Behav Ecol Sociobiol (1985) 17:313–323

Behavioral Ecology and Sociobiology

Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation?

Paul W. Sherman
Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA

Received May 22, 1984 / Accepted February 14, 1985

Summary. Belding's ground squirrels (*Spermophilus beldingi*) give acoustically distinct alarm calls to aerial and terrestrial predators. The animals typically give multiple-note trills to predatory mammals, and single-note whistles to flying hawks. During a 9-year study of free-living *S. beldingi* at Tioga Pass, California, the adaptive significance of the whistle call was investigated. Data were gathered on 664 ground squirrel-hawk interactions, most of which were induced by flying trained raptors over individually marked study animals of known sex and age. The sight of a flying hawk and the sound of whistles stimulated widespread calling and running to shelter by the ground squirrels (Fig. 1). Wild raptors were rarely successful at capturing the rodents once a whistle had been given, and fewer callers than noncallers were killed (Table 1). Individuals of both sexes and all ages whistled equally often (Fig. 4), and females' tendencies to whistle were not affected by the presence of relatives, including offspring (Fig. 5). The most frequent callers were animals in exposed positions: far from cover and close to the predatory bird (Table 2). Taken together the data suggest that unlike trills, which increase vulnerability to terrestrial predators (Table 1) and function to warn relatives, whistles directly benefit callers by increasing their chances of escaping from hawks.

Introduction

Alarm calls, vocalizations given when predators are detected, appear to be altruistic because they alert other animals to impending danger. Recently considerable interest has focused on determining the adaptive significance of alarm calling among mammals generally (e.g. Cheney and Seyfarth 1981; Ivins and Smith 1983) and ground-dwelling sciurids particularly. Field studies of ground squirrels (*Spermophilus*: Sherman 1977; Dunford 1977; Leger and Owings 1978; Schwagmeyer 1980; Davis 1984), chipmunks (*Eutamias*: Smith 1978), prairie dogs (*Cynomys*: Hoogland 1983), and marmots (*Marmota*: Barash 1975, 1976) have revealed sexual and seasonal differences in tendencies to give alarm calls to terrestrial predators. In general, the likelihood of calling is greatest when offspring or siblings are nearby, suggesting that warning relatives is a common function of such calls and implicating kin selection in their evolution.

Belding's ground squirrels (*S. beldingi*) typically give multiple-note alarm trills when predatory mammals approach. The function of these calls has been investigated in a free-living population located near Tioga Pass, in the central Sierra Nevada of California (Sherman 1977, 1980a). Data from 102 predator appearances that occurred naturally during 1974–77 were used to test among six hypothetical advantages of giving alarm calls; the disadvantages of calling were also investigated. It was found that calling was dangerous, that females called more frequently than males, and that females' calling tendencies were highest in the presence of descendant and collateral kin. These results, coupled with the ground squirrels' matrilocal population structure, suggested that alarm trills warn relatives and thus are expressions of nepotism (Sherman 1980b; but see Shields 1980).

Belding's ground squirrels also vocalize when aerial predators appear. The calls are usually single-note whistles, acoustically quite distinct from trills (Turner 1973; Robinson 1980, 1981; Leger et al. 1984). The adaptive significance of whistling was studied from 1974 to 1982 at Tioga Pass. Data were gathered during 664 ground squirrel-hawk interactions, some of which occurred naturally but most of which were induced by flying trained raptors over the study area. The use of semi-tame hawks allowed for control over the timing of the birds' appearances and flight trajectories, and for the preselection of ground squirrels to observe closely. Two main questions were addressed with the data that were gathered: (1) does giving whistles increase or decrease the vulnerability of callers?, and (2) is alerting relatives a primary function of whistling?

Methods

Study animals. Belding's ground squirrels are diurnal, social rodents that inhabit the Sierra Nevada and southern Cascade mountain ranges in the western United States (Jenkins and Eshelman 1983). For 14 years (1969–82) Martin L. Morton and I and our students studied a population of 200–250 *S. beldingi* near Tioga Pass, California (38° N, 119° W; elevation: 3,040 m). The study area is a gently sloping subalpine meadow, 1.1 km long by 0.5 km wide. It is bordered on three sides by stands of pine trees (*Pinus contorta* and *P. albicaulis*) and on the fourth by Tioga Lake. Rock outcrops and 0.5–1.0 m tall willow bushes (*Salix exigua* and *S. planifolia*) are interspersed among the study meadow's grassy areas.

At this study site, Belding's ground squirrels are typically surface-active from mid-May until early-October; the rest of the year they hibernate (Morton 1975; Morton and Sherman 1978; also French 1982). In the spring adult (≥ 2 year) males emerge from hibernation 1–2 weeks before females begin emerging. A female becomes sexually receptive 4–8 days after emergence, and behavioral estrus lasts 1–5 h on a single afternoon. Both males and females mate polygamously (Sherman 1976) and as a result the majority of litters are multiply sired (Hanken and Sherman 1981). Each female rears a single litter of 3–5 pups per season (range 1–11) in a solitary, multiple-entrance burrow that she digs herself. Gestation generally lasts 23–25 days, and the pups are nursed for an equivalent length of time.

Several weeks after they are weaned, juvenile male *S. beldingi* begin dispersing (Holekamp 1983, 1984a); they will never return to their natal area. Adult males are also nomadic, emigrating between seasons. Females, by contrast, seldom disperse and they spend their lives in the area where they were born (Sherman 1977, 1980a). In addition to the sexual dimorphism in dispersal, there is also a marked difference between the sexes in age-specific survival. Males apparently live only about half as long as females on average and at the maximum (Sherman and Morton 1984). Males disappear from the population more rapidly due to both the dangers of dispersal and to the serious physical injuries they inflict on each other during fights over estrus females. As a result of sexual asymmetries in dispersal and longevity males seldom interact with either descendant or collateral kin, and they do not behave parentally. On the other hand, females interact frequently with near and distant matrilineal relatives throughout life, and nepotism has been highly elaborated among females (Sherman 1980a, 1981a, 1981b; Holmes and Sherman 1982). Female philopatry, male dispersal, and the formation and persistence of female kin groups are typical of mammals generally (Greenwood 1980) and ground-dwelling sciurids particularly (Dobson 1982; Michener 1983; Holekamp 1984b).

Marking. Ground squirrels were captured in single-door live-traps and handled without anesthesia, using gloves. They were permanently marked by attaching uniquely numbered metal (fish fingerling) tags to both ears or, when an eartag was lost, by clipping off unique combinations of toes. To facilitate individual identification at a distance, each study animal was also marked with black hair dye. In the course of the research described here, more than 3,500 *S. beldingi* were permanently marked, including ca. 2,000 pups in 400 litters. Juveniles were captured and marked within five days (usually two days) of their first emergence above ground and because females nested alone, assignment of young to sibling groups was unambiguous. As a result of our consistent marking efforts, the exact ages and maternal ancestries of most of the study animals were known.

