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Nepotism and the Evolution of Alarm Calls

Alarm calls of Belding's ground squirrels warn relatives, and thus are expressions of nepotism.

Paul W. Sherman

Alarm calls, vocalizations that alert other animals to impending danger, give the appearance of altruism. Identifying the function of the alarm calls of any species has proved difficult, both because predation is rarely seen in the field (*1*) and because individual identity of and kinship among members of prey species are usually unknown. Moreover, members of many species give several different, predator-specific alarm calls.

During a 3-year field study, I investigated the function of the alarm call that Belding's ground squirrels (*Spermophilus beldingi*, Rodentia: Sciuridae) give when a terrestrial predator approaches. Because the ground squirrel population that I studied contains individually marked animals of known age, among which familial relationships through common female ancestors are also known, discriminating among several hypothesized advantages of giving alarm calls is for the first time possible. A disadvantage of calling is also demonstrated. My investigation indicates that assisting relatives, nepotism, is the most likely function of the ground squirrels' alarm call; this result implicates kin selection (*2*) in the evolution of a behavior that, because it may involve risks to the alarm caller's phenotype, appears to be altruistic.

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Functions of Alarm Calls

Individuals may benefit from giving alarm calls in any of several contexts, because alarm calls may result in one or more of the following six effects.

1) *Diversion of predators' attention to other prey.* This hypothesis would be implicated if, in the absence of cover, alarm calls or screams from captured individuals stimulate aggregation (*3*), group mobbing (*4, 5*), or pandemonium (*5–7*); or, if the prey are already hidden, alarm calls cause them to behave in a manner that would enhance their crypticity (*6, 7*). Observations suggesting that "ventriloquial" alarm calls occur that increase the jeopardy of others (*8*) or that callers mislead or manipulate conspecifics so as to increase their own safety (*6*) would also support this hypothesis for the species and call at issue.

2) *Discouragement of predator pursuit.* By calling, potential prey may reduce the likelihood and costs of attacks on themselves, if calls cause predators to terminate pursuits. For example, fleet and elusive prey might discourage predators by indicating to the predators that they have been seen and that the advantage of surprise has thus been removed (*9*). Sudden or erratic changes in prey behavior as well as alarm calls may startle or momentarily confuse predators, and may indicate to them that an attack is unlikely to succeed (*10*). In addition, poisonous prey might signal their distastefulness by giving an alarm call (*4*). Under this hypothesis, callers gain by indicating to a predator that it has been detected or that the probability of a successful or profitable attack is low. This second hypothesis would thus be implicated if predators consistently turn away from or suddenly release callers, regardless of the presence, proximity, or behavior of other suitable prey.

3) *Alerting relatives.* Callers may gain by having placed themselves in some jeopardy if kin are thereby consistently warned (*2, 11, 12*). Captured individuals might also give distress (alarm) calls in this context, thereby soliciting assistance from relatives (*4*) or else warning them to flee or to hide. Under this, the third hypothesis, year-round alarm calls must be associated with the continuous presence of relatives [compare Williams (*12*, p. 206)]. If alarm calls are given during only part of the year, they must coincide with proximity of kin. For a given species, this hypothesis would be strongly supported if individuals with relatives living within earshot call more frequently than do conspecifics without them.

4) *Helping the group.* Alarm calling might spread by a process of between-group selection, either if (i) prey populations are composed of small, genetical-

ly isolated demes (*13*) or if (ii) between periods of dispersal and panmixia, prey populations are sedentary and composed of isolated aggregations of individuals that are similar to each other in their propensity to call (*14*, *15*). Then either (i) the persistence of groups must be proportional to the percentage of callers within them and groups containing more callers must recolonize areas left vacant by the extinction of groups containing fewer callers (*13*) or else (ii) temporary aggregations of sedentary individuals must produce dispersing young in proportion to the percentage of callers within each aggregation (*14*). In both cases (i) and (ii), unlike the case where the nepotism hypothesis (that is, the third hypothesis) is applicable, fully or partially isolated groups of conspecifics must be identifiable (*13–16*), and these groups must differ in the proportion of alarm callers versus noncallers. If identifiable groups exist and if between-group differences in percentage of callers are demonstrable, the familial relationships among group members must then be considered (*16*, *17*) because between-group differences in the percentage of callers could be brought about by the association of either family members or of nondescendants. If the former, the differential reproduction of such groups is most appropriately analyzed in terms of kin selection [(*16*, *17*); but see (*18*)]. If the latter, hypothesis 4 can be distinguished from hypothesis 3.

