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## The functional significance of infanticide in a population of California ground squirrels (*Spermophilus beecheyi*)

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**Abstract** Naturally-occurring infanticide was observed in a population of California ground squirrels (*Spermophilus beecheyi*). In four seasons, 40 infanticides were observed. All victims were post-emergent pups. Of 37 killings in which the killer was sexed 36 were by females. All infanticidal females were mothers at the time they killed, but in no case was a mother seen to kill or harm her own young. The victim was cannibalized in 22 cases and taken immediately into the killer's burrow in 16 others. In no case did killers gain access to the victimized mother's burrow or territory and female pups were not killed preferentially over males. In light of evolutionary explanations, infanticide in this population may best fit the resource exploitation hypothesis, in which killers commit infanticide to gain a nutritional benefit. Resource competition is a possible auxiliary explanation, since any time a female kills unrelated young she is eliminating possible competitors to her own offspring. This behavior could confer a fitness advantage on killers or it could be an adaptively neutral, alternative feeding strategy. More data are necessary to distinguish between these hypotheses.

**Key words** *Spermophilus beecheyi* · Infanticide · Resource exploitation

### Introduction

Infanticide in free-ranging mammalian populations, though difficult to document (Hrdy and Hausfater 1984), has been observed in a variety of species (Hrdy

1979; Leland et al. 1984; Packer and Pusey 1984; Parmigiani and vom Saal 1994). The most widely known cases are those in the primates (Hrdy 1979; Leland et al. 1984), but the largest body of data on naturally occurring infanticide is that for the marmotine sciurids: ground squirrels, prairie dogs and marmots (order Rodentia, family Sciuridae, tribe: Marmotini). Sherman (1981), studying Belding's ground squirrels (*Spermophilus beldingi*), was the first to systematically examine infanticide in the sciurids. Other studies of ground squirrel infanticide have shown that infant killing occurs throughout the taxa (Balfour 1983; McLean 1983; Waterman 1984; Brody and Melcher 1985; Hoogland 1985).

Infanticide is defined as the killing of dependent young, who have not yet dispersed from their natal territory, by members of their own species (Brody and Melcher 1985). The significance of this behavior has recently been considered in light of evolutionary hypotheses, especially those proposed by Hrdy (1979), which view killing from the standpoint of gain to the perpetrator. With respect to sciurids, killing appears to have a variety of functions throughout the group. Sherman (1982) found Belding's females kill to gain territory, while males kill for nutritional gain. Black-tailed prairie dog mothers (*Cynomys ludovicianus*) may kill their own young (Hoogland 1985, 1994) and male arctic ground squirrels (*Spermophilus parryii*) commit infanticide to gain territories (McLean 1983).

This paper presents data from a four-year study of naturally-occurring infanticide in free-living California ground squirrels. Although Linsdale (1946) and Fitch (1948) both found dead *S. beecheyi* pups on burrows and suspected infanticide, infant killing in this species has only recently been observed (Trulio et al. 1986). The results given here present the largest body of published data on observed infant killing in a free-ranging mammalian population. Infanticide in this colony exhibits a distinct pattern and its possible adaptive significance is examined.

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## Materials and methods

California ground squirrels are large, diurnal rodents which live colonially in short-grass habitats from California to Washington state. They weigh 500–1000 g and live in burrow systems they dig themselves. A colony of these squirrels was observed at Camp Ohlone, a park in the East Bay Regional Park system, Alameda County, California. The site was an abandoned walnut orchard about 0.5 ha in size, in which the trees had been planted 10 m apart to form a grid. Squirrels were trapped in Tomahawk single or double door traps, sedated with Ketamine and marked with Nyanzol pelage dye. Numbered fingerling ear-tags were clipped on each ear for permanent identification. Squirrels were weighed, sexed, examined for reproductive status, and checked for scars and other identifying marks. Trapping took place approximately once a week during non-observation hours. There were 31 adults living on the site in May 1984, 36 in May 1985, 32 in May 1986, and 39 in May 1987, an average of 34.5 adult squirrels in May.

