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Why do Gunnison's prairie dogs give anti-predator calls?

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Abstract. At a colony of Gunnison's prairie dogs, Sciuridae: *Cynomys gunnisoni*, containing marked individuals of known genetic relationships, anti-predator calling was investigated in response to moving, stuffed specimens of a natural predator, the American badger, *Taxidea taxus*. Females with kin in the home territory called more often than females without nearby kin, and females with nearby offspring were especially likely to call. Male gunnisons commonly gave anti-predator calls as well, but male calling was unrelated to kinship of nearby listeners.

Unique calls in response to predators (anti-predator calls) are common among colonial birds and mammals. Why, however, should an individual draw a predator's attention to itself by giving an anti-predator call? Anti-predator calls function mainly to warn offspring for animals such as hoary marmots, *Marmota caligata*, Sonoma and eastern chipmunks, *Eutamias sonomae* and *Tamias striatus*, respectively, and California, Belding's, Columbian, Richardson's, round-tailed, and thirteen-lined ground squirrels, *Spermophilus beecheyi*, *S. beldingi*, *S. columbianus*, *S. richardsonii*, *S. tereticaudus*, and *S. tridecemlineatus*, respectively (Dunford 1977b; Sherman 1977, 1980a; Smith 1978; Yahner 1978; Noyes & Holmes 1979; Owings & Leger 1980; Schwagmeyer 1980; Davis 1984; Owings et al. 1986; MacWhirter 1992). Anti-predator calls thus resemble other risky parental behaviours, such as mobbing, by which individuals endanger themselves to increase the safety of their own offspring.

Black-tailed prairie dogs, *C. ludovicianus*, commonly give anti-predator calls not only to warn offspring, but also to warn non-descendant kin such as siblings, nieces and nephews, and cousins (Hoogland 1983, 1995). Do other animals give anti-predator calls specifically aimed at non-descendant kin, and do anti-predator calls increase the susceptibility of callers to predation? I investigated these questions for a second species of prairie dog, the Gunnison's prairie dog, *C. gunnisoni*.

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THE STUDY ANIMAL

Gunnison's prairie dogs, here referred to as 'gunnisons', are large (250–1100 g for adults), hibernating, colonial rodents of the squirrel family (Sciuridae) that live in the 'four corners' area of the southwestern United States, i.e. the convergent boundaries of Arizona, Colorado, New Mexico and Utah (Burnett & McCampbell 1926; Longhurst 1944; Scheffer 1947; Pizzimenti & Hoffmann 1973; Pizzimenti 1975). Within colonies, gunnisons live in harem-polygynous family groups called clans (Fitzgerald & Lechleitner 1974; Rayor 1985, 1988; Slobodchikoff et al. 1990, 1991). Clans typically contain one breeding male and three to four breeding females. Clan members defend a home territory of about 1.0 hectare, but commonly forage in areas as far as 100 metres from the home territory.

Mortality in the first year is approximately 50% for both male and female gunnisons. Females that survive the first year sometimes live as long as 6 years, but no males at the study colony have lived longer than 4 years.

Gunnison females usually copulate in their first breeding season, when they are about 11 months old. Age of sexual maturation is more variable among males: in some years up to 75% of males copulate as yearlings, but in other years as few as 10% of yearling males copulate (Rayor 1985, 1988; this study).

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Gunnison females, like females of other ground-dwelling squirrels (Holekamp 1984; Holekamp & Sherman 1989), usually remain in the natal area for their entire lives and thus are markedly philopatric. Young gunnison males, by contrast, disperse before reaching sexual maturity, and older males usually do not remain in the same breeding territory for more than one year (Fitzgerald & Lechleitner 1974; Rayor 1985, 1988; this study). Sexually immature yearling males usually remain in the natal territory, but some disperse into adjacent or more distant territories.

In response to predators, gunnisons run to burrow mounds and commonly give anti-predator calls, also known as repetitious barks (Waring 1970) or alarm calls (Fitzgerald & Lechleitner 1974; Slobodchikoff & Coast 1980; Slobodchikoff et al. 1986, 1991). Each call consists of individual barks grouped into sets of 2–25 barks per set, with a pause of 3–15 seconds between each set (Waring 1970).