5) *Reduction of the likelihood of later attacks by the same predator.* If predators become better at hunting similar prey with experience or if they return to hunt near sites of previous successful kills [for examples, see (*19*)], alarm callers may benefit by warning conspecifics if by so doing they deny predators sustenance and a search image (*20*). Hypothesis 5 implies that the phenotypic risk of calling is at least lower than the danger of being surprised during a later hunt by the same predator. The hypothesis requires that predators are more often successful in populations without alarm callers than in populations containing them. Hypothesis 5 does not require a particular population structure or familial relationship among callers and those warned. If predators return to sites of previous successful kills, hypothesis 5 predicts that the most sedentary individuals should call most frequently, because they will be in jeopardy from returning predators more often than less sedentary conspecifics.

6) *Warning of others likely to reciprocate.* If individual callers and listeners associate long and consistently enough for them to exchange risks associated with alerting each other and benefits accompanying being alerted, alarm calling may spread on the basis of reciprocity (*20*). As proposed by Trivers, this hypothesis assumes that callers and warned individuals are either distantly related or unrelated (*20*); however, reciprocity may also occur among related conspecifics [(*21*); see also (*15*)], complicating efforts to contrast hypotheses 6 and 3. Hypothesis 6 would be supported if the likelihood of calling increases directly with the probability of warning reciprocators or if this likelihood decreases with the probability of warning nonreciprocators [for a possible example of reciprocity among primates, see (*22*)].

Under hypotheses 1 and 2, alarm calling is favored because of benefits to the caller's phenotype. Under hypotheses 3 to 6, alarm calls are phenotypically but not genotypically altruistic (*21*, p. 336).

Study Area and Study Animal

During the summers of 1974 through 1976, ten different field assistants (three in 1974, five in 1975, and five in 1976) and I studied the responses of Belding's ground squirrels (Fig. 1) to terrestrial predators at Tioga Pass Meadow, in the Sierra Nevada mountains of California (*23*). Ground squirrels in the study population have been permanently marked yearly since 1969: between 1969 and 1973, M. L. Morton and his students individually toe-clipped 731 of them; from 1974 to 1976 my assistants and I double-ear-tagged another 1135, including the 451 young from 101 complete litters. Therefore, exact ages (up to 8 years) of and familial relationships through common female ancestors among groups of ground squirrels are known. Most animals were marked with human hair dye for visual identification at a distance, and their burrows were marked with stakes and painted rocks.

During 3082 hours of observation, members of five species of terrestrial predators and marked ground squirrels of known age were seen simultaneously 102 times: long-tailed weasels (*Mustela frenata*) 67 times, badgers (*Taxidea taxus*) 11 times, dogs (*Canis familiaris*) unaccompanied by humans 11 times, coyotes (*Canis latrans*) 10 times, and pine martens (*Martes americana*) 3 times. On these occasions nine ground squirrels (six adults and three juveniles) were killed (that is, one was killed every 342 observation hours): two by pine martens, three by coyotes, and four by long-tailed weasels. I use these observations to discriminate among hypotheses 1 to 6 for this species' alarm call.

