NEPOTISM AND ALARM CALLING IN THE BLACK-TAILED PRAIRIE DOG (*CYNOMYS LUDOVICIANUS*)

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Abstract. At a colony containing 200 individuals of known ages and genetic relationships, I investigated alarm calling by black-tailed prairie dogs (Rodentia: Sciuridae: *Cynomys ludovicianus*) during experiments with a stuffed specimen of a natural predator, the badger (*Taxidea taxus*). As in other species of burrowing squirrels, female alarm calls are evidently nepotistic (i.e. function to warn genetic relatives). Male alarm calls are also nepotistic, and individual males vary their rate of alarm calling in response to the presence or absence of close genetic relatives in the home territory. Beneficiaries of alarm calls in other species of squirrels usually include adult or juvenile offspring, but beneficiaries of black-tailed prairie dog alarm calls frequently include only non-descendant kin.

The evolution of alarm calling has puzzled evolutionary biologists for a long time (Hamilton 1964; Maynard Smith 1965; Williams 1966; Trivers 1971; Alexander 1974; Wilson 1975; West Eberhard 1975; Dawkins 1976). Why should an individual risk exposing himself to a predator by calling in order to save competing conspecifics? Two studies of ground squirrels (*Spermophilus*) published in 1977 (Dunford, working with round-tailed ground squirrels, *S. tereticaudus*; Sherman, working with Belding's ground squirrels, *S. beldingi*) showed that alarm calls by adult females are nepotistic (i.e. function to warn genetic relatives). Other studies of squirrels have also indicated that alarm calls of adult females are nepotistic (Leger & Owings 1978; Smith 1978; Yahner 1978; Noyes & Holmes 1979; Owings & Leger 1980; Schwagmeyer 1980). In all of these cases, female alarm calls probably function mainly to warn descendant kin (i.e. offspring and grand-offspring). From a seven-year study of 213 individuals of known ages and genetic relationships, I here report alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*) during experiments with a stuffed specimen of a natural predator, the badger (*Taxidea taxus*). For both male and female black-tails, the warning of non-descendant kin (e.g. parents, grandparents, siblings, aunts, uncles, nieces, nephews, first cousins, etc.) has probably been as important as the warning of descendant kin in the evolution of alarm calling.

Methods

The Study Animal

Black-tails are large (700–1500 g), diurnal, colonial rodents of the squirrel family (Sciuridae).

At Wind Cave National Park, Hot Springs, South Dakota, where I study them, black-tails breed in February and March, and weaned juveniles first emerge from their natal burrows in May and June. Black-tails live in social groups called coteries (King 1955) which typically contain one adult (≥ 2 years) male, 3–4 adult females, and several yearlings and juveniles of both sexes. Males and females usually first breed as 2-year olds (Hoogland 1982). Individuals remain within contiguous coterie territories and interact more amicably with members of their own coterie than with members of other coteries (King 1955; Hoogland 1981b). My study colony covers approximately 500×130 m (6.6 hectares), and in late spring of each year contains a mean $\pm$ SD of 142.9 ± 33.6 adults and yearlings and 72.4 ± 36.9 weaned juveniles (Hoogland 1979a); the mean $\pm$ SD number of coteries present each year is 24.5 ± 1.05. Since 1975, all young weaned at the study colony have been marked with numbered eartags and fur dye before they have mixed with young from other litters. In this way I have determined exact genetic relationships through common female ancestors, and I now know probable genetic relationships through common male ancestors of more than 90% of all colony residents (Hoogland 1979b; Foltz & Hoogland 1981; Hoogland & Foltz, in press). Females usually remain in the natal coterie for their entire lifetimes, but males usually depart before sexual maturity (Hoogland 1982). Consequently, the females and yearling males within a coterie are almost always close genetic relatives. An oestrous female usually copulates with the single unrelated adult male in the home coterie (Foltz & Hoogland 1981; Hoogland & Foltz, in press); thus, a male's

confidence of paternity within a coterie is high, and black-tail littermates, unlike Belding's ground squirrel littermates (Hanken & Sherman 1981), are usually full siblings.

