Langur Social Behavior and Infant Mortality

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Behavior of the Indian langur monkey is highly variable but follows two general patterns. A pattern of multi-male troops and relatively low levels of aggression occurs in a wide range of habitats, but a pattern of one-male troops and extremely high levels of aggression have been reported from crowded habitats and those radically altered by human influence. High infant mortality accompanies the replacement of adult males in troops within the second pattern, and this mortality has been explained by a model of evolved male reproductive strategy that includes infanticide. The present paper reviews variabiility within the first pattern and presents a model in which the second arises directly as the result of ecological pressure upon the first, and infant mortality has no evolutionary significance beyond the obviously detrimental. Research strategies are proposed that will allow a choice between the two models.

Presbytis entellus, the langur monkey of India, is now the most thoroughly studied species in the colobine subfamily. In part due to the colobine ability to digest mature leaves, langurs can adapt to a wide range of ecological conditions, and they live in most parts of the Indian sub-continent except the western deserts. The species has been studied at sites from Nepal to Sri Lanka and in habitats ranging from Himalayan meadow to central Indian forest, and it provides an excellent opportunity to investigate the relationship between differences in habitat and variation in social behavior.

Langur social behavior is highly variable, but under most conditions it follows a pattern in which troops usually contain several adult males and levels of aggression are relatively low. However, a distinctly different pattern was observed at the three sites of Dharwar, Jodhpur and Abu, India, where population densities were high and ecological conditions heavily influenced by man. Troops contained only single adult males, and some of the most violent fighting ever observed among monkeys occurred when males were displaced from troops. Large numbers of unweaned infants disappeared during these displacements, and the explanation of their deaths is the subject of this paper.

Hrdy (1974) explained the infant deaths in terms of Trivers' (1972) discussion of sexual selection. The deaths were attributed to male infanticide, and infanticide was explained as behavior that evolved because it acted directly to increase a male's reproductive success at the expense of his competitors. Infanticide was an evolutionary adaptation to conditions in which males were frequently displaced from troops; when a male established himself in a troop, he killed infants fathered by the male previously in the troop so that their mothers would more quickly become available for reproduction.

This paper will question whether a phenomenon that can lead to the loss of up to eighty-two percent of a langur troop's infants over two birth seasons[1] is likely to be the result of langur evolution. The occurrences at Dharwar, Jodhpur and Abu will be viewed from a perspective that emphasizes the uniqueness of both the ecological conditions and the behavior at the three sites, and a model will be presented that explains the behavior as the result of ecological pressure on the pattern of langur social organization typical of less disturbed conditions. Infant mortality at the three sites will be explained as being simply incidental to high levels of aggression characteristic only of crowded habitats and conditions far different from those in which langur behavior evolved.

Variation in Langur Social Behavior

Nine studies of *Presbytis entellus* of at least four months duration were carried out. The behavior observed during these studies was highly variable, but two basic patterns are apparent. The first was reported from the wide range of ecological conditions at the first six sites in Table 1. At these sites, several adult male langurs typically lived in the same troop, and males could move from troop to troop without major social disruption. Non-troop males were few, and there was no male interference with female reproduction. The second pattern has only been reported from Dharwar, Jodhpur and Abu, sites either crowded or radically transformed by man. Very high proportions of troops contained only single adult males, and there were numerous non-troop males. Males could apparently enter troops only through a process of male takeover in which males previously in the troops were expelled, and the disappearance of unweaned infants frequently accompanied these takeovers.

Differences in the behavior of adult male langurs are fundamental to the two patterns. An inability of one male langur to tolerate another in his reproductive troop appears basic to the second pattern, but highly variable relations among males in the same troop occur within the first. A careful consideration of