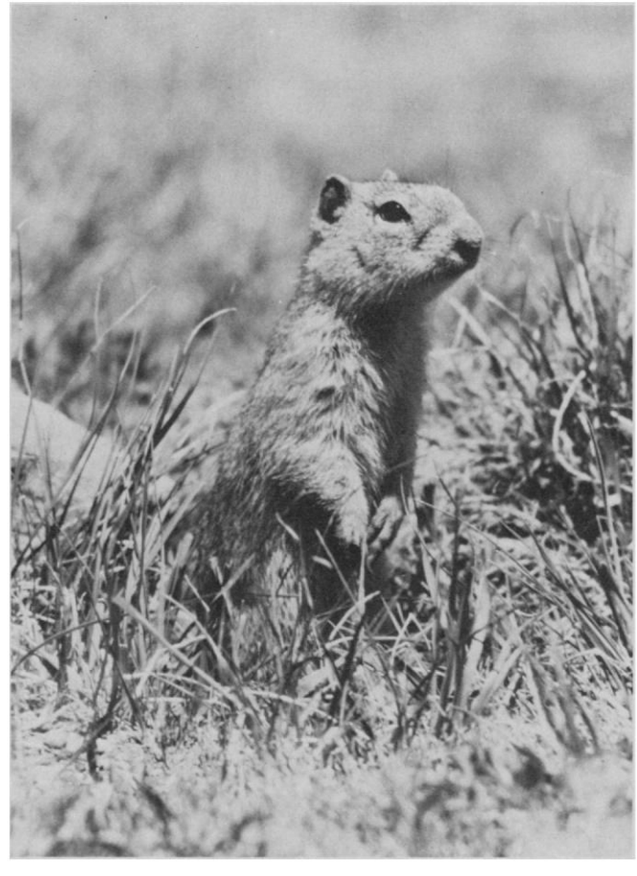

Fig. 1. Belding's ground squirrel at Tioga Pass, Mono County, California.

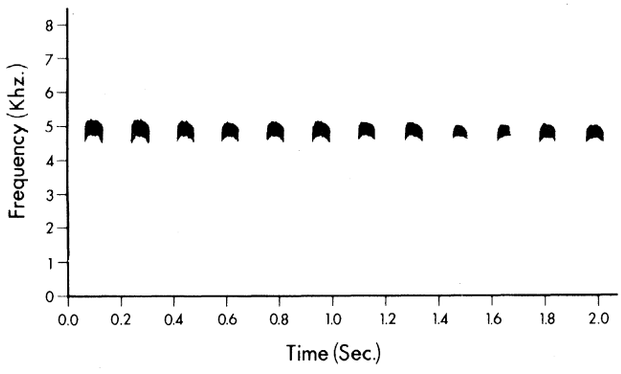

Fig. 2. Sound spectrogram of the alarm call that Belding's ground squirrels give when predatory mammals appear. No frequency harmonics between 6 and 16 khz were found. Frequency is given in kilohertz and time in seconds.

Belding's ground squirrels are diurnal rodents that inhabit alpine and subalpine meadows in the Far West (*24, 25*). At the study area, elevation 3040 meters, they are active from May through September, and they hibernate the rest of the year (*23*). Although conspecific ground squirrels interact daily, they do not group their burrows into circumscribed aggregations nor do they produce young synchronously as do colonial species such as black-tailed prairie dogs (*Cynomys ludovicianus*) (*26–28*).

Like many other terrestrial sciurids (*29, 30*), Belding's ground squirrels give a segmented alarm call in the 4- to 6-kilohertz range when a predatory mammal approaches them (Fig. 2); by contrast they give a single-note, high-pitched whistle to aerial predators [(*31*); see also (*32*)]. Their alarm call to terrestrial predators is easily localized by humans, perhaps because of certain acoustical properties of the sound (*33*) (Fig. 2) and because individuals usually call repeatedly [$\bar{X}$ ± standard error (S.E.) = 27.8 ± 3.8 calls per individual per predator appearance, with N = 13; $\bar{X}$ = 6.1 ± 1.3 minutes of calling per individual per predator appearance, N = 16], even after a predator has apparently disappeared ($\bar{X}$ = 3.7 ± 0.9 minutes of calling per individual, after the predator disappeared from an observer's view; N = 19). Vigorous vibrations of chest cavities of calling ground squirrels and their open mouths enhanced our ability to determine callers' identities, even when several animals were close together. Eighty-two times ground squirrels gave calls that sounded like alarm calls (that is, Fig. 2) when no predator was seen. Because these calls might not have been predator-related, I report here only behavior taking place on the 102 occasions when predators and ground squirrels were simultaneously seen, regardless of whether or not alarm calls were heard. For Tables 2 and 3 and Fig. 3, I combined data from appearances of all five species of predatory mammals after determining that neither the proportions of sex and age categories of ground squirrels present when a predator appeared (Fig. 3) nor the percentage of animals that called differed among predator species (all $P \geq .1$, two-tailed G statistics).

Table 1. Within-family sexual asymmetries in emigration distances among Belding's ground squirrels at Tioga Pass Meadow, California. For females, the home burrow is either the one from which their offspring emerged or, if their young died or disappeared before emergence, the burrow to which they carried nesting material and in which they spent the nights at about the time the young were emerging. For males, the home burrow is the one to which they carried nesting material and in which they spent the nights at about the time the young were emerging. All distances were measured in the field.