Like white-tailed prairie dogs and round-tailed and Belding's ground squirrels (Clark 1977; Dunford 1977b; Sherman 1977), gunnisons vigorously move the lower jaw when giving an anti-predator call. Partly for this reason, gunnison callers are easier to identify, at least for humans, than more ventriloquial black-tailed prairie dog and Olympic and hoary marmot callers (Barash 1975, 1989; Hoogland 1995).

METHODS

From 1989 to 1995, I studied the ecology and social behaviour of Gunnison's prairie dogs at Petrified Forest National Park in northeast Arizona (elevation: 1700 m above sea level). The study site contained about 120 breeding gunnisons each year, and was part of a large colony that contained about 300 adults. Using binoculars and a 60-power telescope, field assistants and I watched gunnisons from 4-m-high observation towers.

The methods for studying gunnisons are almost identical to those used in my long-term study of black-tailed prairie dogs (Hoogland 1995). For permanent identification of individuals, I used National fingerling eartags. For visual identification from a distance, I used Nyanzol fur dye. Dye markings on the flank included numbers, spots, stripes and combinations thereof.

Like mothers of other ground-dwelling sciurid species such as black-tailed prairie dogs and Belding's, Columbian, round-tailed, and Uinta, *S. armatus*, ground squirrels (King 1955; Dunford 1977a, c; Sherman 1981; Festa-Bianchet & Boag 1982; Balph 1984), gunnison mothers reared their offspring in separate nursery burrows until the juveniles first appeared above-ground when they were about 5 weeks old. Except when mothers shared the same nursery burrow (J. L. Hoogland, J. O. Seamon, N. Lawrence and R. H. Tamarin, unpublished data), maternity was thus easy to establish. By completely surrounding nursery burrows with traps shortly after juveniles first appeared above-ground (Hoogland 1995), I captured, ear-tagged, and marked all litter-mate siblings before they mixed with juveniles from other litters.

The gunnison mating season at the study colony (i.e. the interval during which copulations occurred) extended from late March through early April. Each individual female restricted her oestrus and sexual receptivity to several hours of a single day. Females usually copulated with more than one male, and sometimes with as many as four or five. Precise assignment of paternity was thus usually impossible from behavioural observations alone. Cuckoldry sometimes occurred, but resident breeding males none the less sired most of the offspring produced by females in their home territories (J. L. Hoogland, D. A. Gilbert & A. Lowe, unpublished data). I assumed that a male sired offspring in his home territory if he copulated with at least one of the females there that subsequently reared juveniles to first emergence.

I scored gunnisons without living nearby offspring as having non-descendant nearby kin if one parent or at least one sibling, aunt, uncle, niece, nephew or cousin lived in the same home territory. I assumed that litter-mate siblings were full siblings, but realize that they sometimes might have been half-siblings instead (i.e. same mother, different father; J. L. Hoogland, D. A. Gilbert & A. Lowe, unpublished data; see also Travis et al., in press).

To investigate gunnison anti-predator calling, I used two stuffed specimens of a natural predator, the American badger, mounted on plastic sleds. I concealed the badger in a brown cloth bag at the edge of the home territory and then waited in the observation tower. When one or more clan

members were foraging above-ground, a field assistant pulled the badger at a constant rate of 22 cm/s (Hoogland 1983, 1995). Meanwhile, I recorded whether each gunnison gave an anti-predator call while the badger was crossing the home territory. Waiting at least 30 minutes between trials in the same territory, I performed all trials in June (1990, 1992–1994), 1–3 weeks after juveniles had first emerged from their natal burrows.

Shortly after first emerging from the natal burrow, juveniles sometimes give anti-predator calls for sciurids such as Sonoma chipmunks and round-tailed, Belding's, Richardson's and thirteen-lined ground squirrels (Dunford 1977b; Sherman 1977; Smith 1978; Schwagmeyer 1980; Davis 1984). Gunnison juveniles, like black-tailed prairie dog juveniles (Hoogland 1995), however, only rarely called during their first month above-ground. Here I have only considered anti-predator calling of adults and yearlings.