Adult and yearling black-tails respond to a predator by running to a burrow mound, where they commonly give an alarm call (Waring 1970; Hoogland 1981a). An individual's alarm call alerts other coterie members who have not yet detected the predator, and they also run to a burrow mound after hearing the call. Unlike juvenile ground squirrels (Dunford 1977; Sherman 1977; Schwagmeyer 1980) and juvenile Sonoma chipmunks (*Eutamias sonomae*) (Smith 1978), juvenile black-tails rarely give alarm calls; in this report I do not examine juvenile alarm calls, which for obvious reasons can only be heard by non-descendant kin. Because field assistants and I observed only three successful predations on adults and yearlings during the 7-year study, I was unable to determine if callers are more vulnerable to predation than are non-callers.

Experiments with the Badger and Other Methods

To investigate alarm calling under natural conditions, I conducted field experiments with a stuffed badger mounted on a plastic sled. Before each experimental run, the badger was concealed in a brown cloth bag to which the prairie dogs had become habituated for several days. The concealed badger was positioned at the edge of a coterie territory, and was introduced when all coterie members were foraging above ground under undisturbed conditions. He was pulled across the central portion of the coterie territory at a rate of 22 cm/s by means of fishing wire wound around a garden hose reel. From an observation tower, an assistant pulled the badger while I recorded whether each coterie member did or did not give an alarm call. Most experiments were conducted in May and June of 1978 through 1981, after weaned juveniles had emerged from their natal burrows. Conclusions are based on 698 experimental runs, involving 4019 responses from 87 different males and 126 different females. Each year, I calculated for each prairie dog the proportion of times that the individual gave an alarm call in response to the badger; proportions were based on 7.21 ± 3.53 experimental runs per year for males and 7.72 ± 3.61 runs per year for females. If an individual's status regarding the presence of close genetic relatives in the home coterie did not change between years, then data from the

different years were combined for calculating proportions. When there was a change in status between years (e.g. no close genetic relatives in one year versus offspring the next year), data from the different years were considered independent (i.e. as if from different individuals); such a change in status occurred for 25 of the 87 different males (28.7%) and 29 of the 126 different females (23.0%) under investigation. Older individuals are more likely than young individuals to call in both Belding's ground squirrels (Sherman 1977) and several species of marmots (*Marmota*) (Barash 1975), but alarm calling in black-tails is evidently unaffected by age (in 1979, for example, when known ages ranged from 1 to ≥ 5 years, $P = 0.895$ for males and $P = 0.450$ for females, Kruskal–Wallis ANOVA). To investigate the possibility of habituation to the stuffed badger, I compared alarm calling frequencies of adult males and adult females from the early half of experimental runs in 1979 and 1980 with frequencies from the later half of runs; had habituation occurred, then individuals should have called less frequently during the later runs than during the early runs. However, for both sexes, calling frequency did not significantly decline during later runs ($P > 0.050$ each year, one-tailed Wilcoxon matched-pairs signed-ranks test; see Table I, where there is evidence for the opposite trend among reproductive males and females in 1979). Given a coterie containing two adult males (King 1955; Hoogland 1981b), I do not yet know whether a male can discriminate between his own offspring and the offspring sired by the other male; consequently, I classified both adult males in a two-male coterie as having offspring if any offspring were weaned there. During pregnancy and lactation, females defend specific burrows and subterritories within the home coterie territory; following weaning, when most experiments were conducted, no individuals are territorial within the home coterie territory, and coterie members forage over the entire home coterie territory (King 1955; Hoogland 1981b). Consequently, different individuals were closest to the concealed badger during different experimental runs, and 'vulnerability' to the badger was approximately randomized among coterie members. I assumed that the prairie dogs responded to the stuffed badger as though it were alive. I could not rigorously evaluate this assumption, since live badgers were seen at the study colony only five times, and at those times only twice could I record alarm calling. Both times, as

in experiments with the stuffed badger, some individuals called while others in the same coterie remained silent; the same was true during attacks by live coyotes (*Canis latrans*).

I use the term 'close genetic relative' in this report to include parents, offspring, grand-parents, grandoffspring, siblings, aunts, uncles, nieces, nephews, first and second cousins, and first and second cousins once removed. In-dividuals are known to interact more amicably with all of such relatives than with more dis-tantly related individuals (Hoogland 1981b, unpublished data). The 'natal coterie' is the coterie into which an individual is born, and the 'home coterie' is the coterie in which an indi-vidual is living at a particular time; for yearling males and for all females, the home coterie is almost always the natal coterie as well (Hoogland 1982). For those individuals with at least one close genetic relative in the home coterie, there is no evidence that calling frequency varies either directly or inversely with the number of relatives (in 1980, for example, $P = 0.271$ for adult males and $P = 0.438$ for adult females, two-tailed Kendall rank correlation test); for this reason, I followed the example in previous studies of alarm calling and did not distinguish in my statistical analyses among those individuals having different numbers of close genetic rela-tives in the home coterie.

