all the other males, except the fourth-ranking male No-No Man, did respond to mild estrous solicitations from Itch and Oedipa. During February and

⁴ Visible menstrual blood is uncommon among langurs [DAVID and RAMASWAMI 1969] but in some cases, flows ranging from spotty to copious are detectable.

Table IV. Displacements among B-6 males over positions and preferred food items

	Mug	Righty	Kali	No-No	Blue-beard	Pequeno	Total
Mug displaces	–	12	5	3	4	4	28
Righty	0	–	13	3	8	5	29
Kali	0	0	–	0	0	0	0
No-No Man	0	1	0	–	0	1	2
Bluebeard	0	0	0	0	–	1	1
Pequeno	0	0	0	0	0	–	0
							60

March, these two females were mounted on more than forty-three occasions by Righty (29 times); Kali (6 times); Bluebeard (6 times); and Pequeno (2 times). Mug never overtly interfered with these copulations, but harassment by other males was intense. Righty mounted Sol, Oedipa and Itch on forty-seven occasions, and was harassed during thirty-eight of these. The low-ranking male Bluebeard was responsible for 71 percent of this attempted interference. Though No-No Man never participated in copulations, he joined in the harassment of other males on eleven occasions.

Given that Mug was dominant to these newcomers and that I never saw any evidence which suggested that they formed alliances among themselves, why did Mug allow the five males to remain? One possibility is that Mug tolerated the presence of these males in order to dissuade Shifty from his periodic visits. This view was supported indirectly by two forays into B-3's range which were made by the six males. On February 22, all six males, with Mug in the lead, approached within two hundred feet of where Shifty and his B-3 troop sat, on the other side of a low gully. This confrontation was preceded by whoops on both sides, and throughout it, Mug and his band ground their teeth and grunted. On February 28, the six males made a noisy early morning foray into B-3's range at a time when I knew (and I presume that the males did also) that Shifty and B-3 were at Sanand House, at the furthest corner of their range from the B-6 males' invasion.

If Mug was in fact tolerating alien males in order to keep Shifty out of B-6, the strategy was unsuccessful. Even though Mug in 1973 may have been more brazen in the face of his antagonist, whenever Shifty actually approached, the six males fled. During 334 hours that B-6 individuals were kept under observation in 1972 and 1973, the proportion of daytime that Mug was able

to spend in B-6 did not change despite the presence of five extra males in 1973.⁵ In 1972, Mug was with B-6 for 118 of 172 hours (66 percent), while in 1973, he spent 98 of 156 hours (63 percent) with the females. During this same period, Shifty was observed with the troop about 20 percent of the time, while the females (not including Pawless' 1973 wanderings which are discussed below) travelled on their own without any male present about 15 percent of the time. In interpreting these figures, it is important to note that they do not represent absolute proportions of time that the males were either present or absent from the troop due to a prevailing bias: if Mug *was* with the troop, I would observe them for a longer period of time than if he were not. In my estimation, the amount of time that Mug actually spent with the troop was around 10 percent lower, closer to 55 percent of the time, while the figures for females travelling without a male should be greater, around 25 percent of the time. In any event, Mug did not seem to improve his position by the addition of the new males since the bias presumably acted equally in 1972 and 1973.

Shifty's superiority was strikingly apparent when, on February 15, 1973, all six males were dozing in a fig tree across from Hillside House; Bilgay, Itch and Oedipa were feeding nearby. Suddenly, without a sound, all six males leapt from the tree and ran to the north. I looked over my shoulder to find Shifty standing on a wall, twenty yards from the base of the fig. More remarkable than the B-6 males' reaction to his presence, was Shifty's utter silence, totally uncharacteristic of a langur male approaching foreign males. After a moment's pause, Shifty took off to the north in pursuit of the six males; I did not see any of them again that day. On four other occasions, Shifty displaced the six males from B-6, at 10:00 and again at 15:55 on March 3; at 13:50 on March 6; and around 15:50 on March 13.

D. Assaults on B-6 infants in the absence of Shifty (1972 and 1973)

Throughout August and September of 1972, Mug stalked B-6 mothers with infants during periods when he was with the troop. On nine occasions, a mother-infant pair was actually contacted by him, and in three such assaults, the infant was injured. In six of these witnessed attacks, Itch and her infant Scratch were the target. In the other three, no definite identification was made, though in one case the target was probably Bilgay and her dark infant, Mira.

⁵ However, in 1973, Mug was no longer spending the night with the B-6 troop. Instead, he accompanied the five new males to one of two sleeping sites northeast of B-6 troop's home range.



Fig. 5. Sol and Pawless charge Mug who has just attacked and severely wounded Itch's infant (September 9, 1972).

Nine assaults observed in 1972 are summarized in table V. In every case, females other than the mother intervened. Sol and Pawless repeatedly played the most daring roles in defense of the infant (see fig. 5). These same two females also interposed themselves between the male and a mother-infant pair on numerous other occasions, when Mug attempted to approach them. The following description of Mug's stalking, his thwarted assaults, and the intervention by other females is rewritten from my field notes for August 12, 1972.

On August 12, 1972, the B-6 troop feeds near the Phiroze School. Throughout the early afternoon, the females have been deliberately avoiding Mug. If he climbed into the tree where they were, the females immediately moved to another tree. If Mug followed, the females returned to the tree where they had been before. Around 16:00, Mug grunts and looks off into the distance. He climbs to a nearby rooftop, apparently to obtain a better vantage. He strikes a sentinel pose there and stares off first in one direction and then in another.

Minutes later, Mug descends abruptly from the roof and charges Itch. He grabs at the infant clinging to her belly (normally, a 4-5 month old infant would be moving beside a mother as she fed). Itch whirls to face Mug, planting both her front paws as she lunges at him, grimacing and baring her teeth. Within seconds of Mug's attack, Sol, Pawless, and an unidentified mother who does not have her infant with her, join the counter-attack. These three females interpose themselves between Mug and Itch; they lunge at the male and chase him up a tree.

These events happened very fast. Though I did not see it happen, Mug must have

contacted the mother-infant pair, because when I saw Itch and Scratch moments later both their rumps were spattered with blood.

From the tree that he had retreated to, Mug stares down at the pursuing females and begins to bark ('agh, agh, agh') and to give convulsive threats (a relatively rare and particularly violent male vocalization composed of a sequence of spasmodic brays). Moments later, Mug descends and again charges Itch. Almost simultaneously with his charge, Sol intercedes. She lunges at the male, slapping at and contacting him with her forepaws. Mug returns to his tree and resumes barking.

During these events, Bilgay carrying Mira, and Harrietta carrying Harry move to a tall grevillea tree nearby. They are joined there by Oedipa and her infant, and by Sol. Momentarily, the females relax and begin to feed. At 16:18, Mug retreats from Sol into the tree which Itch and the other females have moved to. Mug barks and then moves towards the females grunting. They scatter again except for Sol who climbs up the tree where Mug is and for the third time, charges him. Pawless comes up behind Sol and both older females leave the tree together. The male barks continuously at approximately three second intervals for about ten minutes. At 16:30 Sol and the mothers disperse into three trees adjacent to the tree that Mug and Pawless are in.

At 16:40, Mug moves to the furthest of the three trees, where Itch is, and approaches her. She moves approximately fifteen feet away, towards the end of the limb she is on, while Bilgay moves to the bottom of the tree. As Itch moves to a branch below Mug, he first crouches and then leaps down onto her. Itch evades him and Mug gives up temporarily.