Home burrow distance category	Sample size	Distance (m)	
		Mean ± S.E.	Range
2- to 8-year females, interyear	24	17.4 ± 3.2	0.0– 60.0
2- to 5-year males, interyear	10	175.0 ± 25.4*	56.0– 288.0
Females' mating site(s)—her burrow that year (13 different females)	19	36.4 ± 18.1	13.6– 148.9
Males' mating site(s)—his burrow that year (5 different males)	10	176.3 ± 37.1*	106.7– 380.0
1-year females' burrow—their natal burrow	27	38.4 ± 6.3	5.5– 140.8
1-year males' burrow—their natal burrow	13	223.7 ± 39.9*	58.3– 510.0
2-year females' burrow—their natal burrow	9	47.1 ± 13.7	7.6– 132.4
2-year males' burrow—their natal burrow	7	449.7 ± 161.3*	113.0 – 1385.0
1-year sisters' burrows	17	38.5 ± 7.2	2.9– 115.0
1-year brothers' burrows	6	273.2 ± 49.0*	108.9– 437.8
2-year sisters' burrows	7	71.8 ± 21.2	14.0– 171.5
2-year brothers' burrows	4	325.0 ± 94.8†	87.9– 393.0
Mother—1-year daughter	21	49.7 ± 5.9	2.7– 158.0
Mother—1-year son	10	239.4 ± 37.8*	61.5– 537.6

*Differences significant, $P < .005$. †Difference significant, $P < .01$, Mann-Whitney U test.

Population Structure and Mating System

At Tioga Pass Meadow, the average genetic relatedness among female ground squirrels inhabiting any small area is high as a result of common ancestry. As in several other terrestrial sciurids (*34, 35*), females successfully rearing young are sedentary between years, and daughters mature and breed near their birthplaces until they die or disappear from the study area. In contrast to their sisters (Table 1), males permanently emigrate from the area where they were born, usually before their first winter hibernation (*36*). Males do not return to their natal area to copulate, and brothers do not aggregate elsewhere. Seven males born in 1974 were sexually active for the first time in 1976 (that is, as 2-year-olds), and the mated 422.0 ± 89.8 m ($\bar{X}$ ± S.E., N = 11 copulations) from their natal burrows; the brothers' matings took place 341.3 ± 107.6 m from each other (N = 6 pairs of copulations by brothers). By contrast, 12 females born in 1974, each a sister of one of the 2-year-old males, mated 43.2 ± 11.7 m from their natal burrows [N = 19 copulations; some females mate more than once (*36*)]; the sisters' matings took place 39.2 ± 9.2 m from each other (N = 7 pairs of copulations by sisters).

Some male Belding's ground squirrels are apparently highly polygynous. In 1975, for example, the three most successful males in one area of Tioga Pass Meadow that was under nearly continuous observation (21 percent of the sexually active males present) accounted for 21 of 37 completed copulations (57 percent); the most successful male mated with eight different females and he accounted for 22 percent of all completed copulations. Similarly, in 1976, of ten males the top two (20 percent) accounted

for 19 of 32 completed copulations (59 percent); the most successful male mated with nine different females and he accounted for 31 percent of all completed copulations (*36*). Unlike males in harem-polygynous sciurid species (*27, 37, 38*), male Belding's ground squirrels do not defend mating areas or territories after mating, identifiable physical resources valuable to females or to young, or sexually receptive females. Nor do males appear to behave parentally toward their mates' offspring.

During their 4- to 6-hour period of sexual receptivity, females mate with a mean of 2.1 ± 0.2 different males (± S.E., N = 34 females, 69 copulations). Females rear their young alone, and they protect their offspring from conspecifics that find neonatal ground squirrels acceptable prey by excluding nondescendants from the area surrounding their nest burrows (*36*). About the time that their mates' young are born, the males that copulated most frequently abandon areas where their mates will rear young and inhabit burrows elsewhere (Table 1); unsuccessful males do not move. The successful males usually remain near their new burrows until after they have attempted to mate there the following spring. During the lactation period, a male that had mated to completion with more than one female returned to and entered the area defended by one of his mates only once every 19.3 ± 3.2 hours (data from 7 males, 17 females); similarly, nonmates entered a female's defended area during the same period only once every 16.9 ± 4.1 hours (data from 11 females, 13 adult males). A returning mate was chased away by the resident female 42 of 53 times (79 percent). Similarly, during the lactation period, males who had either not mated at all or else had not copulated with particular females were chased, if they trespassed, from the defended areas of those nonmates 32 of 38 times (84 percent).

