

Chapter 47

Infant Killing as an Evolutionary Strategy: Reality or Myth?

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The students nodded. They had all studied animal behavior, and they knew, for example, that when a new male took over a lion pride, the first thing he did was kill all the cubs. The reason was apparently genetic: The male had evolved to disseminate his genes as widely as possible, and by killing the cubs he brought all the females into heat, so that he could impregnate them.

(Michael Crichton, *Jurassic Park*)

Infanticide (as seen in lions) also occurs in the entellus langur (Presbytis entellus). Marauding bands of nomadic males raid a troop, drive off the resident males, kill all the juveniles, and quickly mate with the females.

(The Oxford Companion to Animal Behavior)

Among many primate biologists, infant killing by conspecific males is thought of as an evolutionary strategy giving adaptive advantage to the infanticidal male (Hrdy 1977, Hausfater and Hrdy 1984). In fact, as can be seen from the above, the use of the sexual selection hypothesis to explain infanticide has become a widespread, almost mythological belief, even in the popular literature. The theory is as follows. An infanticidal male gains reproductive advantage by selectively killing the unweaned offspring of his male rivals. In addition to the relative gain in genetic representation, the infanticidal act terminates lactational amenorrhea, shortening the interbirth interval of the infant-deprived female. This ensures the earli-

est possible opportunity for the infanticidal male to mate with and inseminate the infant-deprived female. Theoretically, the most likely context for this to occur is during male takeover in species with one male groups.

Recently, this theory has been expanded to include seasonally breeding species, such as the ring-tailed lemur (*Lemur catta*), in which the infanticidal male cannot immediately mate with the dead infant's mother. If a male's infant is the subject of infanticide, he is unlikely to be chosen again as a mate in subsequent years (he becomes an "incompetent father") (Perreira and Weiss 1991, Kappler 1993). Thus, females select infanticidal males to father their offspring.

There are two major problems with the sexual selection explanation for infant killing among primates. The first involves the data; the second the theory itself.

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THE DATA

Recently, we examined the literature to determine precisely how many cases of infant killing actually have been observed by primate researchers. Further, we examined the context of these incidences of infanticide (Bartlett et al. 1993). We found that there were only 48 cases in which the death of the infant was observed. These cases occurred in thirteen species of primate, and almost half of the killings (21) were done by Hanuman langurs. More than half of the langur deaths occurred at one Indian site, Jodhpur (Sommer 1994).

One might argue that predation also is rarely observed and yet it is an important cause of death among primates. But the numbers are not comparable. First, the database for predation is quite broad relative to that for infanticide (Anderson 1986, Hart in prep.). A review of the literature reveals a large number of observed cases (Sussman et al. in prep.), even though documenting predation is very difficult (Isbell 1994). Second, primatologists rely on studies of very small prey populations (e.g., one or two primate groups) rather than studies on predators. Field studies of predators indicate that primates are important prey items for many species (Goodman et al. 1993, Hart in prep., Rettig 1978). Finally, primates display typical antipredator defense behaviors outlined by Endler (1991). Yet no such mechanisms exist to deter infanticidal attacks by males. A fixed action pattern towards specific predators is quite different from males associating with infants, females protecting their infants from strange males, or monogamy. In fact, Sommer notes that mothers sometimes "allowed even infanticidal males to come so close to their infants that a sudden jump would have been sufficient to grasp the hopping infant from the ground or from the mother's breast" (Sommer 1987).

A second, even more serious problem with the data is the fact that the context rarely fits the pattern predicted for sexual selection. In only eight of the 48 cases was the infanticidal male observed mating with the mother. In two of these, the male was the most likely father of the infant that he killed! Only six cases involved direct attacks on independent infants, and in an additional three cases a mother-infant pair was the subject of direct repeated attacks. The majority of infant deaths occurred during general aggressive episodes. There is evidence, among Hanuman langurs in particular (Dolhinow in press), that in these situations infants often place themselves into danger by their own actions (e.g., clinging to their mothers during attacks, or being attracted to action and excitement). Thus, of the 48 cases, only 12.5 percent fit the requirements of the sexual selection hypothesis. In 87.5 percent of observed infant killings, the context is not compatible with this hypothesis.

