Infanticide Among Animals: A Review, Classification, and Examination of the Implications for the Reproductive Strategies of Females

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Infanticide among animals is a widespread phenomenon with no unitary explanation. Although the detrimental outcome for the infant is fairly constant, individuals responsible for infanticide may or may not benefit, and when they gain in fitness there may be considerable variation in how they gain. Sources of increased fitness from infanticide include: (1) exploitation of the infant as a resource, (2) elimination of a competitor for resources, (3) increased maternal survival or lifetime reproductive success for either mother or father by elimination of an ill-timed, handicapped, or supernumerary infant, and, finally, (4) increased access for individuals of one sex for reproductive investment by the other sex at the expense of same-sex competitors. Predicted attributes of the perpetrators (such as sex and degree of relatedness to the infant), attributes of the victim (i.e., age and vulnerability), as well as schedule of gain, vary for each class. Under some circumstances, individuals commit infanticide which does not result in any prospect for gain; such instances are considered nonadaptive or "pathological." In those cases where infanticide does on the average increase fitness, selection pressures favoring it have arisen as a result of the extensive and time-consuming investment involved in production of young, and the extreme vulnerability that characterizes infancy in many animals.

The scattered but nevertheless extensive occurrence of infanticide among primates raises the question of inter-specific variation. Factors such as seasonality in breeding, cooperation between individuals in defense of infants, marginal habitats, and low intrinsic rates of natural increase may outweigh other pressures, such as short male tenure lengths, which select for infanticide. Within the same species, infanticide may occur in some areas but not others, as evidenced by the variable expression of infanticidal behavior among Hanuman langurs. At present, the most obvious factor influencing facultative expression of the infanticidal trait is population density.

Where it occurs, sexually selected infanticide is a significant cause of mortality. As such, it has important implications for the evolution of behavior, particularly for patterns of association between males and females, for female reproductive physiology, and for the patterning of sexual receptivity by females. It is hypothesized that the threat posed by infanticide is one of several pressures selecting for a shift among higher primates away from strictly cyclical estrous receptivity towards socially determined or situation-dependent receptivity.

Key Words: Infanticide; Female reproductive strategies; Population density.

INTRODUCTION

Offspring are vital to the continued survival of any species. At first glance, it seems surprising to find selection for behavior that does not contribute to the survival of infants, adder still to find selection for behavior that actually decreases infant survivorship. Yet nature provides abundant examples, many of them paradigms for the evolutionary process: natural selection at the individual level may—at least temporarily—preempt species advantage.

The most widely reported cases of infanticide involve adult males, but adult females and even
other immatures are sometimes implicated. Infants may be killed not only by outsiders but by members of their own group, even their parents. As diverse as the perpetrators are the selection pressures that promote infanticidal behavior. Infanticide among animals cannot be understood as a unitary phenomenon.

This paper attempts to classify manifold instances of infanticide into categories with some explanatory and predictive potential. In general, examples of infant-killing by either males or females can be explained by recourse to one of five classes of explanation. The first four—exploitation, resource competition, parental manipulation, and sexual selection—all assume that infanticidal behavior is evolved and adaptive for those individuals who perpetrate the killing. The fifth class of explanation—social pathology—does not assume that infant-killing is adaptive. Cannibalism is not considered here as a separate category. Typically, cannibalism falls under exploitation of the infant as a resource, but it may also occur opportunistically in conjunction with other classes of infant-killing.

### CLASSES OF INFANTICIDE

**Exploitation**

When individuals responsible for an infant's death directly benefit from consumption or use of their victim, infanticide can be said to be a form of "exploitation": the infant itself becomes a resource, either a food resource, a protective buffer against aggression by third parties, or a "prop" for obtaining maternal-like experience.

The most obvious widespread form of such exploitation is cannibalism. The victim must be killed in order for the resource to be exploited, and infants are particularly vulnerable targets. Among some ground squirrels (Steiner, 1972), hyenas (Kruuk, 1972), occasionally in lions (Schaller, 1972), and other predatory creatures, particularly some fish and insects (Fox, 1975), cannibalism appears to be an end in itself, not clearly distinguished from predation except that immatures are more likely to be eaten than adults because of the size differential among animals that would otherwise be nearly equals.

The extensive literature on intraspecific predation in natural populations has been recently reviewed by Laurel Fox (1975). Contrary to a common misconception, cannibalism is not just an artifact of disturbed settings (e.g., Calhoun, 1962), but rather a widely spread phenomenon in natural populations, particularly among predatory fish, rotifers, and insects which live in fresh water.

Rotifers such as *Asplanchna sieboldi*, for example, provide elegant evidence for the extent and duration of selective pressures from cannibalism. Male rotifers, which are smaller than females in this group, have evolved a variety of major structural adaptations (such as protrusions in the body wall) and other features which specifically protect them from being eaten by other rotifers, including clone mates (Gilbert, 1976).

Lethal exploitation of an infant is not limited to eating it. Among various primates, for example, infants may be used as "buffers" in agonistic episodes (Deag and Crook, 1971, and especially, Popp, 1978) or as an object for "play mothering" (Lancaster, 1971): such episodes may on rare occasions lead to injury or starvation of the infant as an incidental byproduct of exploitation. Among primates, the majority of infant deaths so far attributable to adult females do not occur as a result of violence, but rather starvation. This phenomenon, known as "aunting to death," results when nonlactating females take an infant from its mother and forcibly retain it (Hrdy, 1976). As was true with the early reports of infanticide by male primates, there has been a general tendency to dismiss deaths due to "kidnap" or "aunting" as quirks or pathologies in an otherwise benign system of cooperative infant care which is primarily geared to benefit the infant. However, this view accords with neither the abusive treatment sometimes dealt to borrowed infants (Hrdy, 1977), nor with accumulating case histories of infant fatalities (Quattr, 1977).

In most cases of infant transfer between females belonging to the same group, the mother is able to retrieve her infant without difficulty. Sometimes, however, as has been reported on multiple occasions for rhesus macaques (Hinde and Spencer-Booth, 1967; Quatt, 1977) and squirrel monkeys (Rosenblum, 1972) and in a single case among wild Lowe's guenons (*Cercopithecus campbelli lowei*) (Bourlière et al., 1970) and captive colobus monkeys (Horwich and Manski, 1975), the infant is taken by females who, because of their ability to dominate the mother, prevent her from retrieving her infant.
Infanticide among Animals

Where observers did not intervene, infants "kidnapped" by nonlactating females have died.

The threat of losing an infant to a more dominant female may contribute to maternal possessiveness, and restrict the occurrence of postnatal infant-sharing to species with less pronounced dominance hierarchies (Hrdy, 1976; McKenna, in press). Only among colobines, where dominance relations are typically less rigid than among macaques or baboons, do mothers routinely give up their infants in the first hours after birth.

Among colobines such as the Hanuman langur, mothers are virtually always able to retrieve infants from troopmates, although not necessarily from females belonging to different troops. Intertroop kidnappings that resulted in prolonged separation from the mother or starvation have been reported for Dharwar, Jodhpur, and Mount Abu (Sugiyama, 1965; 1966; Mohnot, 1974; Hrdy, 1977).

Resource Competition

This model applies to competition between individuals (often females or lineages) for physical resources such as food or nest sites. Typically, such resources are related either directly (in the case of nest sites) or indirectly (as in parental food supplies) to the production or rearing of offspring. The resource competition hypothesis predicts that the death of an infant will on the average result in increased access to resources for the killer and his or her descendants. Because other members of a population often stand to gain from reduced pressure on resources, animals may gain from infanticide in this respect even when resource competition is not the primary selective agent for infanticide. In reviewing the literature on cannibalism, Fox, for example, stresses the multiple advantages for animals which prey on conspecifics: "The cannibal gains a meal at the same time that it eliminates a potential competitor and perhaps a potential conspecific predator as well. Because population size is reduced, more food will be available to each survivor. . . ." (1975, p. 97).

Because of their vulnerability, infants are an obvious target for extermination, particularly among fish and insects where parental protection may be absent. In mammalian species where mothers remain near and protect their young, orphans and offspring of subordinate females may be particularly at risk. Among wild dogs, pups born to a subordinate pack member may be murdered by the dominant female, thereby garnering for her own offspring a larger proportion of the pack's resources, including not only meat brought back by other pack members but the milk of the mother who lost her pups (van Lawick, 1972). Mother's milk may also figure in infanticide by female elephant seals who attack and kill infants who become separated from their mothers: such "orphans" survive only by stealing milk from other mothers and, hence, compete with the legitimate offspring of those females (LeBoeuf and Briggs, 1977).