For statistical analyses of anti-predator calls, I used data from 32 males ($N = 75$ responses to the stuffed badgers) and 56 females ($N = 144$ responses). For each individual, I used one data point that was equal to the percentage of trials when it gave an anti-predator call in response to the stuffed badger. The mean ± SD number of trials for each prairie dog was 3.26 ± 1.66 (range = 1–9).

I assumed that gunnisons responded to the stuffed American badgers as they would have responded to live American badgers. I was unable to evaluate this assumption rigorously because live badgers at the study colony were rare. In these few encounters ($N = 2$) and also in encounters ($N = 7$) with live coyotes, *Canis latrans*, gunnisons responded as they did in experiments with the stuffed badgers: some called while others watched in silence. Similar patterns of anti-predator calling during attacks by live terrestrial mammalian predators occur for Belding's ground squirrels, black-tailed prairie dogs, and alpine, *M. marmota*, hoary, Olympic, *M. olympus*, and yellow-bellied, *M. flaviventris*, marmots (Barash 1975, 1989; Sherman 1977, 1985; Armitage 1982; Hoogland 1995).

Regarding kinship of their listeners in the home territory, gunnison callers were of four types: with offspring (for which the coefficient of genetic relatedness, $r = 0.50$); with parents ($r = 0.50$) or litter-mate siblings ($r = 0.50$ or less; see above) but no offspring; with non-descendant kin that did not include parents or litter-mate siblings ($0.0625 \leq r < 0.50$); and with no known kin ($0.0625 > r \geq 0.0$).

Some ground squirrels have more than one distinct anti-predator call (see below). For all interspecific comparisons, unless noted otherwise, I have considered only those calls usually given for terrestrial mammalian predators such as coyotes and American badgers.

All significance levels (*P*-values) result from two-tailed nonparametric statistical tests. Means in the text show one standard deviation (SD), but means in figures show one standard error (SE). The number above each SE line indicates the sample size. When $P \geq 0.001$, I have shown the exact *P*-value. I have shown cases of $P < 0.001$, even when $P < 0.0001$, as simply $P < 0.001$.

RESULTS

I recorded responses of Gunnison's prairie dogs during 126 experimental trials with the stuffed American badgers. At least one gunnison called in 67% of these experiments (85/126). With only a few exceptions, individuals called only when the badger was moving across the home territory. Some gunnisons consistently called in response to the stuffed badgers, but others never called (Fig. 1).

After hearing an anti-predator call, gunnisons in the home and adjacent territories ran to burrow mounds, where they stood and scanned for the enemy. Alerted gunnisons sometimes initiated their own calls after detecting the moving stuffed badger, so that 2 or 3 gunnisons called simultaneously. I did not distinguish between first and second callers in any of the statistical analyses.

With mean calling frequencies of 34% and 41%, respectively, males and females were about equally likely to call (Fig. 1).

If anti-predator calls inflict a cost by rendering callers more vulnerable to predation, then individuals close to a predator should probably call less frequently than more distant, safer individuals. If anti-predator calls do not involve any risk, on the other hand, then, as for Belding's and Columbian ground squirrels (Sherman 1977; MacWhirter 1992), calling should be unrelated to distance from a predator searching for prey in the home territory. In the

