

## Infanticide as a Primate Reproductive Strategy

*Conflict is basic to all creatures that reproduce sexually, because the genotypes, and hence self-interests, of consorts are necessarily nonidentical. Infanticide among langurs illustrates an extreme form of this conflict*

The Hanuman langur, *Presbytis entellus*, is the most versatile member of a far-flung subfamily of African and Asian leaf-eating monkeys known as Colobines. Langurs are traditionally classified as arboreal, but these elegant monkeys are built like greyhounds and can cover distances on the ground with speed and agility. Far more omnivorous than "leaf-eater" implies, Hanuman langurs feed on fully mature leaves, leaf flush, seeds, sap, fruit, insect pupae, and whatever delicacies might be fed them or left unguarded by local people. In forests, langurs spend much of their days in trees, but near open areas the adaptable Hanuman descends to the ground to feed and groom and may spend as much as 80 percent of daytime there. Monkeys are considered sacred by Hindus. This tolerance and their flexibility of diet and locomotion combine to make the Hanuman langur the most widespread primate other than man on the vast subcontinent of India. Ranging from as high

as 400 meters in the Himalayas down to sea level, and living in habitats that grade from moist montane forest to semidesert, this flexible Colobine occurs in pockets and in connected swaths from Nepal, down through India, to the island country of Sri Lanka.

The stable core of langur social organization is overlapping generations of close female relatives who spend their entire lives in the same matrilineally inherited 40 hectare plot of land. Troops have an average of 25 individuals, including as many as three or more adult males, but more often only one fully adult male is present. Whereas females remain in the same range and in the company of the same other females throughout their lives, males typically leave their natal troop or are driven out by other males prior to maturity. Loose males join with other males (in some cases brothers or cousins) in a nomadic existence. These all-male bands, containing anywhere from two to 60 or more juvenile and fully adult males, traverse the ranges of a number of female lineages. They will not return again to troop life unless as adults they are successful in invading a bisexual troop and usurping resident males.

With the exception of male invasions, langur troops are closed social units. Troops are spaced out in separate ranges with some areas of overlap between them. When troops meet at the borders of their ranges, both males and females participate in defending their territory. Males are especially active, relying on a wide repertoire of impressive audiovisual displays, such as whooping, canine grinding, and daring leaps that create a swaying turmoil in the treetops. Despite chases and lunges, the ap-

parent aggressiveness of intertroop encounters is largely bravado and almost never results in injuries. Serious fighting among langurs is largely confined to the business of defending troops against invading males; invasions are the only encounters in which males have actually been seen to inflict injuries on one another.

Because of the close association between man and langurs in a part of the world where monkeys are considered sacred, the earliest published accounts of their behavior date back before the time of Darwin and provide us with extraordinary descriptions of langur males battling among themselves for access to females and of females going to great lengths to defend their own destinies. In the 1836 issue of the *Bengal Sporting Magazine*, for example, we are told that in langur society, males compete for females and "the strongest usurps the sole office of perpetuating his species" (Hughes 1884). Another account (see also Hughes 1884) was written by a Victorian naturalist who witnessed invading males attack and kill a resident male followed by a counterattack against the invaders by resident females, who—if we are to believe the account—castrated and mortally wounded one of the invaders:

In April 1882, when encamped at the village of Singpur . . . my attention was attracted to a restless gathering of Hanumans. . . . Two opposing troops [were] engaged in demonstrations of an unfriendly character. Two males of one troop . . . and one of another—a splendid looking fellow of stalwart proportions—were walking round and displaying their teeth. . . . It was some time—at least a quarter of an hour—before actual hostilities took place, when, having got within striking distance, the two monkeys made a rush at their adversary. I saw their arms