There appears to be no underlying consistent context in which infanticide takes place, such as group

takeover. The circumstances surrounding infant deaths are highly variable and the use of a single term, with all its implications, to refer to the numerous phenomena involved in infant killing misrepresents the complexity of primate social behavior.

THE THEORY

The fundamental assumption of the sexual selection hypothesis concerns the genetic basis for infant killing behavior. Although the inheritance of the "infanticidal trait" (Hrady 1979, 1984, Newton 1988) is crucial for the operation of the sexual selection model, there is no evidence supporting its genetic inheritance. Are the sons of infant-killing males more likely to be infant killers themselves because of genes they inherit from their fathers?

In addition to the lack of data on genetic inheritance, selection for infant killing has never been demonstrated. Selection can be measured by quantifying the covariance between the character and relative fitness in a population that includes infanticidal males (Arnold and Wade 1984, Phillips and Arnold 1989, Schluter 1988). Relative fitness is the relative intrinsic rate of increase of the individual compared to that of the population as a whole. When lifetime relative fitness is unavailable, its time-specific components can be analyzed, with the caveat that the selection measured may be counteracted at other life stages. What is the increase in relative fitness associated with infanticide behavior?

Selection for infant killing, if it exists at all, is likely to be weak. First, variance in infant killing is low because it is a rare event (Bartlett et al. 1993) and low variance limits the covariance of the trait with relative fitness. Second, the only indication of fitness differences we have are a few cases of small decreases in interbirth intervals for females who lost infants relative to those who did not (Sommer 1987). However, a large proportion of infants die within the first months of life regardless of infant-killing males (Jacquish et al. 1991, Sade et al. 1976, Sussman 1991). Some of these infants would have died anyway. The shortening of the interbirth interval due to infant killing needs to be discounted by the underlying death rate so that selection is much weaker than indicated by interbirth interval differences reported in the literature. Furthermore, differences of a few months in the timing of offspring born to infant killers compared to non-killing males who take over a group will only have a slight effect on relative lifetime intrinsic rate of increase. In fact, the necessity of using year-long age intervals in primate demography makes the likely effect smaller than measurable error. It is important to remember that the fitness increase due to infant killing would only be the slightly earlier production of offspring, since the benefits of controlling a breeding group would also accrue to non-killing males.

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Even given a slight increase in fitness for infant-killing males, this increase could well be due to selection on other, correlated traits (Lange and Arnold 1983). We must avoid considering individual traits as independent evolutionary entities rather than as parts of integrated character complexes. Differences in fitness associated with infant killing may actually be due to direct selection on other functionally related characters such as overall aggression (Lange and Arnold 1983, Moore 1990). If there is direct selection on aggressiveness and aggression and infant killing are correlated, infant-killing males may have the same or lower fitness than non-killers. In this instance, infant killing would increase as a correlated response to selection for increased overall aggressiveness not due to independent adaptation.

Most witnessed cases of infant killing appear to be simply genetically inconsequential epiphenomena of aggressive episodes. At this stage, there is little evidence to suggest that infant killing is anything but a rare and evolutionarily trivial phenomenon. No evidence of genetic inheritance or direct selection for the trait has been provided, just non-quantitative plausibility arguments based on anecdotes. Until more specific evidence is available, the concept that infanticide in nonhuman primates is a widespread, adaptive behavior must be approached with appropriate caution. The burden of proof remains, as it always has, with those who favor the sexual selection hypothesis.