Natural observations of direct attacks upon infants by primate females belonging to the same group have been confined to the great apes, and involve cannibalism. In three cases of intracommunity infanticide by female chimpanzees, the mothers of the infant killed (the same female "Gilka" in two cases) suffered from a disability—in both cases partial paralysis due to polio—and both females were lower in rank than the females who killed their infants (Goodall, 1977). A suspected case of cannibalism among wild gorillas (Fossey, 1976, and personal communication) was similarly attributed to a dominant female. By and large, these attacks follow the pattern reported for wild dogs in which a dominant female murders the offspring of a subordinate. It is of some interest therefore, that in wild dogs, gorillas, and chimpanzees, females, or else both males and females, move between communities. This contrasts with the far more typical mammalian pattern of sedentary sisterhoods with migrating males (Frame, 1976; Harcourt et al., 1976; Tutin, 1975, Wrangham, in press). One outcome of such a breeding structure would be lower degrees of relatedness among females in wild dog packs, gorilla troops, or chimpanzee communities, and hence the possibility of harming a close relative would be reduced.

Although the chimpanzee cases may represent elimination of offspring in competing lineages, it is not clear what resources are at stake. Possible additional explanations include exploitation of the infant as a food source, but it is not known how important the food value of a cannibalized infant might be.

In some cases, offspring may be associated with some particular resource. Paul Sherman's observations of Belding's ground squirrels
(Spermophilus beldingi) provide a classic mammalian case in point (1976, 1978, and in press). Among these squirrels of the high California Sierras, infanticide by females is the leading cause of mortality. By an extremely conservative estimate (that is, only killings which were directly witnessed, and none which were inferred, were counted) 8% of infants born are killed by conspecifics. The major killers were adult females distantly related to their victims. Females who lost infants left their seemingly "unsafe" borrows. Sherman hypothesizes that abandoned nest sites become available to the infanticidal female.

A number of animals, including hyenas, wolves, chickens, gese, and various primates (Mech, 1966; Kruuk, 1977; Bygott, 1974; Southwick et al., 1974; Wilson, 1975) exhibit hostility towards strangers of other groups. Southwick et al. have labelled this behavior "xenophobia." Instances of infants being killed in the course of intergroup hostilities have been recorded for rhesus macaques at Cayo Santiago (Carpenter, 1942; D. Sade, personal communication) and, in one instance involving an adult female among Hanuman langurs at Poonnamruwa, Sri Lanka (S. Ripley, personal communication). In addition, Camenzind (1978) reports infanticide by intruding females among coyotes. Specific selection pressures favoring xenophobic infanticide have not been identified, other than marginal benefits to be gained from reduced pressures on resources used by adjacent groups. Not surprisingly, xenophobic infanticide occurs opportunistically. An infant which becomes separated from its mother during an intertroop encounter may be killed, almost incidentally, in the course of the conflict. By contrast, in the wild dog case cited above—which was recorded in detail in a film by van Lawick—the behavior of the killer was systematic, goal-directed, and to an anthropocentric viewer premeditated, since the narrative indicated that the killer waited for the opportunities to enter the burrow containing the pups unobserved by the mother. The paucity of reports of xenophobic killing of alien infants may attest to the minute gain to individuals from elimination of infants in other groups, and hence, the weak selection pressure for such behavior.

The most common and intense competition for resources not infrequently occurs among members of the same family. There is an extensive literature for example on brood reduction among raptorial birds such as hawks, buzzards, crows, owls, skuas, and perhaps especially, eagles (Lockie, 1955; Schuz, 1957; von Wendland, 1958; Ingram, 1959; Meyburg, 1974; Procter, 1975). In several eagle species (e.g., Aguila pomarina, A. verreauxi), two eaglets are hatched, but almost invariably only one fledge. The extraordinary aggressiveness between eaglets of the same eyrie among golden eagles (A. crysaetos) has led observers to the conclusion that one eaglet was murdering the other, and the term "cainism" is used to describe this phenomenon (von Wendland, 1958). In fact, however, as Bernd-Ulrich Meyburg (1974) points out in his review of sibling aggression among nestling eagles, the actual killing of one eaglet by another is probably rare. Instead one hatching (typically the firstborn) contributes indirectly to the demise of the other hatchling through intimidation which predisposes the second eaglet to die of starvation or exposure. Similar patterns apply to other raptors with slight variation. In some cases, the dead hatchling is eaten by siblings, parents, or both. In his 1959 review of juvenile cannibalism among birds of prey, Collingwood Ingram pointed out that such "fratricide" is made feasible by marked disparity in age and size. Since staggered production of young is probably a parental strategy to allocate reproductive effort according to available resources, allowing parents to focus on just one infant if food is in short supply, it becomes difficult in some of these instances to separate fratricidal cannibalism from parentally manipulated infanticide.

Parental Manipulation

The death of an infant and termination of parental investment will sometimes improve the chances for survival of either the mother or existing offspring, or otherwise lead to greater net reproductive fitness of either the mother or the father. Such circumstances include the destruction of imperfect or debilitated offspring whose chances of survival and reproduction would be poor: suboptimal ecological conditions or dangerous circumstances which might make it advantageous for a parent to defer parental investment: existence of older offspring whose future would be jeopardized if parental resources were diverted to a new infant: and, mar-
riage or mating potentialities, or patterns of resource use, that would make one sex of offspring less valuable than another. Examples of infants being killed or abandoned for each set of conditions can be found in the ethnographic record for the human species and have been reviewed by Richard Alexander (1974) and Mildred Dickeman (1975). Dickeman (in press) explores in depth the pressures for preferential elimination of female infants in stratified human societies where hypergamy ("marrying up") is the norm.

In some cases, a mother confronted with poor or dangerous conditions for childrearing may abort, or, where physiologically possible, reabsorb the foetus prior to birth (see Baird, 1945; Roberts and Lowe, 1975, for humans; and Bruce, 1960; Stehn and Richmond, 1975; Mallory and Brooks, in preparation; and Labov, 1978, for rodents). Similarly, it has been suggested that the marsupial style of viviparity may be an adaptation to uncertain environments which permits termination of investment in a given infant without the attendant risks of abortion while also providing the mothers flexibility in timing the discard (Low, 1978). For example, a mother kangaroo closely pursued may jettison joeys from her pouch, thereby eliminating an encumbrance and perhaps simultaneously distracting the predator (Ealey, 1963, cited in Low, 1978). Even where parental investment is not terminated outright, nurture may be reduced, and offspring neglected, as in the case of some humans (Daly and Wilson, in press).

In rare instances, exploitation of the offspring as a resource may increase future breeding opportunities for the parent. Cannibalism of fertilized eggs by a three-spined stickleback father guarding his own eggs may be such an example (Rohwer, 1978). The male stickleback benefits from consuming his own genetic investment by staying in competitive condition for subsequent brood cycles at the expense of whichever female's cytoplasmic investment is parasitized. Not surprisingly, parental cannibalism appears to be related in some cases to social conditions as well as availability of resources (which are often related). The success of litters of Norway rats (Rattus norvegicus) was found to be related to social rank of the parents. Low ranking, scarred females ate more than 60% of their young, while high ranking, unscarred females weaned all of their offspring (Boice, 1972; cited in Fox, 1975).

Ultimately, most instances in which parents destroy or consume their own offspring relate in some way to resource availability. For example, if resources and parental energy were limitless, there would be little (if any) penalty attached to rearing defective offspring. The justification for separating "parental manipulation" and "resource competition" into different explanatory categories derives from the concept of parental effort which combines utilization of material resources with other less tangible costs to the parent, such as risk taking and time (Williams, 1966; Low, 1978; and references therein). In poor or uncertain environments, continued investment by the parent in defective offspring (or alternatively, nondefective offspring born at a bad time), which had low productive value, would be heavily penalized not only because of the environmental resources deflected to a poor bet, but because of the cost to the parent in terms of lifetime allocation of effort in the production and rearing of offspring. Whether infanticide by parents is viewed as a subset of "resource competition" or as a separate category, some distinction is worthwhile, since attributes of both the perpetrators of infanticide and their victim will differ in important ways. In the case of parental manipulation, the victim is a close relative and age, dependence, quality of infant, and amount of parental investment necessary for survival are all crucial, while in the case of resource competition, the victim is typically unrelated, parents are predicted to resist if present, and vulnerability of the victim is the important attribute.

Sexual Selection

Competition between members of one sex for reproductive investment by the other sex may make it advantageous for an animal (usually a male) to destroy another animal's offspring. This sexual selection model relies on arguments laid out by Charles Darwin (1871) and later refined by Robert Trivers (1972). It predicts that (1) infant-killing will be directed at offspring unlikely to be direct descendents of the killer, thereby reducing the reproductive success of competitors, and (2) that, on average, elimination of the infant increases the infanticidal's male's own opportunities to breed, typically by shortening the interval until next ovulation in the mother of the infant killed.
Typically, as in the case of parental manipulation, infants are killed during the period of maximal parental investment (e.g., lactation). Whereas in the case of exploitation of the infant as a resource, or elimination of a competitor for resources, vulnerability of the victim is paramount, in sexually selected infanticide, age of the infant is crucial.

In rare instances, competition for reproductive investment by the opposite sex may apply to infanticide by females, for example in sex-reversed species where females compete for parental investment by males (Trivers, 1972). The button quail (Turnix sylvatia) may provide such an example. Females compete for male services and are responsible for the destruction of eggs laid by other females (Hoesch, 1959).