Staged hawk encounters. During 1974–82 I often observed wild raptors attempting to capture the ground squirrels, especially in mid- to late-summer. However, because the hawks appeared suddenly and moved rapidly, my observations of their behavior and that of the ground squirrels were often fragmentary. In 1977 I attempted to increase the predictability of interactions between ground squirrels and aerial predators by sailing various hawk-like objects over the study area. Hawk-shaped kites, silhouette models (e.g. Müller-Schwarze and Müller-Schwarze 1971), and model heliopters were used, as well as frisbees (e.g. Davis 1984), boomerangs, and gliders (e.g. Noyes and Holmes 1979). All these attempts failed because the ersatz hawks did not consistently elicit either alarm calls or evasive behaviors that were similar to the animals' responses to wild raptors. Therefore this approach was abandoned in favor of staging encounters with live hawks.

During 1978–81 my assistants and I conducted field experiments with two different trained Harris's hawks (*Parabuteo unicinctus*). These are large buteos which are native to the southwestern United States. Although in the wild Harris's hawks prey heavily on diurnal mammals, particularly ground squirrels (e.g. Table 7 in Mader 1975), in my studies they attacked only edible lures (and not *S. beldingi*). My experiments consisted of inducing a hawk to fly in a straight line over Tioga Pass Meadow while the behavior of focal ground squirrels was being observed. A total of 141 such raptor experiments were conducted, on 26–27 July 1978 ($n=26$ flights), 12–13 August 1978 ($n=19$), 30 June–1 July 1979 ($n=31$), 28–29 July 1979 ($n=32$), 27 June 1981 ($n=6$), and 25–26 July 1981 ($n=27$). In the course of these trials, 583 ground squirrel-hawk interactions were observed, involving 306 different marked *S. beldingi*.

To begin a trial, 2–6 field assistants and I stationed ourselves in widely separated observation posts on boulders, 2 m tall tripods, or in trees. Then two handlers slowly entered the study area, one carrying a (hooded) hawk and the other a lure. The falconers stayed 100–200 m apart and I positioned them, using walkie-talkies and hand signals, so that a number of active ground squirrels were between them. Once everyone was in place, we all remained still for at least 10 min to allow the animals to resume their activities. During this period, each observer located a ground squirrel to watch closely during the ensuing trial. I then signalled the falconers to start the experiment, and they slowly stood up and simultaneously unhooded the hawk and held the out the lure.

Upon noticing the lure the bird typically took off and flew toward it, at heights of 1–5 m above the ground. A trial ended when the bird landed on or near the lure. Then the hawk was rehooded and carried back to its original location via a circuitous route, to avoid disturbing the ground squirrels further. Three precautions were taken against habituating the ground squirrels to the hawks. First, when a set of four trials had been completed, the observers and falconers moved to a distant part of the study meadow before repeating the procedures. Second, at least 15 min were allowed to elapse between the end of one trial and the start of the next; the mean inter-trial interval within a set of four was 27 min ± 13 min ($n=11$ days of trials). Third, no more than four sets of trials (i.e. 16 flights) were conducted on a given day, and usually half that day's experiments took place in the early morning, and the other half late in the afternoon.

Data were gathered on the behavior of as many different ground squirrels as possible during every trial. Just before an experiment began, each observer recorded his location on a gridded map of the study meadow, the time and trial number, the identity of the chosen focal animal, and its location, body position, and distance from the nearest known burrow or bush. At the signal to begin a trial, observers directed their attention solely to the behavior of their focal animal and recorded the following information in a notebook or on tape: (1) whether or not the focal animal moved and, if so, the distance and direction of its movements relative to the hawk's flight path, (2) whether the focal animal ran to cover (e.g. bushes or burrows), to promontories (rocks), or to conspecifics, (3) whether or not the focal animal called and, if so, at what point relative to its movement, and (4) whether the hawk was visible to the observer and thus conceivably to the focal animal either before or during its flight, or was instead hidden by a hill or rock outcrop from the observer's view and thus presumably the ground squirrel's. In addition, I recorded the bird's exact flight path and distance, and estimated its maximum and minimum height. If the hawk failed to fly within 5 min of being unhooded, if it soared higher than 10 m, or if it did not fly toward the lure, the trial was stopped. Data from such aborted trials were not included in any of the analyses.

Data analyses. Data obtained during encounters with wild and semi-tame hawks were combined because I observed no differences in the ground squirrels' behavior in these contexts. Furthermore, neither the fraction of animals that gave alarm whistles ($\chi^2=1.7$; $P>0.1$) nor the proportion of them running to promontories versus to burrows or bushes differed significantly ($\chi^2=1.0$; $P>0.3$) between natural and experimental circumstances. Data from all 11 days of experimental trials were also combined after testing for habituation. To do this I examined the relationship between trial order and both the fraction of animals that whistled and the proportion that ran to pronontories versus to burrows or bushes on each of the trial days. No correlations were found for either measure of the animals' responses on ten of the days (i.e. all $P>0.05$); on the eleventh, the proportion of animals that called actually increased slightly ($P=0.03$) as the day wore on. These data suggest that the precautions taken to avoid habituation were reasonably effective, and justify combining the data from the different trials across days.

Information on the frequency of *S. beldingi* alarm calling and evasive behaviors was summarized with regard to each animal's age, sex, relatedness to conspecifics, and stage in the breeding cycle. No ground squirrel was observed in more than 3 trials on one day, or more than 7 trials in a year. The ground squirrels' responses to aerial predators were tested for similarities with their behavior toward terrestrial predators and for differences from randomness using the G-test statistic corrected for continuity (Sokal and Rohlf 1981, pp. 704–716). Under the null hypothesis, ground squirrels should have called in proportion to the number of times they were above ground when predators appeared. Thus the expected frequency of random response was calculated by counting the total number of focal animals in each age/sex/relatedness category observed during censuses taken immediately prior to each raptor appearance.

The ground squirrels' directional movements relative to the hawk's flight path were plotted on a scale map of the study area. For analysis of these data, a perpendicular line was drawn between each animal's position at the moment the hawk took off and the bird's eventual flight line. Then the minimum angle between this line and the ground squirrel's escape path was measured. The directional movements of animals that called and those that did not call to the hawk were analyzed separately. First each distribution was tested for orientation using Rayleigh's statistic (Batschelet 1981, pp. 54–58), and then the two distributions were compared directly using Watson's U^2-test (Batschelet 1981, pp. 114–118).