At 16:47, Mug throws back his head and whoops; both Itch and Bilgay leave the tree he is in. As the females pause for a moment on the ground, Itch's infant tries to leave his mother, but she restrains him. By 16:55, the two mothers have settled themselves in another tree. Mug approaches Bilgay, displacing her, and then moves slowly towards Itch and Scratch. He climbs to a branch just above them and begins to feed.

As Mug calms down, Itch allows Scratch to move four feet from her; he returns within one minute. Moments later, Mug moves towards Itch, who continues to eat the branchlet she is holding. Mug stands nearby, staring at Bilgay and at Harrietta, though occasionally he looks over his shoulder, very briefly, at Itch, whom I believe is the true focus of his attention. At 17:00, Mug leaps onto a branch directly above Itch's head which does not interrupt her vigorous feeding until seconds later when she moves to another tree.

Once again, Itch lets her infant wander three feet from her. As she does so, Mug's attention is riveted to Scratch. Mug moves slowly down from the tree that he is in. Itch gathers up her infant and climbs higher in their tree. At 17:05, Mug climbs into Itch's tree. Itch, and a second, unidentified, female who is there leave abruptly. As Mug continues to stalk the mothers, following Itch and Bilgay out onto a limb, Sol accosts Mug, grimacing and grunting as she does so. Mug threatens and lunges at her, and she turns away. Mug continues to stalk Itch. They exchange positions as she evades him. By this time, Mug as well as most of the females are grunting.

At 17:15, Mug abandons his quarry and turns to threaten Pawless and Sol. He moves towards them, then pauses and slaps the ground after them as they move away. At 17:19, Mug turns and races to the tree where Itch and Scratch are. As the mother moves out on a limb, Mug follows with his eyes. Itch's branch snaps, and she falls a short distance. Mug moves towards her at a walk. Itch runs away along a wall with the male following her. Pawless and Sol join Itch and another chase through the trees ensues. Earlier patterns are repeated until 17:30 when the monkeys are driven away by a gardener.

Table V. Summary of witnessed assaults by Mug upon B-6 infants in August and September of 1972 during the period in which Mug and Shifty were vying with one another for control of B-6

Date and time	Identity of infant	Identity of defending females	Male vocalizations	Location	Outcome
8/10 1440	Unknown	Unknown	teeth grinding grunts	Church	attack thwarted
8/12 1618	Scratch	Pawless, Sol, Itch and unknown female	continuous barks and convulsive threats	Phiroze	Scratch superficially wounded
		Male continues to stalk Scratch until 1740; Sol intervenes by contacting male on 3 occasions.			
8/13 0910–1100	Stalking of previous day resumed; Sol alone once, and Sol and Pawless together twice, intervene contacting and slapping at Mug. Phiroze				
9/1 0955	Scratch	Sol engages Mug	grunts	Eagle's nest	thwarted
9/1 1530	Unknown	Sol and Pawless engages Mug	grunts, barks and convulsive threats	Hillside	thwarted
9/1 1750	Scratch	Sol and Pawless engage, and chase Mug	continuous grunts	Boulders	Scratch superficially wounded
9/5 1645	Unknown	Sol and Pawless	soundless	Hillside	Mug grabs infant before thwarted
9/5 1718	Scratch (falls from tree)	Sol and Pawless engage, grapple with and then chase Mug	soundless	Hillside	Mug grabs infant before thwarted
9/9 1830	Scratch	Sol and Pawless ¹ contact, slap at, and chase Mug	continuous barks; convulsive threats; whoops; teeth grinding ²	Phiroze	Scratch severely wounded in thigh

¹ See figure 5.

² Moments after the assault, the neighboring B-4 troop's leader appeared and chased Mug. He may have been incited to do so by Mug's threatening vocalizations.

To summarize events on August 12: Mug repeatedly charged Itch and attempted to grab her infant. On each occasion other females, almost always including Sol and Pawless, two low-ranking females who had no infants of their own that year, intervened. Mug's stalking was single-minded and was sustained over a ninety-minute period. The action was interspersed with long pauses during which Mug may have been dissimulating his intent by staring in another direction while actually maneuvering closer to Itch. By 09:10 the next morning, Mug had already resumed stalking B-6 mothers, though on this occasion, no contact was made.

During August and September, all four mothers, but especially Bilgay, went to extreme lengths to avoid Mug. By contrast, the mothers' response to Shifty during this same period was quite different. On September 8, 1972, Shifty chased Mug away and then joined B-6. He approached Harrietta, who did not move away. She was not protective of her infant and allowed Harry to clamber about the rock where Shifty sat. On September 27, Bilgay allowed Mira to play within inches of Shifty, as did Oedipa with her daughter, Virginia. None of these mothers showed any sign of avoidance or fear.

According to my calculations, both Bilgay and Itch's infants were sired by Shifty shortly after his take-over in 1971 (discussed in section IV-B). Given that Mug was probably unrelated to either infant, it is interesting to speculate on his bias for attacking Scratch (i.e., in seven of nine observed assaults – see table IV). One possibility is that Mug's antagonism was influenced by Scratch's sex⁶, though more probably, Mug was responding to Itch's carelessness. All the B-6 mothers were restrictive of their infants in Mug's presence, but Bilgay was especially so. She rarely allowed her infant to wander, and she almost never allowed Mug to get close to her. The close contact may have been related to Mira's age (she was the youngest infant in the troop). In contrast to Bilgay, Itch may have been more casual about allowing Mug to approach her (see description of August 12). Maternal negligence was almost surely at issue in the second attack on Scratch that I witnessed on September 5, when Itch let Scratch fall out of a jacaranda tree. Mug was sitting alertly on a wall fifty feet away. When the infant fell, he raced to it, reaching it just split seconds before Sol and Pawless, who had been sitting on the wall on either side of him. The mother was the last of these four individuals to reach her infant. Only by

⁶ A folk belief that I frequently encountered when asking local people about langurs was that langur males routinely kill all male infants. This theory has the obvious merit of explaining why there were more females than males in troops. However, I found no evidence to support this, and I knew of cases in which both male and female infants were killed by incoming males.



Fig. 6. Itch holds her wounded infant (note left thigh) on morning following September 9th attack.

a fierce assault were the females able to wrest the infant from his attacker. After Itch had retrieved her infant, Sol persisted in chasing and slapping at Mug.

On August 12 and September 1, Scratch received superficial cuts as a result of Mug's assaults. On September 9, Scratch was severely wounded when he was attacked by Mug near the Phiroze. Toothmarks were inscribed on his skull, and he had a deep gash across his left thigh (see fig. 6). The crippled infant was helpless without his mother, and she did not desert him, as has been reported under similar circumstances at Dharwar [SUGIYAMA 1967: 229; YOSHIBA 1968: 236; discussed in section IV-C]. When I left Abu on September 12, 1972, I did not expect that the wounded infant could survive. I was informed later however [pers. comm. from MONA ALI] that Scratch did in fact recover and was able to walk again. Mrs. ALI also told me that two days after I left, a dark infant was killed by an adult male near Boulders.