It is both important and enjoyable to formulate scientific hypotheses, and it is not difficult to fit them into an evolutionary framework. However, this in itself is not science. Good science begins when one collects the relevant data needed to test these hypotheses. Hypotheses that are untestable or that cannot be disproved are not useful to science. As we have indicated, there are a number of ways the sexual selection hypothesis can be tested, and we urge those interested in this question to collect the necessary data. An infant killing or disappearance does not in itself support the hypothesis of selection and selection does not cause cases of infanticide. Selection is the relationship between relative fitness and a character caused by environmental factors, and these factors, fitness, and the character itself must be measured to determine whether infant killing is an evolutionary strategy.

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Chapter 48

Infanticide: Let's Not Throw out the Baby with the Bath Water

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As originally defined by Darwin (1871), sexual selection refers to a struggle between members of one sex for access to the other with the result for the unsuccessful competitor being not death, but few or no offspring. The sexual selection hypothesis for infanticide proposes that a male increases his reproductive success by killing unrelated infants if the infant's death makes the female return to receptivity sooner than would otherwise have been the case and if it does not decrease his likelihood of subsequently mating with her. Sussman et al. (1995) first dispute the observational evidence for this hypothesis. Second, they argue that no genetic basis for infanticide has been demonstrated. Last, they assert that the proposed genetic benefits to infanticidal males are not sufficient to be subject to selection. Instead, they argue that infant deaths are incidental byproducts of generalized aggression.

Before we address Sussman et al.'s objections, let's be clear on where we agree. First, we agree that the sexual selection hypothesis is perhaps too readily invoked in both the popular and scientific literature. In the first general review of infanticide in animals (1979), the first sentence of the abstract reads: "Infanticide among animals is a widespread phenomenon with no unitary explanation." Five explanatory hypotheses for infanticide, each generating a different set of predictions concerning who would kill whom when, were laid out. The possibility that infanticide would occasionally occur as an unselected by-product of inter-group aggression or other social conflict was one of those five possibilities (see Table 48-1). If Sussman et al. wish to argue that not every case

of infanticide in nature is due to sexual selection, or even natural selection, who disagrees?

Secondly, we concur that we need more field data, and that larger sample sizes as well as experimental data collected under controlled conditions as exist for rodents (Parmigiani and von Saal 1994) are scientifically—if not always ethically—desirable.

THE OBSERVATIONAL EVIDENCE

Now for the disagreements. In an effort to underscore how limited the evidence for infanticide is, Sussman et al. (1995) point out that half of all 48 (their tally) published cases of observed infanticide come from just a single species, *Presbytis entellus*, and that half of these all come from a single site, Jodhpur—the implication being that infanticide is not so widespread after all, and may largely be peculiar to some langur populations. However, this representation is misleading. First, what counts are rates of infanticide. Without information on how many animals were monitored and for how long, it is meaningless to say more killings were witnessed at one study site than another. Roughly 1000 langurs were studied at Jodhpur, over 18 years (1969–1987), by more than ten full-time doctoral or post-doctoral observers working together with local assistants in the largest scale project ever undertaken for any colobine. Second, infanticide is very widespread, having now been observed in conditions predicted by the hypothesis in species of five of the six primate radiations (the exception being tarsiers), in both captive and field conditions. Infanticidal attempts can predictably be provoked by removing a group's resi-

TABLE 48-1 Predictions Generated by Five Explanatory Hypotheses for Infanticide (From Hrdy and Hausfater 1984)