Results
Evidence that black-tail alarm calling is nepo-tistic is fivefold. (1) Yearling males with non-descendant close genetic relatives in the home (natal) coterie called significantly more often in response to the badger than did yearling males that had immigrated into a coterie where they lacked close genetic relatives (Fig. 1). A similar comparison was not possible for females, because yearling females are almost never in a coterie without close genetic relatives (Hoogland 1982). (2) Similar to females of other burrowing squirrels (Dunford 1977; Sherman 1977, 1980b; Leger & Owings 1978; Smith 1978; Yahner 1978; Noyes & Holmes 1979; Owings & Leger 1980; Schwagmeyer 1980), black-tail adult females with non-descendant or descendant close genetic relatives in the home coterie called significantly more often than did adult females without close genetic relatives in the home coterie (Fig. 1). Adult females without close genetic relatives in the home coterie were either immigrants into the study colony ($N = 7$) or individuals whose relatives had all disappeared ($N = 3$). Similarly,

adult males with offspring in the home coterie called more often than did adult males without offspring in the home coterie, but the difference here was not significant (Fig. 1). (3) Adult females called significantly more often in May and June of a year when they were weaning off-spring than in May and June of the previous year, when (as adults) they did not wean any offspring ($P = 0.030$, $N = 29$ females, one-tailed Wilcoxon matched-pairs signed-ranks test). Six of eight adult males showed a similar trend, but the differences here were not significant ($P = 0.200$, one-tailed Wilcoxon matched-pairs signed-ranks test). (4) Juvenile black-tails are presumably more vulnerable to predation following the first emergence from the natal burrow. Like female Sonoma chipmunks (Smith 1978) and female thirteen-lined ground squirrels (*S. tridecemlineatus*) (Schwagmeyer 1980), black-tail adult females called significantly more often during the 1–3 weeks after their offspring first emerged from the natal burrow than during the previous breeding–pregnancy–lactation stage (Table I). Adult males showed a similar but insignificant trend (Table I). (5) Table I com-pares the responses of individuals before and after a single change in the presence of close genetic relatives in the home coterie. During my study period, five different individuals, all males, experienced two changes in the presence of close genetic relatives in the home coterie. For example, one of the five individuals, male 35, had non-descendant close genetic relatives in his
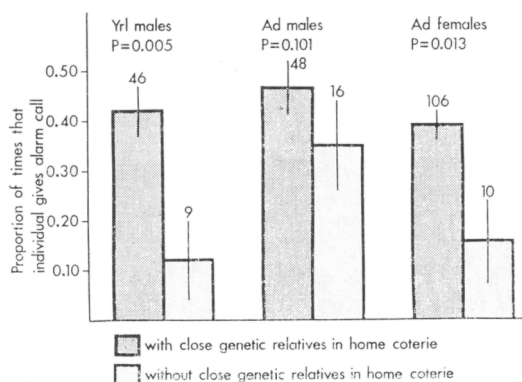

Fig. 1. Alarm calling by individuals with and without close genetic relatives in the home coterie. Lines on bars indicate one standard error (SE). The number above each SE line indicates the number of different individuals observed (each approximately seven times) during 698 experimental runs with the stuffed badger. All data were analysed by the one-tailed Mann–Whitney *U*-test.

Table I. Alarm Calling Before and After the First Emergence of Young from the Natal Burrow*

	No. of individuals that called more often before the first emergence of young	No. of individuals that called more often after the first emergence of young	No. of individuals whose calling frequency was the same before and after the first emergence of young	Significance of these differences
Adult males	4	5	4	$P = 0.221$
Adult females	4	11	7	$P = 0.005$

*During experiments with the stuffed badger, alarm calling was recorded during the stage of breeding–pregnancy–lactation and during the 1–3 weeks following the first emergence of young from the natal burrow. Only data from known parents are shown here (i.e. data from reproductively unsuccessful individuals were excluded). The mean ± SD number of experimental runs before the first emergence of young was 9.11 ± 3.93, and the mean ± SD number after the first emergence of young was 7.69 ± 2.99. Data were analysed by the one-tailed Wilcoxon matched-pairs signed-ranks test.

