Infanticide in tree squirrels — a male reproductive strategy?

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A recent report on the killing of juveniles by an adult tree squirrel, *Paraxerus cepapi*, focuses attention on the adaptive nature of such behaviour. The interpretation of infant killing as a sexually selected male reproductive strategy has been favoured by many sociobiologists, despite the fact that much of the data that are needed for rigorous testing of this hypothesis are lacking. Some postulates and assumptions of the hypothesis are discussed here. Most recent systematic field studies of infanticide in rodents have been conducted on ground squirrels (genus *Spermophilus*). However, observations indicate that males rarely kill juveniles in this group. The lack of male – male competition over mates in the tree squirrel, as well as seasonal breeding in certain ranges of this species, lead me to conclude that infanticide does not represent a sexually selected male reproductive strategy.

'n Onlangse verslag oor die doodmaak van kleintjies deur 'n manlike boomeekhoring, *Paraxerus cepapi*, stel ondersoek in oor die adaptiewe aard van sulke gedrag. Die doodmaak van onvolwassenes deur manlike diere is deur baie dierkundiges beskou as 'n geslag-selektiewe manlike reproduktiewe strategie, alhoewel die data wat benodig word om hierdie hipotese volledig te toets tot dusvêr ontbreek. Sommige stellings en aannames van die hipotese word hier bespreek. Onlangse stelselmatige studies van 'kindermoord' deur knaagdiere is in grondeekhorings (genus *Spermophilus*) uitgevoer. Mannetjies maak selde onvolwassenes dood in hierdie groep diere. Weens die afwesigheid van manlike kompetisie vir wyfies in die boomeekhoring, asook die bestaan van 'n teelseisoen in sommige dele van die spesie se gebied, kom ek tot die gevolgtrekking dat die doodmaak van onvolwassenes nie 'n geslag-selektiewe manlike reproduktiewe strategie in boomeekhorings is nie.

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Recently, de Villiers (1986) reported the killing of three juvenile tree squirrels, *Paraxerus cepapi*, by an adult male. He speculated that, unless the behaviour of the male was aberrant, he was gaining an advantage by killing the juveniles; the advantage being an increase in inclusive fitness (*sensu* Hamilton 1964). ['Inclusive fitness' is a quantitative measure of total genetic success via personal reproduction and effects on relatives' reproduction. It is based on gene frequency rather than on numbers of offspring. Hamilton (1964) introduced the term, and recognized that it is theoretically possible for an individual, under the right circumstances, to have a higher inclusive fitness by aiding relatives, rather than by attempting to reproduce itself. The use of 'inclusive fitness' by de Villiers (1986) is erroneous and should read 'reproductive success' (i.e. classical fitness).] In this paper, I propose to outline the development of the sociobiological interpretations of infanticide. Also, some difficulties underlying the 'sexual selection hypothesis' (Hrdy 1979) are discussed. Finally, a brief summary of observations of infanticide in ground squirrels is presented. I conclude that infanticide by an incoming male is unlikely to have evolved as a male reproductive 'strategy' in the tree squirrel.

In *The Descent of Man*, Darwin concluded that infanticide was one of the most important Malthusian checks on human population growth, adding:

> 'Our semi-human progenitors would not have practiced infanticide . . . for the instincts of the lower animals are never so perverted as to lead them regularly to destroy their own offspring' (1874, p.52).

The killing of conspecific young was thus seen as a purely human phenomenon.

Prior to 1970 most reports of infanticide in animals were merely anecdotal, with no concurrent investigations of causes and functions (Labov, Huck, Elwood & Brooks 1985). Then, Trivers (1972) viewed infanticide as a possible outcome of extreme male – male competition (sexual selection) in rare instances. Infanticide, therefore, became incorporated into the existing sociobiological framework. Once hypotheses had been erected to explain infanticide, the observations of it (often indirect or 'presumed') increased, and explanations of its adaptiveness were sought.

Observations on the Hanuman langur, *Presbytis entellus* (Hrdy 1974, 1977a, b; Sugiyama 1967) formed the cornerstones of the sexual selection hypothesis of infanticide. The argument can be summarized as follows: by killing the nursing infants, a male that takes over a troop of females shortens lactation in the mothers, thereby speeding up the onset of oestrus. Theoretically, therefore, only unweaned young are expected to be killed. (The killing of older offspring, however, does not reduce the proposed selective advantage, provided younger offspring are killed as well.) The usurping male thus gains a reproductive advantage, this being inversely correlated with age of the victim. Many primatologists favour this explanation, but by no means all (e.g. Boggess 1979; Curtin 1977; Curtin & Dolhinow 1978; Dolhinow 1977).

