should help explain the pathophysiology of diseases having immune and neuroendocrine components.

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Infanticide in Prairie Dogs: Lactating Females Kill Offspring of Close Kin

Abstract. *Infanticide, although common in a wide range of species including humans and other primates, is poorly understood. A 7-year study under natural conditions reveals that infanticide within colonies of black-tailed prairie dogs* (Cynomys ludovicianus) *is striking for three reasons. It is the major source of juvenile mortality, accounting for the total or partial demise of 51 percent of all litters born. The most common killers are resident lactating females. The most common victims are the offspring of close kin.*

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Infanticide, the killing of conspecific juveniles, has been observed in numerous species from diverse taxonomic groups including rotifers, insects, fish, amphibians, birds, and mammals (*1*). Infanticide has often been regarded as a pathological and maladaptive response to overcrowding (*2*), but evidence suggests that infanticide in some contexts may lead to increased reproductive success (*1, 3, 4*). Here I describe four different types of infanticide that occur in natural populations of black-tailed prairie dogs (*Cynomys ludovicianus*).

Black-tails are large, diurnal, colonial, harem-polygynous squirrels (Rodentia: Sciuridae). In Wind Cave National Park, South Dakota, they breed in February and March, and weaned or nearly weaned juveniles emerge from their burrows in May and June (*5–9*). Colony residents live in contiguous territorial groups called coteries (*7, 8*), where one adult (≥ 2 years) male, three or four adult females, and several yearling and juvenile offspring typically live. Since they usually remain in the natal coterie territory for life, females within a coterie are almost always genetically related (*9*). Males usually disperse as yearlings and attempt to enter another coterie (*9*). Estrous females usually mate with the adult male in the home coterie (*10*). Breeding within a coterie is synchronous (*7*), and inbreeding is rare (*9, 11*); with some exceptions, breeding in both sexes is deferred until individuals are 2 years old (*8, 10*). The study colony, inhabited for at least 35 years, is approximately 500 m by 130 m (6.6 hectares), and in late spring of each year (1976 through 1984) contains an average of 132.8 adults and yearlings [standard deviation (S.D.), ±8.9; range, 117 to 143], 84.1 juveniles (±20.2; range, 58 to 119), and 23.2 coteries (±2.3; range, 19 to 26). Through eartagging, observing, and electrophoretic analysis of blood samples, maternal, sibling, and putative paternal genetic relationships have been determined for all young weaned at the study colony since 1975 (761 young from 257 litters) (*9, 10, 12*). Since 1975, only 5 females and only 14 males have immigrated into the study colony and produced weaned offspring.

The average gestation period for black-tails is 34.8 days (S.D., ±0.7; range, 34 to 37 days; $n = 32$), and the average time between parturition and the first emergence of weaned or nearly weaned juveniles is 43.4 days (S.D., ±3.5; range, 38 to 50 days; $n = 17$). Infanticide occurs both before and after weaning and sometimes involves cannibalism. Infanticide before weaning usually occurs in the burrow, and detection requires watching burrows with young for possible marauders (*13*). Postweaning infanticide also frequently occurs underground and is detected by the abrupt, simultaneous disappearances of several marked juveniles or by finding maimed carcasses above ground (*14*). Because breeding is so seasonal, females that lose a litter to infanticide lose an entire breeding season. From 1978 through 1984, the study colony was observed for a total of more than 20,000 man-hours of observation; during this time field assistants and I detected 73 cases of infanticide.

Almost all adult females at the study colony mate each year (*10*), after which they typically build an underground nest. After parturition females usually defend their burrows from all conspecifics and sleep with the young at night (*8, 15*). Unguarded by the mother, unweaned offspring may be killed by another lactating female of the home coterie. Only 11 of 36 mothers (31 percent) whose burrows were marauded weaned a litter, compared to 57 of 97 (59 percent) whose burrows were not marauded [$P = 0.004$, χ^2 (1) = 8.36] (*16*).

Infanticide by females of the home coterie was the most common type: we detected 40 cases (three litters were marauded two times), 22 different killers, and 28 different victimized mothers (*17*). These infanticides accounted for the partial elimination of 11 percent (15 of 133)

and total elimination of 19 percent (25 of 133) of litters born from 1981 through 1984 (Table 1) (*14*). The killers were almost always genetically related to mothers (Table 2). Most killers were lactating (n = 32), some had recently lost their own litters (n = 6), and others had already weaned a litter (n= 2). The average age of victims was 17.3 days (±11.0; range, 1 to 41 days; n= 38 litters); the average age of the marauder's offspring (when she still had them) was 17.5 days (±11.6; range, 3 to 47 days; n = 31 litters).