home (natal) coterie A as a yearling, but as a 2-year-old moved to coterie B, where he had no non-descendant close genetic relatives and sired no offspring; as a 3-year-old he moved to coterie C, where he sired offspring. For all five males, the frequency of alarm calling decreased when a change (a move to a new coterie) resulted in the absence of close genetic relatives in the home coterie. Also for all five males, the calling frequency increased again when a change (the emergence of the male's offspring from the natal burrow) resulted in the presence of close genetic relatives in the home coterie. The association between male calling frequency and the presence or absence of close genetic relatives in the home coterie was significant (Fig. 2).

To investigate whether alarm calls of black-tails function mainly to warn either descendant or non-descendant close genetic relatives, I analysed data from three different types of males and females. Type A individuals had no close genetic relatives of any kind in the home coterie. Type B individuals had only non-descendant close genetic relatives in the home coterie. Type C individuals had offspring in the home coterie; type C females also usually had one or more non-descendant close genetic relatives in the home coterie. For both sexes, type C individuals called more often than did type B individuals, who called more often than type A individuals. This trend was significant for both sexes (Fig. 3).

Discussion

This study differs from previous studies in at least five important ways. (1) The proximity of a predator and its hunting technique affect alarm calling by ground squirrels (Dunford 1977; Sherman 1977) and black-tails (Hoogland, unpublished data). But natural predators and live

trained predators attack in unpredictable ways, and it is difficult to determine in such attacks which individuals are actually threatened and are thus more or less likely to call. By pulling a stuffed badger at a constant rate through the central portion of each coterie territory, I increased the probability that all individuals were exposed to the same level of (simulated) danger. (2) Previous studies of alarm calling have used multiple observations from the same individuals for statistical analyses, and sample sizes of different individuals have usually been small
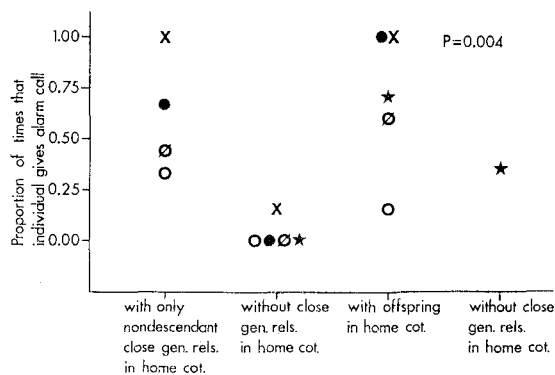

Fig. 2. Alarm calling by males that experienced two changes in the presence of close genetic relatives in the home coterie. Each set of three identical symbols represents data from a single male. The mean ± SD number of experimental runs with the stuffed badger at each stage was 7.60 ± 4.53. The absence of close genetic relatives in the home coterie followed a male's movement into a new coterie. All changes resulting in the presence of close genetic relatives in the home coterie led to increased alarm calling, and all changes resulting in the absence of close genetic relatives led to decreased alarm calling; this association was significant ($P = 0.004$, 2×2 one-tailed Fisher Exact probability test).
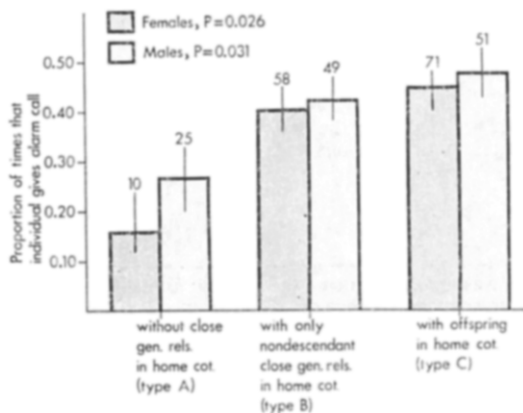
Fig. 3. Alarm calling in three different classes of males and females. Lines on bars indicate one SE. The number above each SE line indicates the number of different individuals observed (each approximately seven times) during 698 experimental runs with the stuffed badger. Because alarm calling is not significantly affected by age, data from all age classes were combined for this analysis; data from yearlings and adults are shown separately in Fig. 1. Data were analysed by the Kruskal–Wallis ANOVA. Many of the pairwise comparisons were also significant (one-tailed Mann–Whitney U-test): for females, $P = 0.012$ for type A versus type B, $P = 0.004$ for type A versus type C, and $P = 0.212$ for type B versus type C; for males, $P = 0.022$ for type A versus type B, $P = 0.005$ for type A versus type C, and $P = 0.263$ for type B versus type C. For males, most of the type A and type B individuals were yearlings, and most of the type C individuals were ≥ 2-year-olds; for females, most of the type B individuals were yearlings and 2-year-olds, and most of the type A and type C individuals were ≥ 2-year-olds.