Results

Alarm calling

Belding's ground squirrels are known to give single-note whistles in the 4–6 kHz frequency range when raptors fly into view, and multiple-note 4–6 kHz trills to predatory mammals. Sonagrams of both these calls have been multiply published and analyzed (e.g. Robinson 1980, p. 841; 1981, pp. 153–154; Leger et al. 1984, p. 756).

During the present study, at least one alarm call was given on 172 of the 199 occasions (86%) when a wild or semi-tame hawk flew low (< 50 m) over Tioga Pass Meadow; typically several individuals whistled during each hawk appearance. Whistles were given by 240 of the 664 focal ground squirrels (36%), and trills were given by 31 (5%). In other words, 240 of the 271 callers (89%) gave whistles, demonstrating that whistles are indeed the predominant vocalization to flying raptors. In comparison, alarm trills were heard on 133 of 198 occasions (67%) when terrestrial predators appeared during 1974–82. Trills were given by 139 of 402 focal individuals (35%) and whistles by 14 (3%); so, 139 of 153 calls (91%) to terrestrial predators were trills. There is thus a highly significant difference ($\chi^2=57$; $P<0.001$) in the vocal responses of *S. beldingi* to predators on the ground and in the air, in agreement with the aforementioned prior reports. Occasionally the ground squirrels also gave acoustically distinctive single-note calls to stationary predators; such vocalizations, called "chirps" by Leger et al. (1984), were not heard in response to flying raptors.

Of 473 ground squirrels that apparently had a clear view of an approaching hawk, 222 (47%) whistled. By contrast only 15 of 158 individuals (9%) whose view of the hawk was blocked by hills or rock outcrops (but who could hear conspecifics' calls) whistled. This suggests that vocal responses of *S. beldingi* are stimulated mainly by the sight of the predatory bird (Leger et al. 1979 made similar observations on California ground squirrels, *S. beecheyi*). Interestingly, on 21 of the 31 occasions

Table 1. Alarm calling and survival in Belding's ground squirrels at Tioga Pass, California. All data are from observations made during attacks by hawks ($n=58$) and predatory mammals ($n=198$) that occurred naturally during 1974–82

Category	No. of ground squirrels Captured	Escaped	Percent captured	P (χ^2 test)
Aerial Predators				
Callers	1	41	2%	
Non-callers	11	28	28%	<0.01
Total	12	69	15%	
Terrestrial Predators				
Callers	12	141	8%	
Non-callers	6	143	4%	<0.05
Total	18	284	6%	

(68%) when ground squirrels gave trills to a hawk, the bird was either perched or walking along the ground and in 3 other cases (10%) the hawk was >100 m away from the caller. Conversely, 12 of the 14 (86%) whistles to terrestrial predators were given when the caller was being closely pursued. These observations suggest that the dichotomy in *S. beldingi* alarm vocalizations relates more to the imminence of danger than to predator taxonomy.

Natural hawk encounters

During 1974–82 detailed data were gathered on the behavior of 81 *S. beldingi* during 58 naturally occurring attacks by wild raptors. Goshawks (*Accipiter gentilis*) swooped down on the ground squirrels most frequently ($n=27$ times), followed by Cooper's hawks (*A. cooperi*; $n=17$), prairie falcons (*Falco mexicanus*; $n=8$), peregrine falcons (*F. peregrinus*; $n=4$), and golden eagles (*Aquila chrysaetos*; $n=2$). On these occasions 12 ground squirrels (10 adults and 2 juveniles) were killed: 6 by goshawks, 4 by Cooper's hawks, and 1 each by prairie and peregrine falcons. Thus the known hunting success of wild raptors at Tioga Pass (12 kills/58 hunts = 21%) was similar to that reported in other studies of aerial predation on ground squirrels (e.g. Pfeifer 1980).

Interestingly, there was a positive association between giving an alarm whistle and escaping from wild raptors (Table 1). A far smaller fraction of callers than non-callers were captured, and only one of the 12 ground squirrels that were killed had whistled. Was escape related to calling per se or simply to being alerted? Of the 42 callers that exhibited escape behavior, only 1 (2%) was caught; in contrast, of 23 non-callers that exhibited escape behavior, 5 (22%) were killed ($\chi^2=6.6$; $P<0.01$). These data indicate that wild raptors were rarely able to capture alerted ground squirrels, especially if they whistled. In contrast, terrestrial predators attacked (Sherman 1977) and killed (Table 1) a greater proportion of callers than non-callers. Giving alarm trills to predatory mammals is apparently more dangerous than whistling in the presence of hawks.

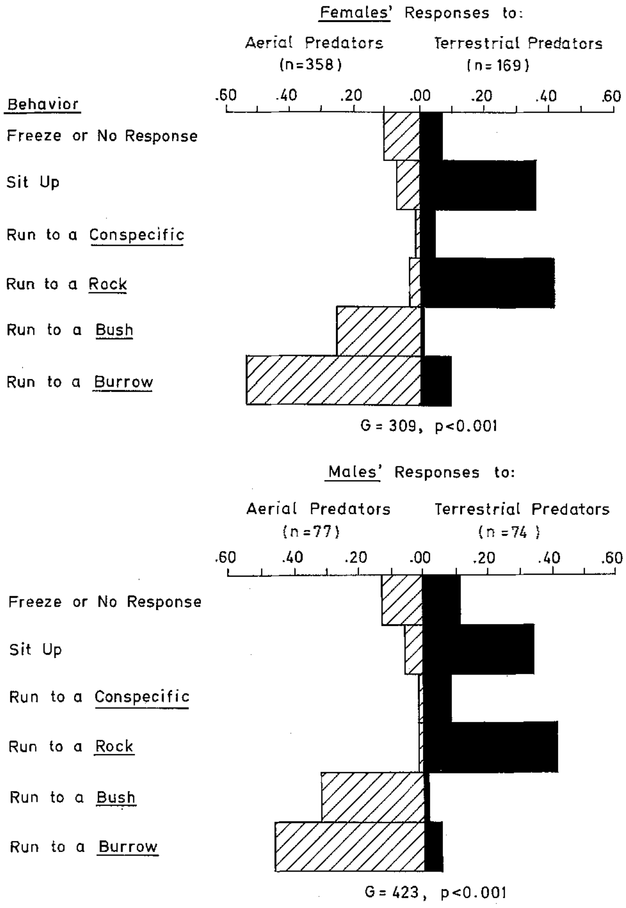

Fig. 1. Behavior of female (upper) and male (lower) Belding's ground squirrels at Tioga Pass, California toward aerial predators or conspecifics' alarm whistles versus terrestrial predators or alarm trills. The number of responses observed (n) and the results of G-tests comparing responses to aerial and terrestrial predators are shown. The data on responses to hawks are presented for the first time here; data on responses to predatory mammals are from Sherman 1977 (Table 3, p. 1251)

Evasive behavior

When wild or trained raptors flew low over Tioga Pass Meadow, the ground squirrels quickly sought cover (Fig. 1). Males and females behaved similarly, and usually they scurried to burrows or bushes.