The site was observed for over 1500 h from 1984 to 1987. Field seasons ran from 8 March to 24 August 1984, 17 March to 28 August 1985 and 22 March to 22 July 1986. In 1987, data collection from 20 February to 29 July was performed primarily by three other researchers. Observations were taken from an elevated blind at the east edge of the colony with 10 × 40 binoculars. Scan samples (Altmann 1974) of each animal's identity, location, posture, orientation and behavior were taken every half-hour in 1984 to 1986 and each hour in 1987. A running log of interactions and pertinent information (predation, carnivory, agonism) was kept.

Throughout this study, infanticide was counted as “observed” only if the killing was actually witnessed. Cases in which an animal was seen in possession of a freshly dead pup (but the actual killing was not seen) were called “strongly suspected” infanticides. Cases in which an adult had a pup, not recently killed, were called “suspected”. When a pup carcass was found on a squirrel's burrow with no other evidence as to the cause of death, these were called “inferred” infanticide. Only observed cases were analyzed to provide insight into the possible adaptive significance of infant killing. For each infanticide, the observer tried to determine the killer's identity, the location of the killing, the victim's sex and mother and the ultimate fate of the carcass.

Statistical analyses included Mann-Whitney *U*-tests and  $\chi^2$  tests for non-parametric data, and *t*-tests when the data did not violate assumptions of normality. All statistical tests used an  $\alpha$  level of 0.05 (two-tailed tests). For all tests, multiple weights or multiple litters per female were averaged together giving a single value for each animal, to eliminate biases arising from individual idiosyncrasies in behavior and non-independence of data.

## Results

### Reproduction

The breeding season at Camp Ohlone ends in late February or early March (D. Owings personal communication). Females were observed to be lactating and presumed to have given birth in late March or early April. Pups remained below ground 5–6 weeks and began emerging in early to mid-May. Litters tended to emerge fairly synchronously, within about a 2-week period (Fig. 1). Numbers of pups emerging were consistent, a total of 73, 56 and 78, respectively, each year from 1985 to 1987 (Table 1). Pup counts in 1984 were not accurate enough to be included. All but 1 of the