(Barash 1975, 1976; Dunford 1977; Sherman 1977, 1980b; Leger & Owings 1978; Smith 1978; Yahner 1978; Noyes & Holmes 1979; Owings & Leger 1980; Schwagmeyer 1980; Hoogland 1981b). In this study, each individual prairie dog was represented one time only in statistical analyses by a single proportion of times that the individual called during numerous experimental runs with the stuffed badger, and calling frequencies were available for 87 different males and 126 different females. (3) Data in Table I and Figs 1–3 indicate that alarm calling by adult and yearling black-tail males functions to warn kin. Similar male nepotism in alarm calling has not been previously demonstrated among squirrels, presumably because adult and yearling males in the other sciurid species studied rarely live near descendant or non-descendant close genetic relatives. Male alarm calls may function to warn offspring in alpine marmots (*M. marmota*) (Barash 1975, 1976) and California

ground squirrels (*S. beecheyi*) (Owings & Leger 1980), but exact paternities in these species have not yet been determined. (4) Data in Table I and, especially, Fig. 2 show that alarm calling frequencies of the same individuals correlate with changes in the presence of close genetic relatives in the home coterie. No other study has followed individuals over long periods of time and shown similar correlations. (5) In all previously studied sciurid species, adult female alarm callers usually have either adult or juvenile offspring nearby and within earshot, and they sometimes have non-descendant adult or juvenile kin nearby and within earshot as well (Dunford 1977; Sherman 1977, 1980a, 1980b; Leger & Owings 1978; Smith 1978; Yahner 1978; Noyes & Holmes 1979; Owings & Leger 1980; Schwagmeyer 1980; Shields 1980). In no case is there unequivocal evidence that adult females call to non-descendant kin in the absence of adult or juvenile offspring; possible exceptions were noted by Sherman (1977, 1980b), but in all cases the callers were 'reproductive' (i.e. pregnant, lactating, or living with weaned young of the year) females. It follows that female alarm calling in ground squirrels and chipmunks may have evolved primarily in the context of parental care (Shields 1980), with the consequence that non-descendant kin may be common secondary beneficiaries. In black-tails, on the other hand, beneficiaries of alarm calls by adult and yearling females frequently include non-descendant adult, yearling, or juvenile kin in the absence of adult, yearling, or juvenile offspring. Thus, while warning of offspring has evidently been important in the evolution of alarm calling by adult and yearling black-tail females (Table I, Figs 1 and 3), warning of non-descendant kin has perhaps been equally as important (Fig. 3), and female alarm calling in this species cannot be explained solely in terms of parental care.

Why do non-descendant kin benefit from female alarm calls more frequently in black-tails than in ground squirrels and chipmunks? At least two factors probably are involved: (a) demography and (b) vulnerability of the caller to predation. Regarding (a), Sherman (1981) recently emphasized the importance of demographic parameters such as mortality and dispersal patterns in the evolution of nepotism. Because females of round-tailed, Belding's, and thirteen-lined ground squirrels and females of Sonoma and eastern chipmunks usually reside near their mothers and usually first breed as yearlings (see above references), females of these