Kinship and Asymmetries in Tendencies to Give Alarm Calls

When a predatory mammal appears, adult and 1-year-old female Belding's ground squirrels give alarm calls more frequently than would be expected if the animals called in direct proportion to the number of times they were present when a predator arrived (that is, expected if calls were "random"); by contrast, males call considerably less often than would be expected under randomness (Fig. 3). Twenty-two times only males were present (that is, no females were there) when a predatory mammal appeared, and four times (18 percent) alarm calls were given by one of them. Conversely, only females were present 47 times when a predator appeared, and alarm calls were given in 40 (85 percent) of these cases. (For this comparison, the number of males present in alarm-call-evoking situations when no females were there and the number of females present when no males were there did not differ significantly; $P > .09$, Mann-Whitney U test.) Because of the matrilineal kin group structure of Belding's ground squirrel populations (Table 1) and because females are the more parental sex in this species, the sexual dimorphism in calling frequency (Fig. 3) suggests that the alarm call under consideration might function to warn kin (that is, hypothesis 3).

In apparent support of the nepotism hypothesis (*2, 11*) are data (Table 2) suggesting that when a predatory mammal appears (i) reproductive females without living mothers, sisters, or descendants call more frequently than do nonreproductive females similarly lacking close female relatives, (ii) reproductive females without living mothers or sisters but with at least one living female descendant (that is, a daughter or a granddaughter) call more frequently than do reproductive females without living mothers, sisters, or descendants, (iii) reproductive females without living female descendants but whose mothers or at least one sister are alive call more frequently than do reproductive females lacking all three classes of close female relatives, and (iv) temporary "invaders," reproductive but nonresident females, known not to have lived on a study plot within Tioga Pass Meadow in the previous year or years and present less than 1 hour, call less frequently than

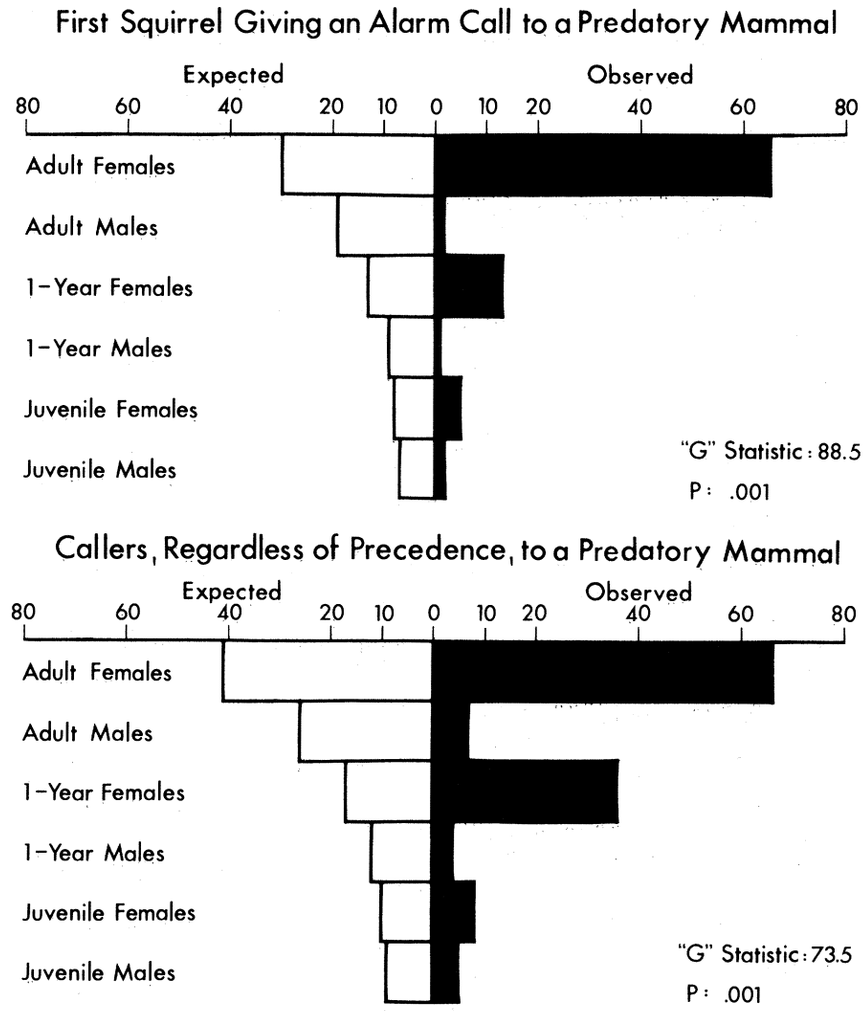

Fig. 3. Expected and observed frequencies of alarm calling by various sex and age classes of Belding's ground squirrels. "Expected" values were computed by assuming that animals call randomly, in direct proportion to the number of times they are present when a predatory mammal appears. The overall significance of both comparisons is largely due to females calling more often than "expected" and males calling infrequently. Data are from 102 interactions between ground squirrels and predators (1974–76).

do reproductive residents (*39*) (for this latter comparison, all reproductive females were considered whether or not their family members were alive).