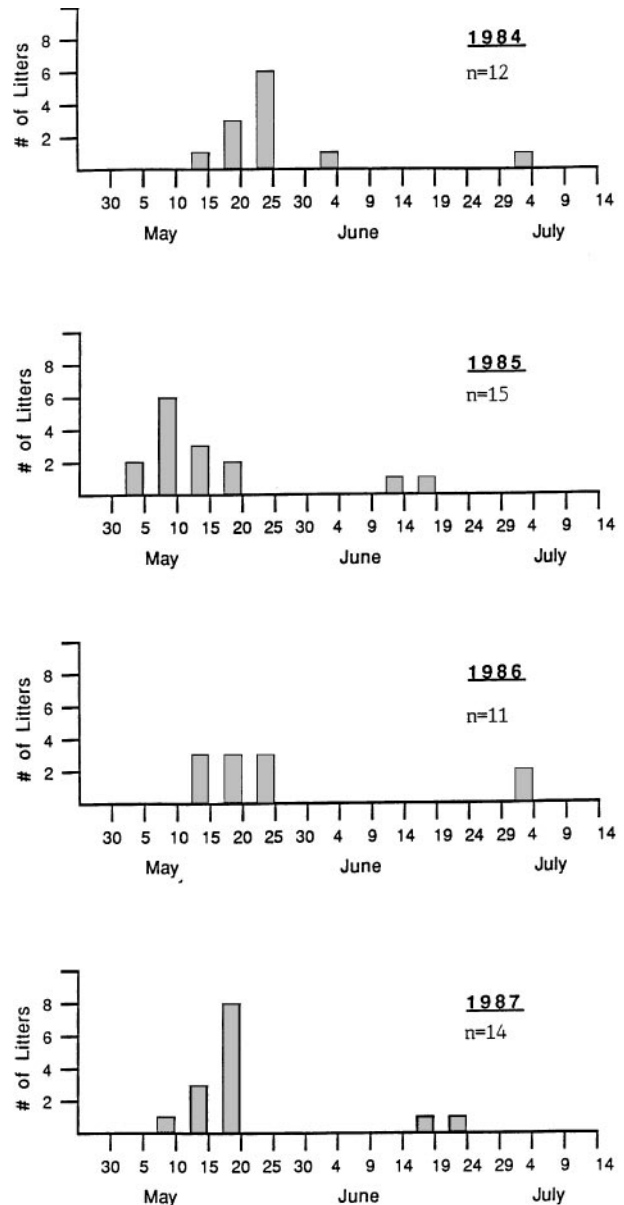


Fig. 1 Distribution of litter emergences in 5-day intervals at the Ohlone Colony over a 4-year observation period

39 reproductive females in these 3 years had one litter/season. One female produced a second litter and pups emerged a month and a half after she lost both pups of the first litter, one to infanticide. Although researchers have long suspected that California ground squirrels might be able to produce two litters a season (Tomich 1962; Simpson and Lamunyon 1980), this may be the first record of the behavior. At emergence, litter sizes ranged from one to eight, with an average of 5.0 pups/litter ( $n = 40$ , 1985–1987). Pups remained in the immediate area of their home burrow for the 1st week and began feeding further away after that time. Pups were considered weaned at 4 weeks post-emergence, the age at which they begin to disperse (Holekamp 1984).

**Table 1** Reproductive data for the Camp Ohlone population, 1984–1987

	1984	1985	1986	1987
Number of litters	12	15	11	14
Number of reproductive females	12	14	11	14
Number of females in the colony (May)	–	17	18	17
Percent of females with litters	–	88.2%	61.1%	82.4%
Total Number of pups	~40	73	56	78
Litter size: average	–	4.9	5.1	5.5
Litter size: range	–	1–8	2–7	1–8

**Table 2** Infanticide data for the Camp Ohlone population, 1984–1987

	1984	1985	1986	1987	Total
<i>I. Observed infanticides</i>					
Observed infanticides	2	6	15	17	40
Perpetrated by females	2	5	13	16	36
Perpetrated by males	0	0	1	0	1
Eaten by killer	2	2	7	9	22
Taken into killer's burrow	0	2	7	7	16
<i>II. Suspected infanticides</i>					
Strongly suspected	2	0	1	1	4
Suspected	1	0	0	2	3
Inferred	0	1	2	5	8
Female suspected killer	3	1	1	6	11
Male suspected killer	0	0	0	0	0

## Infanticide

Over the 4-year study, 40 infant killings were observed at the Ohlone site (Table 2). Of 37 cases in which the sex of the killer was known, 36 killings were committed by females and 1 by a male. Since the average sex ratio of adults over the 4 years was 13.8 females to 11.5 males, females were significantly more likely to be killers than males ( $\chi^2 = 15.1$ ,  $df = 1$ ,  $P < 0.001$ ). Killers were always more than two generations removed from their victims and were always mothers themselves at the time they killed. There was no evidence that mothers ever harmed or killed their own young. Of 38 cases in which the immediate fate of the victim was known, the pup was eaten in 22 cases and taken immediately into the killer's burrow in 16 others. Infanticides were observed from 22 May to 18 June, 1984, 4 May to 19 June, 1985, 15 May to 2 July, 1986, and 16 May to 5 July, 1987.

All 40 victims were post-emergent pups. There was no evidence of pre-emergent pup infanticide such as dead pre-emergent pups on burrow mounds (Sherman 1981) or unrelated females entering a natal burrow and later emerging with dead pups or blood on her mouth (Sherman 1981; Hoogland 1985). In addition, all 25 females seen lactating in two seasons (data complete only in 1985 and 1986) had emergent litters. The age

of victims at the time they were killed ranged from 2 to 13 days post-emergent, with an average age of 5.5 days post-emergent ( $n = 23$ ). Of 11 victims who were sexed, 5 were males and 6 were females. From 1985 to 1987 (1984 excluded because litter counts were not complete), the colony produced 207 pups. During these years, 28 of the 38 pups lost to infanticide were identified as unequivocally from the colony. Thus, over the 3 years, at least 28 of 207 pups or 13.5% of the pup population was lost to infanticide.