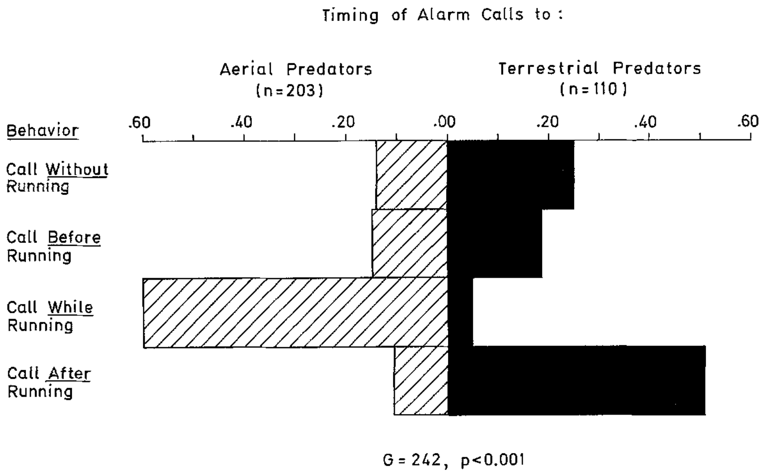

Fig. 2. Timing of alarm calling to predators by Belding's ground squirrels relative to their escape behaviors. Calling responses to aerial (left) and terrestrial predators (right) are shown, along with the number of individual responses observed (*n*) and the results of a *G*-test comparing the animals' behavior toward the two types of predators

Upon reaching safety they occasionally sat up and looked toward the predator with only their head and shoulders exposed. The ground squirrels' responses to mammalian predators were quite different (Fig. 1). When coyotes (*Canis latrans*), badgers (*Taxidea taxus*), long-tailed weasels (*Mustela frenata*), or dogs appeared, both males and females typically ran to a rock or else sat up in place. Thus the ground squirrels behaved in ways that enhanced their view of terrestrial predators and, incidentally, their visibility to human observers.

Most *S. beldingi* that whistled to flying hawks vocalized while running to safety, rather than prior to movement or subsequent to reaching refugia (Fig. 2). By contrast, relatively few individuals trilled to terrestrial predators when they were on the run; instead they generally called after reaching a vantage point and standing up. Because whistles were unmodulated, of short duration (see Fig. 2C in Leger et al. 1984), and were usually given only once or twice by a moving ground squirrel, callers were exceedingly difficult for humans and perhaps predators to locate (e.g. Marler 1955, 1956).

When hawks were seen or alarm calls were heard, ground squirrels typically ran to the shelter nearest them. Of 57 animals that entered a burrow after a raptor appeared, 49 (86%) went to the nearest hole and did not pass up hiding in any other known burrow or any bush during their dash for safety; in 18 of these cases (32%) the nearest hole was the animal's own burrow. Likewise, of 40 ground squirrels that entered bushes as refugia, 36 (90%) did not pass by any other bushes or any known burrow. Turner (1973) also observed that when hawks appeared, *S. beldingi* dove into the nearest burrow, regardless of its number of surface openings; additionally, he found that the animals

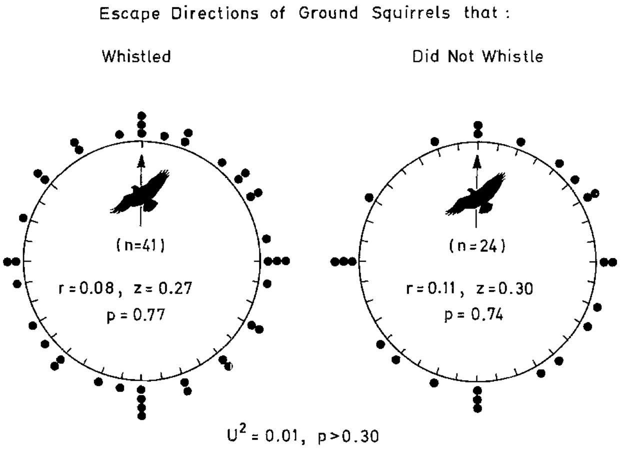

Fig. 3. Directionality of Belding's ground squirrels' escape movements relative to the hawk's flight path (0°). The number of responses observed (*n*) is indicated for ground squirrels that called (left) or did not call (right). The latter animals could not have seen the predatory bird (due to an intervening hill or rock outcrop). Also shown are the results of Rayleigh's tests for orientation of each distribution, and a Watson's U^2-test directly comparing the orientation of the two distributions

reacted to terrestrial predators by seeking out burrows with $\geqq 2$ openings.

The escape movements of ground squirrels that whistled to a flying raptor were similar to those of animals that did not call (Fig. 3). Whether or not they vocalized, individuals attempted to escape by running to the nearest shelter, and their directional movements were random relative to the position of the bird. In this comparison (Fig. 3) the 41 callers were in the hawk's path of flight (< 50 m away), while the 24 non-callers could not have seen the predator because of their positions behind obstructing hills or rock outcrops. The implication

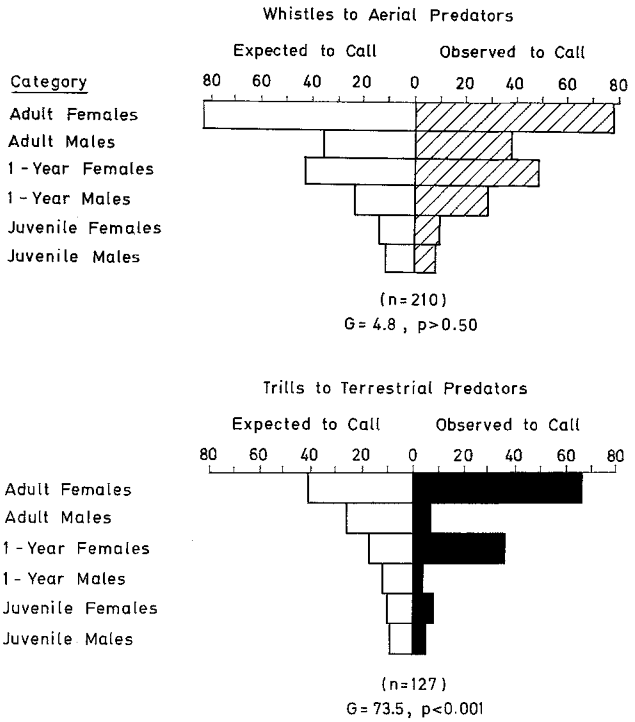

Fig. 4. Expected and observed frequencies of alarm calling to aerial (upper) and terrestrial (lower) predators by various age/sex classes of Belding's ground squirrels. Expected values were determined by assuming that animals called randomly; that is, in proportion to the frequency with which they were present in censuses of all above ground animals taken just prior to the appearances of predators. The number of individuals that gave calls (*n*) is shown, along with the results of *G*-tests comparing expected and observed calling frequencies. The data on whistles are new; the comparative information on trills are redrawn from Sherman 1977 (Fig. 3, p. 1249)