To date, the only published study which has examined predictions of the sexual selection hypothesis under controlled conditions is that of Mallory and Brooks with collared lemmings (Dicrostonyx groenlandicus). Three sets of 16 females with newly born litters were exposed to either a strange male, or to the “stud” male with whom the mothers had previously mated. An additional group of females with three-day-old infants were exposed to a strange male, and finally, 16 females with new litters were allowed to rear their infants without interference, as a control. Forty-two percent of the day-old newborns, and 13% of the three-day-old infants exposed to a strange male were killed by him. None of the infants exposed to their father or in the control group were killed (Mallory and Brooks, 1978). Elapsed time till the next litter, his own, averaged 21 days when the male killed the infants, compared to an average of 28 days if infants were not killed. As in house mice (Mus musculus), pregnant females exposed to strange males may reabsorb foetuses, a phenomenon known as the “Bruce effect.” Quite possibly, the Bruce effect represents a maternal strategy to reduce—and even partially recoup—her investment in offspring liable to be killed; Jay Labov (1978, and in preparation) details evidence supporting this hypothesis.

In the case of collared lemmings, both predictions from the sexual hypothesis are met. Male attacks are aimed exclusively at unrelated infants and death of infants reduces the period of time till the mother gives birth again. As Mallory and Brooks point out, lemmings live in the Arctic where the breeding season is short: time would be a critical factor in reproductive success for both males and females who, with luck, can produce two litters in a summer.

The conclusive nature of the lemming results, and especially the male’s tolerance for his own offspring, are all the more remarkable given the artificial conditions of the experiment. Evidence from other taxonomic orders, while less precise, has been collected under more realistic conditions. Infanticide has been reported among Serengeti lions (Panthera leo) by Schaller (1972a; 1972b) and Bertram (1976) and a diverse array of wild primates including species from both the cercopithecine and colobine branches of the Old World monkeys, the Great Apes, and a single genus (Alouatta) from the generally little-known New World monkeys (discussed in Section “Intraspecific Variation in Infanticide”). In both lions and the primate examples, males kill infants when they enter a new breeding situation from outside it. Based on limited information available for Hanuman langurs (Presbytis entelus) at Dharwar (Sugiyama, 1965) and Mount Abut in western India (see Map 1), males apparently do gain from infanticide; in three troops where post-infanticide birth intervals were known, 70 percent of the females who lost infants gave birth within eight months—just over one gestation period (6.5 months) later (Hrdy, 1974). Such gains may be habitat-specific. In the harsh near-desert environment at Jodhpur, the post-infanticide birth interval from a small sample of four cases was longer (17 months), and up to 27 months in one extreme case (personal communication from S. M. Mohnot). Duration of interbirth intervals, as demonstrated by comparisons between captive and wild primates, is highly dependent on food availability and other factors: monkeys in zoos, for example, typically have shorter interbirth intervals than their wild counterparts. More field evidence on average birth spacing in different environments and under different social conditions is needed to specify how much, in terms of reproductive effort by females, males gain from infanticide.

On a theoretical level, there can be little question that males gain, provided the interval between births is shortened if an infant dies before weaning, as has been demonstrated for wild savanna baboons (Altman et al., 1978) and for humans (Ring and Scrapp, 1973; and other references reviewed in Hrdy, 1977). A recent computer simulation by Chapman and Hausfater
based primarily on data from Dharwar and Mount Abu, calculates the reproductive advantage for males who eliminate unweaned infants at various tenure lengths (cited in Hausfater, 1978; and in press). The model makes explicit the gain to males from infanticide in the langur breeding system under conditions such as those that prevail at Dharwar and Abu where takeovers occur on average every 27 months.\(^1\) According to the simulation, the infanticidal trait, once evolved should sweep through the population under those conditions. The simulation also points to the existence of tenure lengths at which infanticide will not be advantageous.

If infanticide is a male reproductive strategy, the question arises of how males avoid killing their own offspring. The cost to a male of killing his own offspring would be far greater than the "error" of permitting a competitor's offspring to survive. Naturally occurring experiments among langurs provide two lines of evidence suggesting that it is the female rather than the infant who provides langur males with the cue to attack or tolerate her infant. As reported by Sugiyama (1965), Mohnot (1974), and Hrdy (1977), infants are sometimes kidnapped from a neighboring troop and taken by females back to their own troop. Kidnapped offspring are unfamiliar, and almost certainly not sired by the resident male, and yet the infant is never attacked while in the possession of familiar females. Secondly, infants that were probably not sired by a usurper but that were born into a troop after his takeover are not attacked (Sugiyama, 1966; Hrdy, 1977). These observations are compatible with an experiment by Thompson (1967) with caged Macaca fascicularis, the crab-eating macaque, indicating that only the offspring of unfamiliar females would be attacked. There are of course difficulties in interpreting captive observations, particularly since infanticide has never been observed in the wild among these evasive Southeast Asian forest dwellers. Nevertheless, there is preliminary evidence indicating that Thompson's findings may be relevant to the natural history of this species. Several primatologists have independently reported the occurrence of male invasions and takeovers among wild M. fascicularis (Wheatley, 1978; personal communication from C. and E. Shurmann). In addition, there are a number of different reports of infanticide for this species in captivity (Washburn and Hamburg, 1967; Angst and Thommen, 1977; personal communication from Elizabeth Larsen of the Primate Research Colony, Kuala Lampur, Malaysia; and N. Herrenschmidt of the Primatological Research Station, University of Strasbourg, France). Angst and Thommen have catalogued 16 instances in which caged crab-eating macaque males attacked and wounded infants, resulting in the death of six. Thirteen of the infants attacked were offspring of a preceding male: only three were sired by the male who attacked them.

So far as the human case is concerned, there is little or no reliable evidence to support the hypothesis that human males have been selected to murder infants in order to decrease the reproductive success of competitors and increase their own—the most widely reported form of infanticide among other primates. As discussed above, the majority of known human cases fall into the category of parental manipulation, and economic constraints and sex preferences figure importantly (Alexander, 1974). Typically, the parents themselves decide to terminate investment in an infant. Occasionally, a male may kill an infant fathered by some other male (examples are reported for Eskimos, Balikci, 1970; among the Tikopia, Lorrimer, 1954; and among the Mundurucu, Murphy and Murphy, 1974, cited in Hrdy, 1977). In our own society, infants with unrelated males in the household may be very slightly more at risk from abuse (Gil, 1970, discussed in Hrdy, 1976; Daly and Wilson, in press) but, by and large, developmental and economic factors in the lives of the adults involved are primary (Kempe and Kempe, 1978), and adequate evolutionary explanations for child abuse remain elusive. To date, Daly and Wilson (in press) provide the only serious effort to understand child abuse from an evolutionary perspective. I know of only one description of the actual murder of children by invading males, reported by an eye-witness among the Yanamamo tribe.

\(^1\) It should be noted, however, that in real life there is great variation from troop to troop. For example, in the case of a particularly vulnerable troop (Hillside troop, described in Hrdy 1977) the minimum rate of takeovers between 1971 and 1979 was at least every ten months, compared to minimum estimates for more stable neighboring troops (the School and Toad Rock troops) of once every 7.8 years. These estimates were based on the assumption that if the same male was present from year to year, no takeover had occurred (unpublished field notes of S. Hrdy and D. Hrdy for 1977 and 1979).
of Brazil (Biocca, 1971). More commonly, Yanamamo mothers are kidnapped, while their infants left behind are not killed. However (as Yanamamo women themselves are aware), this is functionally equivalent to infanticide since unweaned infants separated from their mothers typically starve (Chagnon, 1968). Interestingly, Yanamamo society is characterized by raiding for women and by the tendency for a few males to be disproportionately represented in the gene pool of succeeding generations (Neel, 1970; Chagnon, 1972). Apart from the oft-cited Yanamamo case, other instances derive from literature (notably, the story of Herod who "sent forth and slew all the children that were in Bethlehem, and in all thecoasts thereof, from two years old and under," in Matthew 2:16, and the command of Pharaoh that all Hebrew sons should die at birth, Exodus 1:16) or from the rumors and propaganda about genocide that accompany war.

Social Pathology

Even evolved behaviors, which on average are adaptive, are not necessarily so under all circumstances. Put another way, an adaptive strategy is probabilistic: animals sometimes make mistakes—often for no reason more mysterious than an inability to predict the future. Such "mistakes" cannot properly be considered pathological and belong to other categories. Technically speaking, the classification "pathological" applies to behaviors which could not evolve because on balance they decrease the individual and inclusive fitnesses of infanticidal animals. In practice, however, it is extremely difficult to discriminate such behaviors from mistakes. Take, for example, a captive animal who is disturbed by her keepers while giving birth: she responds by devouring her own offspring. Is this deranged behavior, or have some animals been selected to respond to danger and potential threats to her infant by eliminating the current offspring (like the pursued kangaroo who jettisons her joey) and deferring further parental investment until a more opportune birth?