Table 1
SELECTED RESULTS OF STUDIES OF *PRESBYTIS ENTELLUS* OF AT LEAST FOUR MONTHS DURATION

Site	Dates	References	Habitat and Human Influence	Population Dentsity
Orcha, Madhya Pradesh, India	11/58-11/59	Jay 1962, 1965; Dolhinow 1972.	Deciduous forest, full complement of predators. Little human influence.	7/km²
Kaukori, Uttar Pradesh	12/1/59-3/30/60		Rural cultivation, no predators.	7/km²
Polonnaruwa, Sri Lanka	10/26/62-5/11/63	Ripley 1965, 1967.	Partially cleared forest at archeological site surrounded by cultivation, few predators. Some human harassment of the monkeys.	58/km²
Melemchi, Helambu, Nepal	11/71-9/72	Bishop 1975.	Oak-broadleaf forest with low level of human use, probably full complement of predators. Occasional human harassment.	15/km² (min.)
Junbesi, Solu Khumbu, Nepal	10/72-2/74	Curtin 1975; Boggess 1976.	Meadow and mixed forest, full complement of predators. Occasional human harassment.	1/km²
Simla, Himachal Pradesh, India	8/72-1/73	Sugiyama 1976.	Oak - coniferous forest; human influence not described but main study area the "western suburb of Simla."	25/km²
Dharwar, Mysore, India.	10/61-3/63	Sugiyama 1964, 1965a, 1965b, 1966; Sugiyama, Yoshiba and Parthasarathy 1965; Yoshiba 1967. Reviewed in Sugiyama 1967, and Yoshiba 1968.	Dry forest, partially cleared, surrounding forest recently cleared, few predators. Harassment by domestic dogs.	134/km² (forest)
Jodhpur, Rajasthan India	7/67-7/70	Mohnot 1971a, 1971b.	Cultivation at edge of town and desert. Human feeding and harassment, harassment by domestic dogs.	not reported
Abu, Rajasthan, India	6/27/71-9/13/71 6/19/72-9/12/72 2/11/73-3/26/73	Hrdy 1974.	Town and surrounding cultivation. Human feeding and harassment, harassment by man and domestic dogs.	50/km² (min.)

*The population studied near Dharwar included troops living in roadside trees and creek beds in cultivated areas; under these conditions, home range was estimated at 38 ha (30th troop). See Sugiyama, 1964.

the behavior at sites where it has been found that more than one adult male langur *can* exist in a single troop is necessary both to delineate the differences between the two patterns and to illuminate the possible forces involved in their origin.

Jay (1962, 1965; Dolhinow 1972) described the relations among adult males as relaxed in both the virtually undisturbed forest at Orcha and the cultivated fields at Kaukori. Superior observation conditions allowed the detection of a stable dominance hierarchy among the Kaukori troop's six males; a shift in rank within this hierarchy was accompanied by fighting but followed by a return to stability with both participants remaining in the troop. Non-troop males were present at both sites. At Orcha, a single male lived in the area of overlap of two troop home ranges but was never seen to interact with either troop, and at Kaukori, one of a three member male group twice tried to join the study troop but was rebuffed.

Sugiyama (1976) found that the langurs near Simla followed a similar pattern. Most troops contained two or more adult males, and relations among males were usually calm with some evidence of stable dominance hierarchies. Some males lived outside of troops for at least the five months of the study, and their relatively infrequent attempts at entering troops were actively and successfully resisted by troop males.

Despite a much higher population density and frequent, aggressive territorial behavior, Ripley (1965, 1967) found essentially the same situation at Polonnaruwa. Troops contained two or more adult males in stable dominance hierarchies, and although there was some tension and a tendency towards spatial avoidance among males, relations were usually calm. Male groups of seven and eleven members were seen on single occasions about six months apart, but no permanent non-troop males were known. Non-troop males could enter troops at least on occasion, since two sub-adult males successfully migrated between troops.

Two studies from Nepal both extended the area in which multi-male troops were found and documented the existence of powerful male rivalries within them.

Group Size	Home Range and Inter-troop Relations	Takeover?
10-28	Mean home range 380 ha; home range overlap, avoidance between troops.	No
54	Home range 770 ha; only one troop at site.	No
19-c42	Estimated home range 32-128 ha; considerable overlap with territorial defense by chasing and display.	No
32	Home range 220 ha; considerable home range overlap and possible inter-troop avoidance.	No
3-c19	Home range of main study troop 1200 ha; inter-troop interactions rare because of range size.	No
16-98	Home range in Simla region 100 ha; little inter-troop interaction.	No
9-24	Mean home range 16.8 ha;* territories with mean size 8.9 ha are actively defended.	Yes
29-82	Not reported.	Yes
c20	Average home range 38 ha; inter-troop relations not described.	Yes

The langurs that Bishop (1975) studied at Melemchi showed a pronounced annual reproductive cycle, and behavior among males changed with it. Sexual behavior was least frequent during winter, and interaction among males was frequent and included grooming, embracing and play. As the year progressed, male-male grooming, then huddling and finally adult male participation in play dropped from the repertoire of observed behavior. By the mating peak in late summer, agonistic behavior among males had risen to the highest levels observed, and male wounds were most frequent. Summer also brought changes in the troop's male membership; a large adult male left the troop in late spring or early summer, and smaller ones both left and entered in August. The great majority of sightings of non-troop males also took place during the summer, and these males were usually in the vicinity of the troop rather than elsewhere as at other times of the year.