is that alerted individuals behaved similarly, regardless of whether or not the predatory bird was visible to them (Turner 1973 and Robinson 1981 made similar observations).

Effects of sex and age

Belding's ground squirrels of both sexes and all ages gave alarm whistles to hawks (Fig. 4). Surprisingly, there was no significant difference between the observed number of callers in various age/sex categories and that expected under the null hypothesis that calls were given randomly. Although females called more often than males, this difference was proportional to the greater number of females in the population (Sherman and Morton 1984). The data indicate that the probability of a ground squirrel giving an alarm whistle at the approach of an aerial predator was independent of its sex or age.

The pattern of calling to terrestrial predators was considerably different from the vocal response to hawks (Fig. 4). When predatory mammals appeared, adult and yearling females called more often than random expectation, while adult and yearling males called less frequently than expected. These asymmetries implied a nepotistic function for the *S. beldingi* alarm trill (Sherman 1977). The vastly different pattern of vocal response to aerial predators at the same study site suggests that alarm whistles may function in a different context.

Effects of kinship and season

The likelihood that female *S. beldingi* would give alarm whistles to hawks did not vary significantly with the time in the breeding season. Females called equally frequently regardless of whether they were pregnant (41 of 109 pregnant females called: 38%), lactating (35/101 called: 35%), or living with weaned young (86/214 called: 40%). Kinship also did not seem to affect calling tendencies (Fig. 5), and females whistled equally frequently regardless of whether offspring, sisters, or their mother were alive. Reproductive "nonresident" females, known to be >100 m from their nest burrows when the hawk flew over, called slightly more often than reproductive residents.

In contrast, reproductive condition and the existence of both descendant and collateral kin strongly affected females' calling behavior to predatory mammals (Fig. 5). Females trilled when relatives were most likely to be alerted and remained silent when no kin lived nearby. Furthermore, reproductive residents called more frequently than nonresidents. Again the data imply that different factors affect the ground squirrels' tendencies to trill and to whistle.

Effects of vulnerability

The likelihood that a ground squirrel would give an alarm whistle varied with its proximity to both the predatory bird and to refugia (Table 2). Interestingly, the most consistent callers were animals who were farthest from a burrow or bush when a low-flying raptor suddenly appeared close to them. At the other extreme, ground squirrels near safety rarely whistled at distant hawks. Between these extremes the frequency of calling varied systematically: the closer an animal was to a hawk and the farther it was from a hiding place the more likely it was to whistle.

Proximity to conspecifics also appeared to affect *S. beldingi* calling tendencies. During 1978–82

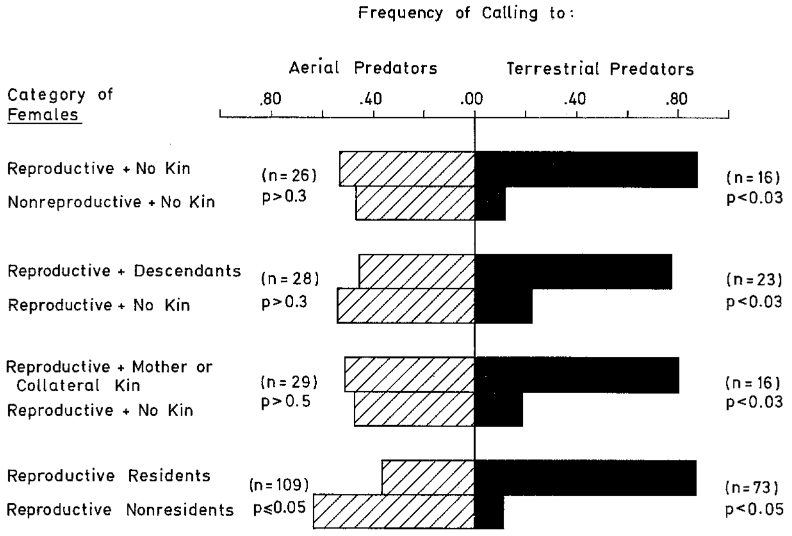

Fig. 5. The effects of kinship and residency on the frequency of alarm calling to aerial (left) and terrestrial (right) predators by female Belding's ground squirrels. The total number of times that calls were given (*n*) by females in each paired category is shown, along with the results of *G*-tests comparing the distribution of calling in each category with that expected if calls were given randomly (see Fig. 4). "Reproductive" females were either pregnant, lactating, or living with weaned young. The data on whistles are new; the comparative information on trills are from Sherman 1977 (Table 2, p. 1250)

Table 2. The effects of proximity to cover and to a hawk on the frequency of alarm whistling. The proportion of ground squirrels that whistled is shown as a function of the distance between the animal's position when the hawk took off and both the bird's flight line (rows) and the closest burrow or bush (columns). Sample sizes are in parentheses

Distance to the hawk (m)	Distance to nearest burrow or bush (m)				
	0.0[a]	0.1–0.5	0.6–2.0	2.1–5.0	>5.0
>100	0% (8)	0% (13)	13% (15)	25% (4)	20% (5)
81–100	0% (5)	13% (8)	11% (9)	0% (3)	50% (4)
61–80	0% (4)	6% (17)	25% (12)	66% (3)	– (0)
41–60	6% (17)	9% (44)	32% (22)	22% (9)	75% (4)
21–40	18% (17)	9% (41)	45% (42)	50% (18)	71% (7)
6–20	18% (22)	33% (49)	58% (52)	79% (14)	100% (5)
0–5[b]	28% (18)	63% (51)	88% (26)	88% (8)	100% (7)

[a] These animals were partially in a burrow or bush when the hawk took off

[b] These animals were directly under the hawk's flight path

nine different females nested on one of several grassy hillocks that were surrounded by willows. The burrows of these "island" nesting females were relatively isolated, and their nearest neighbors lived 108.7 ± 17.4 m away. By comparison, the inter-burrow distance of females not living on these habitat islands was 36.1 ± 11.6 m ($n = 52$). The alarm calling behavior of the nine isolated females was compared with that of 17 others who nested <30 m from conspecifics. All 26 females were either two or three years old, and were lactating at the time their behavior was observed; none had any living daughters or sisters. An "isolate" female was sitting <0.5 m from a burrow or bush and <20 m from the trained hawk's flight path on 28 occasions; five times (18%) such females gave alarm whistles. In contrast, "social" females were observed in the same proximity to safety and to the hawk on 81 occasions, and 40 times (49%) they whistled. Thus social females were significantly more likely to give whistles than solitary females ($\chi^2 = 7.3$; $P < 0.01$).