When I returned in February 1973, Scratch, Mira and Virginia were missing. Based on: (1) Mrs. ALI's report; (2) the fact that Boulders was well within B-6's home range; (3) the conviction that Mira was the only dark infant in the vicinity at that time; and (4) the observation that Bilgay was

more than five months pregnant in February (which meant that she must have resumed cycling around September or October), I am relatively certain that the infant killed by a male was Mira. Based on observed behavior of the two most likely male suspects, Mug and Shifty, and on the reaction of the mothers to each of these males, I assume that Mug was the killer.

The cases of Scratch and Virginia are more problematic. When I re-contacted B-6 in February, both Itch and Oedipa were probably in the first months of pregnancy, suggesting that either of these infants could have been lost as late as December or January. This timing is also in line with Mrs. ALI's report that Scratch had time to recover before he disappeared. The seven observed assaults on Scratch, which included three near-misses, make it plausible that Mug was finally responsible for Scratch's death. I suspect that Virginia was also killed, but not necessarily by Mug. On my return, five new males in addition to Mug were present in B-6.

The changes in the B-6 troop as of February 11, 1973 can be summarized as follows: (1) Only Harrietta's fifteen-month old son had survived from the previous season; (2) around November, Pawless had given birth to a daughter who was 3-4 months old; (3) Bilgay was in the last months of pregnancy; (4) from the extremely mild form of estrous behavior that they exhibited, I inferred that Oedipa and Itch were in the first months of pregnancy; (5) five adult males in addition to Mug were present in the troop whenever he was (see also tables III and IV).

In 1973, females with infants reacted to the five new males just as mothers had reacted to Mug in 1972: by avoiding them. On February 11, the day that I first saw her, Pawless' daughter had superficial cuts on her head in very much the same pattern as cuts which I had seen Mug inflict on Scratch's skull in September 1972. On February 26, I witnessed males assault Pawless and her infant near Jodhpur house and inflict a four inch cut down the infant's back. The circumstances surrounding this attack are described below.

On February 25, Pawless and her infant spent the day alone, returning to B-6 at 17:20. No male had been in B-6 that day in almost seven hours of observation. Pawless was still with the group at 08:35 the next morning when Righty followed by five other males cantered up the road from their sleeping trees beyond the Phiroze School. About thirty minutes later, Kali and other males attacked Pawless and her infant.

Even though I watched the February 26 attack from fifteen feet away and I was able to make a super-8 film record, it was not always clear which males were actually attempting to injure the infant. From my firsthand impression and from replays of the film, Kali appeared to be the most persistent attacker.

In one sequence, Pawless jumped three feet into the air, onto a wall. As she was in midair, Kali leaped up and tried to pull her infant from her chest. Subsequently, Kali pursued Pawless far out onto a limb and forced her to jump to the ground among males who were sitting below.

At the time I was aware of Itch's attempted but ineffectual intervention. She lacked the aggressiveness that both Sol and Pawless had displayed the year before when defending Itch's infant. What I did not notice at the time, was the possibility of Mug's assistance. From the film, Mug appears to be supporting rather than harassing Pawless. In one scene, Mug joins Pawless in the center of a cluster of males who have been grabbing at her infant. Even though he is beside her, Mug shows no interest in her infant; his threatening posture is directed outwards towards the other males.

After the first of four attacks, Pawless was panting, diarrhetic, and apparently quite shaken. At 0915, fifteen minutes later, she left the troop for an *Anogueissus* tree several hundred feet away. Minutes later, she descended and sat in the midst of some builders who were quarrying stone – though normally langurs avoided such violently noisy human activity. When the males, followed by the rest of B-6, headed her direction, Pawless doubled back in the direction that she had come from. She did not return to the troop that day. When I was able to get a close look at Pawla, seven hours later, I noticed that she was wounded superficially on her back. The cut healed within a few days.

It may have been in order to avoid such attacks that Pawless no longer spent much time with the B-6 troop. Of 156 hours that B-6 was observed between February 11 and March 25, Pawless and her daughter were absent during 111 of these. Including February 26, the day Pawla was wounded, Pawless and her daughter were present when Mug and the five males were during only eight observation hours. On ten different days Pawless and Pawla were spotted travelling apart from the group. On four of these occasions, Harrietta, the only other B-6 mother, and her son, were with them. On at least five other occasions, however, Harrietta and Harry were seen with the group when Pawless and Pawla definitely were absent. Pawless' new range was the area of overlap between B-3 and B-6's home ranges, though she also entered sections which I had previously designated as B-3's core area, normally used exclusively by them. On March 4, for example, I followed Pawless, Harrietta and their offspring into the Bazaar, west of B-6's usual range.

After the February 26 attack, Pawless was observed with the troop on five occasions; only once, on March 25, were any of the six males present when she was. Except for this day, Pawless returned to B-6 only when Shifty

was nearby (a proximity which was invariably correlated with the absence of the six males), or else she arrived in the evening after the males had departed for their sleeping trees to the northeast of B-6's range and she left at sunrise before the males rejoined the group. On at least six occasions Pawless was observed either at the B-6 sleeping trees with the other females, or else she was spotted alone on the following morning in the vicinity of their sleeping trees.

IV. Discussion

A. Population density, political change and infanticide

Ten take-overs by males from outside the troop have been reported at Dharwar, Jodhpur and Abu; seven of these were accompanied by infanticide and resulted in the deaths of about thirty infants. These events are summarized in table VI. At all three locations, temporary invasions by male-bands which did not necessarily entail eviction of the leader also occurred. At Abu, invasions in two troops (B-6 and the B-1 troop near Chippaberi) coincided with wounded, dead, or missing infants, though only in the case of B-6 were such males actually observed to attack an infant. To date then, assaults by langur males upon infants have only been reported when a male enters, or re-enters, the troop from outside it, indicating a definite correlation between political change and infanticide.

A more tentative correlation may exist between frequency of such political changes and population density. At Orcha and Kaukori, where langur population densities are as low as seven to sixteen animals per square mile, only one instance of change was observed in sixteen months of observation. This shift involved the replacement of a leader by another troop member and took place with relatively little conflict [JAY 1965]. By contrast, in areas with much higher population densities, there was a higher frequency of troop take-overs. At Dharwar where population densities are between 220 and 349 langurs per square mile [YOSHIBA 1968] males outside the troop wrested control in four of nine troops under surveillance between March 1961 and April 1963 [SUGIYAMA 1967]. Including surveyed troops, ten major changes, six witnessed and four inferred, were reported for Dharwar in a two-year period [YOSHIBA 1968]. At Abu where population densities exceed one hundred and thirty animals per square miles, three major changes occurred in two of five troops under intermittent observation between June 1961 and March 1973. Data on population density and on rates of change are not yet published for Jodhpur, but it is worth noting that due to the