species regularly have adult or juvenile offspring nearby and within earshot. Although black-tail females also usually reside near their mothers, they usually do not breed until two years of age and frequently do not wean a litter until they are three or four years old (King 1955; Hoogland 1981b, 1982). Consequently, black-tail adult and yearling females frequently do not have adult, yearling or juvenile offspring in the home coterie, but they do regularly have adult, yearling, or juvenile non-descendant kin in the home coterie. During experiments in 1979, for example, only 35 of the 72 adult and yearling females (49%) with known reproductive histories had offspring in the home coterie, but 58 of these 72 females (81%) had non-descendant kin in the home coterie; 35 of the 72 females (49%) had only non-descendant kin in the home coterie. It follows that selection for warning non-descendant kin in the absence of offspring has probably been more intense in black-tails than in ground squirrels and chipmunks. (b) Because black-tails may be the most colonial of all the sciurid species (King 1955; Hoogland 1979b), 'selfish herd effects' (Hamilton 1971) and 'dilution effects' (Bertram 1978; Rubenstein 1978) are probably more pronounced for black-tails than for ground squirrels and chipmunks (Hoogland 1981a). Consequently, vulnerability of alarm callers to predators may be lower for black-tails than for ground squirrels and chipmunks, and this factor may partially account for the frequent calling of black-tail females with either descendant or non-descendant kin in the home coterie. However, vulnerability of alarm call beneficiaries to predators is probably also lower for black-tails than for ground squirrels and chipmunks; that is, both the costs and benefits of alarm calling may be lower for black-tails. At this point I do not know how the decreased vulnerability of black-tail alarm callers is offset by the decreased vulnerability of alarm call beneficiaries.

A black-tail female that is familiar with the nature and positioning of the burrows within the home coterie territory might be more likely to give an alarm call than an individual less familiar with the home coterie territory, because the former could presumably reach safety more quickly than the latter. Harvey & Greenwood (1978; see also Sherman 1977) pointed out that it is difficult to separate the effects of site familiarity and nepotism on alarm calling in a species of sedentary individuals. Three lines of evidence indicate that alarm calling in black-tails is based

on nepotism rather than on site familiarity. First, alarm calling does not vary with female age as noted above, even though older females are presumably more familiar with the home coterie territory than are young females. Second, Table I shows that maternal black-tails call significantly more often following the first emergence of offspring from the natal burrow. Although the first emergence of offspring represents a dramatic change in the presence of above-ground close genetic relatives in the home coterie, it does not obviously correlate with increased site familiarity. Third, calling by adults with either descendant or non-descendant kin in the home coterie is more common in males than in females (Figs 1 and 3). However, because females usually remain in the natal coterie for their entire lifetime while males frequently change coteries after a residency of one or two years (Hoogland 1982), adult females should call more than adult males if site familiarity is important.

Data in this report show that alarm calling by both male and female black-tails can be partially explained as an attempt to warn close genetic relatives of danger. Factors other than nepotism must also be involved, however, because recent immigrants into the study colony, who have no close genetic relatives in either the home coterie or anywhere else in the colony, sometimes call (Figs 1 and 3). Additionally, individuals with either descendant or non-descendant close genetic relatives in the home coterie frequently do not call (Figs 1, 2, 3). Furthermore, same-age, same-sex full siblings in the same coterie sometimes differ markedly in alarm calling frequencies (Hoogland, unpublished data). Previous investigators have suggested numerous non-nepotistic factors which may be important in the evolution of alarm calling, such as reciprocity, reduced likelihood of later attacks by the same predator, discouragement of continued hunting by the predator, and possible manipulation of other group members (Hamilton 1964; Maynard Smith 1965; Williams 1966; Perrins 1968; Trivers 1971; Alexander 1974; Charnov & Krebs 1975; West Eberhard 1975; Wilson 1975; Dawkins 1976; Sherman 1977; Cheney & Seyfarth 1981). I am currently investigating the importance of such non-nepotistic factors in black-tail alarm calling.

REFERENCES

Alexander, R. D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.*, **5**, 325–383.

Barash, D. P. 1975. Marmot alarm calling and the question of altruistic behavior. *Am. Midl. Nat.*, **94**, 468–470.

Barash, D. P. 1976. Social behaviour and individual differences in free-living alpine marmots (*Marmota marmota*). *Anim. Behav.*, **24**, 27–35.

Bertram, B. C. R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 64–96. Sunderland, Mass.: Sinauer.

Charnov, E. L. & Krebs, J. R. 1975. The evolution of alarm calls: altruism or manipulation? *Am. Nat.*, **109**, 107–112.

Cheney, D. L. & Seyfarth, R. M. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour*, **76**, 25–61.

Dawkins, R. 1976. *The Selfish Gene*. New York: Oxford University Press.

Dunford, C. 1977. Kin selection for ground squirrel alarm calls. *Am. Nat.*, **111**, 782–785.