In other animals, infanticide has been variously explained (e.g. Hausfater & Hrdy 1984; Hrdy 1979). In rodents, adaptive explanations include the elimination of weak individuals, reduction of future competitors, acquisition of food or nest sites, reduction of an overlarge litter size, as well as sexual selectionist interpretations (Labov *et al.* 1985).

The points listed below form some untested postulates and assumptions of the sexual selection hypothesis. Many of the criticisms can also be levelled at other adaptationist hypotheses.

Population demography

A polygynous breeding system and intense male – male competition are prerequisites of the sexual selection hypothesis. A large number of females must be dominated by a few males, so that takeover of a group of females by an incoming, foreign male is the only access to reproductive females for that male. Also, the infanticidal male has to mate with the victimized female. Struhsaker (1977) suggested that male takeovers and infanticide may be phenomena characterizing one-male social systems. In addition, observed takeovers and infant deaths increase with population density (Boggess 1979; Curtin 1977; Hrdy 1979). Most observed cases of infanticide, therefore, occur in high density populations, characterized by a high frequency of takeovers and intense male – male competition. These conditions do not preclude the interpretation of infanticide as social pathology (e.g. Calhoun 1962; Curtin 1977).

Reproductive physiology and breeding season

The sexual selection argument rests on the assumption that the killing of preweaned young speeds the return to oestrus in the victimized female (Hrdy 1979). Thus continual breeding is a prerequisite of this hypothesis.

> 'There would be little reproductive gain for a male who killed an infant among strictly seasonal annual breeders . . .' (Hrdy 1979, p.22).

Field observations suggest that infant loss has little impact on female oestrus patterns in seasonally breeding langur populations (Hrdy 1977b).

Kin or individual recognition

The infanticidal male would clearly be at a disadvantage if he killed his own young. Therefore, a male has to 'assess' his relationship to the potential victim. Hrdy (1974, 1977a) suggested that male langurs base their decision whether to kill an infant or not on previous consort relationships with the infant's mother (i.e. whether the mother is known to the male or not). Langurs are thus credited with remarkable abilities (Curtin & Dolhinow 1978), especially as multiple mating of females may occur (Boggess 1979).

If there is no kin or individual recognition, dispersal of males becomes important. If a male is nomadic during some stage of his life, this decreases the chance that the infants in the recently usurped group are his own offspring. Theoretically therefore, infanticide is expected to show a correlation with nomadism.

The genetical basis of infanticide

The idea that infanticide is adaptive and has evolved (for example Hrdy 1974, 1977a, b; Wilson 1975) implies that the behaviour is heritable. Although there are tenuous indications of genetically based strain differences in the occurrence of infanticide in laboratory mice (Svare, Broida, Kinsley & Mann 1984), such differences may be the result of differing laboratory management techniques (Labov *et al.* 1985).

Underlying all discussions of the adaptiveness of infanticidal behaviour is the assumption of relatively simple inheritance of 'infanticide genes'. For the sexual selection hypothesis specifically, the infanticidal behaviour is manifested only in the males (that is, it is sex-limited), and it is difficult to envisage the inheritance of a behaviour pattern which is detrimental to females, but has to be passed on from a female to her son.

The evolution of infanticide

Even if it can be shown that infanticide is heritable, will this behaviour evolve? Recently, mathematical modelling of infanticide in a hypothetical population has substantiated the possibility that infanticidal behaviour can evolve (Chapman & Hausfater 1979; Glass, Holt & Slade 1985; Hausfater, Aref & Cairns 1982). It becomes apparent, however, that it is adaptive only under certain, restricted conditions. For example, as the frequency of infanticidal behaviour increases in a population, so the chance that an infanticidal male will be replaced by another infanticidal male increases. The advantage gained by the initial male thus decreases (Chapman & Hausfater 1979). Also, the number of offspring gained by an infanticidal male relative to a non-infanticidal male is never more than one brood per female per takeover. Therefore, an infanticidal male has to risk many takeovers for his theoretical reproductive advantage to be substantial.

Physical injury caused by the male – male conflict that accompanies a takeover as well as by postpartum aggression of females protecting their young may preclude frequent takeovers and infanticide. Furthermore, no data are available to show that infanticide increases the fitness of a male. Certainly lack of this behaviour does not preclude reproductive success.

With the social disruption that often follows infanticide (Hrdy 1979; Hausfater 1984) and the impact such behaviour has on the population age structure through removal of juveniles, it is unlikely that such behaviour represents an adaptive male reproductive strategy, given only a slight advantage (if any) of infanticidal over non-infanticidal males.