Table VI. Political changes and infanticide at Dharwar, Jodhpur and Mt. Abu

Location	Troop	Source	A Number of invad- ing males	B Number of resident males before take-over	after take-over	C Number of males excluded invaders	residents	D Infants killed
1. Dharwar (June 1962)	XXX	SUGIYAMA 1965b	7	1	1	6	1 adult 6 juvs.	6
2. Dharwar (July 1962)	II	SUGIYAMA 1966	1	0 (leader removed)	1 (leader IIIrd troop)	0	0	4
3. Dharwar (July 1962)	V	YOSHIBA, in SUGIYAMA 1967	59 (including males X, Y, and Z)	1	1	ca. 58	1	-
4. Dharwar (October 1962)	VII	YOSHIBA in SUGIYAMA 1967	3 (X, Y, and Z)	1	1 (X)	2 (Y and Z)	1	-
5. Dharwar (March 1963)	I	KAWAMURA in SUGIYAMA 1967	2 (Y and Z)	3	2 (Y and Z)	0	3	4-5
6. Jodhpur (July 1969)	B-26	MOHNOT 1971	22	0 (leader died)	1	21	0	5
7. Mt. Abu (July-August 1971)	B-6	BLAFFER	1 (Shifty)	1 (Mug)	1 (Shifty)	0	1 adult 1 juv.	6
8. Mt. Abu (May 1972)	B-3	BLAFFER	1 (Shifty)	3	1 (Shifty)	0	3 adults 2 juvs.	4
9. Mt. Abu (June-August 1972)	B-6	BLAFFER	1 (Shifty)	1 (Mug)	1 or 0	1	1	3
10. Mt. Abu (February 1973)	B-6	BLAFFER	5	1	6 or 0	5 (or 0)	1 (or 0)	-
		Total:	102			114		

extremely arid conditions under which these langurs live, even though langurs have large open spaces available to them, they tend to concentrate about intensively used garden spots and watering places. Similar correlations between adult male replacements, death of infants, and high population densities have been reported for *Presbytis senex* in Sri Lanka [RUDRAN 1973b].

As YOSHIBA [1968] and others have pointed out, the most obvious link between population density and increased frequency of political change is the increased numbers of non-troop males who come into contact with bisexual troops and who are available to instigate male attacks against them. At Dharwar where non-troop males are abundant (as opposed to Kaukoir where they are rare), SUGIYAMA estimates that political change occurs in troops on average once every three to five years [1967: 71; YOSHIBA 1968]. Even faster rates of change have been hypothesized [SUGIYAMA 1966] but for several reasons these may be too high. To the extent that take-overs are related to numbers of non-troop males, social change is self-accelerating. As can be calculated from columns A, B, and C of table VI, the number of adult and juvenile males expelled from a troop may exceed the number who originally invaded it. Furthermore, this increase in potential invaders may be accentuated by a 'ricochet' effect, as seen at Dharwar in cases 3-5 of table VI. Within a matter of months, males X, Y, and Z, who were evicted from one troop, attacked another, followed by ousted males Y and Z attacking yet a third troop [SUGIYAMA 1967].

Despite this apparent correlation between density and rate of political change, it is obvious that chance, historical factors, as well as the individual personalities of the males involved are important. In two cases for example, take-overs only occurred after the absence of the troop leader was discovered by neighboring males. At Dharwar, the leader of the IIInd troop was experimentally removed before the leader of neighboring IV troop entered and killed all infants. [SUGIYAMA 1966]. At Jodhpur, troop B-26 was rendered vulnerable to attack by a male band when the leader and sixty-eight troop members died, apparently from drinking contaminated water [MOHNOT 1971]. At Abu, nomadic non-troop males were able to enter the particularly vulnerable B-6 troop on three (and possibly four, judging from the composition of the troop when first encountered in 1971) years in a row. During a twenty-two month period, nine of eleven infants born (82 percent) were killed. By contrast, four infants in B-3 were killed after Shifty took over, but subsequently, this male remained with the troop, and no other males were able to enter. Whereas B-6 faces the possibility of extinction, troop B-3 seems on the verge of stability and growth.

It has been suggested that the high population densities reported for Dharwar are recent, the result of deforestation and the resulting compression of the langurs' habitat and reduced predation [SUGIYAMA 1967, discussed in CROOK 1971]. One of the implications of the view that langurs are living under new conditions to which they are not adapted is that the aggressive

behavior reported for crowded langurs is somehow pathological [as in CALHOUN 1962] or that langur infanticide is 'dysgenic' [WARREN 1967: 257]. Several lines of evidence however suggest that such behavior is in fact adaptive: (1) Intense competition between langur males for access to females, and resulting high levels of aggression have been ongoing for at least 130 years, and probably much longer (see below). (2) In contrast to pathological behavior, observed assaults upon infants have been highly goal-directed and organized (see for example section III-D). (3) As far as can be determined, assaults upon infants have been directed with reference to roughly accurate assessments of paternity. That is, the infants attacked were those sired by competitors. (4) The existence of counter-strategies among females (discussed in section IV-C) also suggests that infanticide has been going on long enough for adaptations to it to have arisen.

As early as 1836, fighting among langur males was a well-known phenomenon among British and Indian naturalists, and was described in the August issue of the *Bengal Sporting Magazine* as:

'... a story of the stronger sex trying conclusions amongst themselves for the charms of the gentler one. The males are exclusively the combatants and the strongest usurps the sole office of perpetuating his species through the reciprocal agency of his female associates... At a particular season of the year the great body of he-monkeys which had been leading a monastic life deep in the woods, sally forth to the plains and mixing with the females a desperate conflict ensues for the favours of the fair lady pugs... This continues for several days at the end of which time, one male more valorous than the rest will be found in possession of the flock... (after which)... a kind of conference takes place, the females delivering up their half-grown male offspring to the care of the (defeated males) who troop away to the jungle re-inforced by hopeful juniors.' [Quoted in HUGHES 1884: 147-148].

Attacks by male bands upon bisexual troops were witnessed by several naturalists who published detailed accounts [HUGHES 1884; J.F.G. 1902]. According to HUGHES' account, the troop leader was killed by one of the invading males, after which one of the invaders was himself killed by resident females (p.149). In addition, a female carrying a young infant was killed when a pursuing male shook her from the branch onto which she had attempted to escape – exactly the strategem that the invading male Kali used in pursuit of Pawless and her infant in 1973.

*B. Infanticide as a reproductive strategy.*⁷

If conditions such as those at Dharwar and Abu are in fact not due to recent changes, then intense competition between males for females, a high

⁷ It should be clear that motivational terminology and discussion of 'strategy' as they appear in this paper refer to theoretical interpretations of behavior. It is assumed that on

rate of political change, and pressure on males to maximize their reproductive success within a short period of time, constitute the conditions under which some langurs evolved. In this case, infanticide might permit an incoming male to use his short reign over a troop more efficiently. By eliminating an infant unlikely to be his own, a newcomer could hasten the mother's return to sexual receptivity so that she could then bear his own offspring.

Such an hypothesis assumes that in the competition between males for females, take-over of a troop is more or less equivalent to reproductive access to females and that insofar as these females are fertile, such access is correlated with differential reproductive success. To the extent that death of her infant induces a female to resume cycling in the presence of the male who killed her infant, infanticide should *on average* increase the reproductive success of those males who practice it.

Precise measures of reproductive success for males who take over a troop and kill infants as well as for those males who do not, are crucial for the acceptance of this sexual selection hypothesis. Unfortunately, even though paternity exclusions from primate blood samples are technically feasible, it was not possible to gather such samples at Abu. Nevertheless, in at least three troops (Dharwar troop XXX, the experimental IInd troop at Dharwar; and troop B-3 at Abu) females whose infants were killed were observed copulating with the new male, and 70 percent of these (four of six in troop XXX; three of four in troop II; and four of five in B-3) gave birth between six and eight months later. The average time was just over one normal langur gestation period (see table VII: footnote 1). Barring the possibility that another male besides the new leader was the actual progenitor, it is hard to see how infanticide in these cases did not increase the reproductive success of those males who committed it.