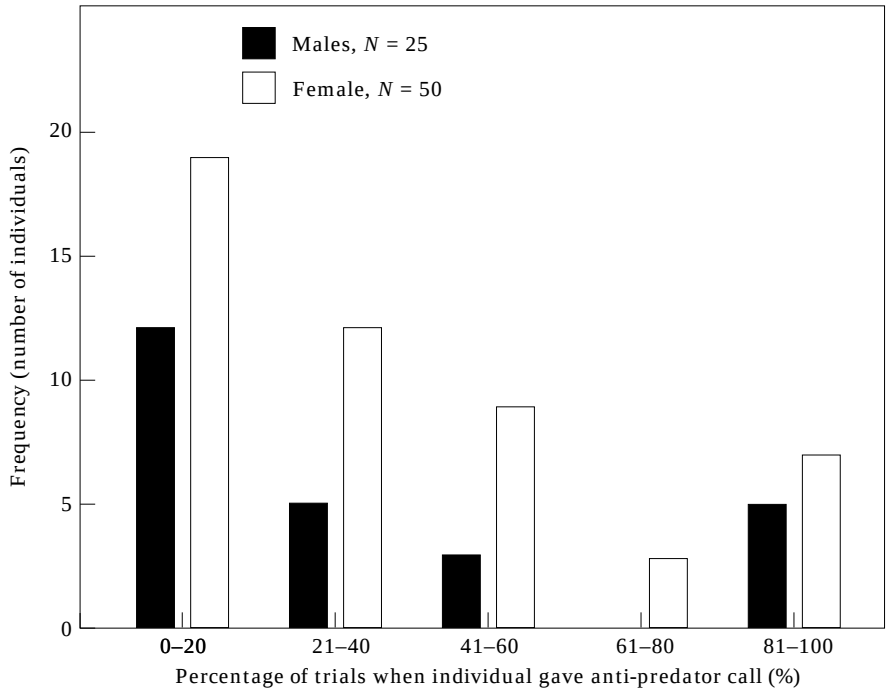

Figure 1. Variation between gunnisons in anti-predator calling. The percentage of anti-predator calling for each individual results from approximately three experimental trials with the stuffed American badgers. Excluded are data from 7 gunnison males and 6 females that were available for only one trial. Mean calling frequencies for males and females were 34% and 41%, respectively (*NS*, Mann–Whitney *U*-test).

present study, gunnison anti-predator calls evidently increased susceptibility to predation, because individuals closest to the badger were less likely to call (Fig. 2a).

Like Belding's and Columbian ground squirrels and black-tailed prairie dogs (Sherman 1985; MacWhirter 1992; Hoogland 1995), Gunnison's prairie dogs did not automatically submerge into a burrow after hearing or giving an anti-predator call. Rather, alerted individuals remained on burrow mounds and carefully watched the predator until its departure. Only when the predator came close (sometimes as close as 5 metres) did a gunnison usually submerge.

Gunnisons that are forced into burrows by predators are presumably in more danger than are gunnisons that remain above-ground. It anti-predator calls inflict a cost by rendering callers more vulnerable to predation, then submergers should probably call less often than individuals that feel safe enough to remain above-ground. If anti-predator calls do not involve any risk, on the other hand, then calling should be unrelated to submergence coerced by a predator that approaches too closely. Figure 2b indicates that gunnison anti-predator calls are costly, because individuals that submerged in response to the badger were less likely to call.

Gunnison females with any type of kin in the home territory were more likely than females without nearby kin to give an anti-predator call (Mann–Whitney *U*-test, $P = 0.034$; Fig. 3). Furthermore, females with offspring in the home territory were more likely to call than were females that had only other types of kin (i.e. parents, litter-mate siblings, nieces and nephews, or cousins) in the home territory ($P = 0.001$; Fig. 3). Females with non-descendant kin but no offspring in the home territory did not call significantly more often than did females with no nearby kin ($P = 0.167$; Fig. 3).

For gunnison males, by contrast, anti-predator calling seemed unaffected by kinship of nearby listeners (Fig. 3). Specifically, males without kin in the home territory called as often as did males with offspring, siblings, parents, or other kin in