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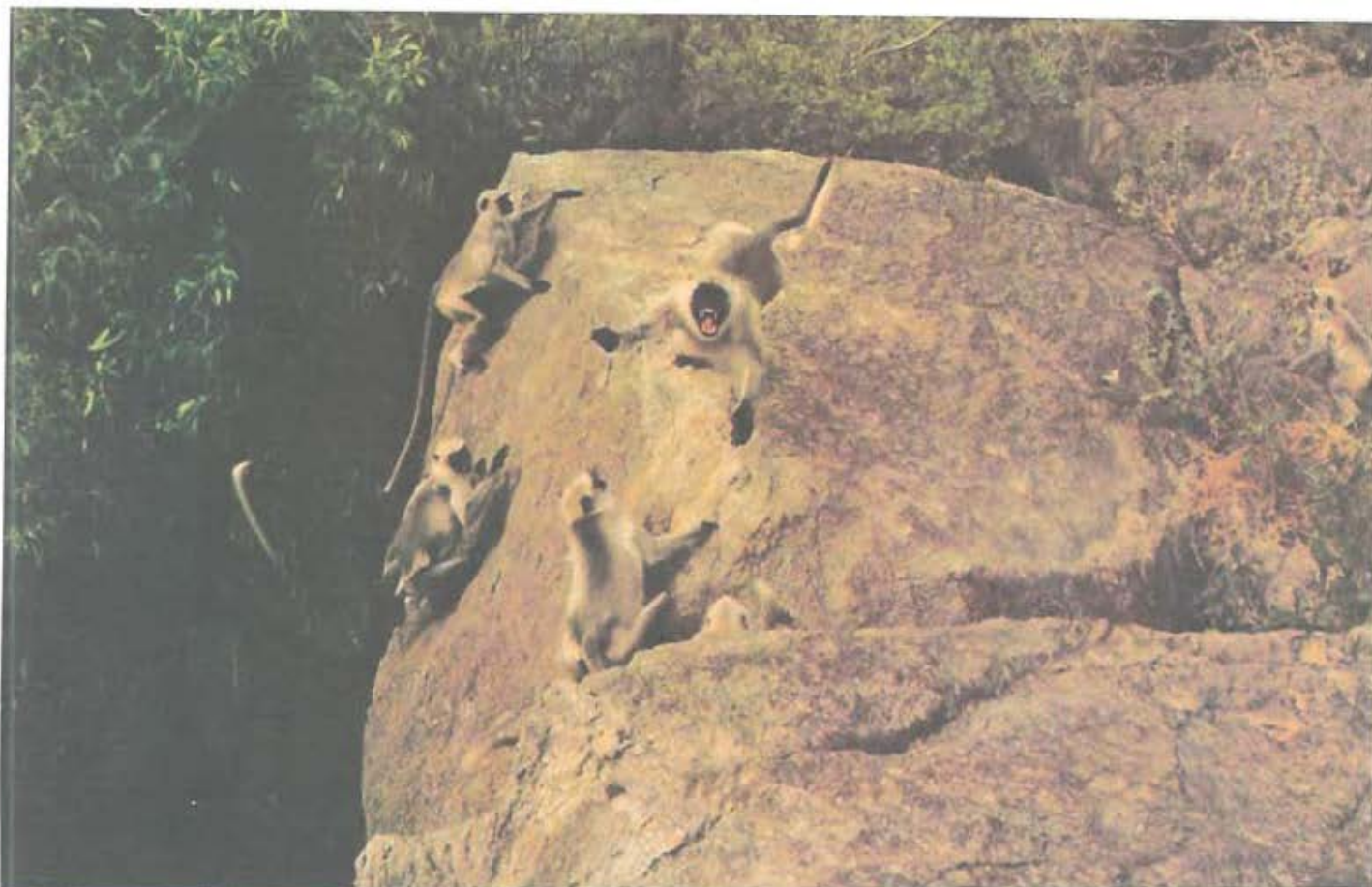


Figure 1. Aggressive behavior in encounters between troops of Hanuman langurs is largely bluff. Here, a spread-eagled, open-mouthed male hurtles dangerously through space. In

fact, he landed nowhere near his opponent, the familiar resident male from the neighboring troop. (Photos by D. B. Hrdy and author.)

and teeth going viciously, and then the throat of one of the aggressors was ripped right open and he lay dying.

He had done some damage however before going under having wounded his opponent in the shoulder. . . . I fancy the tide of victory would have been in [this male's favor] had the odds against him not been reinforced by the advance of two females. . . . Each flung herself upon him, and though he fought his enemies gallantly, one of the females succeeded in seizing him in the most sacred portion of his person, and depriving him of his most essential appendages. This stayed all power of defense, and the poor fellow hurried to the shelter of a tree where leaning against the trunk, he moaned occasionally, hung his head, and gave every sign that his course was nearly run. . . . Before the morning he was dead.

### Social pathology hypothesis

Despite the vivid accounts of langur aggression set down by early naturalists, one of the first steps of modern

primatology was to put aside these anecdotes so that the fledgling science of primatology could be laid on a purely factual foundation. By the late 1950s the modern era of primate studies, launched primarily by social scientists, had begun. The early workers were profoundly influenced by current social theory and in particular by the work of Radcliffe-Brown, who believed that any healthy society had to be a "fundamentally integrated social structure" and that in such a society every class of individuals would have a role to play in the life of the group in order to ensure its survival.

In 1959, Phyllis Jay went out from the University of Chicago to the Indian forest of Orcha (Fig. 2) and to Kauri, a village on the heavily cultivated Gangetic plain. Jay found among North Indian langurs a remarkably peaceful society. She reported that relations among adult male langurs were relaxed, domi-

nance relatively unimportant, and aggressive threats and fighting exceedingly uncommon (1963 diss., 1965). All troop members, she wrote, were functioning so as to maintain the fabric of the social structure. Because of the overriding conviction that primates behave as they do for the good of their group, the early naturalists' descriptions were dismissed as "anecdotal, often bizarre, certainly not typical behavior" (Jay 1963 diss.).

Nevertheless, a second study turned up findings that forced reconsideration of the question of langur aggressiveness. In 1963, a team of Japanese primatologists led by Yukimaru Sugiyama were tracking langurs through the teak forests near Dharwar, South India, when they witnessed a band of seven langur males drive out the leader of a bisexual troop, after which one male from among the invaders usurped control and remained in sole possession of the troop. Within days of this takeover,

all six infants in the troop were bitten to death by the new male. Curiously, and contrary to all previous reports concerning the solicitude of langur mothers (who have been known to carry the corpse of a dead infant for days), mothers whose infants were wounded by the usurping male abandoned them (Sugiyama 1967).

It was difficult to explain such behavior in terms of group survival and of a "fundamentally integrated" social structure. To circumvent this problem, it was suggested that there was something abnormal about the langurs of Dharwar and that their extreme aggressiveness was somehow pathological. In fact, if Jay's Kaukori study—the only other one available at that time—was taken as the norm, there was something unusual about Dharwar: langurs there were living in an area of rapid deforestation and of environmental disruption. Population densities (84–133 langurs per

km<sup>2</sup>) were some 30 times higher than the very low density recorded at Kaukori (3 per km<sup>2</sup>).