The langurs that Curtin (1975) and Boggess (1976) studied at Junbesi showed the same annual reproductive cycle, and male behavior again varied with the cycle. Either an absence of interaction or low levels of tension usually marked relations among males, but agonistic interaction led on several occasions to males being driven at least temporarily from the troop. These peripheralizations were most frequent and profound during the summer mating peak. All peripheralizations during winter were temporary, but two of the main study troop's four males were permanently driven from the troop in May and a third was periodically excluded until November, when the troop's male membership stabilized at two. Behavior consistent with this was observed in other troops. Both fully isolated and peripheralized males were seen at all times of the year, but most frequently in summer, and non-troop males coordinated their movements with nearby troops. One of the males driven from the main study troop in May successfully entered a nearby troop.

This pattern of increased agonistic behavior and male peripheralization during the peak mating season may have been present in the Melemchi forest as well. Bishop's observations of changes in the male membership of her study troop during the summer, and particularly of the increased number of isolates apparently attracted to the troop then, are entirely consistent with a model in which some adult males are at least temporarily excluded from troops during the peak mating season. It is possible that this pattern is quite widespread, since both Jay's intensive study of social behavior at Kaukori and Ripley's at Polonnaruwa were carried out outside of peak mating seasons, and Sugiyama's study included only the end of the peak season at Simla.

The langurs discussed above share a social structure in which most troops contain more than one adult male but male rivalry exists. Rivalry varies in its expression from the relaxed dominance hierarchy at Kaukori to the high levels of agonistic behavior during peak mating seasons at Melemchi and Junbesi. Fighting between males occurred even at Kaukori during shifts in dominance rank, and there was an apparent pattern of exclusion of males from troops during mating peaks at Junbesi and possibly Melemchi. Relations between troop and non-troop males were usually tense and accompanied by at least aggressive display, and the success of non-troop males attempting to enter troops was variable. Males were driven away from troops at Kaukori and Simla, but entered troops at Polonnaruwa, Melemchi and Junbesi.

Male rivalry within this pattern could cause changes in troop membership, but there was no evidence that these changes had any regular effect of reducing numbers of troop males, and they took place without any major disruption of troop structure. The tendency for male exclusion from troops was balanced by the observed ability of peripheralized males to successfully enter their original or other troops, and so the number

of males in any given troop could rise or fall. Exclusions from troops were of long-term members in the context of agonistic interaction with other long-term members. Entry was a gradual process, and although entries could follow prolonged agonistic behavior, they were never linked with the exclusion of males already in troops. The process of male takeover was never observed, and changes in male membership were never associated with infant injury or disappearance.

Studies at Dharwar, Jodhpur and Abu revealed a sharply contrasting pattern of langur behavior under conditions of high population density and substantial human interference with the animals. The situation at Dharwar exemplified the remarkably similar social behavior at the three sites. Most troops contained only single adult males, and the rare multi-male troops usually contained but one large, fully adult male; almost half the adult males in the population lived outside of troops in male groups. Relations between these male groups and the one-male troops formed the heart of a pattern unique to these three sites among all those where langurs have thus far been studied.

Male groups at Dharwar included individuals as young as one year old and ranged in size up to thirty-two members. They occupied relatively large areas that overlapped the home ranges of several troops but normally avoided contact with the troops. This pattern of avoidance was frequently broken, particularly during mating periods, by attacks by male groups on troops. These attacks led to the most severe fighting that has ever been observed among langurs, and they were variable in their detail and their outcome. Any number of the members of a male group might join in an attack, and their incursion into a troop could be met by female reactions ranging from flight to approach and copulation. The male in the troop always resisted the encroachment of the male group and could successfully drive off even a number of males, but he might be defeated and himself expelled. Sometimes part of the troop left with the male group. When a male group succeeded in expelling a troop's male, a period of heightened agonistic behavior followed until males of all post-weaning ages, whether originally members of the troop or the invading male group, were driven out and a single adult male remained with the troop. Five of these takeovers were observed at Dharwar, and the interval between their occurrence in any given troop was estimated at three to five years.

Increased sexual activity and, frequently, attacks on females with infants followed invasions by male groups, and three takeovers were followed by the disappearance of unweaned infants from the affected troops. The investigators at Dharwar interpreted these disappearances as being the results of attacks on the infants by the males newly established in the troops and noted that the mothers of the missing infants soon became pregnant.

Mohnot (1971a and b) described similar occurrences at Jodhpur. One-male troops were again typical, and the number of non-troop males exceeded even that at Dharwar. Mohnot witnessed the intrusion of a male group on the surviving females and young of a troop that had suffered mass mortality from unknown causes. A single male drove out the others and remained with the troop, and Mohnot saw this male kill three infants and suspected that he was responsible for the disappearance of two more. The Jodhpur sequence then departed from that observed at Dharwar in that none of the mothers of the killed infants became pregnant. The only female who conceived shortly after the takeover had not been a mother, and hers was one of the infants that disappeared.