Females typically lose weight during lactation, and weaning a litter 1 year reduces the probability of successfully weaning a litter the next. Thus, lactation is evidently costly to individual black-tail females as it is to females of other mammalian species (*18*). Marauding may be beneficial: a comparison of marauding and nonmarauding lactating females showed that marauders (i) were more likely to successfully wean a litter, (ii) had larger litters at weaning, (iii) had heavier young at weaning, and (iv) were heavier themselves at weaning (*19*). Marauders may also gain by removing future competitors from themselves and their offspring (*4, 20*).

Some females that mated each year did not act maternally—that is, they did not build underground nests, guard burrows, or sleep alone (*8, 10, 15*), or they showed these behaviors only sporadically. We assumed that such females either failed to conceive or aborted and resorbed their litters, as has been observed for prairie dogs under laboratory conditions (*21*). In 1983 and 1984, we found from daily live-trapping that these females usually did give birth (*22*) but abandoned their offspring immediately after parturition. In many cases other coterie members were in the burrow at the time of parturition. Abandoned young were apparently killed and cannibalized by other coterie members or by the mother herself. In the best documented case, a female gave birth above ground and then joined two females of the home coterie in cannibalizing her newborn offspring. Putative infanticide in this context accounted for elimination of 13 percent (15 of 112) of litters born in 1983 and 1984 (Table 1). Presumed killings of abandoned young usually involved yearling males and nonlactating females but occasionally also lactating females.

When a yearling male was successful in entering a new coterie with recently weaned juveniles, all juveniles in the invaded coterie frequently disappeared within several days. In five of nine such cases, all juveniles (from seven litters) disappeared within 5 days; in three of the four other cases, some, but not all, the juveniles disappeared within 5 days. In coteries without yearling male invaders, juveniles disappeared abruptly after weaning in only three of 108 cases; this difference in juvenile survivorship was statistically significant ($P < .001$, two-tailed Fisher exact test). Male invaders presumably killed the unrelated juveniles that disappeared, and maimed carcasses were found above ground following four invasions, but actual killing was observed only once. In eight of the nine cases, the invading male remained in his new coterie until the following spring and sired offspring there. Postweaning infanticide by invading yearling males accounted for the partial demise of 2 percent (7 of 431) and for the total demise of 2 percent (7 of 431) of all litters born from 1978 through 1984 (Table 1). In 1984, presumed preweaning infanticide by invading yearling males removed an additional 4 percent (2 of 53) of litters born (Table 1) (*23*).

Infanticide after invasion by a new male has been observed in numerous other harem-polygynous mammals, including lions (*Panthero leo*) (*24*) and several primate species (*1*). The payoff for the males may be that females that lose lactating offspring come into estrus and conceive more quickly than females that continue lactating. In prairie dogs, however, many of the infanticides by invading males occurred after the termination of lactation; further, since prairie dog females come into estrus for only 1 day each year in either February or March (*10*), infanticide by an invading male in May or June evidently does not reduce the time until the next estrus of the females. Weaning success varies inversely with the number of yearlings in a coterie—perhaps because of increased competition from yearlings for food (*15*); the killing of juveniles by an invading male reduces the number of competing yearlings present in the next breeding season. Females in the year following infanticide are more likely to wean a litter. Thus, infanticide by invading prairie dog males may lead to increased male reproductive success by a mechanism unknown for other harem-polygynous species.

Female immigrants are also infanticidal. Of the two female immigrants from 1978 through 1984 that invaded established coterie territories that contained recently weaned juveniles, one permanently evicted the single resident female and her two juveniles (*25*). The other sequestered part of the established coterie territory, excluded the five resident females from that area, and evidently killed the three juveniles there, one of

Table 1. Summary table of infanticide in prairie dogs. Frequencies are the ratios of the number of observed infanticides to the number of litters born that could be monitored for infanticide as represented by numbers in parentheses (*14*).