Almost concurrently, John Calhoun (1962), at the National Institutes of Health, was studying the effects of crowding on the behavior of rats. He demonstrated that when the animals were crowded, normal rat social conventions broke down. The rats sank into a "pathological" state characterized by excessively high infant mortality due to inadequate maternal care, infanticide, and cannibalism. Comparisons between Calhoun's rats and the langurs of Dharwar were inevitable. A number of explanations were offered as to why langur infants were killed, and the social pathology hypothesis figured prominently among them. It was suggested that infanticide was a product of crowding (Sugiyama 1967; Eisenberg et al. 1972) and as such a mechanism for population control (Rudran 1973;

Kummer et al. 1974). Alternatively, it was suggested that the behavior had no adaptive value (Bygott 1972) or that it was "dysgenic" (Warren 1967). Functional explanations for infanticide included the idea that males were somehow displacing aggression built up by the "simultaneous sexual excitement and enragement" of the new leader (Mohnot 1971) or that the male attacked infants in order to strengthen his "social bonds" with females in his new troop (Sugiyama 1965). All of these explanations derived from the basic assumption that under normal conditions animals act so as to maintain, not disrupt, the prevailing social structure.

Only one of the early explanations focused on the possible advantages of infanticide for the animal actually responsible for the act—the male. In 1967, Sugiyama suggested that the male attacked infants to avoid the two- to three-year delay in female sexual receptivity while she continued to nurse her offspring. This argument has been expanded into the more general sexual selection hypothesis that will be offered here.

It was to find out whether crowding really was at issue in infant-killing and desertion that in 1971 I first went to India. By the time I arrived, there was a new report of infanticide, this time from the desert region near Jodhpur, far to the north of Dharwar at a location where the Indian primatologist S. M. Mohnot had been studying langurs for several years. Already it seemed possible that infanticide was a more widespread and normal behavior than the social pathology hypothesis suggested.

From Jodhpur, I traveled southwestward to Mt. Abu. For 1,503 hours during five annual two- to three-month study periods between 1971 and 1975 I monitored political changes in five troops of langurs in and around the town. In the following section I will summarize the evidence—based largely on work at Abu, but drawing also on the detailed observations of Y. Sugiyama and S. M.

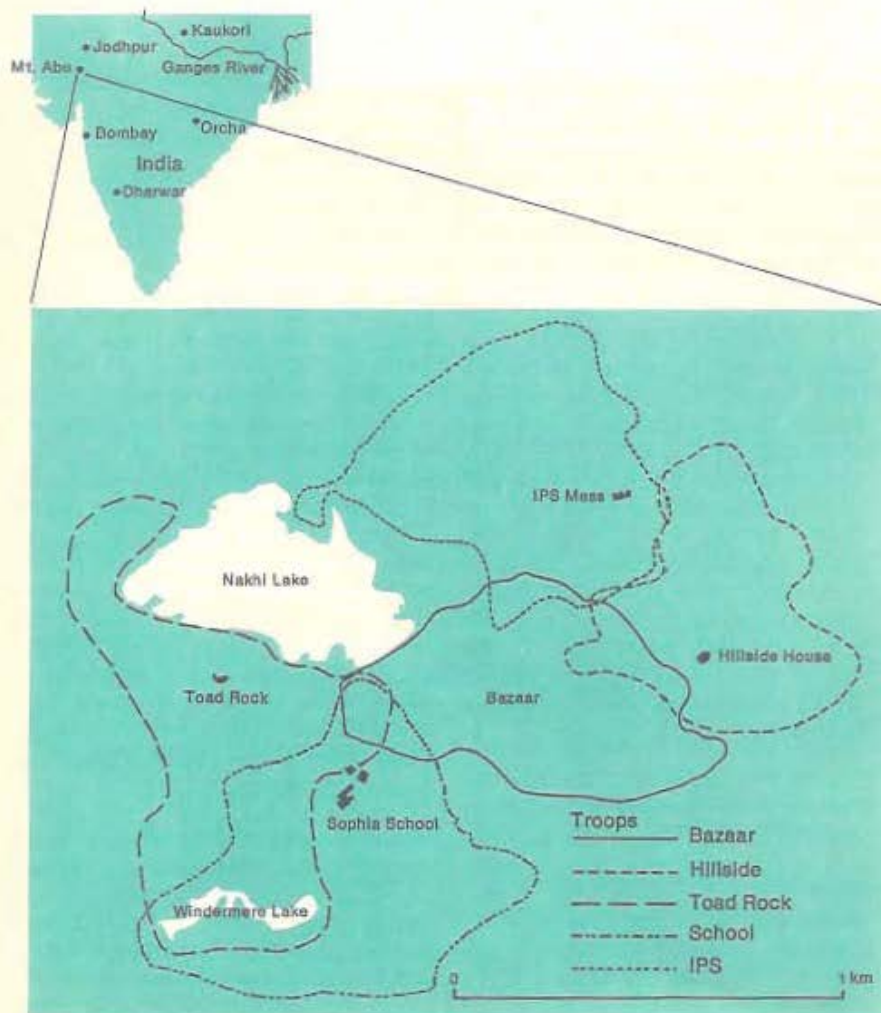


Figure 2. Over a 5-year period, the author studied five troops of Hanuman langurs in and around Mt. Abu, one of several sites on the Indian subcontinent where these widespread monkeys have been investigated.