In order for such an infant-killing male to leave a disproportionate number of surviving offspring however, he must possess some means of discriminating between infants likely to be his own and those belonging to another male. A male who attacked his own infants would be rapidly selected against.

To some extent, differential treatment of infants is incumbent in male roles [RANSOM and RANSOM 1971; HRDY, in press]. Among langurs for

average the genes of those animals who respond to certain situations in certain ways are disproportionately represented in subsequent generations. On one level of causation, this is a sufficient explanation for extant behavior [discussed in TINBERGEN 1963; WILLIAMS 1966]. At no time do I mean to imply by these terms proximate causation. Nothing is known concerning mechanisms (endocrinological or other) which directly determine langur behavior.

example, a troop leader who is likely to be the progenitor of infants born in his troop is normally tolerant of infants [JAY 1965], active in troop defense [RIPLEY 1967], and occasionally heroic in the rescue of infants [McCANN 1934; and pers. observation). Troop leaders have an investment in keeping other troops and especially extra-troop males away from harem and offspring, and behave accordingly. By contrast, lower ranking adult males within the troop are less likely to be progenitors and they participate less in troop defense. The special role of subadult males in inter-troop encounters will be discussed at greater length elsewhere.

The behavior of non-troop males is quite different. These nomadic males haunt the vicinity of bisexual troops. If they do enter, they ignore infants except when their intentions are specifically hostile (e.g., Kali's towards Pawla). One exception to this however has been reported in which an invading male held a newborn infant on his lap [YOSHIBA 1968: 236]; unfortunately, no further information regarding their relationship is available. Generally, alien males are either scrupulously avoided or else attacked by mothers with infants, though estrous females may approach them.

At present it is not clear what determines when a male band will skulk about a troop, and when it will attack. Nor is it clear what determines which male is able to drive out other males and remain by himself as the new leader. A consistent linear hierarchy was observed in the dominance relations among the five males who entered B-6 in 1973 (see section III-C), and it may be that such hierarchies are typical of male bands. If this is the case, when troop take-overs occur the future leader may to some extent be predetermined. In the case of this particular band, the five males may have formed a temporary alliance with the sometimes B-6 leader Mug in exchange for the opportunity to 'steal' copulations even though in fifty-two such mounts which were observed the females involved were probably not fertile (see section IV-C).

Even beyond differential treatment of infants by males fulfilling different roles, some males behaved in accordance with a roughly accurate ability to discern probable paternity. That is, the behavior of some males coincided with information (admittedly incomplete) recorded by human observers. According to my calculations for Abu, for example, the two infants born in B-6 in March and April of 1972 must have been conceived around the time of observed copulations in August and September of 1971, just after Shifty took over the troop. Whereas Shifty was tolerant of these two infants, whenever the pre-August 1971 leader (Mug) was with the troop, he repeatedly stalked, and in the case of Scratch, severely wounded, these infants who were in all probability *not* his. Pawless' infant Pawla was conceived around April

of 1972, just before Shifty left the B-6 troop for B-3. Even though Pawla was born around November, while Shifty was no longer in sole possession of that troop, whenever he visited, he tolerated Pawla as though she were his own infant. The mother made no attempt to avoid Shifty, and in fact throughout February and March of 1973 she sought him out (see section III-D). Had the resident females in B-3 permitted her, I suspect that Pawless would have joined Shifty's troop; however, relations between females in the two troops were antagonistic [HRDY, in prep.].

It would be of great interest to know exactly what means the langur male has at his disposal for discriminating his own infants from those of a previous leader. One possibility is that his behavior is influenced by previous consort relationships with the mother [cf. RANSOM and RANSOM 1971 for anubis baboons] or the lack of them [e. g., THOMPSON 1967 for crab-eating macaques].

Familiarity alone however does not explain the case of Mug the former B-6 leader who returned a year later and attacked Scratch, an infant who almost surely was sired by his rival. Barring coincidence, one possibility is that males are roughly able to evaluate the *timing* of previous consort relationships. If this is so, the mechanism is apparently imperfect. There is one problematic account of a langur who attacked an infant which was probably his own [pers. comm. from S. M. MOHNOT]. More often however, the converse has been observed: a troop leader allows another male's offspring, born after his take-over, to survive. At Dharwar, for example, the leader of neighboring troop IV took over troop II after the IIInd troop leader was experimentally removed. The new leader killed four infants and as the mothers came back into estrus, copulated with them (see table VII). The leader of IV troop was unable to unite females from Troop II with his own troop and as sexual activity in II troop subsided, he returned to his own troop, whereupon another neighboring troop leader, III male, began consorting with the leaderless troop II females. Four months after III male's accession of troop II, four infants, sired by the first usurper, IV male, were born. Subsequently, troop II merged with troop III, yet the III male never attacked the new infants who were not his own [SUGIYAMA 1966: 61-62]. The fact that the females in troop II exhibited estrous behavior and solicited the new male, even though they were already pregnant may have been an important inducement for III male's tolerance (see next section). Another possibility is that infanticide is not a universal pattern among langurs.

Besides the absence of precise information concerning male reproductive success, there are several other problems which complicate acceptance of a sexual selection hypothesis. Though infanticide is a relatively effective means

Table VII. Approximate time elapsed between death of infant, estrous behavior and birth of subsequent offspring in three cases of infanticide

Troop and location	Female	A Date of death or disappearance	B Estrous behavior observed	C Days elapsed between death and estrus	D Date of subsequent birth	E Months elapsed between observed estrus and next birth ¹
30th troop Dharwar	A	June 6-11, 1962	June 12-16	1-5	not observed	>9
[SUGIYAMA 1965b]	B	June 6	June 12-13	6	late December to Mid January, 1963	ca. 7
	C ²	June 29	not observed	-	late January to early February	(ca. 7.5?)
	F	June 17-18	June 23-25	ca. 6	late January to mid February	ca. 7.5
	I ³	July 9	July 18	10	early to late January	ca. 6.5
	E ⁴	August 4	September 6	ca. 33	late December to mid January	4.5
2nd troop Dharwar	K	June 28, 1962	July 11	14	(female disappeared)	
[SUGIYAMA 1966]	R	June 30	July 15	15	mid January to February 5, 1963	6-6.5
	S	June 29	July 11-18	13	mid January to February 5	6-6.5
	U	June 28	June 29	1	mid January to February 5	6.5-7
B-26 troop Jodhpur	Ti	July 24, 1969	July 28-31	5	October 1971	27 months
[MOHNOT 1971 and pers. comm. from MOHNOT 1973]	Ni	July 27	August 5-8	9	June 28, 1970	11 months
	Ri	August 3	August 4-7	1	August 1970	12 months
	Pi	July 29	August 8-12	11	(a) Stillbirth (b) July 1972	19 months

Average: (deleting female E) = 8 days

¹ The gestation period of 168 days reported by HARMS [1956] and cited in NAPIER and NAPIER [1967] may be too short. Gestation periods of 200 ± 10 days at the National Center for Primate Biology at Davis are close to those of 6-7 months observed by SUGIYAMA in South India [Pers. comm. from L.J. NEURATER, 1971].

² Presumably then female C came into estrus about the time of the take-over and the death of her infant (June 1962) since she gave birth seven and one-half months later.

³ There is a discrepancy [SUGIYAMA 1965b] between table III and the text (p.398); it is assumed that the date mentioned in the text and cited here is the correct one.