Type of infanticide	Frequencies							
	1978	1979	1980	1981	1982	1983	1984	All years
Lactating female kills								
Some unweaned offspring of close kin				3.1 (1/32)	20.8 (5/24)	8.3 (2/24)	13.2 (7/53)	11.3 (15/133)
All unweaned offspring of close kin				21.9 (7/32)	20.8 (5/24)	12.5 (3/24)	18.9 (10/53)	18.8 (25/133)
Mother and other coterie members kill all abandoned newborn offspring in litter						10.2 (6/59)	17.0 (9/53)	13.4 (15/112)
Invading female immigrant kills all weaned offspring in litter	1.3 (1/77)	1.4 (1/69)	0.0 (0/56)	0.0 (0/64)	0.0 (0/53)	0.0 (0/59)	0.0 (0/53)	0.5 (2/431)
Invading yearling male kills								
All unweaned offspring in litter							3.8 (2/53)	3.8 (2/53)
Some weaned offspring in litter	6.5 (5/77)	0.0 (0/69)	0.0 (0/56)	0.0 (0/64)	0.0 (0/53)	3.4 (2/59)	0.0 (0/53)	1.6 (7/431)
All weaned offspring in litter	2.6 (2/77)	0.0 (0/69)	0.0 (0/56)	7.8 (5/64)	0.0 (0/53)	0.0 (0/59)	0.0 (0/53)	1.6 (7/431)

which was found dead above ground. This type of infanticide (or eviction) is similar to that reported for female Belding's ground squirrel (*Spermophilus beldingi*) immigrants (*4*), and accounted for the partial (*25*) or total loss of 0.5 percent (2 of 431) of all litters born in 1978 through 1984 (Table 1). Increased weaning success in smaller coteries (*15*) is the presumed payoff for female immigrants that kill unrelated juveniles.

In other mammalian species in which infanticide has been observed, the usual killers are invading adult males (*1, 3*), or, less commonly, nonbreeding immigrant females (*4*). For prairie dogs, the most common killers observed were resident lactating females. Except anecdotally (*26*), resident lactating females have not previously been implicated as infanticidal.

The study colony, surrounded by trees on three sides, cannot readily expand, and it is possible that some or all of the 73 observed cases of infanticide resulted from overcrowding (*2*). To investigate this possibility, we observed two other colonies at Wind Cave National Park that contained marked individuals; both colonies were young (one less than 5 years old, the other less than 15 years old), expanding, and presumably uncrowded. During 900 man-hours of observation, we detected one case of infanticide at the first colony and two cases at the second (*27*). The frequent failure of adult females to wean a litter reported in other studies (*8, 28*) may have resulted largely from infanticide. Thus, the evidence to this point suggests that infanticide in prairie dogs is widespread (*29*).

Accurate estimates of the frequency of infanticide under natural conditions are elusive. Combining frequencies of the different types of prairie dog infanticide indicates that 51 percent of litters were partially (13 percent) or completely (38 percent) affected (Table 1) (*30*). Only rarely has infanticide been implicated as such a major source of juvenile mortality (*31*). Increased mortality due to infanticide must be added to increased aggression and increased ectoparasitism as an important cost of prairie dog coloniality (*5*).

Natural selection favors individuals who are most successful at transmitting copies of their own alleles to future generations through the reproduction of either themselves or their kin. In general, individuals should behave preferentially toward kin and should aid the reproduction of such kin when possible (*32*). If a female can successfully wean her own litter only if she can obtain sustenance from infanticide and cannibalism, it follows that females should kill the offspring of nonkin rather than the offspring of kin. All prairie dog coterie members defend the home coterie territory (*8, 15*), but within the coterie only the mother defends her burrow and young (*8, 15*). Killing unrelated juveniles in an adjacent coterie would require eluding the defenses of all members of that coterie, whereas killing related juveniles in the home coterie requires only eluding one mother. This difference in accessibility may explain why marauding lactating females regularly kill the offspring of kin rather than the offspring of nonkin (Table 2) (*33*).

Table 2. Genetic relationship of killer to mother of victims for cases of infanticide perpetrated by lactating females.

Mother	9
Daughter	6*
Full sister	8
Half-sister	9
Full aunt	1
Half-aunt	1
Full niece	2†
Full first cousin	1
No known kinship	3‡
Total	40

*Males do not usually remain in the same breeding coterie for more than two consecutive years, and females do not usually breed until 2 years old (*9, 10*). Thus, when a daughter kills her mother's young, the victims are usually half-siblings rather than full-siblings. In five of the six cases reported here, the daughter killed half-siblings rather than full-siblings. †In one of these cases, the marauder killed juveniles of her father's full-sister who was living in an adjacent coterie. ‡In two of these cases, the marauder killed juveniles in a different coterie. In the other case, the marauder was living in a coterie into which she had immigrated from an adjacent coterie; before killing, the marauder permanently evicted the mother of the victims from the home coterie territory.