Mohnot—that led me to reject my initial crowding hypothesis in favor of the theory that infanticide is adaptive behavior, extremely advantageous for the males who succeed at it.

## The langurs of Abu

The forested hillsides of Mt. Abu rise steeply from the parched Rajasthani plains. The town itself is an Indian pilgrimage and tourist center 1,300 m above sea level. My study concentrated on five troops in the vicinity of the town, but I will focus here on just two of these: the small Hillside troop and its neighbor, the Bazaar troop, whose name derives from the fact that these langurs spent a portion of almost every day scavenging in the bazaar (see Fig. 2).

In June 1971 the Hillside troop contained one adult male, seven adult females, six infants, and one juvenile male. In August of that year, Mug was replaced by a new male, Shifty Leftless—named for a bite-sized chunk missing from his left ear. At the time of the takeover, one adult female and all six infants disappeared from the troop. Soon after, mothers who had lost infants came into estrus and solicited the new male. Local inhabitants witnessed the killing of two infants by an adult male. Each killing took place at a site well within the range of the Hillside troop; in fact, one occurred at a location used exclusively by that group. It seemed highly probable that the missing infants had been killed, and that the usurping male Shifty was the culprit. (These events are discussed in greater detail in Blaffer Hrdy 1974 and 1975 diss.)

On my return to Abu in June 1972, I was surprised to find that the same male, Shifty, had now transferred to the neighboring Bazaar troop. In 1971, Bazaar troop had contained three adult males, ten subadult and adult females, five infants, and four juveniles. Three of these infants were

now missing. The killing of one had been observed by a local amateur ornithologist who lived beside the bazaar. The three Bazaar troop males remained in the vicinity of their former troop; the second-ranking of these bore a deep wound in his right shoulder.

During 1972, Mug took advantage of Shifty's absence to return to his former troop. At this time Hillside troop consisted of the same six adult females and their four new infants. Two females, an older, one-armed female called Pawless and a very old female named Sol, had no infants. Although Mug was able to return to his troop for extended visits, whenever Shifty left Bazaar troop on reconnaissance to Hillside troop, Mug fled. On at least eight occasions, Mug left the troop abruptly just as the more dominant Shifty arrived, or else the "interloper" was actually chased by Shifty. Typically, Shifty's visits to

Hillside troop were brief, but if one of the Hillside females was in estrus he might remain for as long as eight hours before returning to Bazaar troop.

During the periods Mug was able to spend with his former harem he made repeated attacks on infants that had been born since his loss of control. On at least nine occasions in 1972, Mug actually assaulted the infants he was stalking. Each time one or both childless females intervened to thwart his attack. Despite their heroic intervention, on three occasions the infant was wounded. During this same period, other animals in the troop were never wounded by the male. When the same male, Mug, had been present in the troop in 1971, he had not attacked infants. Similarly, during Shifty's visits to the Hillside troop in 1971, his demeanor toward infants was aloof but never hostile. Whereas Hillside mothers were very



Figure 3. This Hillside infant was conceived in 1971, during the time that Shifty was the troop's resident male, and was later killed by an adult male langur, probably Mug. The age of langur infants can be determined with some precision: between the third and fifth months of life, the all-black natal coat changes to cream color, starting with the top of the head and a little white gontee.



Figure 4. Juveniles and subadults threaten and lunge at two females from another troop. The adult male looks on calmly but does not participate.

restrictive with their infants when Mug was present, gathering them up and moving away whenever he approached, these same mothers were quite casual around Shifty. Infants could be seen clambering about and playing within inches of Shifty without their mothers' taking notice.

In 1973, Mug was joined by a band of five males. Nevertheless, the double usurper Shifty could still chase out all six males whenever he visited the Hillside troop. A daughter born to Pawless during the period when both Shifty and Mug were vying for control of Hillside troop was assaulted on several occasions by the five newer invaders; the infant eventually disappeared and was presumed dead.

By 1974, Mug was once again in sole possession of the Hillside troop and holding his own against Shifty. When the Hillside and Bazaar troops met, Mug remained with his harem. On several occasions, the newly staunch Mug confronted Shifty and in one instance grappled with him briefly before retreating behind females in the Hillside troop. Mug resolutely chased away members of a male band who attempted to enter his troop. By 1975, Mug's star had risen.

When I returned to Abu in March of that year, Shifty was no longer with

the Bazaar troop. In his place was Mug. It was not known what had become of the extraordinary old male with the bite out of his left ear. Perhaps he died or moved on to another troop, or perhaps he was at last usurped by his longtime antagonist Mug.

Mug's former position in the Hillside troop was filled by a young adult male called Righty Ear. Righty (with a missing half-moon out of his right ear) was one of the five males who had joined Mug in the Hillside troop two years previously. Since that time, Righty had passed in and out of the troop's range, traveling with other males but not (so far as I knew) attempting to enter the troop. Righty's "waiting game" apparently paid off that March, when he came into sole possession of the Hillside troop. But, as in the case of his predecessors, Hillside troop was only a stepping stone: in April 1975, Righty replaced Mug as the leader of Bazaar troop.