⁴ Female E's infant was more than a year old at the time of the take-over, and it is possible (note short gestation period) that she was already pregnant, and that her estrous behavior was 'mock estrus' as discussed in this paper.

of inducing estrous behavior (doing so within about eight days of the death of her infant in most cases for which there is information - Column C of table VII) in many cases it is an imperfect means of inducing a female to ovulate, conceive and to subsequently give birth to a live infant (e.g., Jodhpur cases,

column E of table VII). In the case of female T_1 at Jodhpur for example, twenty-seven months elapsed between her infant's death and birth of a subsequent one. At Jodhpur, the average time between the killing of an infant and the next live birth was seventeen months, two and one-half times the average time at Dharwar and Abu. One possibility is that this lag may have been due to the harsh conditions under which these desert-living langurs dwell, but more information is needed about the mechanisms of birth spacing among langurs living in natural (including harsh) conditions before any conclusions are possible.

Whatever its cause, however, the cost of this lag is borne largely by the female whose infant was killed, not by the male who killed it. Assuming that he is the father of her subsequent offspring, however delayed, the incoming male may fare better than if he had waited for the mother to wean her first infant and resume cycling naturally. By that time, the usurper might no longer be in control of the troop. Another risk for the male is that after inducing a female to ovulate, he may not be able to retain exclusive access to her. At both Jodhpur and Abu, females who resumed estrus after the death of their infants solicited males outside the troop [MOHNOT 1971 and section III-A of this paper]. Even if a usurping male is successful in inseminating females, if he then leaves the troop, another male may come in after the infants are born and kill them. This is what happened to the ambitious Shifty when he left B-6 for B-3. Nevertheless, if Shifty's switch was a gamble, he won insofar as B-3 offered twelve females of breeding age as opposed to five in B-6, and insofar as one of three B-6 infants that he probably sired was still alive in March of 1973.

Another factor which may contribute to less than the maximum possible reproductive success for infanticides is incompetence. A male such as Shifty may be more proficient than a male such as Mug who attacked Scratch more than ten different times before the infant was killed. Pawless' infant was also attacked more than once, and possibly will survive. It is unknown to what extent infanticide is learned behavior. It seems unlikely to me though that practice can be very important since exposure to such chances during the lifetime of any given male would be limited.

C. Female counter-strategies

In almost every instance that the strategy of infanticide seems inefficient, the cause can be attributed either to interference from another male (discussed above) or to noncooperation from females. Confronted with a population of males who are competing among themselves, often with adverse

consequences for females and their offspring, it is plausible that natural selection would have favored those females inclined and best able to protect their interests.

When an alien male approaches a troop, he is fiercely attacked by females as well as by the resident male. Even when the resident male for whatever reason 'decides' to tolerate alien males (see section III-C and footnote 7), females with infants or juveniles do not; they may either actively resist such males or leave the troop. After a new male takes over, females may form temporary alliances to prevent him from killing their infants (e.g., Sol and Pawless' repeated interventions when Mug attacked Itch's infant). Even after a female loses her infant and resumes cycling, for whatever reason, the female may thwart the male who killed her infant by soliciting some other male (see section III-A).

In several cases mentioned above, females were able to delay infanticide. Only rarely could they prevent it. For this reason, one of the most effective counter-infanticide tactics may be post-conception estrous behavior. That is, if males are actually able to evaluate past consort relationships (see previous section), a pregnant female may induce a male to tolerate her subsequent infant (not necessarily his) by soliciting this male in the months before her infant is born. Though the term estrus usually connotes a cycling female, post-conception periods of estrus have been reported for macaques as well as langurs [CONAWAY and KOFORD 1965: 586; ROWELL 1972: 83]. At Dharwar, Jodhpur, and Abu, pregnant females confronted with a new leader displayed the traditional estrous signals – presenting to the male and shaking their heads. The shuddering in such pseudo-estrus is usually less frenzied than normal, and the duration of estrus is shorter.

Female E in the XXXth troop at Dharwar exhibited estrous behavior and copulated with the new leader even though she gave birth four months later, three to four months short of a normal gestation period. Females in the IIInd troop at Dharwar exhibited estrous behavior fewer than four months before delivery [SUGIYAMA 1965b and 1966: 61]. Female 0 at Jodhpur exhibited estrous behavior in early August and gave birth in January, five months later [MOHNOT 1971]. At Abu, Pawless exhibited estrous behavior in early August and again in early September, and was seen at different times in consort with *both* Shifty and Mug, even though she was four to five months pregnant with her daughter (Pawla) at that time. Pawla was probably conceived in March of 1972, while Shifty was still in sole control of the troop.

After birth, an infant's survival is best insured if its mother is able to associate with the father, or at least with a male who 'thinks' he is the father

or who acts like one; that is, a male who tolerates the infant. Such a strategy might explain Pawless' shift in allegiance between August 1971 when she fought Shifty, and March 1973 when she sought him out.

If none of the above tactics are possible, a mother may leave the troop (e. g., Pawless in February of 1973; female K at Dharwar – see table VII), though this may not be an equally attractive option for all females. At Abu, two older females (Sol in B-6 and a female named Quebrado from B-3) occasionally left the troop for periods of five hours or more. Younger females were never observed to do so. More information on this age distinction, if it does exist, is needed. If departure is not feasible, and if the infant is attacked and wounded, a mother may continue to care for it, or abandon it as was the case at Dharwar [SUGIYAMA 1967: 229–230]. RUDRAN [1973b: 184] has suggested that the mother abandons her wounded infant for fear of injury to herself. But, it is also possible that desertion reflects a practical evaluation of what *this* infant's chances of survival are, weighed against the probability that her next infant will survive (refer back to footnote 7 for a discussion of 'evaluation'). For example, from the point of view of her reproductive success, it was a waste of energy for Itch to continue to care for her wounded infant in 1972. Soon after Scratch recovered, he was killed. Given the circumstances, desertion and quick return to estrus might have been her optimum strategy.

Relative to other primate species, such as anubis baboons in which males play an important role in troop defense [HALL and DEVORE 1965] and in child-rearing [RANSOM and ROWELL 1972], langur females are remarkably self-sufficient. Outside of insemination, the only crucial function fulfilled by an adult male is to keep another male from taking over the troop. At Abu, for example in 1972 and 1973, the B-6 females spent approximately 25 percent of their daylight hours with no adult male present. In February and March 1973, adult males almost never spent the night at the same site with these females. These females suffered no ill-effects other than their vulnerability to alien males coming in. The troop foraged as usual and even engaged in two inter-troop conflicts with B-3 (once, when Shifty was also off chasing the B-6 males).

It is not known of course how male absence over a long period of time would affect a troop and its range. In any event, it is unlikely that such a situation could occur. It is worth noting though that despite multiple changes in male leadership, langur home ranges and habitat usage remain remarkably stable over time. It must be assumed that such traditions are passed on by females.

A further consequence of female stability is that females in langur troops are liable to be closely related to other troop members *except* adult males coming in from the outside. This high degree of relatedness may explain the extraordinary altruism exhibited by Pawless and Sol in 1972 in defense of another female's offspring; that is, fitness in such cases may also encompass the fitness of close relatives who share genes by common descent [see HAMILTON 1964; 1971]. In addition to such 'inclusive fitness', reciprocity may also be involved. In 1972, Itch's infant was defended by Pawless and Sol, while in 1973, Itch was the only female who came to the rescue of Pawless' infant when she was attacked. The two explanations are by no means incompatible. In fact, this is precisely the sort of situation in which genes for altruistic females might be selected for [TRIVERS 1971].