Despite this difficulty, social pathology has been widely invoked to account for infanticide among primates (Warren, 1967; Curtin, 1977; Dolhinow, 1977; Curtin and Dolhinow, 1978; 1979). Applications of the hypothesis range from the nearly incontestable position that wild animals sufficiently stressed under artificial conditions, particularly in captivity, may exhibit unnatural, destructive, and even self-destructive behaviors, to the extreme position that any destructive behavior must be maladaptive (Dolhinow, 1977). Hence, infanticide among primates is regarded as an epiphenomenon, a byproduct of abnormally high levels of aggression and social "chaos." As it is applied by its major proponents (e.g., see Curtin and Dolhinow, 1978; 1979), the social pathology hypothesis predicts that infanticide should be limited to areas recently disturbed (typically by humans). According to Curtin and Dolhinow, behaviors, and particularly infant deaths occurring in the course of such "chaos," will not be predictable. Infant deaths will simply be a consequence of their increased vulnerability.

INTERSPECIFIC VARIATION IN INFANTICIDE

In no species is infanticide a common event. When it occurs, the sequence of events may transpire in the space of minutes. A lethal attack on an infant by an adult male langur which was witnessed by S. M. Mohnot took under three minutes. Not surprisingly, records of this phenomenon are scanty and often incomplete. With the exception of the exemplary study by Paul Sherman—a study which involved a team of researchers monitoring 1,981 animals at a single site over a period of years—much of the evidence on infanticide is based on isolated cases, and on inferences derived from witnessed attacks which were followed by disappearance of infants. Existing reviews of infanticide among mammals focus on the relatively well-studied order Primates (Angst and Thommen, 1977; Hrdy, 1977). The majority of these cases involve infant-killing by males and appear to fit the sexual selection pattern: discussion here of interspecific variation will focus on this evidence only.

In the roughly 16,000 hours that Hanuman langurs have been studied, some 46 infants have disappeared when males entered troops from outside. In the type case, reported by Yukimaru Sugiyama at Dhawar (1965a), a band of males usurped a bisexual troop and ousted the resident male. Subsequently, one of the invaders drove out all other males. This new "leader" bit to
Infanticide among Animals

death unveaned infants presumably sired by the former resident. Mothers resumed cycling and copulated with the usurper (1965b).

By comparison with *Presbytis entellus*, other members of the subfamily Colobinae have scarcely been studied, but even from preliminary observations it is apparent that male takeovers and infanticide occur in other colobines. Rasanayagam Rudran (1973) has reported adult male replacements accompanied by the wound- ing or disappearance of infants among purple-faced langurs (*Presbytis senex*) in Sri Lanka. Similar patterns have been reported for *P. cristata* in Malaysia (Wolf and Fleagle, 1977), and in a single, problematic case among the rare Mentawei Island leaf-monkey (*P. potenziani*) (personal communication from R. Tilson). A continent away, in Africa, John Oates has recorded the disappearance of infants coincident with male takeovers among *Colobus guereza* (1978).

Outside of the Colobinae, the highest incidence of infanticide among wild primates is among the great apes. As the work of Fossey among gorillas (*Gorilla gorilla beringei*) and Goodall among chimpanzees continues, these apes are checking in with a record of infanticide made even more impressive by the comparatively small numbers of births among apes. In some 7,000 hours of observation, Dian Fossey witnessed three cases of infanticide by adult males, and inferred three others. In the best documented cases, the mother subsequently copulated with the male who killed her infant (Fossey, 1974; 1976; personal communication).

The gorilla reports indicate that infant killing is not necessarily confined to species in which males drive out other males and usurp harems, since the typical pattern for gorillas is for an extra-troop male to ‘steal’ or lure away young females from an established group without taking over the group itself. The same point is driven home by accumulating evidence for infanticide and cannibalism among chimpanzees, a species with a multimale breeding system in which females initiate transfers between communities. Five cases of infanticide by adult males have been reported for chimpanzees at the Gombe Stream Reserve (Bygott, 1974; Goodall, 1977). Researchers at the Budongo forest in Uganda and in the Mahale mountains of southern Tanzania have witnessed similar instances of adult males killing and cannibalizing infants (Suzuki, 1971; Nishida, 1979; Goodall, 1977, reviews this evidence). In virtually all cases where details were known, the mother of the infant belonged to a different community from the males who killed her infant. Based on the reports of her field assistants, Goodall believes that “attacks which led to the killing of stranger infants were aimed as much (or more so) at injuring the mother as her infant.” In support of conclusion that the killings reflect xenophobia, Goodall cites (1) observations of a chimpanzee which became separated from its alien mother and was subsequently “rescued” by a resident male and (2) observations of attacks on a strange female even after her infant was killed. However, on the basis of similar evidence from the Mahale mountains population of chimpanzees, Toshisada Nishida attributes infanticide and cannibalism there to reproductive advantages gained by males (1979).

The langur pattern of male takeover and infanticide is paralleled almost exactly in the case of redtailed monkeys (*Cercopithecus ascanius*) studied in the Kanyawara district of the Kibale forest in Uganda (Struhsaker, 1977; 1978) with two important exceptions. First, Struhsaker’s site is one of the least disturbed forest habitats where monkeys have ever been carefully studied. Secondly, the two infants killed were also partially cannibalized by the new male. Other cases of infanticide occurring after adult male replacements include Rudran’s observations among Venezuelan howler monkeys, *Alouatta seniculus* (1979; see also suspected cases among *A. palliata* in Collias and Southwick, 1956).

Hence, adult male infanticide has been reported for all the major groups of higher primates: the Old World monkeys, the New World monkeys (in the genus *Alouatta* only), and the Hominoidea (apes and man). These cases appear to primarily fit the sexual selection hypothesis, with several possible exceptions. Patterns of infanticide among chimpanzees and redtail monkeys, where the victim is eaten, might also suggest exploitation of the infant as a food resource, though in neither case is there any estimate of the food value of the infant for conspecifics. Moreover, some of the evidence for infanticide among howler monkeys fails to fit predictions.

* Fox (1975) reviews additional cases of primarily herbivorous or granivorous animals which engage in cannibalism.
from the sexual selection hypothesis. Rudran, who first observed infanticide in this species, favors an explanation based on resource competition. Rudran hypothesizes that howlers are food-limited and an invading male is eliminating vulnerable immatures who would subsequently compete with his own offspring. Rudran notes for example that in several male takeovers accompanied by infanticide, the usurper did not appear to gain increased reproductive opportunities (1979: in preparation). In the best documented of these cases, the usurper was lethally wounded in a fight with the former leader, and it was the former resident who mated with females whose infants had been killed by his competitor. Future observations should be aimed at clarifying whether howler males do or do not on average gain reproductive advantages from infanticide, and whether the males in Rudran's sample were typical or just "unlucky." Since females as well as males move between groups in howler societies, one would predict on the basis of the resource competition hypothesis that incoming individuals of either sex, not just males, would kill distantly related immatures if the opportunity arose. Furthermore, vulnerability of the victim rather than age should be paramount. By contrast, in sexually selected infanticide, the gain to the male is inversely correlated with the age of the victim. Among Presbytis entellus, no male has ever been observed to kill a weaned infant.

According to the sexual selection hypothesis, infant-killing is a reproductive strategy whereby an invading male increases his own reproductive success at the expense of the former leader or dominant male (who would typically be the father of the infant killed), the mother, and of course the infant. Close relatives of the infant would be expected to resist; such defense imposes a potential cost upon the infanticidal male. Hence, on average, the gain to the male must outweigh such risks if infanticide is to evolve. Crucial to the evolution of infanticide are factors which augment the relative gain to a male from eliminating unweaned infants. For example, sexually selected infanticide depends for its evolutionary feasibility on a flexible female reproductive physiology such that it is both feasible and advantageous for a mother to conceive again soon after the death of an infant. There would be little reproductive gain for a male who killed an infant among strictly seasonal annual breeders, such as rhesus macaques. At whatever point he killed the infant, the timing of the mother's next conception would be roughly the same. Similarly, circumstances promoting infanticide—for example, male takeovers resulting in replacement of one adult male by another—may not be feasible in marginal environments where the energetic costs for one male to aggressively exclude another are prohibitive. An example might be the high altitude site of Solu Khumbu at 3,500 meters in the Himalayas, where invading males do not completely drive out their competitors (Boggess, 1977). By contrast, infanticide would be most advantageous under conditions where male replacements occurred and the tenure of male access to females was on average short, and where females responded to loss of an infant by conceiving again as soon as possible, regardless of season.