The first indication I had of Righty's arrival in Bazaar troop was a report from local inhabitants that an adult male langur had killed an infant. On the following day when I investigated this report, the young adult male with the unmistakable half-moon out of his right ear was present in Bazaar troop; Mug was nowhere to be found.

An elderly langur mother still carries about the mauled corpse of her infant by the following day, she had abandoned it. Righty subsequently made more than 50 different assaults on mothers carrying infants. Nevertheless, only one other infant disappeared. Five infants in the Bazaar troop remained unharmed when my observations terminated on June 20.

After Righty switched from Hillside to Bazaar troop, there followed some nine or more weeks during which the Hillside females had no resident male except for brief visits from Righty. Whenever the two troops met at their common border, Hillside females sought out Righty Ear and lingered beside him. These females were fiercely rebuffed by resident females in the Bazaar troop. Hostility of Bazaar troop females toward "trespassers" from Righty's previous harem prevented a merger of the two. The troops were still separate when Harvard biologist James Malcolm visited Abu in October 1975, but the vacuum in Hillside troop had been filled by a new male, christened Slash-neck for the deep gash in his neck.

### The evolution of infanticide

Over a period of five years, then, political histories of the Hillside and Bazaar troops were linked by a succession of shared usurpers. First Shifty, then Mug, and finally Righty switched from the small and apparently rather vulnerable Hillside troop to the larger Bazaar troop (Fig. 5). Possibly the shifts were motivated by the greater number of reproductively active females in Bazaar troop. Between 1971 and 1975, at least four different males usurped control of Hillside troop. Infant mortality in this troop between 1971 and 1974 reached 83 percent, and extinction of the troop loomed as a real possibility. In contrast, during the same period, another troop at Abu, the School troop, was exceedingly stable, retaining the same male throughout.

Figure 5. The vicissitudes of male tenure in two troops of langurs are charted during the months the author spent observing the troops at intervals during 1971-75. Observations of infants missing, killed, or assaulted coincided with tenure shifts (as shown in italics in the chart).

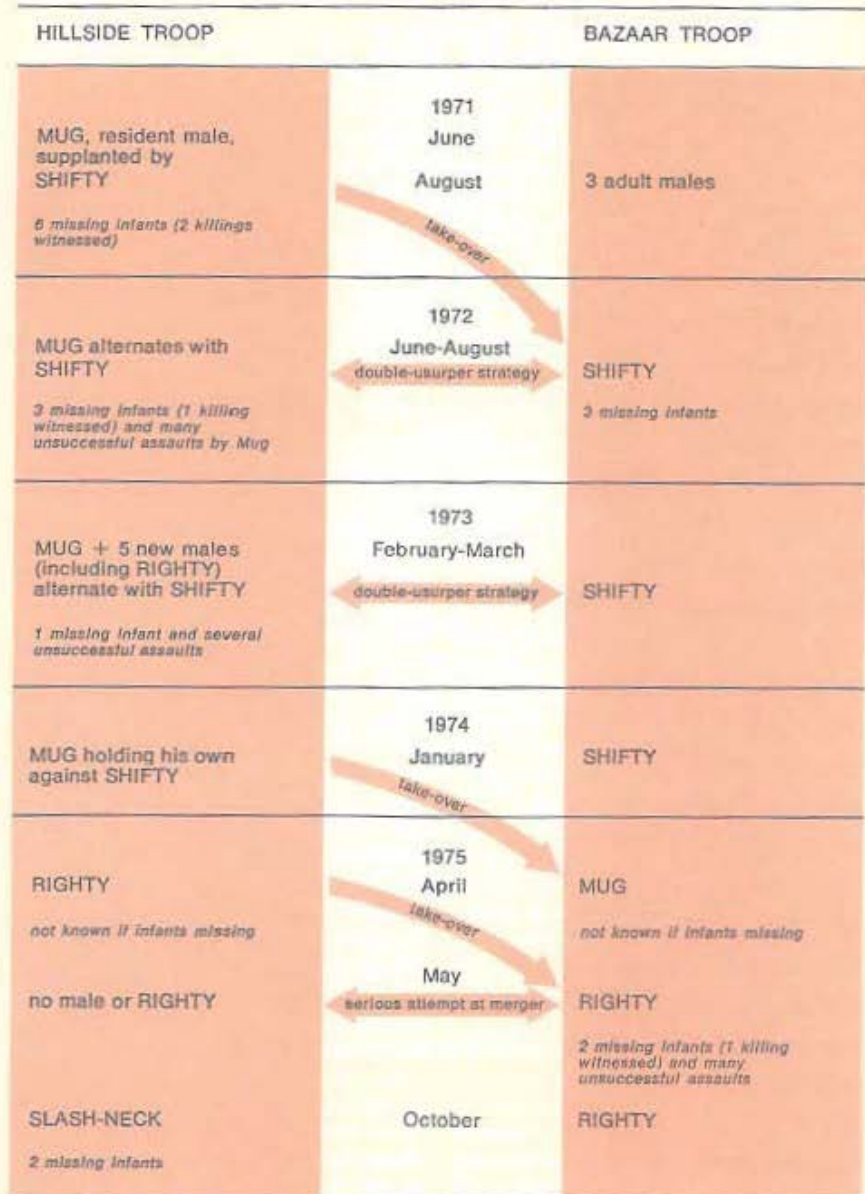
Combining all troop studies, the average male tenure at Abu was 27.5 months, a figure astonishingly close to the average tenure of 27 months calculated by Sugiyama for Dharwar (1967).