Despite the self-sufficiency of langur females, when a mother is confronted with a male determined to kill her infant, the odds are in his favor. In almost every case (Pawless being the possible exception) that a male tried repeatedly, he eventually succeeded. But females do have a last recourse. To the extent that infanticide is advantageous for males, and to the extent that it is a heritable disposition, females may 'choose' to breed with an infanticide so that their own sons will profit from killing another male's offspring.

D. Social conditions conducive to infanticide

The langur pattern of invasion by nomadic males, defeat and ouster of resident males, annexation of their females and the killing of their offspring is not unique in the animal kingdom. Serengeti lions provide the closest parallel. In both lions and langurs the stable reproductive unit is composed of matrilineal relatives encompassing several generations. These 'sisterhoods' are closed social units, difficult for any alien female to join [SCHALLER 1972a].

Male lions are usually forced out of their natal groups before reaching adulthood; if they ever rejoin the pride, it will be as a nomad who actively expels resident males and appropriates their lionesses [SCHALLER 1972b]. At such times, infanticide may occur [SCHALLER 1972b]. Occasionally, male lions try, as Shifty Leftless did, to maintain jurisdiction over two prides at once [SCHALLER 1972a].

Among most pre-industrial human societies, infant-killing appears to be primarily practical; it is determined by economic constraints, probability of infant-survival, and future marriage potentialities [BALIKCI 1970: 147ff; LANGER 1972; LAUGHLIN 1968; KONNER 1972; MEAD 1971; WAGLEY 1969]. Occasionally, a husband may attempt to kill an infant sired by another male [BALIKCI 1970: 150; FIRTH cited in LORRIMER 1954]. I encountered only one,

anecdotal, description of children being killed by invading males, among the Yanamamö tribe of Brazil [BIOCCA 1971: 35-37]. Interestingly, the Yanamamö are a society characterized by raiding for women [CHAGNON 1968] and by the tendency for a few males to be disproportionately represented in the gene pool of succeeding generations [NEEL 1970: 818].

In the case of both the Serengeti lion, and the langurs of Abu and Dharwar, there is (1) intense competition between males and the monopolization by a few males of genetic representation in succeeding generations; and (2) a high rate of political change so that the opportunity for the male to reproduce is of short duration, an average of three to five years among langurs, and potentially ten but closer to two among lions [SCHALLER 1972a: 40-42]. Since captured females would have infants sired by some other male, by killing them a male proportionally decreases the reproductive success of his competitors; by inseminating such females himself, he insures his own.

Summary

Langurs at Abu were observed for a total of 986 hours during three study periods between June 1971 and March 1973. During this time, a single male (Shifty) took over first the B-6 troop (in 1971) and then the larger B-3 troop (in 1972). In each case, resident adult and subadult males were driven out, and all unweaned infants disappeared. In the cases of three of thirteen infants who disappeared local inhabitants witnessed an adult male killing them.

After leaving B-6 for B-3, Shifty still attempted to retain control over it. In 1972 and 1973, Shifty and the former B-6 leader male (Mug) vied with one another for control of this troop. On fifteen occasions when Shifty returned to B-6, Mug was displaced. Even after Mug was joined by five other males in 1973, he was unable to improve his position.

During August and September of 1972, Mug stalked and repeatedly attacked a B-6 infant conceived shortly after his loss of control in August 1971. Nine assaults were witnessed in which the infant was contacted, and on three of these occasions he was wounded. Three of four infants present in B-6 at that time subsequently disappeared and were presumed to have been killed, though only one killing was actually witnessed (by a local person). In 1973, a fifth B-6 infant was attacked and wounded by one of the five new males.

To date, infanticide has been reported for seven langur troops at Dharwar, Jodhpur and Abu. In each case, infants were killed when males from outside the breeding system entered or re-entered it. Though precise information on paternity does not exist, the evidence available suggests that these males were killing infants sired by their competitors. Females whose infants were killed exhibited estrous behavior within days of the deaths of their infants, and in most cases these females copulated with the new male. In three of four troops for which information on subsequent births is available, 70 percent of these females gave birth just over one langur gestation period later. In a fourth troop, from the arid region of Jodhpur, the interval between the killing of one infant and the birth of a subsequent live infant was over twice as long as the intervals at Dharwar and Abu.

It appears that at least in some cases (at Dharwar and Abu) males are able to short-cut two to three year birth intervals by killing infants. In the case of langurs living in conditions of high population densities where troop take-overs occur approximately every three to five years, and where the reign of a given male is a potentially short one, any male strategy which increased female fertility *during his tenure* would be extremely advantageous.

Confronted with a male reproductive strategy disadvantageous for them, females exhibit counter-infanticide strategies which include leaving the troop and temporary alliances between females against the usurping male. Seven of nine assaults by Mug upon a B-6 infant in 1972 were thwarted when two females who did not have infants of their own audaciously intervened between the male and his victim. In addition, it was hypothesized that desertion of a wounded infant and rapid return to estrus by the mother, as well as post-conception estrous behavior may also be adaptive behavior for females in the presence of an infanticidal male.

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References

- BALIKCI, A.: *The Netsilik Eskimo* (Natural History Press, New York 1970).
- BIOCCA, E.: *Yanoama* (E. P. Dutton, New York 1971).
- BOWDEN, D.; WINTER, P., and PLOOG, D.: Pregnancy and delivery behavior in the squirrel monkey (*Saimiri sciureus*) and other primates. *Folia primat.* 5: 1-42 (1967).
- BURTON, F. D.: The integration of biology and behavior in the socialization of *Macaca sylvana* of Gibraltar; in POIRIER *Primate socialization*, pp. 29-62 (Random House, New York 1972).
- BYGOTT, J. D.: Cannibalism among wild chimpanzees. *Nature* 238: 410-411 (1972).
- CALHOUN, J. B.: Population density and social pathology. *Scient. Am.* 206: 139-148 (1962).
- CHAGNON, N.: *Yanomamö, the fierce people* (Holt, Rinehart and Winston, New York 1968).
- COLLIAS, N. E. and SOUTHWICK, C. H.: A field study of population density and social organization in howling monkeys. *Proc. Amer. Phil. Soc.* 96: 143-156 (1952).
- CONAWAY, C. H. and KOFORD, C. B.: Estrous cycles and mating behavior in a freeranging band of rhesus monkeys. *J. Mammal.* 45: 577-588 (1965).