Foltz, D. W. & Hoogland, J. L. 1981. Analysis of the mating system in the black-tailed prairie dog (*Cynomys ludovicianus*) by likelihood of paternity. *J. Mammal.*, **62**, 706–712.

Foltz, D. W. & Hoogland, J. L. In press. Genetic evidence for outbreeding in the black-tailed prairie dog (*Cynomys ludovicianus*). *Evolution*.

Hamilton, W. D. 1964. The genetical evolution of social behaviour, I, II. *J. theor. Biol.*, **7**, 1–51.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, **31**, 295–311.

Hanken, J. & Sherman, P. W. 1981. Multiple paternity in Belding's ground squirrel litters. *Science, N.Y.*, **212**, 351–353.

Harvey, P. H. & Greenwood, P. J. 1978. Anti-predator defence strategies: some evolutionary problems. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 129–151. Sunderland, Mass.: Sinauer Associates.

Hoogland, J. L. 1979a. The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Anim. Behav.*, **27**, 394–407.

Hoogland, J. L. 1979b. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae, *Cynomys* spp.) coloniality. *Behaviour*, **69**, 1–35.

Hoogland, J. L. 1981a. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology*, **62**, 252–272.

Hoogland, J. L. 1981b. Nepotism and cooperative breeding in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). In: *Natural Selection and Social Behavior* (Ed. by R. D. Alexander & D. W. Tinkle), pp. 283–310. New York: Chiron Press.

Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. *Science, N.Y.*, **215**, 1639–1641.

Hoogland, J. L. & Foltz, D. W. In press. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behav. Ecol. Sociobiol.*

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. *Contrib. Lab. Vertebr. Biol. Univ. Mich.*, **67**, 1–123.

Leger, D. W. & Owings, D. H. 1978. Responses to alarm calls by California ground squirrels. *Behav. Ecol. Sociobiol.*, **3**, 177–186.

Maynard Smith, J. 1965. The evolution of alarm calls. *Am. Nat.*, **99**, 58–63.

Noyes, D. H. & Holmes, W. G. 1979. Behavioral responses of free-living hoary marmots to a model golden eagle. *J. Mammal.*, **60**, 408–411.

Owings, D. H. & Leger, D. W. 1980. Chatter vocalizations of California (USA) ground squirrels (*Spermophilus beecheyi*): Predator-role and social-role specificity. *Z. Tierpsychol.*, **54**, 163–184.

Perrins, C. 1968. The purpose of the high-intensity alarm call in small passerines. *Ibis*, **110**, 200–201.

Rubenstein, D. I. 1978. On predation, competition, and the advantages of group living. In: *Perspectives in Ethology* (Ed. by P. P. G. Bateson and P. H. Klopfer), pp. 205–231. New York: Plenum Press.

Schwagmeyer, P. L. 1980. Alarm calling behavior of the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*. *Behav. Ecol. Sociobiol.*, **7**, 195–200.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. *Science, N.Y.*, **197**, 1246–1253.

Sherman, P. W. 1980a. The meaning of nepotism. *Am. Nat.*, **116**, 604–606.

Sherman, P. W. 1980b. The limits of group squirrel nepotism. In: *Sociobiology: Beyond Nature/ Nurture?* (Ed. by G. W. Barlow & J. Silverberg), pp. 505–544. Boulder, Colorado: Westview Press.

Sherman, P. W. 1981. Kinship, demography, and Belding's ground squirrel nepotism. *Behav. Ecol. Sociobiol.*, **8**, 251–259.

Shields, W. M. 1980. Ground squirrel alarm calls: nepotism or parental care? *Am. Nat.*, **116**, 599–603.

Smith, S. F. 1978. Alarm calls, their origin and use in *Eutamias sonomae*. *J. Mammal.*, **59**, 888–893.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.*, **46**, 35–57.

Waring, G. H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. *Am. Midl. Nat.*, **83**, 167–185.

West Eberhard, M. J. 1975. The evolution of social behavior by kin selection. *Q. Rev. Biol.*, **50**, 1–33.

Williams, G. C. 1966. *Adaptation and Natural Selection.* Princeton, N.J.: Princeton University Press.

Wilson, E. O. 1975. *Sociobiology: The New Synthesis.* Cambridge, Mass.: Belknap Press.

Yahner, R. H. 1978. Seasonal rates of vocalizations in eastern chipmunks. *Ohio J. Sci.*, **78**, 301–303.