The short average duration of male tenure among langurs underlies the most crucial counterargument against the social pathology hypothesis: the extent to which adult males appear to gain from killing infants. Given that the tenure of a usurper is likely to be short, he would benefit from telescoping as much of his females' reproductive career as possible into the brief period during which he has access to them. By eliminating infants sired by a competitor, the usurping male hastens the mothers' return to sexual receptivity; on average, a mother whose infant is killed will become sexually receptive again within eight days of the death. In other words, infanticide permits an incoming male to use his short reign more efficiently than if he allowed unweaned infants present in the troop at his entrance to survive, to continue to suckle, and thus to delay the mother's next conception.

In three troops at Dharwar and Abu for which we have reliable information on subsequent births, 70 percent of the females who lost infants gave birth again within 6 to 8 months of the death of their infants, on average—just over one langur gestation period later. In the harsh desert environment of Jodhpur, however, the postinfanticide birth interval was much longer, up to 27 months.

Once infant-killing began, a usurper would be penalized for *not* committing infanticide. If a male failed to kill infants upon taking over a troop, and instead waited for those infants already in the troop to be weaned before he inseminated their mothers, then his infants would still be unweaned and hence vulnerable when the next usurper (presumably an infanticidal male) entered.

Other variations in the social system



might likewise be expected to select for changes in male behavior. For example, if the rate of takeovers were speeded up and then held constant over time, male tolerance toward weaned immatures might be drastically altered. With a faster rate of takeover, it would be unlikely that one male could remain in control of a troop long enough for immature females to reach menarche and to give birth to an infant that would in turn grow old enough to survive the next takeover. Immature females, then, would be worth no more to the usurper than young males would be, and they might compete with the productive females of his harem for resources. Under these circumstances, it would behoove a usurper to drive

out immatures of both sexes. This is precisely what occurs among a related langur species, *Presbytis senex*, living at very high densities (as high as 215 animals per km<sup>2</sup>) at Horton Plains in Sri Lanka (Rudran 1973). The ousted females travel with former male troopmates in mixed-sex bands.

Up to this point, I have not dealt with the apparent correlation between male takeovers and high population density. At both Dharwar (84-133 langurs per km<sup>2</sup>) and Abu (50 per km<sup>2</sup>), population densities are relatively high. In the desert region near Jodhpur, langurs have vast open areas available to them but tend to cluster about waterholes and garden spots. Infanticide has been reported

at all three locations, but it has been recorded for none of the areas with low densities (at Jay's Orcha and Kaukori study sites or at any of three Himalayan sites where langurs have been studied by N. Bishop, the Curtins, and C. Vogel). This finding is inconclusive, however, since observations in the low-density areas were comparatively short, ranging from several months to a year. If the correlation does turn out to be valid, a possible explanation may be the greater numbers of extratrop males in heavily populated areas. If the possibilities for male recruitment are greater at high densities, and if a band of males has a better chance of usurping a troop than a single male would, then there would be more takeovers in crowded areas.

An alternative explanation has been offered by Rudran (1973), who has suggested that takeovers occur in order to maintain the one-male troop structure and infanticide occurs so as to curtail population growth in crowded areas. Unquestionably, one-male troops and reduced infant survival are outcomes of the takeover pattern. However, if takeovers and infanticide are advantageous to the individual males who engage in them, then the above outcomes are only secondary consequences and not explanations for them.

To date, we have information on 15 takeovers, 5 at Dharwar, one at Jodhpur, and 9 at Abu. At least 9 coincided with attacks on infants or with the disappearance of unweaned infants. A conservative estimate of the number of infants who have disappeared at the time of takeovers is 39. The important point (and this is the second line of evidence against the social pathology hypothesis) is that attacks on infants have been observed *only* when males enter the breeding system from outside—even if, as in the case of Mug, they have been only temporarily outside it. Such males are unlikely to be the progenitors of their victims. In contrast to what is considered "pathological" behavior, attacks on infants were highly goal-directed. An important area of future research will be learning exactly what means a langur male has at his disposal for discriminating infants probably his own from those probably sired by some other male. Quite possibly, males are evaluating past consort relations with the

mother (Blaffer Hrdy 1976). Interestingly, infants kidnapped by females from neighboring troops were not attacked by the resident male so long as they were held by resident females from his own troop and were not accompanied by their (alien) mothers (Blaffer Hrdy, 1975 diss.).

The third line of evidence against the social pathology hypothesis is the length of time that conditions favoring infanticide have persisted. Nineteenth-century accounts describing male invasions and fierce fights among males for access to females undermine the position that langur aggression and infanticide are newly acquired traits brought about by recent deforestation and compression of langur ranges. More important (and this constitutes the fourth line of evidence), recent findings concerning other members of the subfamily Colobinae suggest that a time span much longer than a few centuries is at issue. In addition to good documentation for male takeovers and infanticide among the closely related purple-faced leaf-monkeys of Sri Lanka (*Presbytis senex*) (Rudran 1973), adult male replacements coinciding with the death or disappearance of infants have been reported for *Presbytis cristata* of Malaysia (Wolf and Fleagle, in press); *P. potenziani*, the rare Mentawai Island leaf-monkey (R. Tilson, pers. comm.); and among both captive and wild African black and white colobus monkeys (S. Kitchener and J. Oates, pers. comm.). This recurrence of the takeover/infanticide pattern among widely separated members of the subfamily in Africa, India, and Southeast Asia argues strongly for its antiquity. Though the possibility of environmental convergence cannot be ruled out, the case of phylogenetic inheritance of these traits among geographically disparate relatives is a compelling one. Far from being recent responses to crowded conditions, it appears that a predisposition to male takeovers and infanticide has been part of the colobine repertoire since Pliocene times, some ten million or more years ago, when the split between the African and Asian forms occurred.