Hrdy (1974) found the same pattern at Abu. She reported the successive takeovers of two troops by the same male, and then the return in the company of a male group of the first male to be displaced. Unweaned infants disappeared during these takeovers, and in several cases their mothers subsequently became pregnant. Hrdy witnessed male attacks on mother-infant pairs in one troop and received reports from townspeople of males killing infants.

Two models of langur behavior

There are three major differences between the two patterns discussed in the last section. In the first, most troops contain more than one adult male and non-troop males are few, males can move between troops without major disruption, and infant mortality is independent of changes in the male membership of troops. In the second, most troops have single adult males and there are large numbers of non-troop males, male entry into troops takes place within the disruptive process of male takeover, and infants frequently disappear during and after takeovers.

Neither geography nor subspecific differences sort the two patterns. Populations following the first have been reported from Nepal to Sri Lanka, and the full expression of the male takeover/infant disappearance pattern has been described from Mysore to Rajasthan; both patterns occur within the subspecies *Presbytis e. entellus*. The patterns are thus unlikely to be the results of genetic differences between populations, and the key to their differences must be sought in the details of behavior and ecology. The successful model of langur behavior must explain both.

Hrdy (1974) interpreted the behavior observed at Dharwar, Jodhpur and Abu as being evidence of highly regular patterns that were universal among langurs. Her model followed that of the Dharwar investigators in its description of the history of a langur troop as cyclic. Like Sugiyama, she believed that fathers would tolerate their male offspring as adults, and one-male troops would grow into multi-male troops as infants matured within them (age-graded troops as described by Eisenberg, Muckenhirn and

Rudran, 1972). The process of male takeover, however, was normal, and when it occurred, the growth of a multi-male troop would be checked. A male group would invade the troop and drive out all of its male members, thus creating a new male group composed of individuals of all ages, as observed at Dharwar and Jodhpur. One male of the original male group would then drive the others from the troop, and the cycle would begin anew with a one-male troop. Differences in the frequency of male takeover would explain variation in the proportion of one-male and multi-male troops among different populations. At Dharwar, where population density was high and there were consequently large numbers of non-troop males, takeovers were frequent and most troops did not have time to mature into a multi-male configuration. In areas like Orcha, where densities were low, takeovers were so infrequent that troops usually contained two generations of adult males and hence were multi-male.

The evolution of a pattern of male infanticide was a major element of the model. Because they postponed their mothers' fertility, unweaned infants were obstacles to the reproductive success of a male newly entering a troop, and selective pressures favored male behavior that would remove the infants. These pressures were strongest where population densities were high, because frequent takeovers would shorten the average tenure of males in reproductive troops. Since he would probably soon be driven out, a male's promptness in fathering offspring would be crucial. Because killing infants quickly brings their mothers into estrus, infanticide evolved essentially as an extension of male competition for females into the past. An infanticidal male enjoys accelerated and lengthened access to fertile females at the expense of both his predecessor's and the females' reproductive success.

The infant disappearances at Dharwar and Abu, and the observed killings at Jodhpur, were interpreted as being the results of a male strategy of infanticide that evolved in this manner. Hrdy rejected the possibility that the infant deaths were the results of aberrant behavior and argued in favor of an evolutionary explanation of male attacks on the basis of the apparent "goal-directed" and organized nature of those observed (1974: 45), the apparent correlation between attacks and non-paternity, and the existence of female behaviors evidently evolved as "counter-strategies" to male infanticide. An ability to evaluate the timing of previous consort relationships was proposed as the likely basis of a male's ability to avoid the evolutionarily disastrous killing of his own offspring, and suggested female counter-strategies included interference with this mechanism as well as behavior more directly related to male attack. Pregnant females frequently continued to mate after takeovers occurred, and this "pseudo-estrus" presumably could have resulted in a male behaving towards as competitor's offspring as if it were his own. Females sometimes cooperated in defense of infants against male attack, and their behavior during takeovers could include resistance of the attacking male group and departure from the troop if the takeover process was successful. At Dharwar, mothers apparently abandoned their injured infants and subsequently came into estrus, and Hrdy interpreted this as possibly reflecting accurate assessment of the injured infants survival chances in the face of continued attack. It was advantageous for the females to concentrate their reproductive effort on future offspring and to mate with the infanticidal males so that their sons would possess the valuable genetic predisposition towards infanticide (Hrdy 1974: 53).