In the following section, I propose to examine whether field observations of infanticide in rodents support the sexual selection hypothesis.

Ground squirrels

Infanticide is likely to occur infrequently and under circumstances that reduce its detection in nature (Sherman 1981, 1982). Most recent systematic field studies of this behaviour have been conducted on ground squirrels (Balfour 1983; McLean 1983; Sherman 1981; Waterman 1984).

Although infanticide is said to occur widely in the genus *Spermophilus*, it has been observed directly in only a few species (Michener 1982). During a four-year study of Belding's ground squirrels (*S. beldingi*) at least 8% of all young born were infanticide victims (Sherman 1981, 1982). The main perpetrators were adult females and yearling males. The latter consumed their victims (cannibalism); the former gained access to nest sites deserted by the victim's mother. Adult males seldom committed infanticide, and, regardless of the loss of their litters, females were sexually receptive only once per season. Furthermore, Hanken & Sherman (1981) reported multiple matings in this species, so that paternity is confused. In Columbian ground squirrels (*S. columbianus*) only females have been seen to be infanticidal (Balfour 1983; Waterman 1984). McLean (1983) reported ten instances of killing of conspecific young by adult male Arctic ground squirrels (*S. parryii*). In only six of these instances was the actual killing observed. Young that had not emerged from the natal burrow were killed by males that became resident in the area after the mating period. After losing their young, females did not breed again in the same season (McLean 1983).

Tree squirrels

The behaviour of the tree squirrel, *Paraxerus cepapi*, has been studied most completely by Viljoen (1975, 1977). Aggression plays a prominent role in social behaviour, with both males and females being aggressive to either sex. Yet the mortality rate for juveniles up to the age of six months is very low, contrary to predictions if infanticide were important in this species.

Tree squirrels live solitarily or in groups, often with more than one adult male in each group. During oestrus, which lasts about 4 h, the female emits distinct vocalizations. These attract males, often several at a time and often from adjacent territories (Viljoen 1975, 1977). Therefore, multiple insemination in this squirrel cannot be ruled out. The vocalizations of oestrous females have the effect of stimulating oestrus in other, nearby females, so that some degree of synchronization exists. Therefore, intense male – male competition, with only a few males having access to females, is not evident in this species. Viljoen (1977, p.154) wrote:

> '. . . male squirrels are only tolerated on a strange territory during a mating bout which indicates that the limited resource which causes territoriality in this species is something other than a mate.'

Data on male takeovers are also lacking.

Tree squirrels seem to have a distinct breeding season (Viljoen 1975, 1977). However, pregnant females have been collected throughout the year in certain areas (Smithers 1971). It is not known whether these females are polyoestrous, or whether different females are mated at different times of the year (each female coming into oestrus once and being anoestrous for a large part of the year). Under favourable conditions, and in captivity, females may become polyoestrous (Viljoen 1975, 1977; see also de Villiers 1986). However, males show testicular regression between January and June (Viljoen 1975, 1977), but an exception to this was reported by de Villiers (1986).

Although tree squirrels are not strict seasonal breeders in at least certain areas of their range, there is no evidence to indicate whether sexual cycling is resumed shortly after loss of a litter. Attempted copulation by an infanticidal male has been witnessed by de Villiers (1986), but the female was considered anoestrous. The advantage gained by the male will probably be two additional offspring [the average litter size (Smithers 1971; Viljoen 1975, 1977)], but there is no evidence of this ever having occurred.

Conclusion

The data gathered so far do not substantiate the sexual selection hypothesis for ground squirrels. Usually other interpretations, including reduction of future competitors and intraspecific aggression, are proffered (e.g. Sherman 1981). In tree squirrels, *Paraxerus cepapi*, although observations of possible polyoestrus have been made, the lack of intense male – male competition precludes the interpretation of infanticide as a sexually selected male reproductive strategy (*sensu* Hrdy 1979). The behaviour witnessed by de Villiers (1986) should, therefore, be seen as aberrant (as mentioned by the former author), pending further observations.

Infanticide represents a concept with many anthropomorphic connotations. For example, Hrdy (1979) repeatedly uses the word 'murder'. The killing of young, therefore, represents a problem to some workers, unless an adaptive explanation is sought.

Infanticide may be adaptive and may have evolved, but only under conditions where the disadvantages are outweighed by the advantages to the infanticidal party, or more specifically, where infanticidal behaviour becomes a necessary prerequisite for reproduction. These conditions seem to be precise and predictable, and, therefore, should be tested rigorously. Mere anecdotal descriptions of infanticide in conjunction with plausible adaptive explanations will not suffice to resolve the question whether the killing of young is adaptive or not.

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