Killers tended to kill more than once over the season, although only one pup was killed at a time. Seven different marked females killed and five were multiple killers. In total, 9.7% of all females and 13.7% of mothers were killers. When they killed, infanticidal females tended to be farther from their home burrows than victims were from theirs. In 22 cases in which the killer and victim's home burrow were known, killers were an average of 20.2 m from home, while victims were only an average of 6.9 m from their home burrow when killed, a significant difference ( $t = 5.52$ ;  $df = 21$ ;  $P < 0.001$ ). Nine litters were attacked multiple times, and in seven of these sets, the litter was attacked twice by the same killer. The home burrows of both the victim and the killer were known for 26 killings. Of these 26, 13 victims were from the litter closest to the killer which did not belong to the killer's mother or sister.

Fourteen females lost at least one pup to infanticide. In no case did a victimized female losing a pup immediately vacate her burrow ( $n = 25$ ), nor did killers ever attempt to move into the victimized mother's area after infanticide.

Table 3 compares five characteristics of different classes of females in the colony. There was no statistical difference between the weights of infanticidal females and non-infanticidal females, nor did the weights of victimized mothers versus non-victimized mothers differ. The difference in weight between nine infanticidal females and the corresponding nine females they victimized was not significant (only nine paired measures, all in 1987, were close enough together in the pre-infanticidal period to be reliably compared). The ages of infanticidal females, as measured by the ratio of yearling squirrels to mature (2 years or older), did not differ significantly from non-infanticidal females and there was no significant age difference between victimized and non-victimized females.

There was no difference with respect to the average number of pups emerging per litter between infanticidal and non-infanticidal females or between victimized versus non-victimized mothers. Nor was there a significant difference between the number of pups weaned by infanticidal versus non-infanticidal females. The number of offspring lost between emergence and weaning did not differ significantly for infanticidal versus non-infanticidal females.

**Table 3** Statistical comparisons between relevant classes of females

I. Weight comparison					
	Mean weight (g)	SD	<i>n</i>	Test	Significance <sup>a</sup>
Infanticidal versus Non-infanticidal	558.3 566.0	63.5 55.5	6 19	Mann-Whitney <i>U</i> = 50	ns
Victimized versus Non-victimized	557.5 558.4	45.7 57.7	8 16	Mann-Whitney <i>U</i> = 62	ns
Infanticidal versus Victimized female <sup>b</sup>	559.0 567.3	79.9 63.3	9 9	<i>t</i> = 0.189	ns
II. Age comparison					
	No. of yearlings to mature females			Test	Significance
Infanticidal versus Non-infanticidal	2/6 22/30			$\chi^2 = 0.29$	ns
Victimized versus Non-victimized	5/5 19/31			$\chi^2 = 0.08$	ns
Infanticidal versus Victimized female	2/6 5/5			$\chi^2 = 0.35$	ns
III. Pups emergent per female					
	Mean litter size	SD	<i>n</i> Females	Test	Significance
Infanticidal versus Non-infanticidal	4.7 5.3	2.6 1.4	6 24	Mann-Whitney <i>U</i> = 71	ns
Victimized versus Non-victimized	6.0 4.8	1.1 2.0	10 20	Mann-Whitney <i>U</i> = 71	ns
IV. Pups weaned per female					
	Mean no. weaned	SD	<i>n</i> Females	Test	Significance
Infanticidal versus Non-infanticidal	2.6 2.2	2.7 2.1	5 20	Mann-Whitney <i>U</i> = 46	ns
V. Pups lost between emergence and weaning					
	Mean no. lost	SD	<i>n</i> Females	Test	Significance
Infanticidal versus Non-infanticidal	1.8 3.3	1.5 2.4	5 20	Mann-Whitney <i>U</i> = 31	ns

<sup>a</sup>All tests two-tailed; *P* < 0.05 unless otherwise stated; ns = non-significant

<sup>b</sup>Comparison of 9 pairs of killers and females they victimized in 1987

## Suspected infanticide

Table 2 provides data on strongly suspected, suspected and inferred infanticides at Ohlone. In four of five strongly suspected and suspected killings in which the likely killer was identified, the potential killers were reproductive females; the fifth was a non-reproductive female. In 13 of the 14 cases listed, the carcass was eaten. Carcasses were all discovered during the weeks when "observed" infanticide occurred.