Discussion

Research on the adaptive significance of sciurid alarm calls to predatory mammals has proliferated, and the evidence now indicates that warning kin is a common function of such vocalizations (e.g. Hoogland 1983; Davis 1984). Not surprisingly, given the close genetic relationships and thus the similar reproductive interests of callers and warned individuals, considerable "honest" information (Krebs and Dawkins 1984; Markl 1985) appears to be encoded in sciurid alarm calls. For example, California ground squirrels give acoustically discriminable calls to different predator species (Leger et al. 1980; Owings and Leger 1980). In field playbacks of these call variants the ground squirrels' escape responses mimic those observed when the various predators are actually present (Leger and Owings 1978; Leger et al. 1979). Field playbacks of recorded alarm vocalizations also stimulate appropriate escape behavior in thirteen-lined (*S. tri-*

decemlineatus: Schwagmeyer and Brown 1981) and Columbian ground squirrels (*S. columbianus*: Harris et al. 1983). Although the calls of Belding's ground squirrels are apparently not as predator-specific as are those of *S. beecheyi* (Leger et al. 1984), *S. beldingi* do discriminate between dangerous and harmless animals, near and distant predators, and rapidly versus slowly moving predators (Robinson 1980).

Several species of ground squirrels predictably give alarm calls to aerial predators that are audibly distinct from their calls to predatory mammals. As in *S. beldingi* the former are usually single-note calls that are given once or twice, while the latter are multiple-note trills given repetitively. Species with dichotomous alarm vocalizations include Uinta (*S. armatus*: Balph and Balph 1966), Arctic (*S. parryi*: Melchior 1971), California (Fitch 1948; Owings and Virginia 1978), and Richardson's ground squirrels (*S. richardsonii*: Davis 1984; also Koeppl et al. 1978); on the other hand, thirteen-lined (Matocha 1977; Schwagmeyer 1980) and round-tailed ground squirrels (*S. tereticaudus*: Drabek 1970, p. 44; Dunford 1977) trill at predatory mammals but are typically silent when hawks approach. Usually it is argued that as Robinson (1981, p. 163) put it, "... trills and chirps [in *S. beldingi*], and corresponding calls among other ground squirrels, functionally label slow-developing, 'low-risk' and fast-developing, 'high-risk' situations, respectively" (see also Owings and Hennessy 1984). In support of this hypothesis, Arctic (Melchior 1971), California (Leger et al. 1980), and Belding's ground squirrels sometimes trill at perched or distantly soaring hawks and whistle when closely pursued by predatory mammals.

Until recently, the adaptive significance of sciurid aerial predator (or "high risk") alarm calls had not been investigated. In the first of such efforts Davis (1984) compared the vocal responses of Richardson's ground squirrels to predatory mammals with their behavior toward real and artificial aerial predators (hand-thrown frisbees). He reported that both sexes called equally often to all types of "predators," and that adult females with young called significantly more often to frisbees than adult females without young. Because in his study population both male and female *S. richardsonii* lived near kin, Davis concluded that warning close relatives was the most likely function of both the whistled and trilled alarm vocalizations. Interestingly, Davis's data (Table 4 in Davis 1984) also reveal that during the artificial hawk experiments, females with young (the callers) were on average twice as far from their burrows (0.9 m vs 0.4 m) when the frisbee passed directly over them than were females without young (the noncallers). This suggests that alarm whistling by female *S. richardsonii* may be affected by distance from refugia in the same way as in *S. beldingi* (Table 2; also Robinson 1980) and *S. beecheyi* (Leger et al. 1980), and raises the possibility that warning kin is not the sole function of the *S. richardsonii* alarm whistle.

I began the present study to see if Belding's ground squirrels' alarm whistles to flying hawks warn relatives. To my surprise, the data indicated that unlike trilling, whistling tendencies were not affected by age, sex, or kinship (Figs. 4 and 5). Furthermore, predatory mammals were attracted to individuals who trilled, and they attacked (Sherman 1977) and killed (Table 1) more callers than noncallers. In contrast, free-living hawks were rarely successful at capturing callers, or indeed any ground squirrels after an alarm whistle had been given (Table 1). Taken together, these results suggested the intriguing possibility that the whistled and trilled alarm calls involve different costs and benefits, and serve different purposes.

Two sorts of observations support the hypothesis that alarm whistling directly benefits the caller. First, the most frequent whistlers were individuals who were apparently in the greatest danger: those farthest from shelter and those closest to the hawk (Table 2). Second, ground squirrels typically called coincident with running toward shelter rather than after reaching it (Fig. 2). In both cases, callers were animals that had the most to lose if whistling were dangerous and the most to gain if it increased their chances of escape. Parallel observations and reasoning led Noyes and Holmes (1979) to conclude that alarm calls of hoary marmots (*M. caligata*) to aerial predators also involve minimal risk.

During their field study of alarm communication in California ground squirrels, Leger et al. (1980, p. 242) saw "... several raptor attacks aborted when alarm calls rang out and squirrels ran in all directions." They hypothesized that the hawks may have been momentarily startled or confused by the rapid appearance of numerous scurrying, vocalizing animals. Presumably calling *S. beecheyi* benefitted through both "pandemonium" (Neill and Cullen 1974; Owens and Goss-Custard 1976) and "selfish herd" effects (Hamilton 1971). It is possible that this mechanism also could account for the failure of hawks to capture alerted Belding's ground squirrels. At Tioga Pass, the appearance of hawks and/or the sound of whistles stimulated an instantaneous, almost explosive appearance of many calling, dodging animals. To human observers, the scene suddenly became chaotic; then, just as suddenly, the animals disappeared. Although not conclusive, the behavior of female *S. beldingi* who nested in relative isolation supports the mechanism suggested by Leger et al. (1980). Such females could not benefit from confusion or selfish herd effects to the same extent as more group-living conspecifics, and they gave alarm whistles significantly less often. Carrying this argument a step farther, it is interesting that thirteen-lined ground squirrels, which do not call when hawks approach (Schwagmeyer 1980), habitually live at considerably lower densities (Vestal and McCarley 1984) and in deeper cover (Evans 1951) than the five spermophiles with dichotomous alarm calls.