Class of Infanticide	Killer-victim Relatedness	Age of Highest Infant Risk	Age and Sex of Killer	Nature of Gain to Killer
1) Exploitation as resource	Distant	Vulnerability and size more important than age	Either sex at any age large enough to subdue victim	Nutritional gain by killer
2) Competition for resources	Distant	Vulnerability more important than age	Either sex usually (but not always adults)	Increased availability of resources for killer and killer's kin
3) Sexual selection	Distant	Unweaned (but specifically younger than age at which ovulation resumes or amenorrhea terminated)	Adult of sex investing least in offspring, typically male	Additional breeding opportunity
4) Parental manipulation	Close (~0.5)	Just after birth (but any age possible depending on time-course of parental investment)	Either sex, but most likely an individual of the sex investing most in the offspring, typically female	Increased inclusive fitness for one or both parents
5) Social pathology	Not critical for this hypothesis	Size, proximity, and vulnerability more important than age	Adult of sex most likely to respond to social disturbance with increased aggressiveness	None for killer directly, although decrease in population density may eventually result

dent male(s). Reported differences in rates of infanticide are found at least in part because species and populations vary in how often they meet the conditions in which male infanticide is likely (Newton 1986). Indeed, this variation could be put to use in future comparative tests of the sexual selection hypothesis.

Sussman et al. (1995) compare the evidence for infanticide with that for predation, another rare behavior, for which, they argue, the evidence is much better. However, we would argue that, if one uses the same standards of evidence, infanticide is, if anything, better documented than predation on wild primates. Forty-eight observed cases of infanticide is far greater than the number of witnessed cases of predation upon primates that made it into the professional literature. Most published estimates of predation rates for primate populations are inferred (sudden disappearance of healthy animals, cries in the night, bones under a nest, monkey hairs in a scat) (Cheney and Wrangham 1987, Isbell 1990). For example, in her landmark study of relative effects of predation and resource competition on the social system of vervet monkeys, Isbell (1990) did not witness a single predation event even though the disappearance rate for females and juveniles was 65 percent, and the rate of predation was estimated at 45 percent.

Despite the paucity of direct observations, it is widely accepted (and Sussman et al. concur) that predation has been an important selection pressure on primates who have accordingly evolved anti-predator strategies that range from careful selection of sleeping locations and avoidance of dangerous habitats to vigilance, predator-specific alarm calls and sometimes cooperative defense (Cheney and Wrangham 1987). Arguing from the larger sample of observed infanticides, we note that there is a range of male, female, and even infant behaviors that only begin to make sense when we assume that infanticide, like predation, is a recurring threat, even if

the actual events are rarely witnessed. These include adult males who closely associate with the infants they have sired (van Schaik and Dunbar 1990), females with unweaned infants holding back in encounters with strange males or avoiding the boundaries of ranges altogether (Goodall 1986, van Schaik and Dunbar 1990), mothers who attempt to abandon their infants in the company of familiar ousted males rather than take infants with them back to a troop with an interloper in it, transformations of laissez-faire mothers into obsessively restrictive ones in the presence of strange males, mothers avoiding even attacking such interlopers (Hrdy 1977), female migrations into groups coinciding with lowest vulnerability to infanticide (Sterck submitted). These examples suggest to us that behavioral counterstrategies against infanticide are common and successful and help account for its infrequent occurrence in many species. Sussman et al. contest these behavioral observations by citing cases such as some langur females, who, under extreme pressure from an infanticidal male, abandon or cease to defend an infant. Instead, we view such cases as analogous with the well-documented Bruce effect in rodents, whereby a female mouse exposed to an alien male spontaneously resorbs the fetus; such females cut their losses by ceasing to invest on behalf of an infant almost certain to be killed.

THE GENETIC BASIS

So far the criticism has focused on the quality and quantity of the evidence for infanticide in wild primates. Sussman et al. (1995) also argue that for the sexual selection hypothesis to make sense infanticidal tendencies must have some genetic basis, and that we know virtually nothing about this in primates. Indeed, the genetic basis for almost any behavioral trait in primates is unknown.

However, experimental studies on infanticidal behavior in small-bodied, short-lived, and fast-breeding rodents (Perrigo and vom Saal 1994) provide strong evidence that genes are involved.