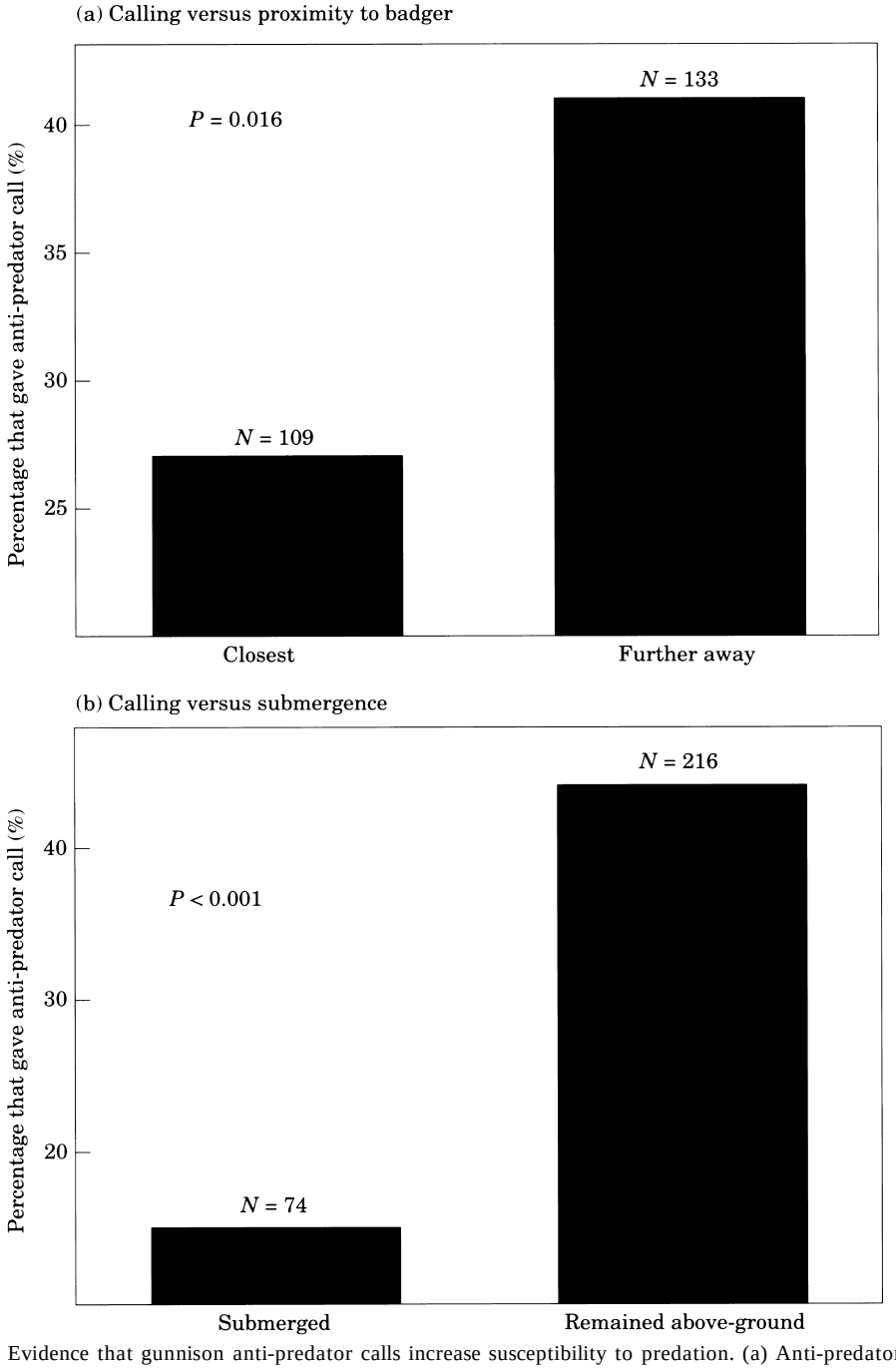

Figure 2. Evidence that gunnison anti-predator calls increase susceptibility to predation. (a) Anti-predator calling versus distance from the stuffed American badger. Before 109 of the 126 experimental trials. I determined which individual was closest to the concealed badger. The number above each bar indicates the number of individuals observed. The *P*-value is from the 2 × 2 chi-squared test. (b) Anti-predator calling versus submergence into a burrow. I recorded anti-predator calling by individuals that did and did not submerge into a burrow in response to the stuffed badger. The number above each bar indicates the number of individuals observed during 126 trials. The *P*-value is from the 2 × 2 chi-squared test. Individuals in more (simulated) danger (i.e. closer to the badger or forced to submerge) were less likely to call.