## Beyond the Colobines

But the tale of infanticide does not stop with the Colobines. In what may be the most startling finding by pri-

matologists in recent years, we are discovering that the gentle souls we claim as our near relatives in the animal world are by and large an extraordinarily murderous lot. It is apparent now that the events witnessed at Abu and Dharwar are not aberrations. Increased observation of primates had led to an increase in the number of species in which adult males are known to attack and kill infants—and, occasionally, each other. Although murder is uncommon, cases of adults fighting to the death have been reported for rhesus, pig-tailed, and Japanese macaques, baboons, and chimpanzees, as well as Hanuman langurs.

At the time of this writing, infanticide, either observed or inferred from the disappearance of infants at times when males have usurped new females, has been reported for more than a dozen species of primates. Every major group of primates, including the prosimians, the New and Old World monkeys, apes, and man, is represented.

Not all these reports parallel the pattern of events recorded for Hanuman langurs, but many are disturbingly similar: males attack infants when they come into possession of females who are accompanied by offspring sired by another male. Typically, these are unfamiliar females. Perhaps the clearest illustration of the potential importance of previous acquaintance is provided by an experiment with caged crab-eating macaques (Thompson 1967). Here, infanticide was the unexpected outcome in a cage study on the effects of familiarity or lack of it in relations between male and female *Macaca fascicularis*. When paired with his accustomed companion and her infant, the adult male displayed typical behavior, mounting the female briefly and then casually exploring his surroundings. He entirely ignored the infant. Paired with an unfamiliar mother-infant pair, the male responded quite differently. After a brief attempt at mounting, the male attacked the infant as it lay clutched to its mother's belly. When the mother tried to escape, the male pinned her to the ground and gnawed the infant, making three different punctures in its brain with his canines.

Two suspected cases of infanticide

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Figure 6. A female langur holding a newborn infant takes food from a priest of Shiva who lives in one of the sacred caves in the hillsides surrounding Mt. Abu.

among wild hamadryas baboons were occasioned by human manipulation. In the course of capture-and-release experimentation on the process of harem formation among *Papio hamadryas* of Ethiopia, two mothers were switched to new one-male units. In one case the infant was missing a day later; in the other, the infant was seen dead, "its skull pierced and its thighs lacerated by large canine teeth." The witnessed killing of two hamadryas infants at the Zurich Zoo just after their mothers changed "owners" adds plausibility to the inference that the wild infants were similarly murdered (Kummer et al. 1974).

Less contrived perhaps is the following account of chimpanzees from the Gombe Stream Reserve in Tanzania, where a young British researcher, David Bygott, happened to be following a band of five male chimpanzees when they encountered a strange female whom "in hundreds of hours of field observation," Bygott had never seen before. This female and her infant were immediately and intensely attacked by the males. For a few moments, the screaming mass of chimps disappeared from Bygott's view. When he relocated them, the strange female had disappeared and one of the males held a struggling infant. "Its nose was bleeding as though from a blow, and [the male], holding the infant's legs, intermittently beat its head against a branch. After 3 minutes, he began to eat the flesh from the thighs of the infant which stopped struggling and calling" (Bygott 1972). In contrast with normal chimp predation, this cannibalized corpse was nibbled by several males but never consumed.

Dian Fossey's remarkable decade-long study of wild mountain gorillas in central Africa provides what may be the most dramatic instances of adult male invaders mauling infants. For several days, a lone "silverback" (or fully mature) male had been following a harem of gorillas, presumably in quest of females. At last, he made his move, penetrating the group with a "violent charging run." A pri-



marous female who had given birth to an infant on the previous night countered his charge by running at him. Halting within arm's reach of the male, she stood bipedally to beat her chest. The male struck her ventrally exposed body region where her newly born infant was clinging. Immediately following this blow, a "thin wail" was heard from the dying infant. On two other occasions, Fossey witnessed silverbacks kill infants belonging to primiparous mothers. In the best documented of these cases, the mother subsequently copulated with the male who had killed her infant (Fossey 1974; pers. comm.). To date, of the killings witnessed, only first-born gorilla infants have been seen to be victims. This could be owing to maternal inexperience, or, as I believe is more probable, to Fossey's finding that in gorilla society only young females routinely change social units. Since an older mother would in all

likelihood not join a usurper anyway, he would rarely benefit from killing her infant.

Isolated instances of infanticide by adult males have also been reported for various prosimians: among free-ranging Barbary (*Macaca sylvana*) and rhesus macaques (*M. mulatta*) (Burton 1972; Carpenter 1942) and among wild *Cercopithecus ascanius*, the red-tailed monkeys of Africa (T. Struhsaker, in press). Infanticide is suspected among wild chacma baboons (*Papio ursinus*) (Saayman 1971); wild howler monkeys (*Alouatta*) of South America (Collias and Southwick 1952); and among caged squirrel monkeys (*Saimiri*) (Bowden et al. 1967).