Except for anecdotal reports on several carnivore species (*26*), there are no mammals for which lactating females are known to regularly kill the offspring of close kin. Acorn woodpeckers (*Melanerpes formicivorus*) (*34*) and certain insects sometimes destroy eggs laid by close kin (*1, 35*), but victimized females in these cases can typically lay additional eggs and thus do not lose an entire breeding season.

While a lactating female is marauding, the offspring in her own burrow are unguarded. Of the 40 observed cases of infanticide by lactating females, 5 (13 percent) occurred when the victimized mother herself was marauding. Thus, although the benefits of kin-directed infanticide are not yet clear, there is at least one serious cost.

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13. Preweaning infanticide was counted when a prairie dog entered the burrow of a lactating female for at least 10 minutes and displayed one or more of a series of specific behaviors. An excavation after a case of presumed infanticide which involved these specific behaviors led to two decapitated juveniles, and two above ground cases of infanticide involving these behaviors were also observed.
14. For the types of infanticide that are relatively easy to detect, we collected reliable data for as many as 7 years (1978 through 1984); for the more difficult types (those requiring live trapping), reliable data covered only 1 or 2 years (Table 1). In some years we were able to monitor all litters for certain types of infanticide but only some litters for other types (Table 1).
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16. In the 11 cases in which weaned juveniles emerged from the burrows that were marauded, partial litter infanticide was probably involved. Whereas the average litter size at weaning at the study colony from 1981 through 1984 for unmarauded home burrows that produced juveniles was 3.16 (±1.18; range, 1 to 6; n = 57 litters), the average litter size for the marauded home burrows that produced juveniles was 2.18 (±0.75; range, 1 to 3; n = 11 litters) (P = 0.012, two-tailed Mann-Whitney U test).
17. Numerous females never marauded, but one marauded seven times and another five times. Some females never lost their litters to infanticide, but one lost her litter in three consecutive years.
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19. Lactating females were classified each year depending on whether or not they marauded that year. Differences between marauders and nonmarauders were: (i) probability of weaning a litter, 15/26 = 58 percent versus 51/104 = 49 percent; (ii) average litter size at weaning among those females who weaned a litter, 3.07 (±1.16; range 1 to 5; n = 15 litters) versus 2.98 (±1.18; range 1 to 6; n = 53 litters); (iii) average juvenile weight at weaning, 158 g (±32; range, 99 to 241; n = 15 litters with a single average juvenile weight used for each litter) versus 145 (±28; range, 82 to 226; n = 53 litters); (iv) average weight of the mother at weaning, 699 (±86; range, 555 to 847; n = 15 mothers) versus 674 (±80; range, 565 to 982; n = 53 mothers). Differences were not statistically significant.
20. If removal of competitors is important, nonbreeding yearling females would presumably gain by marauding (*9, 12*). The restriction of marauding to lactating or recently lactating females suggests that increased sustenance for a lactating female may be more important than the removal of competitors, but the two hypotheses are not necessarily mutually exclusive. Because females that lose their own litters are less likely to maraud and have more time to defend the home coterie territory and to scan for predators, females may sometimes kill to lower the probability of losing their own litters to marauders and to induce victimized females to become better defenders and scanners [that is, better helpers; see (*15*)].
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23. Among squirrels, infanticide by invading males

has also been observed in *S. columbianus* [A. L. Steiner, *J. Mammal.* **53**, 601 (1972)] and *S. parryii* [I. G. McClean, *Anim. Behav.* **31**, 32 (1983)], both of which are probably harem-polygynous.
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25. The evicted mother and one evicted juvenile were never seen again and presumably died. The other evicted juvenile incorporated herself into an adjacent coterie where she weaned a litter 2 years later; no other prarie dog at the study colony ever permanently transferred into a different coterie so soon after weaning.
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29. Coterie members restrict feeding and other activities to the home coterie territory which does not usually fluctuate in size (*8, 15*). Thus, overcrowding within coteries could occur even though the colony as a whole is not overcrowded. Because infanticide sometimes occurs in small coteries with large territories, overcrowding within coteries evidently is not the only reason why lactating females sometimes kill the offspring of close kin. Prairie dogs today occupy less than 10 percent of their former geographic range [T. W. Clark, *Natl. Geogr.* **156**, 270 (1979)], but it is not known whether overcrowding is more serious in South Dakota populations now than in populations over evolutionary time.
30. Black-tail females may sometimes kill their own offspring. This infanticide would be in addition to the 51 percent shown in Table 1. It would be difficult to distinguish between infanticide perpetrated by the mother and that by an undetected marauder.
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Rescue of the *Drosophila* Phototransduction Mutation *trp* by Germline Transformation