One interesting question to arise from a comparative approach is why infanticide is so rare among savanna baboons—especially since infanticide can be easily brought about by the artificial introduction of new males in another member of the genus Papio, the harem-dwelling hamadryas baboon (Zuckerman, 1932; Kummer et al., 1974; Angst and Thommen, 1977). In the thousands of hours that Papio ursinus, P. anubis, and P. cynocephalus have been studied, there have been only a very few, isolated cases of adult males injuring or killing infants (e.g., at Gilgil, Kenya personal communication from N. Nicolson; and at Amboseli, Kenya, in an incident which involved a crippled, older infant, personal communication from G. Hausfater). Such isolated instances have occurred when the infant was some distance from its mother, and hence the cost to the male from adult retaliation greatly reduced. Despite the superior fighting abilities of male baboons relative to females, a wild male baboon has never been known to incur the risk of attacking an infant in the possession of its mother, as wild langur, gorilla, chimpanzee, and howler monkey males have been known to do. Altman et al. (1978) have shown that baboon birth intervals are significantly shortened by loss of an unweaned infant. Based on the work of the Altmanns, Hausfater, and others (see Hausfater, 1975; and references therein), it is apparent that male baboons routinely move between troops and hence enter
troops composed of females whose offspring were sired by some other male.

What has countered selection pressures for infanticide in these species? Explanations to date all focus at some level on the multimale troop organization of savanna baboons. It has been suggested for example that male takeovers and infanticide may be a phenomenon characterizing one-male social systems (see for example, Struhsaker, 1977). However, it is clearly insufficient to argue that a multimale breeding structure by itself precludes the evolution of adult male infanticide since it has not done so among chimpanzees or crab-eating macaques. Furthermore, some langur and howler monkey troops are multimale. To date, three hypotheses have been proposed to explain the absence of infanticide among savanna baboons. (1) It is possible that male baboons entering troops are following their fathers and brothers from troop to troop; hence, the inclusive fitness of a male might be reduced by infanticide. This hypothesis predicts an extremely inbred population of baboons. (2) Terrestrial, savanna-dwelling baboons are uniquely dependent on cooperation from other adult males in defending their troop from predators such as leopards (as is the case at Amboseli, for example). If having a reproductive stake in the troop (such as the presence of his own offspring) is one of the incentives for male defense (as suggested by Popp, 1978), then any male who eliminated the offspring of his rival would jeopardize effective cooperation in troop defense. That is, any male who killed offspring belonging to a male still present in the troop would reduce the stake that male had in risking his life to defend the troop. Hence, all infants in a troop containing an infantilical male (including his own) would have been less likely to survive. This hypothesis predicts that removal of a male’s infants from the troop will decrease his participation in troop defense. (3) Based on her field observations at Gilgil, Kenya, Smuts has suggested that a baboon male would be forestalled from killing another male’s infants by the protective presence of other adult males and females. According to Smuts, female relatives who mobbed the attacking male would quickly be joined in their defense of the infant by other adult males, including relatives, consorts, or potential consorts of the mother. Clearly, the presence of multiple males is an element in this explanation, but it also relies upon the strong affiliative tendencies which characterize baboon social organization (Smuts, in preparation).

**INTRASPECIFIC VARIATION IN THE EXPRESSION OF INFANTICIDE**

With the exception of savanna baboons, rhesus, and Japanese macaques, infanticide by adult males is a recurrent phenomenon among each of those primate species which have been studied for ten thousand or more hours (i.e., Hanuman langurs, chimpanzees, gorillas, and howler monkeys). It is apparent however that within each of those well-studied species, infanticide is not equally likely to occur in all populations. To date, *Presbytis entellus* provides the broadest documentation for such intraspecific variation. At Dharwar, Jodhpur, and Mount Abu, male takeovers and infanticide appear to be routine or regular occurrences (Sugiyama, 1967; Mohnot, 1971; 1974; Hrdy, 1974; 1977; Makwana, in press). Calculations for Dharwar and Mount Abu indicate that successful male invasions and troop takeovers occur on the average once every 27 months. Male takeovers associated with the disappearance of infants have also been reported for langurs at the Gir forest (Starin, 1978) and at Polonnarwa (personal communication from S. Ripley). Infanticide has also been witnessed among langurs at the game sanctuary of Sariska by the warden, Fateh Singh (personal communication). By contrast, neither takeovers nor infanticide have been observed among langurs at orchha, Kaukori, or Singur, North India, nor at Solu Khumbu or Melemchi in the Nepal himalayas (Jay, 1965; Oppenheimer, 1977; Boggess, 1977; Bishop, 1975). (See Table 1 for site descriptions).

Currently, there are three hypotheses to account for differences recorded between sites:

1. Populations of langurs may be gentically dissimilar in regard to the trait of infanticide. Such differences could be a matter of geographic or historical accident, or else due to specific environmental conditions which countered evolution of the trait. Differences could encompass areas as large as eastern and western sides of the subcontinent. Consider for example that infanticide has been reported at four sites, and is
suspected at two other sites which lie towards the west of the Indian subcontinent, while infanticide has never been reported at any of the five sites which lie towards the east (Fig. 1). However, the fact that there are no known geographic, climatic, or population boundaries between these two areas makes the proposition that langurs are divided into two populations unlikely. Alternatively, local circumstances could have selected or failed to select for the trait in numerous small populations.

The main reason for rejecting an explanation based solely on genetic differentiation between populations of langurs is the failure of morphologic differences between populations to accord with any behavioral differences. (Fig. 2 shows subspecific differentiation of *Presbytis entellus* based on Hill, 1939; at that time, the synonym *Semnopithecus* was in use). Langurs at Mount Abu and Jodhpur (*Presbytis entellus entellus*) are easily distinguished from those at Dharwar (*P. e. achates*) by mode of tail carriage and other
morphological differences (Roonwal, in press). There are no known differences however, in the range of behaviors exhibited by these two subspecies. To date, the only subspecific differences which parallel different behavior patterns are those between Himalayan langurs and the rest of the langur on the subcontinent of India and Sri Lanka. These behavioral differences include reduced frequency of aggression, increased male-male tolerance, reduced incidence of long-distance vocalizations (the male whoop), reduced estrous signalling, increased huddling, and increased seasonality of breeding (Vogel, 1973; Bishop, 1975; reviewed in Bishop, in press).

2. Populations of langurs could be genetically similar in respect to behavior, but the expression of specific traits is facultative. That is, expression of the trait occurs along a behavioral scale (Wilson, 1971; 1975) in response to specific en-

Figure 1. Langur study sites; note that sites where takeovers have been reported lie to the west of line, while sites without takeovers lie to the east.
environmental or demographic conditions. Again variation could be due to environmental differences on a large scale, as between eastern and western sides of the subcontinent, or, as seems more probable, to differences between sites or even between populations or groups at the same site. Markedly different social organization in adjacent groups of acorn woodpeckers (Melanerpes formicivorus) provides a case in point (Stacey and Bock, 1978), and stresses the importance of a nontypological perspective and the need to focus on the strategies of individuals which may differ greatly even between closely related animals belonging to the same species.

At present, the chief candidate for determining behavioral differentiation between populations or groups of langurs are human disturbance and population density. Several authors, including Sugiyama (1967), Eisenberg et al. (1972), Rudran (1973), and Hrdy (1974) have suggested

Figure 2. Distribution of races within the genus "Semnopithecus." according to Hill (1939). Note that a new taxonomic classification of Presbytis entellus is being prepared by C. Vogel.
that the frequency of male takeovers among leaf-eating monkeys is a function of population density. As Rudran points out: "there are reasons to indicate that male replacements occur both at high and low densities, but the frequency of aggressive interactions between males which lead to male replacements varies with the density" (1973, p. 179). Not only would the occasion for aggression be increased, but frequent encounters between troop and non-troop males would wear down males in troops, making them more vulnerable to ouster. Furthermore, in most cases, there will be a larger absolute number of extra-troop males at high densities, and larger average sizes for male bands; several authors have suggested that size of male bands, which travel over wide areas and contact a number of different bisexual troops, may be related to success rates for takeovers (reviewed in Hrdy, 1977). Any of these factors, singly or in combination, would contribute to a shorter duration of male tenures in bisexual troops at high densities.

Alternatively, it has been argued that the key variable determining the occurrence of the takeover infanticide pattern is disturbance of the habitat by humans, which creates an "abnormal" environment for the primates living in it. That is, these are the "disturbing results when a species is pushed beyond the range of its flexibility" (Curtin and Dolhinow, 1978; 1979). One difficulty with testing this widely held belief has been a tendency in the literature to define as "crowded," "abnormal," or "disturbed" sites where infanticide has been reported, with no attempt at objective classification of study sites based on tangible features of the habitat (see Curtin, 1977; Dolhinow, 1977). Hence, Dharwar, Jodhpur, and Abu are characterized as "crowded," "stressed," "disturbed," and "harassed" populations, while Kaukori, Orcha, and the two high-altitude sites at Melemechi and Solu Khumbu are referred to as "normal."