Careful consideration of the variability of langur behavior indicates the possibility of a different explanation of the pattern observed at Dharwar, Jodhpur and Abu. This second model emphasizes the crowded ecological conditions at the three sites and states that a conservative interpretation of the data available from them indicates a substantially less regular pattern of behavior than that described in the evolutionary model discussed above. This less regular pattern is explained as the result of the effect of crowding on the widespread, ecologically adaptable pattern of langur behavior discussed in the last section.

Under almost the entire range of conditions in which langurs have been studied, troops were multi-male and male rivalry was expressed solely by agonistic behavior between males. This pattern was present in the cultivated fields near Kaukori and the almost wholly undisturbed deciduous forest at Orcha and was observed in mixed forest and meadow at elevations in excess of 3000m at Junbesi. It persisted under population densities ranging from 1 langur per km^2 at Junbesi to fifty times that in the relict forest surrounding the archaeological site at Polonaruwa.

In contrast to this diversity, the pattern of one-male troops, male takeover and high infant mortality has been found only under crowded conditions or where contact with humans was extensive. At the time of the study there, the Dharwar area had been subject to extensive recent deforestation and only a greatly diminished predator population remained; population densities were as high as 134 langurs per km^2 in what forest survived. The Jodhpur and Abu langurs also lived in habitats drastically altered by human influence. The Jodhpur langurs lived on the edge of the desert surrounding the city, were extensively fed by people and subsisted largely by raiding various types of cultivation. The Abu population was even more urban, consisting of "six troops... in and about the town, and a seventh... at the Chippaberi bus stop," (Hrdy 1974: 21) and again fed by people and frequently harassed. Such close association with human habitation typically denies animals the use of considerable amounts of space, and so the effective population densities at Jodhpur and Abu are greater than indicated in Table 1.

The high population densities at the three sites are probably of quite recent origin. They are almost certainly the results of the combination of habitat destruction by settlement, deforestation and cultivation and the removal of the population check of predation. Mukherjee (1974) states that habitat disruption and faunal impoverishment became dramatic in India only with the advent of the Mughal Empire and accelerated with the coming of the British and again with Independence. Schaller's (1967) work demonstrated that both tigers and leopards frequently prey on langurs, and the numbers of these predators has declined precipitously since the introduction of modern firearms. Orcha, Melemchi and Junbesi, the three sites where habitat destruction was least and predators were most common, all had relatively low population densities.

Of all the sites where langurs have been studied, conditions at Dharwar, Jodhpur and Abu were most different from those in which langur behavior evolved. The three sites are therefore the least likely places to seek evolutionary interpretations of behavior, and data must be unequivocal before a widespread pattern is inferred from occurrences observed at these sites and nowhere else.

Table 2 summarizes the ten instances of male takeover that are described in the current literature. First-hand, eyewitness reports are available only of those of the 30th and 2nd troops at Dharwar and the B-26 troop at Jodhpur, and of the 1972 takeover of the B-6 troop at Abu. Regarding the actual causes of infant disappearance, the genetic relationships of purported infanticidal males to missing infants and the behavior of females within the takeover process, even these accounts indicate a pattern that is much less orderly than that described in the model of the evolution of infanticide.

The only direct observations of a langur male killing infants have been those of Mohnot at Jodhpur, and the takeover that established the infanticidal male in the B-26 troop followed the death of seventy-one members, including the adult male, of an eighty-two member one-male troop. Data were gathered at Dharwar and Abu under less dramatic conditions but did not include the results of any direct investigator observation of infanticide. Behavior observed at all three sites indicated that the takeover process might be expected to lead to an increase in infant mortality even in the absence of any male strategy of infant killing.

Infant langurs are quite vulnerable to injury from attacks on their mothers as well as themselves, and rapid arboreal locomotion exposes them to serious risks of falling. Male takeovers are therefore likely to be especially hazardous for infants; they involve the most intense aggressive interactions ever reported among langurs, and behavior includes extensive attack, display and chasing among both males and females. Sugiyama's (1965b: 387 et seq.) is the most detailed account of the invasion and takeover of a troop by a male group and the subsequent establishment of a single male in the troop. Much of the behavior he describes creates risks to infants. Sexually active females accompanied by infants initiated contact with the male group, and male attacks followed. Females followed the invading males intermittently throughout the takeover process and were sporadically attacked. After a single male was established in the troop, he attacked some mother-infant pairs, and infants disappeared. In at least two instances, how-