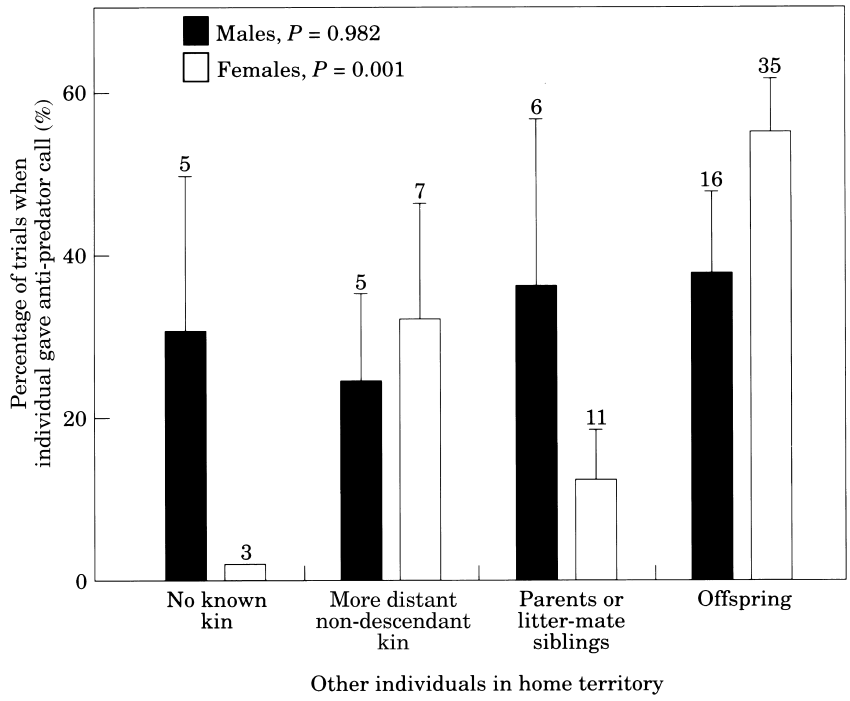

Figure 3. Anti-predator calling by prairie dogs with and without genetic relatives in the home coterie territory. For this analysis, kin were other prairie dogs sharing a coefficient of genetic relatedness (r) of 0.0625 or greater. The number above each SE line indicates the number of adult and yearling individuals observed (each approximately three times) during 126 experimental trials with stuffed American badgers. P-values are from the Kruskal–Wallis analysis of variance (see text).

the home territory (Mann–Whitney U-test: $P \geq 0.700$) for all pair-wise comparisons; Fig. 3). The five males with no nearby kin were all yearlings that had dispersed into new territories where they did not sire any offspring; at least three, and possibly four, of these five males arrived from adjacent territories. Two of the three females with no nearby kin moved into new territories where they did not rear any offspring; one was a yearling, the other a two-year old. The third female's offspring and other close kin had all either died or dispersed to other territories.

DISCUSSION

Both theoreticians (e.g. Hamilton 1964; Maynard Smith 1965; Williams 1966; Alexander 1974; Wilson 1975; West-Eberhard 1975; Dawkins 1976) and field biologists (Dunford 1977b; Sherman 1977; Schwagmeyer 1980; Davis 1984; Owings & Leger 1980) have assumed that individuals must usually increase their susceptibility to predation by giving an anti-predator call. However, supporting data for this logical assumption are scarce. Gunnison's prairie dogs closest to the stuffed badger at the start of each experimental trial, and hence more vulnerable to (simulated) predation, were less likely to call than were more distant, safer individuals. Furthermore, gunnisons coerced to enter burrows by the moving badger were less likely to call than were gunnisons that remained above-ground. These results indicate that gunnison anti-predator calling, like anti-predator calling of Belding's ground squirrels (Sherman 1977, 1985), is dangerous, and that gunnisons assess personal safety before calling. Because field assistants and I observed so few predations at the study colony ($N = 1$ adult victim), I could not directly investigate whether callers were more vulnerable to predation.

Over half of the calling frequencies for gunnisons in response to the stuffed badgers were between either 0% and 20% or 81% and 100%

(Fig. 1). The two single most common frequencies were 0% and 100%. Most of the variation in the probability of calling thus resulted from differences between individuals (i.e. callers versus non-callers) rather than from differences within individuals (i.e. call today but do not call tomorrow).

Sometimes differences in calling frequency between two seemingly equivalent gunnisons were dramatic and inexplicable. For example, consider females H9 and 76, who were same-aged littermate sisters who lived in the same (natal) territory and who both weaned litters as yearlings in 1992. Female H9 called during every experiment with the stuffed badger in 1992 ($N = 5$ trials), but female 76 called at a frequency of only 25% ($N = 4$).