Among rodents marked differences exist in tendencies to commit infanticide that vary between wild-caught and lab-bred strains (Jabukowski and Terkel 1982, Svare et al. 1984). Even in strains known to be highly infanticidal, researchers find pronounced intra- as well as inter-strain differences in probability that a male or female in a given test situation will kill an infant (Perrigo and vom Saal 1994, Svare et al. 1984). Hence a male mouse belonging to the highly inbred C57B1/6KJ strain in which individuals are almost genetically identical, introduced at the age of 65 days to a pup, responds infanticidally 70 percent of the time compared to 25 percent of the time in the case of males from another strain (e.g., DBA/2J). However, even in the extremely infanticidal lines, infanticidal behavior is still facultatively expressed according to circumstances. In a male mouse social status (e.g., dominant versus subordinate), reproductive status, as well as seemingly random developmental factors such as intrauterine position, can be critical (vom Saal 1984). Interestingly, exposure to testosterone in utero appears to have a sensitizing effect on the neural area mediating infanticide (vom Saal 1984), suggesting, as some of us have long suspected, that although some infant killing may well result as an incidental by-product of aggressive thrashing about as Sussman et al. argue, the kind of goal-directed infanticidal behavior being described (Hrdy 1977, Leland et al 1984, Sommer 1994) may best be understood as a separate motivational system from aggression.

As in primates, a male mouse's response towards infants is very context-specific, changing predictably from benevolent, soon after ejaculating with a given female, to infanticidal after the number of light/dark cycles needed to wean the pups has elapsed (Perrigo and vom Saal 1994). While the mechanisms may not be exactly similar in primates, the wealth of evidence from rodents underscores the presence and variability of genetic and other mechanisms underlying infanticide in a group that is more amenable to experimental manipulation. Sussman et al. (1995) ignore these experimental results, while deploring the absence of similar rigor among wild primates. Although it would be scientifically very satisfying to have similar data for primates, various constraints (time, money, and ethical concerns) will probably dictate that advances in this area will continue to come from non-primates.

THE RESOLUTION OF SELECTION

As their final exhibit in the case against sexually selected infanticide, Sussman et al. (1995) claim that no selection on infanticide has been demonstrated, and "if it exists at

all, is likely to be weak" (Bartlett et al. 1993). True, selection on the infant-killing phenotype has never been measured. The selection gradient, commonly used to predict evolutionary change in a trait, can be estimated as the regression of the relative fitness of individuals on their trait values within a population (Arnold and Wade 1984). In practice, there is a major hurdle, because its estimation requires complete behavior records over a male's adult life as well as estimated lifetime reproductive success. No primate data set even comes close to producing these data. Sussman et al. considered this demonstration important because they felt that infanticide is "but a rare and evolutionarily trivial phenomenon" (Bartlett et al. 1993). However, their assertion that selection on infanticide is rare flies in the face of abundant evidence for strong selection on rare alleles. Furthermore, for some other primate species, infanticide is neither rare nor inconsequential.

The question is, will the average adult male ever have the opportunity to commit infanticide during his lifetime? Among Jodhpur langurs, one-third of infants born are killed by males invading the breeding unit from outside it (Sommer 1994). Similarly, 14 percent of infant mountain gorillas are killed by males (Watts 1989), as are 12 percent of red howler infants (Crockett and Sekulic 1984). While the relative mortality risk due to infanticide may be lower in many other species and populations, such numbers indicate that males successful in gaining access to females will have multiple opportunities for infanticide, and that selection could therefore act on infanticidal behavior. These percentages are quite comparable to those of other mammals in which infanticide is common and in which the evidence that it is a significant selection pressure is overwhelming, such as lions (27 percent of all cub deaths in first year due to infanticide, Pusey and Packer 1994) and prairie dogs (39 percent of litters partly or totally killed, Hoogland 1994). In lions, DNA fingerprinting reveals that all cubs born in a pride are sired by the residents (Gilbert et al. 1991), so there can be little doubt that the reproductive benefits of infanticide accrue to the *infanticidal males*. These studies complement the primate studies and demonstrate that the perpetrators of infanticide can derive significant fitness benefits from it.