Table 2
REPORTED CASES OF MALE TAKEOVER AMONG LANGURS*

Site,Troop	Date	Reference	Eyewitness?	Infants Missing	Evidence of Infanticide
Dharwar 30th	6/62	Sugiyama 1965b	Yes	6	Attacks on mother-infant pairs, wounds found on infants.
Dharwar 2nd	7/62	Sugiyama 1966	Yes	4	"
Dharwar 5th	7/62	Sugiyama 1967, Yoshiba notes	Not reported	-	-
Dharwar	10/62	"	"	-	-
Dharwar	3/63	Sugiyama 1967, Kawamura notes	"	4-5	Not reported.
Jodhpur B-26	7/69	Mohnot 1971b	Yes	5	3 cases witnessed; 2 inferred from disappearances.
Abu B-6	7-8/71	Hrdy 1974	No	6	Disappearance, reports of 2 killings by villagers.
Abu B-3	5/72	"	"	4	Disappearance, report of 2 killings by villager.
Abu B-6	6-8/72	"	Yes	3	9 attacks on mother-infant pairs witnessed; disappearance during observer's absence from site; villager reports.
Abu B-6	2/73	"	Yes, after takeover.	-	Attack on mother-infant pair witnessed.

adapted from Hrdy 1974:43

ever, his attacks continued after the disappearances and it was apparent that the mothers, not the infants, were the targets.

Mohnot's report confirms the occurrence of male attacks on females, particularly when they attempt to approach non-troop males. Such attempts do not appear infrequent during the takeover process, and it seems that they lead to substantial threats to infant safety. The dangers inherent in the high levels of aggression that otherwise accompany takeovers are more difficult to evaluate, but inter-male aggression continued during the periods in which infants disappeared at all three sites from which disappearances were reported. Two of the three killings observed by Mohnot followed interactions between the infanticidal male and members of the male troop of which he was formerly a member. It is noteworthy that Mohnot's interpretation of the only observed cases of langur infanticide stressed the male's highly excited state rather than any more ultimate cause.

The presence of more than one male at times of infant disappearance obscures the identity of the male involved in suspected instances of infanticide where there has been no direct observation, but even if such disappearances are assumed to be the results of infanticide by males newly established in the infants' troops, the genetic relationships between killer and killed remain unclear. Studies at both Abu and Junbesi indicated that males frequently move in and out of the same troop, and the possibility that infants disappear during their fathers' return to their troops has yet to be eliminated. Mohnot attributed the disappearance of one infant at Jodhpur to infanticide by the male who was in exclusive consort with its mother at the time of its conception. This and the failure of males to kill infants definitely fathered by rivals but born after takeovers indicates that any correlation between infanticide and non-paternity is incomplete. On the basis of present data, the sounder correlation is between infant disappearance and male takeover and requires no explanation in terms of an evolved male strategy of infanticide.

Proposed female counter-strategies can also be explained without reference to infanticide, and the behavior of females within the takeover process appears to be much more variable than that described by the infanticide model. The phenomenon of females continuing to mate after conception has been observed at both the Berkeley Animal Behavior Research Station and at Junbesi and is a widespread aspect of langur reproductive behavior rather than any adaptation to the specialized conditions at Dharwar, Jodhpur and Abu. Cooperative defense of infants against male attack is part of the pattern of cooperative caretaking that is ubiquitous among langurs and survives even in crowded conditions. Directly counter to predictions in terms of female counter-strategies, females approached male groups at both Dharwar and Jodhpur, and this behavior represented one possible way in which females could contribute to the creation of situations in which infants were endangered. Data from the Berkeley research facility indicate that the length of time between birth and a mother's return to estrus is highly variable among langurs and can be much shorter than a year (P.C. Dolhinow, personal communication), and birth intervals of less than eighteen months were observed at Junbesi. The possibility therefore exists that mothers' resumption of estrous cycling is a factor in their approaches towards male groups. If so, the mothers' estrus precedes the loss of their infants, and there is no need for infanticide to induce female receptivity. Infant disappearances are again most economically explained as results of heightened aggression during the takeover process.

This description of male takeover as a chaotic, irregular process in which infant langurs are endangered indicates that the ultimate cause of infant disappearance should be sought in the origin of the pattern of one-male troops and male takeover. The fact that this pattern is unique to crowded habitats is evidence that its origin lies in the effects of crowding on the widespread pattern of multi-male troops.

A review of Table 1 shows that small home ranges are the most direct results of high population densities. This is especially so in view of the fact that effective home range is smaller in open or settled habitat than in forest and that Dharwar should be compared to Orcha, Melemchi and Polonnaruwa, and Jodhpur and Abu to Kaukori and Junbesi. The effects of small home ranges most likely to influence social behavior probably lie in the proximity of neighboring troops, the reduction of space between individuals within troops and the limiting of areas available for intra-troop social interaction.