## Discussion

Hrды (1974, 1979) suggested that infanticide may be an adaptive behavior and she developed five functional

hypotheses which view infant killing from the standpoint of gain to the killer:

1. Resource competition, in which killers gain access to a resource or reduce competition to themselves or their young
2. Resource exploitation, in which killers gain a food item
3. Sexual selection, in which killers gain a reproductive advantage
4. Parental manipulation, in which parents kill defective or "inappropriate" sex offspring
5. Social pathology, killing which is maladaptive Sherman (1981) produced nine hypotheses which considered the behavior in light of cost to the parents. His formulation expanded on Hrды's five basic points.

With respect to either formulation, infanticide in California ground squirrels seems to best accord with the function of obtaining nutrition by killing, i.e., the resource exploitation hypothesis. This hypothesis predicts that killers will eat the victims, will be unrelated to their victims, and may be energy-stressed. In the 38 cases in which the victim's fate was known, victims were either eaten or taken into the killer's burrow. Kinship data was known for 7 of 16 killer-victim pairs. In each case, perpetrators were more than two generations removed from the pups they killed, with the possible exception of the male whose relationship to any pup could not be known. All female killers (11) were mothers themselves at the time they cannibalized pups (20 cases). Females with nursing young are likely to be highly energy- and nutrient-stressed (Schitoskey and Woodmansee 1978; Wolff and Cicirello 1990) and may require large protein meals to successfully wean their litters (Hoogland 1985, 1994).

While killers ate the victim in 22 cases, in 16 other killings victims were taken immediately into the killer's burrow. Since cannibalism was not observed, these cases cannot unequivocally be categorized as exploitation infanticide. However, victims were never abandoned, as has been seen in other ground squirrel species (*S. beldingi*: Sherman 1981; *S. parryii*: McLean 1983; *S. armatus*: Balph 1984; *C. ludovicianus*: Hoogland 1985). In all 16 cases, killers expended energy to move the carcass to their burrow rather than abandoning the carcass as would be expected if simply killing the infant was the goal. Sherman (1976) has stated that by removing victims to their burrows, killers appear to treat victims as valuable food items. Also, in 8 of the 22 cases of observed cannibalism, the partially-eaten victims were also taken into the killers' burrows.

Infanticide for food may be an extension of the opportunistic carnivory shown by this population. Including data obtained in 1983 (Trulio et al. 1986), there have been 15 cases of carnivory observed. Goodall (1977) suggested the connection between carnivory and infanticide in primates, as did Hrdy (1979; p. 14), who noted that the cannibalism of young "appears to be an end in itself, not clearly distinguished from predation." At Ohlone, *S. beecheyi* females may view unrelated pups as another type of small prey item.

Resource competition is always a theoretical co-function of cannibalism, because whenever an unrelated pup is eaten, a possible competitor is removed (Hrdy and Hausfater 1984). However, in this population, killers did not directly gain a resource such as burrows, since infanticide never resulted in a killer obtaining a victimized female's burrow. Nor did killers preferentially eliminate direct competitors. Since unrelated female pups are considered the greatest competitive threat to other females and their young (Sherman 1981), females should be preferentially killed. But, of the 11 victims sexed, only just over half (6) were females.

Competition infanticide may have been more general and directed against any sex pup competing for local resources with the killer's pups. Of the 26 killings in which home burrows were known, 13 were directed at the nearest litter of non-relatives. Since victimized females had more emergent pups than non-victimized females, competition for food or space is implicated in these nearest-neighbor, large-litter killings. An alternative interpretation is that these numerous, nearby pups simply provided the easiest targets for opportunistic killing.