Only objective measures of human disturbance, however, will allow us to ask whether male takeovers are indeed associated—much less caused—by habitat disturbance. A first effort toward such a classification is provided by Bishop et al. (in press). In Table 2, ten langur study sites are scored according to the degree of human influence on the habitat, harassment of the animals by humans, habituation of the animals to humans, and finally, human influence on local predators. As shown in Table 3, the mean score for human disturbance at five sites without male takeovers was not significantly different (using a Mann–Whitney U-test) from the average score of five sites where male takeovers have been reported and where infanticide was either observed or suspected. Assuming that the measures used do indeed reflect the degree of human disturbance in the habitat, these findings indicate that other factors besides habitat disruption are at issue. Far more promising is a comparison of mean population density at five sites without male takeovers (7.31 langurs per square kilometer) compared with five sites where male takeovers were reported (89.6 per square kilometer) (see Table 4). Mean population density was more than twelve times higher at sites with takeovers, and this difference was highly significant (p < 0.01 using a Mann–Whitney U-test).

Because Christian Vogel's field site at Sariska was not scored for human disturbance in the Bishop study, it was omitted from the above analysis. Nevertheless, information from langurs living at this game sanctuary in western Rajasthan are consistent with the finding that population density rather than habitat disturbance is correlated with the takeover-infanticide complex. Sariska is a protected sanctuary, and one of the few areas in India where tigers are still common. Other predators include leopards and jackals (Sankhala, 1978). According to Vogel (1971, 1973, 1976), population densities at Sariska are approximately 104 langurs per square kilometer, roughly equivalent to the densities recorded by Sugiyama at Dharwar in 1960 and about twice the density recorded for Mount Abu in the early seventies (Hrdy, 1974). (Since these estimates, the population of langurs at Dharwar has decreased, while that at Mount Abu has increased (Sugiyama and Parthasarthi, 1979; S. and D. Hrdy., unpublished field notes for 1979). Although 100 langurs per square kilometer is at the high end of the distribution of population densities for this species, it is questionable whether the designation "crowded" (Curtin, 1977; Curtin and Dolhinow, 1979) is an appropriate one. Oates (1974) found population densities of roughly 100 animals per square kilometer among the related species Colobus guereza living in the Kanyawara forest, part of the Kibale Forest Reserve in Uganda, one of the least disturbed areas monkeys have ever been
Table 2. Qualitative rating of degree of human disturbance at ten langur study sites

<table>
<thead>
<tr>
<th>Site</th>
<th>Disturbance to habitat</th>
<th>Disturbance to animals</th>
<th>Habitation to humans</th>
<th>Presence of predators</th>
<th>Mean score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Singur</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>3.75</td>
</tr>
<tr>
<td>Abu town</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>3.75</td>
</tr>
<tr>
<td>Jodhpur</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3.00</td>
</tr>
<tr>
<td>Kaukori</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>2.75</td>
</tr>
<tr>
<td>Polonnaruwa</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>2.50</td>
</tr>
<tr>
<td>Dharwar forest (16.2–30 km. from Dharwar)</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>2.25</td>
</tr>
<tr>
<td>Melemchi</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2.00</td>
</tr>
<tr>
<td>Solu Khumbu</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2.00</td>
</tr>
<tr>
<td>Gir Forest</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1.75</td>
</tr>
<tr>
<td>Orcha Forest</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1.00</td>
</tr>
</tbody>
</table>

* All scores are from Bishop et al. (in press). C. Vogel’s sites at Sariska and Bhimtal were not included because the authors were not personally familiar with those sites, nor able to discuss them directly with the German investigators.

1. **Undisturbed forest**—primary or mature secondary forest, no human habitations or economic activities; no livestock or dogs.
2. **Disturbed forest**—moderate to extensive exploitation of habitat (e.g., woodcutters or tourists); some livestock may be present in the habitat.
3. **Intermediate habitat**—habitat essentially man-made (i.e., fields, cleared areas) and forested areas adjacent to human settlement.
4. **Urban**—monkeys live in continuous close association with human habitations or activities.

* Animals are undisturbed—contact between humans and monkeys rare.
* Minimal harassment—monkeys are chased or harassed only when they enter fields to raid crops.
* Occasion-specific harassment—monkeys are harassed when they steal food and when they enter area of human habitations.
* Intense harassment—harassment occurs frequently, on a daily basis.

* Wild—monkeys fle when humans appear.
* Moderately wild—monkeys move away if humans actually approach; they may crop raid, but are not provisioned.
* Habituated—monkeys are accustomed to human presence, although they will usually not tolerate approach unless food is thrown to them.
* Habituated and routinely commensal—monkeys do not move away at benign human approach and typically live on human refuse and provisioning.

* Full complement of predators—large cats and other predators are protected.
* Partial complement of predators—predators are represented by a few individuals of some species, but numbers are diminished due to hunting or habitat destruction.
* Impoverished complement of predators—most major predators eliminated; village dogs may harass primates.
* No predators—neither dogs nor humans present a threat to monkeys.

Table 3. Mean score for human disturbance in the habitat and mean population density for langur study sites with and without male takeovers

<table>
<thead>
<tr>
<th>Site</th>
<th>Human disturbance</th>
<th>Population density</th>
<th>x score</th>
<th>x density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Singur</td>
<td>3.75*</td>
<td>12.5 per km²</td>
<td>2.3</td>
<td>7.31</td>
</tr>
<tr>
<td>Kaukori</td>
<td>2.75</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orcha Forest</td>
<td>1.0</td>
<td>4.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melemchi</td>
<td>2.0</td>
<td>16.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solu Khumbu</td>
<td>2.0</td>
<td>1.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Site</th>
<th>Human disturbance</th>
<th>Population density</th>
<th>x score</th>
<th>x density</th>
</tr>
</thead>
<tbody>
<tr>
<td>6. Abu town</td>
<td>3.75</td>
<td>50.0</td>
<td>2.65</td>
<td>89.60</td>
</tr>
<tr>
<td>7. Jodhpur</td>
<td>3.0</td>
<td>18.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Polonnaruwa</td>
<td>2.5</td>
<td>150.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Dharwar Forest</td>
<td>2.25</td>
<td>108.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10. Gir Forest</td>
<td>1.75</td>
<td>121.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Score taken from Bishop et al.
studied on a long-range basis. Oates also reviewed the literature for population densities among other colobines in Africa and Asia. Comparable densities (1 animal per hectare) have been reported for *Presbytis metalophos*, *P. obscurus* and *P. entellus*. Somewhat higher densities (as high as 2 animals per hectare) have been reported by Eisenberg et al. (1972) for *Presbytis senex*. Although *Colobus guereza* (a more folivorous monkey than *P. entellus*, but similar in body weight and social organization) share the forest at Kanyawara with seven other species of primates, no ecologist to date has suggested that monkeys in this habitat are "crowded." Hence, Sariska would appear to provide an example of a relatively undisturbed langur population where a high (but not abnormally high) density of langurs is maintained, and where infanticide is known to occur. These findings fail to support the prediction of the social pathology hypothesis that infanticide only occurs in disturbed or unnaturally crowded areas (see also "Reply" in Dolhinow, 1977).

These findings are instead consistent with the hypothesis proposed by Rudran, Sugiyama, Yoshiba, Hrdy, and others that the incidence of male takeovers among leaf-monkeys is higher at high population densities. The mechanism underlying this association is still not known, but as suggested above, the most obvious link (originally suggested by Yoshiba, 1967) between population density and takeovers is the increased numbers of extra-troop males traversing the home ranges of the bisexual troops at high densities. One striking common denominator between colobines such as *Colobus guereza* and *Presbytis senex*, as well as to some extent *P. entellus*, and the other monkeys in which the male takeover-infanticide complex appears strongly entrenched (such as *Alouatta seniculus* and *Cercopithecus ascanius*) is the relatively high proportion of leaf material in their diets (Hladik, 1978; Kay and Hylander, 1978). An obvious question for future investigators is the extent to which a large folivorous component in the diet allows a population to reach high population densities and to maintain itself at a level close to the carrying capacity of the environment for extended periods. If hypothesis 2 is correct, this capacity would intensify a tendency towards male takeovers.\(^2\) As early as 1972, and before it was apparent just how widespread the male takeover pattern was among monkeys, Eisenberg et al. pointed out that folivorous primates were prone to live in one-male groups. In the light of these speculations, recent demographic information from Dharwar (Sugi-

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\(^2\) Note that an association between infanticide and high population densities is equally compatible with explanations based on sexual selection or resource competition. This is going to further complicate separation of the two models.
yama and Parthasarthay, 1979), Jodhpur (Mohnot et al., 1979), and Mount Abu (S. and D. Hrdy, unpublished field notes for 1979) take on special significance. By and large, the proportion of one-male versus multimale troops in a given population of langurs is a good index of how frequently male takeovers occur. Typically, when there are frequent male takeovers, the majority of troops have only one full adult male (Hrdy, 1977). Whereas population densities at Jodhpur and a predominantly one-male troop organization have remained constant during the decade between 1968 and 1978, population densities at Dharwar and Mount Abu have changed. The population at Mount Abu has grown by 12.3% in the years between 1971 and 1979 and male takeovers continue at a high rate. By contrast, the population of langurs at Dharwar in 1978–79 had declined by 54.5% since 1961 and the troops nearest to the town of Dharwar have disappeared. Based on an interim census at Dharwar in 1976, Sugiyama and Parthasarthay concluded that the most serious decreases had occurred in the last three years and were due largely to felling of forests and the planting of eucalyptus trees, which are not usable for food by langurs. Although the data gathered by Sugiyama and Parthasarathy are not yet fully analyzed, it is apparent that the proportion of multimale troops has increased, while levels of inter-troop aggression and the number of all-male bands have decreased. Based on hypothesis 2 presented here, one would predict that male takeovers and infanticide at Dharwar have also decreased, even though the level of human disturbance has increased dramatically since Sugiyama’s initial study in the early 1960s.