Twenty-six years ago, before kin selection had been implicated in the evolution of alarm calls (e.g. Hamilton 1964; Maynard Smith 1965; Williams 1966, p. 207), Peter Marler suggested (1959, p. 177) that the "calls given by various song birds, including the chaffinch, when a hawk flies over, have precisely the structure we have predicted, namely a high-pitched pure tone, beginning and ending gradually, sounding rather like the squeak of a finger on glass. We must conclude that these small birds have evolved a call for this particular situation that is capable of warning others of their peril while at the same time exposing themselves to a minimum of danger. Even though small birds must also have difficulty in locating this call, this is no disadvantage, for their immediate response is to fly to the nearest cover, irrespective of the direction of the call or of the hawk".

The behavior of alerted Belding's ground squirrels (Fig. 3) paralleled that of the songbirds described by Marler. Furthermore, individual *S. beldingi* whistled in moments of extreme danger, thereby apparently increasing their own chances of escape. By informing conspecifics that danger was imminent, callers enabled listeners to rush for shelter, thereby creating predator-confusing pandemonium and a group in which to hide. This scenario forms the essence of the "manipulation" hypothesis proposed by Charnov and Krebs (1975) to explain the adaptive significance of alarm calls. However in the ground squirrels there was no evidence that the "manipulation" involved misinformation; indeed, the escape responses of callers (Fig. 3) were indistinguishable from those of alerted noncallers who could not see the hawk.

Why were there no sexual asymmetries in alarm whistling, given the ground squirrels' matrilocal population structure? I hypothesize that if the first individual who sees an attacking raptor flees without calling, it not only forgoes the potential benefits of both predator confusion and selfish herd effects, but also risks being singled out because of its movement. On the other hand, any individual who hears a whistle but fails to immediately seek shelter risks being targeted as the only stationary prey or the only animal left once the others have departed. These hypothetical penalties for "cheating" may explain why most hawk appearances elicited whistles and why whistles typically caused rapid escape behavior. Furthermore, they suggest the reason why male ground squirrels called as frequently as did females (Fig. 4). That is, the nomadic, nonparental males gained the same sorts of immediate benefits from calling as did the sedentary, highly parental females; conversely, males did not benefit themselves or their kin by trilling at terrestrial predators, and so they remained silent unless closely pursued.

The foregoing considerations do not rule out two other ways in which *S. beldingi* might benefit themselves by giving an alarm whistle. First, whistles might indicate to attacking raptors that they have been seen, thus discouraging their pursuit (e.g. Smythe 1970; Woodland et al. 1980; Tilson and Norton 1981). Second, whistles might startle predators (e.g. Humphries and Driver 1970), or misdirect their attacks due to the calls' ventriloquial characteristics (e.g. Perrins 1968; Brown 1982). Controlled studies of attacks by raptors on *S. beldingi* and the details of their behavior toward callers and noncallers are necessary to test these alternatives.

Regardless of the outcome of such tests, it is clear that both the form and function of Belding's ground squirrels' alarm calls to terrestrial and aerial predators differ: while trills are expressions of nepotism, whistles involve self-preservation. Thus alarm calls, like other aspects of the animals' social behavior, contain elements of both phenotypic altruism and selfishness. It will be interesting to see if similar functional dichotomies characterize the different alarm calls of other vertebrates.

Acknowledgments. I thank Gary A. Beeman, Jeffrey T. King, and their Harris's hawks "Chapparal" and "Mojo" for participating in these experiments and for their consistent encouragement and good humor. For other assistance in the field, I thank Carlyn A. Clement, Linda Doyle, Barbara Evans, Paul Mead, Martin L. Morton, Barry S. Mulder, Mark A. Newton, Karen Noack, Susan F. Payne, Cynthia Kagarise Sherman, and James Sherman. For comments on the manuscript I thank Richard D. Alexander, Stephen T. Emlen, Daniel W. Leger, John L. Hoogland, Cynthia Kagarise Sherman, and an anonymous reviewer. My studies were supported by the National Geographic Society, the Miller Institute at the University of California (Berkeley), Cornell University, and the National Science Foundation.

References

Balph DM, Balph DF (1966) Sound communication of Uinta ground squirrels. J Mammal 47:440–450

Barash DP (1975) Marmot alarm-calling and the question of altruistic behavior. Am Midl Nat 94:468–470

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

Batschelet E (1981) Circular statistics in biology. Academic Press, New York

Brown CH (1982) Ventroloquial and locatable vocalizations in birds. Z Tierpsychol 59:338–350

Charnov EL, Krebs JR (1975) The evolution of alarm calls: altruism or manipulation? Am Nat 109:107–112

Cheney DL, Seyfarth RM (1981) Selective forces affecting the predator alarm calls of vervet monkeys. Behaviour 76:25–61

Davis LS (1984) Alarm calling in Richardson's ground squirrels (*Spermophilus richardsonii*). Z Tierpsychol 66:152–164

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192

Drabek CM (1970) Ethoecology of the round-tailed ground squirrel, *Spermophilus tereticaudus*. PhD thesis, University of Arizona, Tucson

Dunford C (1977) Kin selection for ground squirrel alarm calls. Am Nat 111:782–785

Evans FC (1951) Notes on a population of the striped ground squirrel (*Citellus tridecemlineatus*) in an abandoned field in southeastern Michigan. J Mammal 32:437–449

Fitch HS (1948) Ecology of the California ground squirrel on grazing lands. Am Midl Nat 39:513–596

French AR (1982) Intraspecific differences in the pattern of hibernation in the ground squirrel *Spermophilus beldingi*. J Comp Physiol 148:83–91

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hamilton WD (1964) The genetical evolution of social behaviour, I and II. J Theor Biol 7:1–52

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Hanken J, Sherman PW (1981) Multiple paternity in Belding's ground squirrel litters. Science 212:351–353

Harris MA, Murie JO, Duncan JA (1983) Responses of Columbian ground squirrels to playback of recorded calls. Z Tierpsychol 63:318–330

Holekamp KE (1983) Proximal mechanisms of natal dispersal in Belding's ground squirrel (*Spermophilus beldingi beldingi*). PhD thesis, University of California, Berkeley

Holekamp KE (1984a) Natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Behav Ecol Sociobiol 16:21–30