Other functional hypotheses are inappropriate explanations of infanticide in this population. Parental manipulation is not supported since mothers were never seen to kill their own young. Sexual selection infanticide is not a likely explanation for females in this species as California ground squirrels exhibit harem polygynous (Dobson 1983) or promiscuous (personal observations) breeding behavior, and in neither system are females likely to compete for matings with males.

Pierotti (1991) has proposed that killing young to prevent the adoption of unrelated individuals may be another adaptive function of infanticide. This hypothesis may be most relevant in cases typically ascribed to competition or pathology. In species exhibiting adoption avoidance infanticide, parents are likely to adopt unrelated young at a time when other young cannot be distinguished from offspring, usually later in rearing. This hypothesis is not a likely explanation in *S. beecheyi*, as infanticide in this species is best ascribed to exploitation. Moreover, females in other *Spermophilus* species have been shown to actively discriminate between their own and other offspring (Sherman and Holmes 1985) and *S. beecheyi* may be able to do the same. Finally, young which are killed to avoid adoption are expected to have wandered into a strange female's territory seeking care (Quinn et al. 1994). In the Ohlone colony, killers, not victims, were the wanderers; killers were significantly farther from their burrows than the victims were from theirs.

While reproductive females can benefit by cannibalizing unrelated young, why particular females become killers is not clear. There was no significant difference between the weights, ages or numbers of emergent pups per litter of infanticidal females versus non-infanticidal females; none of these parameters illuminate why certain females become infanticidal (Table 3). However, why a female became a victimized mother seems clearer. Proximity to an infanticidal female was an important factor. Of 26 victims 13 were taken from the closest unrelated litter to the killer's maternal burrow. Victimized females also had larger litters than non-victimized females. Because they were nearby and large, the litters of victimized females were more accessible than small, distant litters. Hoogland (1994) cited accessibility as a prime reason why female

black-tailed prairie dogs killed local young, even though those pups might be close relatives.

Losses to infanticide in the Ohlone colony can be calculated several ways. If only observed infanticides in which the victims were known to be residents of the colony are counted, then over three years 13.5% of the pup population was lost to infanticide. This figure is comparable to the observed infanticide recorded by Sherman (1981) for Belding's ground squirrels (8.5% of all pups in 3 years). A more liberal estimate can be obtained by counting all the pups killed by local adults and adding the cases of suspected and inferred infanticide (Dobson 1990). From 1985 to 1987, 38 pups were killed by Ohlone adults and there were 12 other cases of possible infanticide, representing a maximum of 24.2% (50/207) of the colony lost to infanticide. Using this formula, Dobson (1990) found 24% of the pups in his colony of Columbian ground squirrels were killed by adults. By either calculation, losses to infanticide in this colony are substantial.

If killing pups is adaptive, then *S. beecheyi* killers might be expected to have higher fitness than non-killers and wean more young. Although over 3 years (1985–1987) infanticidal females weaned more young than non-infanticidal females, this difference was not significant (Table 3). Infanticidal females also lost fewer pups between emergence and weaning than non-infanticidal squirrels, but again the difference was not significant. Infanticide may also confer fitness on killers by eliminating competitors to their offspring from local, large litters (Hoogland 1994), but this benefit could not be tested. It is also possible that killers may obtain higher fitness by killing than if they had not killed (C. Packer, personal communication). Testing this hypothesis would be very challenging.

An alternative view is that resource exploitation infanticide may not result in killers having higher fitness over non-killers, but rather equal fitness with them. If this is the case, then infanticide may be described as an adaptively neutral, alternative feeding strategy for energy-stressed females. Sherman (1981) implied that infanticide may be adaptively neutral in some circumstances. Sample sizes from this study are too small to produce definitive results on weaning success or fitness advantages; much more information from the Ohlone colony is necessary to distinguish between these hypotheses.

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