Infanticide may be a common cause of mortality, but if natural infant mortality is high or reduction in interbirth intervals is modest, benefits to infanticidal males will be diluted. However, among mammals, primates are characterized by slow life histories and relatively low infant mortality rates. Sussman et al. (1995) claim that the only indication of fitness differences we have are small decreases in interbirth intervals for females who lost infants relative to those who did not. They arrive at this conclusion largely on the basis of the Jodhpur results (Sommer 1994). However, because of provisioning, the Jodhpur langurs have the shortest interbirth interval of which the species is capable, virtually identical to captive

animals fed ad lib. By contrast, in wild red howlers, females that lose their infants to observed and inferred infanticide have interbirth intervals 37 percent shorter than other adult females (Crockett and Sekulic 1984). Because of the typically short breeding tenure of males in most infanticidal primate species, even a small reduction in interbirth interval increases the likelihood that a new male will sire offspring before he is ousted, or his progeny are old enough to escape infanticide by the next male. Additional advantages may accrue, as an infanticidal male eliminates offspring sired by rivals as well as future competitors.

ARE THERE PLAUSIBLE ALTERNATIVES?

The alternative proposed by Sussman et al. (1995) is that "most cases of infant killing appear to be simply inconsequential epiphenomena of aggressive episodes." This implies that there has been no selection for any increased tendency for males to eliminate unrelated infants. No doubt, infanticide might once have occurred as a by-product of males encountering unfamiliar females and some infanticides may still be best explained as incidental aggression. However, the deliberate targeting and stalking of infants belonging to unfamiliar females (Hrdy 1977, Leland et al. 1984, Pusey and Packer 1994, Sommer 1994), the widespread occurrence of the male takeover/infanticide pattern, as well as the experimental data on the timing of infanticide in relation to ejaculation in rodents, imply selection for specific responses. Hence, in various rodents, the act of ejaculation with a female partner (spontaneous ejaculation does not suffice) provides a male mouse with a neural fail-safe system for timing when it is safe versus possibly genetically suicidal to destroy pups that he encounters (vom Saal 1984). Such calibrations simply do not strike us as the stuff that "genetically inconsequential epiphenomena" are made of.

CONCLUSION

Where infanticide is a major source of mortality, there is every reason to expect it to affect parental behavior and even social systems. Regardless of the functional significance, if infanticide is likely in certain circumstances and if a particular behavior minimizes their occurrence, we expect selection to favor the behavior. But can such selection actually shape primate social systems (van Schaik and Dunbar 1990)? The idea remains controversial for primates, but consider data for the dung beetle *Nichophorus orbicollis* (Scott 1990). After preparing a dung ball, parents deposit the eggs. Guarding by both biological parents dramatically reduces the probability that conspecifics will usurp the resource, kill the newly hatched brood and produce a replacement clutch. Such

data strongly suggest that infanticide selects for biparental care in this species.

The continuing debate over infanticide among primates reflects two different world views, both of them defensible. Consider the following summation from Bartlett et al. (1993): "Clearly, proponents of the sexual selection hypothesis accept the fact that there is variation in takeover events, yet they maintain that there is an underlying consistency—infant killing follows group takeover. Yet, while this may be true in general terms for many cases (emphasis ours), the use of a single term to refer to the numerous phenomena described above misrepresents the complexity of primate social behavior. . . ." Precisely. While some are interested in emphasizing the uniqueness of each case—a valid position—others are driven by the need to seek for general patterns and to use theory to explain them. For the former it is an insult to the sanctity of the individual and the sacredness of context that generalizations should extend beyond the specifics of the case in hand. The latter derive their greatest pleasure from noting that so many findings could have been correctly predicted on the basis of pitifully incomplete data sets merely by relying on logic, comparisons, and extrapolations guided by evolutionary theory.

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