Animals such as alpine and hoary marmots and Uinta, arctic, *S. parryii*, and Richardson's ground squirrels usually give one distinct anti-predator call in response to aerial, avian predators and another for terrestrial, mammalian predators (Balph & Balph 1966; Melchior 1971; Taulman 1977; Davis 1984; Hofer & Ingold 1984). The same is true for vervet monkeys, *Cercopithecus aethiops*, and ringtailed lemurs, *Lemur catta* (Seyfarth et al. 1980; Pereira & Macedonia 1991). However gunnisons have only one distinct anti-predator call for their aerial and terrestrial predators, and thus resemble yellow-bellied and Olympic marmots, Columbian and thirteen-lined ground squirrels, and black-tailed prairie dogs (Waring 1970; Barash 1973, 1989; Betts 1976; Matocha 1977; Schwagmeyer 1980; Hoogland 1995). Subtle variation between gunnison anti-predator calls, however, might indicate different types of predators or different levels of urgency (Slobodchikoff et al. 1986, 1991). For example, individuals seemed to call at a faster rate (i.e. more barks per minute) when danger was especially imminent (see also Waring 1970), but I did not investigate this possibility.

By dispersing into a new breeding territory, male black-tailed and male Gunnison's prairie dogs separate themselves from close kin. Black-tail males usually do not give anti-predator calls until they sire offspring in the new territory. Male gunnisons without offspring in their territories, however, called as often as did males with either non-descendant kin or offspring nearby (Fig. 3). At least three factors might explain this unexpected difference between black-tail and gunnison males. First, data are available from only five gunnison males without kin in the home territory, compared to data from 43 black-tail males (Hoogland 1995); more data might lead to the predicted result for gunnison males. Second, perhaps gunnison males are more diligent than black-tail males regarding the protection of future mates. Third, gunnison males are more likely than black-tail males to disperse into adjacent, rather than more distant, territories (this study) so that kin in their previous (natal or breeding) territory might still be within earshot. Gunnison territories are larger than black-tail territories, however, so that kin feeding in distant areas of adjacent territories might not easily hear anti-predator calls.

To study the importance of kinship in the evolution of anti-predator calling by Gunnison's prairie dogs, one of the toughest tasks was to identify individuals that did not have either offspring or other kin within the home territory. After locating such individuals, I made a special effort to determine their frequencies of anti-predator calling via experiments with the stuffed badgers. Consequently, gunnison adults and yearlings with no nearby kin are disproportionately represented in Fig. 3. Specifically, Fig. 3 might suggest that the frequencies of males and females with no kin in the home territory within gunnison colonies are 16% (5/32) and 5% (3/56), respectively. The real, natural frequency of adult and yearling males with no kin in the home territory at the time of first juvenile emergences is less than 5% at the study colony each year, and the comparable frequency for adult and yearling females is less than 1%.

Do individuals call to warn offspring, with non-descendant kin sometimes being secondary beneficiaries (Shields 1980 versus Sherman 1980b; MacWhirter 1992)? If so, then anti-predator calling is primarily an expression of parental care. Alternatively, has the evolution of anti-predator calling also involved natural selection for the specific warning of non-descendant kin? Investigation of these questions is difficult when callers consistently live near offspring, as they do for species such as Sonoma chipmunks and California, Belding's, Richardson's, round-tailed, and thirteen-lined ground squirrels (Dunford 1977b; Sherman 1977, 1980a, b, 1981; Smith 1978; Schwagmeyer 1980; Shields 1980; Davis 1984; Owings et al. 1986). Investigation is easier for species such as Gunnison's and black-tailed

prairie dogs, for which callers without nearby offspring commonly live near non-descendant kin. Black-tail males and females call not only to warn offspring, but to warn non-descendant kin as well. Indeed, black-tails with only non-descendant kin in the home territory call as often as black-tails with nearby offspring (Hoogland 1995). The story is different for gunnisons. Anti-predator calling by gunnison males, for example, seemed unrelated to the kinship of nearby listeners (Fig. 3). Further, gunnison females with offspring in the home territory called more often than did females with only non-descendant kin nearby (55% versus 21%; Fig. 3).