Abstract. *Phototransduction is the process by which light-stimulated photoreceptor cells of the visual system send electrical signals to the nervous system. Many of the steps that follow the initial event in phototransduction, absorption of light by rhodopsin, are ill-defined. The fruitfly,* Drosophila melanogaster, *provides a means to dissect phototransduction genetically. Mutations such as* transient receptor potential (trp) *affect intermediate steps in phototransduction. In order to facilitate molecular studies of phototransduction, the* trp *gene was isolated and its identity was confirmed by complementing the mutant* trp^{CM} *allele of the* trp *gene by P-element mediated germline transformation of a 7.1-kilobase DNA fragment. Expression of the* trp *gene begins late in pupal development and appears to be limited to the eyes and ocelli.*

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Phototransduction is a neuronal excitation process that is stimulated by light and results in a change in the flow of ions across the photoreceptor membrane. Physiological studies suggest that several important features of the phototransduction process are similar in vertebrates and invertebrates. In both systems, the pigments that absorb light and undergo photoisomerization are protein-chromophore complexes known as rhodopsins (*1*). It appears that, in vertebrates and invertebrates, there are a series of intermediate steps between the photoisomerization of the visual pigments and the change in permeability of the photoreceptor membrane (*2*). With the exception of vertebrate transducin (*3*), little is known in either system about the proteins that function in the intermediate phototransduction events.

The fruitfly *Drosophila melanogaster* is an excellent system in which to study phototransduction. The anatomical features of the fruitfly's compound eyes have been described in detail, mutations in genes affecting phototransduction have been isolated (*2*), and techniques for germline transformation have been developed (*4*). Many of the *Drosophila* mutants believed to intervene in phototransduction were isolated on the basis of abnormal electroretinogram (ERG) recordings (*2*). ERG's measure the change in potential across the photoreceptor membrane in response to light. Wild-type flies display a sustained receptor potential that decays very gradually during continuous bright illumination. Within 5 seconds of cessation of a light stimulus (dark recovery) the response of wild-type flies to a subsequent stimulus is nearly maximal. Of the mutants thought to affect an intermediate step in phototransduction, the transient receptor potential (*trp*) mutant is among the most intensively studied (*5–8*). The *trp* mutant is characterized by a rapid decay of the receptor potential during illumination with bright light (*5*). It also displays an abnormally slow dark recovery (*5*). Despite many detailed studies, the basis of the *trp* phenotype is not well understood. The *trp* phenotype is not due to quantitative or qualitative changes in the photopigment (*6*). Minke has proposed that the rapid decay of the receptor potential is caused by a light-induced reduction in excitation efficiency resulting from an unknown defect in an intermediate stage of phototransduction (*6*).

Currently, none of the genes encoding products relevant to an intermediate step in phototransduction have been isolated in *Drosophila*. A more thorough understanding of the processes disrupted by the *trp* mutation and other phototransduction mutations would be facilitated by identification and characterization of the corresponding genes and gene products. We now describe the identification of *trp* by a germline transformation procedure that rescues the phenotype (*9*). The developmental expression and tissue localization of the *trp* RNA are also presented.

A gene encoding a product that functions specifically in an intermediate process in phototransduction might be expected to be expressed exclusively in the eyes. Therefore, the criteria used to identify a gene likely to rescue the *trp* phenotype were that it map to the cytogenic position of the *trp* mutation and that it be expressed specifically in the eye. A differential screen of a library of cloned *Drosophila* genomic DNA segments with polyadenylated [poly(A)$^+$] RNA prepared from fly heads and bodies yielded 20 cloned sequences that were expressed more abundantly (by a factor of 10 at least) in the head than in the body (*10*). Among these 20, one (λ559)