3. According to a third hypothesis, male takeovers and infanticide may occur with equal probability at all sites but have been missed due to differences in observation conditions.

A corollary of high population density at a study site is the opportunity for researchers to simultaneously monitor a number of different troops. Hence, the mean number of troop-months langurs were monitored at five low-density sites where no takeovers were ever reported was 29.2, far lower than the mean number of troop-months langurs were followed at sites where takeovers were reported (424.4 troop-months; see Table 5). On the basis of sample size alone, the chances of an observer recording a takeover would be higher at high densities. Nevertheless, examination of Table 5 makes clear that even though only a few troops were observed at Solu Khumbu and Singur, the duration of these studies should have been sufficient to record takeovers if they were occurring at a rate comparable to those reported at Dharwar and Abu (every 27 months). On these grounds, I believe we can discount the possibility that takeovers are occurring at the same rate at all sites.

Having followed these detailed arguments, the reader is perhaps entitled to my own opinion, namely that the second hypothesis is the most promising and that, so far as langurs on the Indian peninsula are concerned, animals from Singur, Orcha, Abu, and Dharwar reared in similar environments would exhibit the same range of behavior. I would not, however, rule out the possibility that Himalayan langurs who have evolved under extreme environmental conditions at the margin of the species’ range will be shown to be genetically different and exhibit corresponding differences in behavior.

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4 Firmly entrenched in the langur literature is the notion that as the habitat is destroyed, animals become more densely packed together in remnant forest. For example, Curtin and Dolhinow write that “The forest near Dharwar [referring to the early ’60s] had recently been cleared and the langurs concentrated in what little remained, with the result that their population density reached 134 langurs per km².” (1978, p. 471). Although such a “refuge effect” may occur immediately after felling of a forest, no habitat can continue to support a population which exceeds the carrying capacity of the environment. Substantial portions of forest still existed at Dharwar through the ’60s and into the early ’70s, and these forests were capable of supporting high densities of langurs. When extensive destruction of the forest did take place, the population dropped rapidly rather than increased as usable habitat was destroyed.

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THE IMPLICATIONS OF INFANTICIDE FOR FEMALE REPRODUCTIVE STRATEGIES

Infanticide has been reported for a broad array of animals in a variety of circumstances. For no species are there precise data on mortality attributable to infanticide, though we have a known minimum of 8% of infants killed by conspecifics at Sherman’s ground squirrel study site, and an estimated minimum of 83% in one langur troop at Mount Abu which happened to be particularly vulnerable to male invasions. In some cases, chiefly those involving resource
competition, the killers may be animals of either sex, and age of the victim secondary to vulnerability. In other circumstances, particularly sexually selected infanticide, males are implicated, and targets are primarily unweaned infants. In all cases however, a situation permitting infanticide is liable to be uncommon (i.e., the presence of infants coincident with the opportunity to kill them and pressures to do so). This makes it all the more striking that scientists witness such fleeting episodes as often as they do (see for example Struhsaker, 1977). One must assume that although uncommon, infanticide is a widely recurrent behavior with drastic consequences for the fitness of individuals. As such, infanticide—like classical predation and other recurrent perils—is likely to have played a significant role in the evolution of infanticidal species.

In the case of primates, studies are now available for a number of species belonging to the same family and even for members of the same species inhabiting different locations. This comparative material permits us to search for adaptations to the threat which infanticide poses for individuals. In this section, I will outline three areas—social organization, the physiology of reproduction, and the patterning of female sexual receptivity—which may have been subject to selection pressure from infanticide.

Social Organization

What sort of effects will the threat of intraspecific damage to infants have on patterns of association? Grouping patterns of the great apes provide some of the clearest examples. Based on the work of Fossey, Harcourt, and Stewart at the Karisoke Research Center in Rwanda, we now know that female gorillas, like chimpanzees, move between groups. The main attraction for transferring females, and the main cohesive focus of gorilla groups generally, is the silverback male of each group (Harcourt, 1977). Harcourt and others have postulated that one source of continuing male attractiveness is his ability to protect the female and any offspring she produces. That is, "subsequent decisions to stay or transfer might rest on the female's success at raising her offspring in the unit: two mothers who successfully raised their offspring in a new unit stayed; three who did not, left. The infants of at least two of the latter were killed deliber-

ately during interunit interactions" (Harcourt et al., 1976, p. 227).

Similarly, Goodall has postulated that chimpanzee females stay close to adult males after the birth of offspring to gain protection against attacks on their infants by other females (Goodall, 1977, p. 276). Analysis of association patterns at the Gombe Stream feeding area indicate that mothers tended to associate more frequently with males after the birth of an infant than they did before. Such increases are apparently due to the mother rather than the male. A parallel pattern has been more tentatively suggested for orangutans by Joel Cohen in his analysis of data collected by John MacKinnon. Typically, an orang mother travels on her own. Nevertheless, a female orang is statistically more likely to be seen travelling with a male if she has an infant (Cohen, 1975). Whereas a gorilla male may help to care for weaned infants (Harcourt, 1977), orang males do not. Neither of these large apes is in much danger from any predator other than man. Although there are a variety of advantages (as well as costs) to group living (see Alexander, 1974; Clutton-Brock and Harvey, 1976), protection of infants from conspecifics must be one of the important determinants of those other animals with which females choose to associate with (Wrangham, in press, makes this same point).

In situations where there are frequent shifts in group memberships, mothers with infants may exhibit clear preferences for one male while avoiding another. After a takeover, Hanuman langur females may leave their natal troop temporarily to travel with ousted males or even, in an extreme case, attempt to follow a male who has left one troop to take over another (Hrdy, 1977, pp. 51 and 266). In the gorilla case, female preferences may be influenced by male care, but this probably is not a factor among langurs, where the main contribution of males to the survival of offspring (at least at high density sites) is to protect infants from other males. Infanticide may also have implications for relations among females as well as between the sexes. As pointed out by Sherman (1978), the threat to offspring from aliens may increase the benefits of remaining near relatives. Furthermore, a hitherto little-considered advantage for a female's high rank would be to reduce interference by other females in her own childrearing while permitting her to harass her competitors.
Among wild dogs and the great apes for example, it was the offspring of subordinate females who were killed by other females in the group. Similarly, Mallory and Brooks (in preparation) report that caged *Dicrostonyx groenlandicus* mothers are better able to defend their one-day old litters from the deprivations of nonpregnant, nonlactating females introduced into the cage if the mother is significantly heavier than the strange female.³

**Female Reproductive Physiology**

The capacity of females to conceive again soon after losing an infant is a crucial preadaptation for the evolution of infanticide through sexual selection. Although it might be advantageous for species if females delayed ovulation and hence "penalized" infanticide, it would be disadvantageous to the individual female. If anything, selection will operate on individual females to ovulate even sooner after the loss of an infant. Females can, however, be selected to reduce investment, or even abandon an infant seriously endangered by infanticide. In the case of a number of small mammals, including *Mus musculus*, *Peromyscus maniculatus*, *Microtus agrestis*, *M. pennsylvanicus*, *M. ochrogaster*, and *Clethrionomys glareolus* (reviewed in Mallory and Brooks, in preparation and Labov, in preparation), females exposed to a strange male early in their pregnancy may reabsorb the foetus, and it seems possible that this is a strategy to reduce the risk of infanticide when the pups are born (Stehn and Richmond, 1975; Hrdy, 1977, p. 308; Mallory and Brooks, 1978; and in preparation; Labov, 1979, and in preparation.). Most of these strategies however mean considerable loss in investment for females.

To date no one has investigated for any primate species whether or not introduction of a new male alters the risk of abortion. Absence of information from field studies, at this point, can only be taken as evidence for the difficulty of collecting information on incomplete pregnancies under field conditions. As Labov (in preparation) has pointed out, females among some other large, infanticidal mammals, such as lions, do abort when new males replace residents (Bertram, 1975). Because of the greater relative investment of a monkey or ape mother per infant, abortion in primates would be a far costlier maternal strategy than it is among lions. If abortion of a nondefective infant is ever selected for among primates one would expect it to be an option of "last resort"—hence a threefold question might be the appropriate one for future research: (1) Does the risk of abortion increase when a new male is introduced? (2) Does the rate of abortion under such conditions differ for infanticidal and noninfanticidal species? (3) Is the likelihood of abortion affected by past sexual encounters? That is, is a pregnant female less likely to abort if she mated with the usurping male prior to takeover? Although highly speculative, I feel it is important to ask these questions to encourage the collection and publication of relevant data from field and laboratory studies. As a parallel example, it is worth noting that prior to the 1970s, when considerable attention was focused on the phenomenon of infanticide in primates, apparent cases of infanticide went unreported.