The high levels of inter-troop aggression observed at Dharwar and Polonnaruwa compared to Orcha and Melemchi demonstrate the importance of the proximity of troops to the nature of inter-troop interaction, but effects on troop structure are likely to be more subtle. The langurs at Polonnaruwa maintained their multi-male troops despite frequent territorial encounters, and it is probable that small distances between troops affect troop structure through their influence on intra-troop behavior rather than directly.

Small home ranges can increase levels of intra-troop aggression by processes homologous to those well known from studies of captive animals: reduction of space between individuals and increases in competition over concentrated resources. None of the studies thus far have reported details of intra-troop spacing, but the observation of the Dharwar investigators that troop spread in normal conditions ranged from 20 to 30 m and rarely exceeded 100 m can be compared to the situation at Junbesi where the troop was frequently spread over distances of 200 to 300m; there is at least a possibility that crowding reduces intra-troop spacing.

The exact relationship between crowding and intra-troop aggression is similarly unclear, but the the tension and spatial avoidance among males at Polonnaruwa contrasts with the relaxed relations at Orcha despite similar troop compositions at the two sites. Any effect of crowding *per se* on aggression is probably greatly exacerbated at both Jodhpur and Abu by substantial levels of human feeding and harassment.

Crowding also reduces the amount of space available for the resolution of aggressive interactions that do occur. Here again, detailed studies have yet to be reported, but agonistic behavior between males at several sites took place across great distances. Males at Dharwar were displaced up to 1 km during interactions between troops and male groups; male groups at Jodhpur have begun attacks on troops from 1.5 km away; and a male at Abu was able to displace males from the troop adjacent to his own. The peripheralization and return of males to the Junbesi troop was accompanied by active searching and threat at distances in excess of 1 km, and peripheralized males elsewhere in the Solu coordinated their movements with troops even more distant. These examples are extreme, but they suggest the probablity that some aggressive interactions between males cannot be resolved within the small home ranges typical of crowded habitats.

The existence of multi-male troops at Dharwar, Jodhpur and Abu would thus be difficult. Crowding *per se* could be expected to exacerbate any chronic inter-male tension similar to that observed at Polonnaruwa and Junbesi, and heightened proximity would increase competition over food, particularly where the langurs were fed, and estrous females. Any serious fighting could easily drive males beyond home range or at least core area/territorial boundaries and into contact with other, nearby troops. Crowding here resembles the caged situation; the loser of an intense aggressive interaction has no way to remain within the social system. He is unlikely to be tolerated in his precipitate entry into the range of another troop, and so what might be a temporary exclusion in a less crowded area will likely drive him permanently from his troop. Processes such as that at Junbesi that involve gradual reduction of great inter-male distances will be interrupted by the intervening presence of other troops. Crowding will thus both increase the frequency of aggression and greatly magnify its effect; losers become non-troop males.

One-male troops and male takeovers follow directly from this creation of non-troop males. The widespread pattern of increased aggression during mating peaks, in combination with less systematic sources of conflict, will regularly cause males to be driven from troops. Since males apparently cannot enter troops in crowded habitats, this will inexorably reduce the numbers of males in troops and finally bring about a one-male troop pattern. The large numbers of non-troop males will form male groups, and their proximity to troops and the impossibility of their assimilation forms the basis of the takeover pattern. Crowding causes male takeovers, and the high infant mortality associated with them is an effect of crowding, not a result of langur evolution.

Conclusion

The essence of the disagreement between the two explanations of langur infant deaths discussed in the last section lies in differing *opinions* of what is happening at Dharwar, Jodhpur and Abu. Such different models arise from the possibility of different interpretations of the data in three areas: the actual causes of infant disappearances, the genetic relationships between infants and purported infanticidal males, and the relation between infant loss and female reproduction and behavior. Interpretation of the available data as evidence of a highly regular pattern supports the evolutionary model, but the same data can be taken as indications of the chaos commonly expected in disturbed ecology.

Conflict between the models will be resolved only when our *knowledge* of langur behavior in crowded habitats becomes more complete. Choice between them awaits detailed understanding of both the pattern of long term processes and the exact nature of rare events, and the controversy over langurs exemplifies the growing need in primate studies for research strategies combining long term observation and field and laboratory experiment.

Long term, continuous observation, preferably conducted simultaneously by several investigators, is needed both to understand processes that occur over long time periods and to maximize opportunities of seeing rare, naturally occurring events. Such study of langurs will be necessary for an understanding of the patterns of male movement among troops and male groups, and in crowded habitats it will gain both the crucial knowledge of the past relations with a troop of the males involved in its takeover and the greatest chance of seeing the takeover itself. Observation by several investigators further increases the possibility of witnessing a takeover and can provide histories of both the troop and the male group involved.