The explanation for infanticide need not be the same in every case, but the parallels with the well-documented



langur pattern are striking. According to the explanatory hypothesis offered here for langurs, infant-killing is a reproductive strategy whereby the usurping male increases his own reproductive success at the expense of the former leader (presumably the father of the infant killed), the mother, and the infant. If this model applies, the primate-wide phenomenon of infanticide might be viewed as yet another outcome of the process Darwin termed *sexual selection*: any struggle between individuals of one sex (typically males) for reproductive access to the other sex, in which the result is not death to the unsuccessful competitor, but few or no offspring (Trivers 1972). Crucial to the evolution of infanticide are, first, a non-seasonal and flexible female reproductive physiology such that it is both feasible and advantageous for a mother to ovulate again soon after the death of her infant and, second, competition between males such that tenure of access to females is on average short.

### Female counterstrategies

Confronted with a population of males competing among themselves, often with adverse consequences for females and their offspring, one would expect natural selection to favor those females most inclined and best able to protect their interests. When an alien langur male invades a troop, he may be chased away and harassed by resident females as well as by the resident male. After a new male takes over, females may form temporary alliances to prevent him from killing their infants (e.g. Sol and Pawless's combined front against the infanticidal Mug).

Females are often able to delay infanticide. Less often are they able to prevent it. Pitted against a male who has the option to try again and again until he finally succeeds, females have poor odds. For this reason, one of the best counterinfanticide tactics may be a peculiar form of female deceit. Almost invariably, langur males have attacked infants sired by some other male; a male who attacked his own offspring would rapidly be selected against. It may be significant then that at Dharwar, Jodhpur, and Abu, pregnant females confronted with a usurper displayed the traditional langur estrous signals: the female presents her rump to the male and

frenetically shudders her head. These females mated with the usurper even though they could not possibly have been ovulating at the time. Postconception estrus in this context may serve to confuse the issue of paternity.

After birth, an infant's survival is best ensured if its mother is able to associate with the father, or at least with a male who "considers" himself the father or who acts like one—in short, a male who tolerates her infant. In at least three instances at Abu, females with unweaned infants left recently usurped troops to spend time in the vicinity of males that on the basis of other evidence I suspected of having fathered their offspring.

If all else fails and her infant is attacked and wounded, a mother may continue to care for it, or abandon it. In several cases at Dharwar and Jodhpur, mothers abandoned their murdered infants soon after or even before death (Sugiyama 1967; Mohnot 1971). Rudran has suggested that the mother abandons her infant for fear of injury to herself and "because an adult female is presumably more valuable than an infant to the troop" (1973). It is far more likely, however, that desertion reflects a practical evaluation of what *this* infant's chances are weighed against the probability that her next infant will survive.

Under some circumstances a mother may opt to abandon an unweaned infant. In a single case from Abu, a female in a recently usurped troop who had been traveling apart from the troop (presumably to avoid the new male's assaults) left her partially weaned infant in the company of another mother and returned to the main body of the troop alone. If this was in fact an attempt to save her infant by deserting it, the ploy failed when the babysitter herself returned to the troop, some time later, bringing both infants with her. Nevertheless, both infants did survive the takeover.

Despite the various tactics that a female may employ to counter males, infanticide was the single greatest source of infant mortality at Abu. The plight of these females raises a perplexing question: How has this situation come about? Langur males contribute little to the rearing of off-

spring; apart from insemination, females have little use for males *except* to protect them from other langur males who might otherwise invade the troop and kill infants. Why then should females tolerate males at all, suffering subjection to the tyranny of warring polygynists? On the vast time scale of evolution, alternatives have been open to the female since the dawn of Colobines. Large body size, muscle mass, and saber-sharp canines might just as well have been selected among females as among males. Why should females weigh only 12 kg, on average, and not the 18 kg that males routinely do? Alternatively, female relatives could ally themselves to a much greater extent than they do. The combined 36 kg of three females operating as a united front against an infanticidal male surely should prevail. Infanticide depends for its evolutionary feasibility on the prior female adaptation of conceiving again as soon as possible after the death of an infant. If females failed to ovulate after a male killed their infants, or if they "refused" to copulate with an infanticide, the trait would be eliminated from the population.

The facts that females do not grow so large as males, that they do not selflessly ally themselves to one another, and that they do not boycott infanticides, suggest that counterselection is at work. Once again, the pitfall is intrasexual competition—this time competition among females themselves for representation in the next generation's gene pool. Whereas head-on competition between males for access to females selects for males who are as big and as strong (or stronger) than their opponents, a female who "opted" for large size in order to fight off males might not be so well-adapted for her dual role of ecological survivor and childbearer. An over-sized female might produce fewer offspring than her smaller cousin. In time, the smaller cousin's progeny would prevail.

Intrasexual competition is mitigated by the close genetic relatedness between female troop members, but it is by no means eliminated. A female in her reproductive prime who altruistically defended her kin, in spite of the cost to herself, might be less fit than her cousin who sat on the sidelines. Finally, if infanticide really is advantageous behavior for males, a female who sexually boycotted in-

fanticides would do so to the detriment of her male progeny. Her sons would suffer in competition with the offspring of nondiscriminating mothers.

For generations langur females have possessed the means to control their own destinies. Caught in an evolutionary trap, they have never been able to use them.

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