**Female Sexual Behavior**

Among mammals where estrous behavior and imminent ovulation are less well correlated than is the case among rodents, counter-strategies less costly to females may be feasible. If males are in fact using past history of sexual relations with the mother as a cue to either attack or tolerate the infant, females capable of exhibiting estrous behavior at all stages of the reproductive cycle possess some control over information available to males concerning possible paternity. Provided extra-troop males cannot detect ovulation, it would behoove females to enter into consortships with potential usurpers. Such a strategy, for example, could account for both the behavior of female langurs who leave their troop to travel and mate with males in all-male bands (Hrdy, 1977: personal communication from Moore and Mohnot), and for the onset of semicontinuous estrous behavior when male invaders approach or enter langur troops. At such times, females without infants may solicit males regardless of their cyclical state, and even if they are already pregnant. Unlike baboons, and other primates with sexual swellings or colora-

³ Mallory and Brooks (work in preparation) tentatively attribute this infanticide to competition among female *Mus musculus* for territories. As in the case of Belding’s ground squirrels, a female who loses her litter moves away to a new nest site.
tion keyed to the menstrual cycle, a langur female signals receptivity by presenting to a male and shuddering her head. Except for the possibility of pheromones (which have never been studied in langurs), the male apparently depends on behavior signals. Female langurs are then in a relatively good position (as are human females) to confuse the issue of paternity, particularly with extra-troop males.  

The hypothesis that pseudo-estrus is a strategy to forestall infanticide predicts that (1) males who have copulated with a female prior to her giving birth will be less likely to subsequently attack an infant associated with her, and that (2) females will solicit extra-troop males both at ovulation when conception is possible, and at other times, when it is unlikely or not possible. This second prediction, already partially substantiated for langurs, is an important one because it allows us to exclude competing hypotheses which would explain female promiscuity, namely that females are increasing their options to choose between males by preventing a dominant animal from monopolizing them, or secondly, that females copulate with a number of different males to insure fertility, or thirdly, that such promiscuity is a mechanism to insure out-breeding.

In the course of primate evolution, there has apparently been a trend away from strictly hormonal determination of receptivity. Based on an experimental study, Eaton (1973) provides an instructive comparison of the invariant relationship between ovarian hormones and mating in a nocturnal African prosimian (Galago crassicaudatus) and the more flexible breeding of higher primates. Among galagos, Eaton found a mean cycle length of 44 days, with a period of estrus (as determined by the presence of cornified epithelial cells in vaginal smears) of 12 days. Within these 12 days, females were receptive (i.e., permitted intromission) for a mean of only 3.8 days, and no galago female was ever receptive outside of that period, even though males attempted to mount. In contrast, among pig-tailed macaques (Macaca nemestrina), female receptivity did not change across the cycle, and the mean number of intromissions did not vary significantly across the cycle. What changed, however, was the "attractiveness" of females, since males inspected the vaginal area and ejaculated more frequently at midcycle. For both pig-tailed macaques, and rhesus macaques (Michael and Zimpe, 1970), the only measure that has been reliably correlated with a particular stage of a female's reproductive cycle is frequency of ejaculation, which was highest at midcycle. Data from free-ranging rhesus macaques corroborate the finding that females in a relatively normal social setting copulate throughout the cycle (Conaway and Koford, 1965; Loy, 1970). Similarly, both captive and wild gelada baboons copulate throughout the cycle (Dunbar and Dunbar, 1974; Smith and Credland, 1977). Unlike the macaques, the gelada males were not more likely to ejaculate at midcycle than at other times, but females were significantly more likely to solicit males in the ten days or so when the vesicles on the bare skin of the gelada chest and perineal region were maximally swollen and pigmented than they were in the ten days surrounding menstruation (Dunbar, 1978). Among captive orangutans (Nadler, 1977) and captive chimpanzees (Lemmon and Allen, 1978) females copulated on any day of the cycle, although there were increases in frequency at midcycle. On rare occasions, a wild chimpanzee has also been known to lapse from cyclicity into semi-continuous receptivity (Tutin, 1975, p. 59). Among humans, females are more or less continuously receptive; tendencies towards increased sexual activity at midcycle (comparable to those reported for macaques and some apes) have been reported among women in both Western and gathering-hunting societies (Udry and Morris, 1968; Adams et al., 1978; Worthman, 1978). Research by Adams et al. (1978) is particularly significant because the study was specifically designed to focus on female-initiated sexual activity. Results from earlier studies have been blurred by the confounding effects of male-initiated sexual relations in the human case.

The lack of any strict correlation between ovulation and sexual receptivity in higher primates has been known since the turn of the century when Walter Heape (1900) presented his

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* Resident males, however, are in a position to monitor the intensity of solicitations from cycle to cycle and to compare estrus at ovulation with pseudo-estrus, just as a human observer watching langurs can; this may be one of several reasons why resident males are more discriminating in their mating activities. A soliciting female ignored by a resident male is frequently sought after by extra-troop males (Hrdy, 1977, pp. 137-141; 16-mm film by D. Hrdy, S. Hrdy, and J. Bishop, entitled "Stolen Copulations").
exhaustive report on estrus in mammals. Heape concluded that in respect to estrous behavior monkeys stood in an intermediate position between other mammals and man. It has been left for modern workers belatedly to agree. Pressure to do so was applied by Thelma Rowell in her review of primate reproductive cycles (1972) which emphasized that there was no necessary correlation between copulation and stage of the menstrual cycle.

These findings raise important issues for primate evolution. Under what conditions do females shift away from cyclical determination of receptivity towards socially determined or situation-determined receptivity? And, in particular, under what conditions do female primates benefit from copulating at times when they will not conceive?

There are at least three possible ways in which females might benefit from concealing ovulation and from mating throughout the cycle, according to circumstances with any of several or a number of partners. Briefly, these involve: increasing options from which to choose an advantageous genotype (Trivers, 1978): cultivating additional male investment—as is the case for barbary macaques, Macaca sylvana, where care from several different males is essential for the survival of infants (Taub, in press); and, forestalling infanticide (Hrdy, 1974). Since females may copulate independently of ovulation in multimale troops (e.g., macaques), one-male harems (e.g., langurs), and in monogamous pairs (e.g., marmosets), and since this phenomenon occurs in both species with and without extensive paternal care, it would be an error to insist on any unitary explanation for continuous receptivity. According to the classic anthropological formulation proposed by Morris (1967), continuous receptivity evolved in human females to maintain the pair bond and to insure paternal care necessary to rear particularly altricial human young (see also Barash, 1977). This proposition—largely untestable—may well be true. Certainly, it accords with such findings as an increase in libido among human females during the first, and particularly the second trimester of pregnancy (Masters and Johnson, 1966, p. 154–159), and it accords with some of the comparative evidence for other primates. For example, marmosets are a group of New World monkeys characterized by both monogamy and extensive male care of offspring. Of all the primates, including humans, ovulation is best disguised among this group. Female marmosets copulate at low level throughout the cycle, exhibit no visible signs of ovulation, and do not menstruate (Hearne, 1978).

Nevertheless, the Morris proposition is clearly insufficient to account for all the evidence, and particularly for the precursors of continuous receptivity among a number of nonhuman primates such as langurs (Hrdy, 1977) and vervets (Struhsaker, 1967) which are characterized by neither pair bonds, unusually helpless young, nor male care. Furthermore, the hypothesis based on female choice cannot account for the widespread occurrence of post-conception estrus among langurs, Japanese and rhesus macaques, patas monkeys, gorillas, sykes monkeys, and chimpanzees (reviewed in Hrdy, 1977: pp. 284–285) because in such cases male genetic contribution to offspring is not at issue, although his subsequent behavior to offspring will be.

In addition to female choice, the cultivation of male investment, and inhibition of infanticide, there is of course a fourth possible explanation for continuous receptivity, namely that it is an endocrinological byproduct of hormonal changes which evolved for some other reason. This alternate hypothesis will be difficult to rule out. However, the hypothesis will be weakened if a female primate is more likely to switch from cyclical to continuous receptivity under specific social conditions, such as those conducive to infanticide. Barring endocrinological accident, the strongest hypothesis to account for the emergence of continuous receptivity among primates is that it first evolved in social contexts where it was beneficial for females to confuse paternity, as in the case of infanticidal species.

This sexuality would constitute the physiological heritage that prehominid females brought to the revolutionary new lifestyle that distinguished our hominid ancestors from other primates—a life centered about a home base, characterized by division of labor into gathering and hunting, and an emphasis on food sharing (Isaac, 1978). Out of gathering–hunting economics would grow the new dimensions to the pair bond postulated by Sahlin (1959), Morris (1967), and others. The helplessness of human young would place strong selective pressures on males to help rear their young. But continuous, situation-dependent sexual receptivity would have predated those developments.
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