Holekamp KE (1984b) Dispersal in ground-dwelling sciurids. In: Murie JO, Michener GR (eds) The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, Neb, pp 297–320

Holmes WG, Sherman PW (1982) The ontogeny of kin recognition in two species of ground squirrels. Am Zool 22:491–517

Hoogland JL (1983) Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). Anim Behav 31:472–479

Humphries DA, Driver PM (1970) Protean defense by prey animals. Oecologia (Berl) 5:285–302

Ivins BL, Smith AT (1983) Responses of pikas (*Ochotona princeps*, Lagomorpha) to naturally occurring terrestrial predators. Behav Ecol Sociobiol 13:277–285

Jenkins SH, Eshelman BD (1983) *Spermophilus beldingi*. Am Soc Mammal, Mammalian Sp 221:1–8

Koeppl JW, Hoffmann RS, Nadler CF (1978) Pattern analysis of acoustical behavior in four species of ground squirrels. J Mammal 59:677–696

Krebs JR, Dawkins R (1984) Animal signals: mind reading and manipulation. In: Krebs JR, Davies NB (eds) Behavioural ecology, 2nd edn. Sinauer, Sunderland, Mass, pp 380–402

Leger DW, Owings DH (1978) Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. Behav Ecol Sociobiol 3:177–186

Leger DW, Owings DH, Boal LM (1979) Contextual information and differential responses to alarm whistles in California ground squirrels. Z Tierpsychol 49:142–155

Leger DW, Owings DH, Gelfand DL (1980) Single-note vocalizations of California ground squirrels: graded signals and situation-specificity of predator and socially evoked calls. Z Tierpsychol 52:227–246

Leger DW, Berney-Key SD, Sherman PW (1984) Vocalizations of Belding's ground squirrels (*Spermophilus beldingi*). Anim Behav 32:753–764

Mader WJ (1975) Biology of the Harris' hawk in southern Arizona. Living Bird 14:59–85

Markl H (1985) Manipulation, modulation, information, cognition: some of the riddles of communication. Fortschr Zool 31:163–194

Marler P (1955) Characteristics of some animal calls. Nature 176:6–8

Marler P (1956) Behaviour of the chaffinch (*Fringilla coelebs*). Behaviour (Suppl) 5:1–184

Marler P (1959) Developments in the study of animal communication. In: Bell PR (ed) Darwin's biological work. Cambridge University Press, Cambridge, pp 150–206

Matocha KG (1977) The vocal repertoire of *Spermophilus tridecemlineatus*. Am Midl Nat 98:482–487

Maynard Smith J (1965) The evolution of alarm calls. Am Nat 99:59–63

Melchior HR (1971) Characteristics of Arctic ground squirrel alarm calls. Oecologia (Berl) 7:184–190

Michener GR (1983) Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Eisenberg JF, Kleiman D (eds) Advances in the study of mammalian behavior. Am Soc Mammal Sp Publ 7, pp 528–572

Morton ML (1975) Seasonal cycles of body weights and lipids in Belding ground squirrels. Bull South Calif Acad Sci 74:128–143

Morton ML, Sherman PW (1978) Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. Can J Zool 56:2578–2590

Müller-Schwarze D, Müller-Schwarze C (1971) Responses of chipmunks to models of aerial predators. J Mammal 52:456–458

Neill SR St J, Cullen JM (1974) Experiments on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. J Zool (Lond) 172:549–569

Noyes DH, Holmes WG (1979) Behavioral responses of free-living hoary marmots to a model golden eagle. J Mammal 60:408–411

Owens NW, Goss-Custard JD (1976) The adaptive significance of alarm calls given by shorebirds on their winter feeding grounds. Evolution 30:397–398

Owings DH, Hennessy DF (1984) The importance of variation in sciurid visual and vocal communication. In: Murie JO, Michener GR (eds) The biology of ground dwelling squirrels. University of Nebraska Press, Lincoln, Neb, pp 169–200

Owings DH, Leger DW (1980) Chatter vocalizations of California ground squirrels: Predator- and social-role specificity. Z Tierpsychol 54:163–184

Owings DH, Virginia RA (1978) Alarm calls of California ground squirrels (*Spermophilus beecheyi*). Z Tierpsychol 46:58–70

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

Pfeifer S (1980) Aerial predation on Wyoming ground squirrels. J Mammal 61:371–372

Robinson SR (1980) Antipredator behaviour and predator recognition in Belding's ground squirrels. Anim Behav 28:840–852

Robinson SR (1981) Alarm communication in Belding's ground squirrels. Z Tierpsychol 56:150–168

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

Schwagmeyer PL, Brown CH (1981) Conspecific reaction to playback of thirteen-lined ground squirrel vocalizations. Z Tierpsychol 56:25–32

Sherman PW (1976) Natural selection among some group-living organisms. PhD thesis, University of Michigan, Ann Arbor

Sherman PW (1977) Nepotism and the evolution of alarm calls. Science 197:1246–1253

Sherman PW (1980a) The limits of ground squirrel nepotism. In: Barlow GW, Silverberg J (eds) Sociobiology: beyond nature/nurture? Westview, Boulder, Col, pp 505–544

Sherman PW (1980b) The meaning of nepotism. Am Nat 116:604–606

Sherman PW (1981a) Kinship, demography, and Belding's ground squirrel nepotism. Behav Ecol Sociobiol 8:251–259

Sherman PW (1981b) Reproductive competition and infanticide in Belding's ground squirrels and other animals. In: Alexander RD, Tinkle DW (eds) Natural selection and social behavior: Recent research and new theory. Chiron, New York, pp 311–331

Sherman PW, Morton ML (1984) Demography of Belding's ground squirrels. Ecology 65:1617–1628

Shields WM (1980) Ground squirrel alarm calls: nepotism or parental care? Am Nat 116:599–603

Smith SF (1978) Alarm calls, their origin and use in *Eutamias sonomae*. J Mammal 59:888–893

Smythe N (1970) On the existence of "pursuit invitation" signals in mammals. Am Nat 104:491–494

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, San Francisco

Tilson RL, Norton PM (1981) Alarm duetting and pursuit deterrence in an African antelope. Am Nat 118:455–462

Turner LW (1973) Vocal and escape responses of *Spermophilus beldingi* to predators. J Mammal 54:990–993

Vestal BM, McCarley H (1984) Spatial and social relations of kin in thirteen-lined and other ground squirrels. In: Murie JO, Michener GR (eds) The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, Neb, pp 404–423

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Woodland DJ, Jaafar Z, Knight M (1980) The "pursuit deterrent" function of alarm signals. Am Nat 115:748–753