Individuals share just as many alleles with their parents and full siblings as with their offspring. Thus, in terms of Hamilton's (1964) coefficient of genetic relatedness (r), parents or full siblings in the home territory are equivalent to offspring there. If kinship per se is primarily important in the evolution of anti-predator calls, then individuals with only parents or full siblings in the home territory should call as often as individuals with offspring there, which is true for black-tailed prairie dogs (Hoogland 1995). If anti-predator calls are mainly expressions of parental care, however, then individuals with nearby offspring should call more often than individuals with only parents and full siblings nearby. As for female Belding's, California, Columbian, and round-tailed ground squirrels (Dunford 1977; Sherman 1977, 1985; Owings & Leger 1980; MacWhirter 1992), anti-predator calling by female gunnisons was largely an expression of parental care. Specifically, gunnison females with offspring in the home territory called more often then females with only parents or full siblings nearby (55% versus 13%; Fig. 3).

Kinship of nearby listeners is not the only factor that affects the evolution of anti-predator calling, of course. Reciprocity, demography, direct benefits to the caller, and age, reproductive value, and vulnerability of both caller and listener are only some of the other factors that might be important (Trivers 1971; Alexander 1974; Sherman 1977, 1985; Hoogland 1995). Suppose, for example, that gunnison female *A* has two yearling offspring but no other kin in the home territory, and that a same-aged female, *B*, has two emergent juvenile offspring but no other kin in the home territory. Because juveniles are more susceptible to predation than adults (unpublished data; see also Hoogland 1995), natural selection for calling probably will be stronger for female *B* than for female *A*, even though the two mothers are equivalent in terms of kinship of nearby listeners. On the other hand, because the older offspring of female *A* have higher reproductive value than the juvenile offspring of female *B*, perhaps natural selection for calling will be stronger for female *A*. Surely one reason for the emphasis on kinship of nearby listeners in studies of anti-predator calling is that measurement is easier and less complicated for kinship than for variables such as reproductive value, reciprocity, and susceptibility of caller and listener to predation.

Unlike their anti-predator calls for terrestrial, mammalian predators, the anti-predator calls of Belding's ground squirrels for aerial, avian predators seem to enhance 'self-preservation' by reducing the susceptibility of the caller to attack (Sherman 1985). The anti-predator calls of black-tailed prairie dogs might also enhance self-preservation, but such direct benefits to the caller must surely be secondary to the indirect benefits that accrue from warning nearby kin (Hoogland 1995). I detected no circumstances under which gunnisons might somehow benefit directly from their own anti-predator calls.

From research involving marked animals of known genetic relationships, information on anti-predator calling to terrestrial, mammalian predators is now available from six species of ground squirrels, two species of prairie dogs, one species of chipmunk, and one species of marmot. Females with nearby offspring are the most common callers among Sonoma chipmunks and round-tailed, Belding's, thirteen-lined, and Columbian ground squirrels (Dunford 1977b; Sherman 1977, 1985; Smith 1978; Schwagmeyer 1980; MacWhirter 1992). Along with mothers, males with nearby offspring commonly call among hoary marmots, Gunnison's prairie dogs, and California and Richardson's ground squirrels (Davis 1984; Owings & Leger 1980; Owings et al. 1986; Barash 1989; Fig. 3). Mothers and fathers also call among black-tailed prairie dogs, but non-parental males and females with nearby non-descendant kin call equally often (Hoogland 1995). Except for gunnison males (Fig. 3), the common theme in all these studies is kinship: individuals with kin within earshot are more likely to call than are individuals without nearby kin. But numerous questions remain. Why, for

example, do anti-predator calls seem to increase susceptibility to predation for some species (Fig. 2; see also Sherman 1977, 1985), but not for others (Barash 1975; Dunford 1977b; Noyes & Holmes 1979; Davis 1984)? Also, why do fewer than 50% of individuals with nearby kin usually call when a predator approaches (Fig. 3; see also Sherman 1977; Davis 1984; MacWhirter 1992; Hoogland 1995)? Conversely, why do individuals with no nearby kin consistently call at a low (Sherman 1977; Davis 1984; MacWhirter 1992; Hoogland 1995) or high (Fig. 3) frequency? More research is imperative for a better understanding of anti-predator calling among Gunnison's prairie dogs and other animals.

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