- CROOK, J.H.: The socio-ecology of primates; in CROOK Social behavior of birds and mammals, pp. 103-166 (Academic Press, New York 1970).
- DAVID, G.F.X. and RAMASWAMI, L.S.: Studies on menstrual cycles and other related phenomena in the langur (*Presbytis entellus entellus*). *Folia primat.* 11: 300-316 (1969).
- DOLHINOW, P.: The north Indian langur; in DOLHINOW, Primate patterns, pp. 181-238 (Holt, Rinehart and Winston, New York 1972).
- EISENBERG, J.F.; MUCKENHIRN, N.A., and RUDRAN, R.: The relation between ecology and social structure in primates. *Science* 176: 863-874 (1972).
- J.F.G.: Habits of the lungoor monkey. *Bombay J. Nat. Hist.* 14: 149-151 (1902).
- HALL, K.R.L. and DEVORE, I.: Baboon social behavior; in DEVORE Primate behavior, pp. 53-110 (Holt, Rinehart and Winston, New York 1965).
- HAMILTON, W.D.: The genetical evolution of social behavior, parts I and II. *J. Theoret. Biol.* VII: 1-51 (1964).
- HAMILTON, W.D.: Selection of selfish and altruistic behavior in some extreme models; in EISENBERG and DILLON Man and beast: comparative social behavior, pp. 57-91 (Smithsonian, Washington 1971).
- HRDY, S.B.: The care and exploitation of non-human primate infants by conspecifics other than the mother; in ROSENBLATT, HINDE and SHAW Advances in the study of behavior VI (Academic Press, New York, in press).
- HUGHES, T.H.: An incident in the habits of the *Semnopithecus entellus*, the common Hanuman monkey. *Proc. Asiatic Soc. Bengal, Calcutta*, pp. 147-150 (1884).
- JAY, P.: The common langur of North India; in DEVORE, Primate behavior, pp. 197-249 (Holt, Rinehart and Winston, New York 1965).
- J.F.G.: Habits of the lungoor monkey. *Bombay J. Nat. Hist.* 14: 149-151 (1902).
- JOLLY, A.: The evolution of primate behavior (Macmillan Co., New York 1972).
- KONNER, M.J.: Aspects of the developmental ethology of a foraging people; in BLURTON JONES Ethological studies of child behaviour, pp. 285-304 (Cambridge University Press, Cambridge 1972).
- LANGER, W.: Checks on population growth: 1750-1850. *Scient. Am.* 226: 92-99 (1972).
- LAUGHLIN, W.S.: The demography of hunters: an Eskimo example; in LEE and DEVORE Man the hunter, pp. 241-243 (Aldine, Chicago 1968).
- LEBOEUF, B.J.; WHITING, R.J., and GANTT, R.F.: Perinatal behavior of northern elephant seal females and their young. *Behaviour* 43: 121-156 (1972).
- LORRIMER, F.: Culture and human fertility. (UNESCO, Zurich 1954.)
- MCCANN, C.: Observations on some of the Indian langurs. *J. Bombay Nat. Hist. Soc.* 36: 616-628 (1934).
- MEAD, M.: Sex and temperament in three primitive societies (Dell, New York 1971).
- MITCHELL, G. and BRANDT, E.: Paternal behavior in primates; in POIRIER Primate socialization, pp. 173-206 (Random House, New York 1972).
- MOHNOT, S.M.: Some aspects of social changes and infant-killing in the Hanuman langur, *Presbytis entellus* (Primates: Cercopithecidae) in Western India. *Mammalia* 35: 175-198 (1971).
- NEEL, J.V.: Lessons from a 'primitive' people. *Science* 170: 818 (1970).
- PRAKASH, I.: Group organization, sexual behaviour, and breeding season of certain Indian monkeys. *Jap. J. Ecol.* 12: 83-86 (1962).
- RANSOM, T. and RANSOM, B.: Adult male-infant interactions among baboons (*Papio anubis*). *Folia primat.* 16: 179-195 (1971).

- RANSOM, T. and ROWELL, T.: Early social development of feral baboons; in POIRIER Primate socialization, pp. 105-144 (Random House, New York 1972).
- RIPLEY, S.: Intertroop encounters among Ceylon gray langurs (*Presbytis entellus*); in ALTMANN Social communication among primates, pp. 237-253 (University of Chicago Press, Chicago 1967).
- ROWELL, T. E.: Female reproductive cycles and social behavior in primates; in LEHRMAN, HINDE and SHAW Advances in the study of behavior (Academic Press, New York 1972).
- RUDRAN, R.: The reproductive cycles of two subspecies of purple-faced langurs (*Presbytis senex*) with relation to environmental factors. *Folia primat.* 19: 41-60 (1973a).
- RUDRAN, R.: Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia primat.* 19: 166-192 (1973b).
- SAAYMAN, G. S.: Behaviour of the adult males in a troop of free-ranging chacma baboons (*Papio ursinus*). *Folia primat.* 15: 36-57 (1971).
- SCHALLER, G. B.: The serengeti lion: a study of predator-prey relations (University of Chicago Press, Chicago 1972a).
- SCHALLER, G. B.: The sociable kingdom; in MARLER The marvels of animal behavior, pp. 66-87 (The National Geographic Society, Washington 1972b).
- SCHALLER, G. B.: Golden shadows, flying hooves (Alfred A. Knopf, New York 1973).
- SPENCER-BOOTH, Y.: The relationships between mammalian young and conspecifics other than mothers and peers: a review; in LEHRMAN, HINDE and SHAW Advances in the study of behavior III (Academic Press, New York 1970).
- SUGIYAMA, Y.: Group composition, population density and some sociological observations of Hanuman langurs (*Presbytis entellus*). *Primates* 5: 7-38 (1964).
- SUGIYAMA, Y.: Behavioral development and social structure in two troops of Hanuman langurs (*Presbytis entellus*). *Primates* 6: 213-247 (1965a).
- SUGIYAMA, Y.: On the social change of Hanuman langurs (*Presbytis entellus*) in their natural conditions. *Primates* 6: 381-418 (1965b).
- SUGIYAMA, Y.; YOSHIBA, K., and PARTHASARATHY, M. D.: Home range, mating season, male group, and intertroop relations in Hanuman langurs (*Presbytis entellus*). *Primates* 6: 73-106 (1965).
- SUGIYAMA, Y.: An artificial social change in a Hanuman langur troop (*Presbytis entellus*). *Primates* 7: 41-72 (1966).
- SUGIYAMA, Y.: Social organization of Hanuman langurs; in ALTMANN Social communication among primates. pp. 221-236 (University of Chicago Press, Chicago 1967).
- THOMPSON, N. S.: Primate infanticide: a note and request for information. *Lab. Primate Newsletter* 6: 18-19 (1967).
- TRIVERS, R. L.: The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35-57 (1971).
- TRIVERS, R. L.: Parental investment and sexual selection; in CAMPBELL Sexual selection and the descent of man 1871-1971, pp. 136-179 (Aldine, Chicago 1972).
- WAGLEY, C.: Cultural influences on population: a comparison of two Tupi tribes; in VAYDA Environment and cultural behavior, pp. 268-280 (Natural History Press, New York 1969).
- WARREN, J. M.: Discussion of social dynamics; in ALTMANN Social communication among primates, pp. 255-257 (University of Chicago Press, Chicago 1967).
- WILLIAMS, G. C.: Adaptation and natural selection. (Princeton University Press, Princeton 1966).

- YOSHIBA, K.: An ecological study of Hanuman langurs, *Presbytis entellus*. *Primates* 8: 127-154 (1967).
- YOSHIBA, K.: Local and intertroop variability in ecology and social behavior of common Indian langurs; in JAY *Primates*, pp. 217-242 (Holt, Rinehart and Winston, New York 1968).
- ZUCKERMAN, S.: *The social life of monkeys and apes* (Routledge and Kegan Paul Ltd., London 1932).

Request reprints from: SARAH BLAFFER HRDY, Department of Anthropology, Peabody Museum, Cambridge, MA 02138 (USA)