Uninterrupted, long term observation is also necessary to provide an accurate picture of female reproductive cycles in habitats where male takeovers and infant disappearances occur. Since birth intervals and periods between birth and the resumption of estrus vary widely from site to site and among captive langurs, an understanding of their pattern at the sites where infant disappearance is studied is necessary for a sound evaluation of the effects of disappearance on female reproduction. The increased chance of direct observation of takeovers will also help to illuminate the phenomenon of female initiation of interaction with male groups reported by Sugiyama and Mohnot.

Shorter or intermittent studies will be much less likely to allow direct observation of takeovers and will yield inadequate data on context. Neither will allow the analysis of behavior in terms of annual reproductive cycles, which are known to have been important at Dharwar, Melemchi and Junbesi. What behavior is seen during short studies must usually be interpreted on the basis of the assumption, shown to be incorrect at both Abu and Junbesi, that males entering troops have no histories of previous membership, and intermittent studies are forced into the dangerous assumption of a static situation during the observer's absence.

By itself, however, even long term study will probably prove inadequate to fully answer questions concerning the takeover process itself and the immediate causes of infant disappearance. Male takeovers and infant disappearances are so rare and by their nature difficult to observe that truly prohibitive investments of observer time would be required to fully describe them. Experiment is necessary both to define the conditions that lead to takeovers and infant disappearances and to create such conditions where the details of the processes can best be observed.

The use of field experiement in primate studies is not new. Kummer's (1971) classic studies of the basis of differences in social structure between common and hamadryas baboons made extensive use of release experiments to demonstrate that the foundation of the one-male troop pattern in hamadryas lay in male herding. Sugiyama (1966) attempted to examine the takeover pattern at Dharwar by removing the adult male from a one-male troop. The results of Sugiyama's experiment illustrate both the problems and promise of the experimental approach to the langur controversy. The male's removal led to attempts, finally successful, by males in adjacent troops to merge the experimental troop with their own, but the normal takeover pattern did not occur. Infant injury and disappearnce followed the experimental removal, but the observers were unable to witness the actual events.

Sugiyama's experiment did clearly demonstrate the possible benefits of manipulation. The removal of males from troops, combined with the release of different males, appears to present a powerful tool for investigating takeovers and and their relation to infant disappearance. This approach will allow direct inquiry into the relation between crowding and the form of the takeover process. If the experiment is performed in an uncrowded habitat, Hrdy's hypothesis predicts that infant disappearance will still occur. The alternative model predicts that the results will resemble behavior already observed at Junbesi: gradual male entry into the troop unaccompanied by any injury to infants.

Experiment will also allow the manipulation of variables within the takeover process in crowded habitats. Troops can be chosen for experiment on the basis of the age of the animals they contain, single or multiple adult males can be released, and males can be removed from and released to the same troops after varying periods to test the correlation between infant disappearance and lack of genetic relationship to males entering troops. The experimental process will also greatly increase the quality of data that can be obtained during a given takeover. The combination of removal and release of males will allow the experimenter to predict when and where a takeover will occur, and observers and film equipment can be prepared and present.

Colony studies are a further area of complementary investigation. Introductions of males to troops containing infants can be observed under optimal conditions, and, uniquely, the effects on female reproductive cycles of male introductions and infant loss can be monitored physiologically as well as behaviorally.

The necessity of such extensive research is not unique to the present controversy. The questions of modern primate studies require both increasingly detailed knowledge of what animals do over long time periods and much clearer understanding of the causes of behavior. The combination of long term observation with experiment is fundamental to the achievement of these goals, and it is crucial to the study of the adaptive significance of social behavior if we recall Williams' (1966: 261) statement in the midst of a different controversy:

> "Parsimony demands that an effect be called a function only when chance can be ruled out as a possible explanation. In an individual organism an effect should be assumed to be the result of physical laws only, or perhaps the fortuitous effect of some unrelated adaptation, unless there is clear evidence that it is produced by mechanisms designed to produce it."

Interpretations of the evolutionary functions of social behavior must be made on the basis of a sound knowledge of the context and the variability of the behavior, particularly when evolutionary significance is sought for only a small fraction of a large range of variation. Variations in habitat — analogous to Williams' physical laws — can be expected to lead to different expressions of variable behaviors. Where ecological change is so rapid that behaviors take place in contexts markedly different from those in which they evolved, the dangers of imputing evolutionary functions to their varying expressions — whatever their effects — should be especially clear to anthropologists.

Notes

[1]Hardy (1974) attributed the deaths of nine of eleven infants born to the B-6 troop at Abu, Rajasthan, over a twenty-two month period to infanticide.

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