Although the data are sparse, it appears that females with living female relatives call whether or not those family members are actually present when a predatory mammal appears (Table 2). Destruction of the current year's litter also does not seem to affect calling tendencies (Table 2).

Analysis of variance of 1974–75 data from 87 encounters between ground squirrels and predators (involving 174 different reproductive females of known age) indicates that time of year (*40*) has no effect on calling frequency ($F = 2.03$, d.f. = 2, $P = .17$), but that the age of the female does have a significant effect ($F = 19.8$, d.f. = 1, $P = .005$); the likelihood that alarm calls will be given by females increases with increasing age (*41*). Among males, alarm calling and copulatory success seem to be unrelated. When predatory mammals appeared in 1975, seven males that had copulated at least once called no more frequently (that is, in no greater percentage of the times when a predator appeared) than did eight males that had not copulated in 1975 ($P > .2$, Mann-Whitney U test). Among the seven 1975 males that copulated at least once, there was no correlation between the number of matings with different females and the percentage of alarm-call-evoking situations in which each male called ($P > .3$, Kendall's rank correlation test).

Neither the first ground squirrel that behaved as if it saw a predator (Table 3), the animal closest to the danger, nor the one closest to its own burrow always sounded the first alarm. On 54 occasions, the animal first reacting to a predator was identified and its sex was ascertained. In 6 of the 31 times that an adult male reacted first (19 percent), the first-reacting male also called first, and in 9 of the 23 times that a reproductive female reacted first (39 percent), the first-reacting female also called first. In 68 instances, the ground squirrel closest to a predator when the predator was first seen by a human observer was identified and its sex was ascertained. In 5 of the 36 times that an adult male was the closest (14 percent), the closest male also called first, and in 9 of the 32 times that a reproductive female was the closest (28 percent), the closest female also called first. Among reproductive residents, 21 females giving alarm calls were no closer to their home burrows than were 19 simultaneously present noncallers ($P > .1$, Mann-Whitney U test). Thus, when a predatory mammal appears, old (that is, 4 to 7+ years), reproductive, resident females with living kin are most likely to call, while males are the most consistent noncallers. Again the implication is that warning family members, hypothesis 3, is a likely function of this alarm call.

Discriminating Among the Alternative Hypotheses

Could these data be better explained by any of the five hypotheses alternative to nepotism? Contrary to hypothesis 1, alarm calls did not divert predators' attention to other prey by causing pandemonium among the ground squirrels, and the animals did not aggregate to mob or to flee from predators (Table 3). Four times an adult female chased a long-tailed weasel from the neighborhood of her burrow, and in none of these cases did any conspecifics aid her (*42*). Whether or not they were near their burrows, most ground squirrels either sat up or ran to a rock upon sighting a predatory mammal or upon hearing an alarm call (Table 3). Occasionally juveniles squeaked when hand-held, and these screams from captured individuals sometimes attracted their mothers or other reproductive females. Such squeaks were clearly different from the alarm calls under discussion (that is, Fig. 2), and they ceased 3 to 4 weeks after juveniles appeared above the ground for the first time. First callers and other alarmers did not seek cover in the center of an aggregation of conspecifics. Neither did alarm callers appear to sequester information on the whereabouts of approaching predators, and the calls did not seem ventriloquial to us or, apparently, to predators (below). Alarm callers usually sat upright, often on prominent rocks, and looked di-

Table 2. Kinship and asymmetries in tendencies to give alarm calls among female Belding's ground squirrels. Expected calling frequencies were computed as in Fig. 3; *N* is the number of times ground squirrels in each category were present when a predatory mammal appeared.

Category of females	*N*	Number observed to call	Number expected to call if calls are "random"	Significance	
				*G**	*P*
Reproductive,† with no known living relatives	19	14	9	5.80	< .025
Nonreproductive, with no known living relatives	14	2	7		
Reproductive, with a living daughter or granddaughter, but no other living relatives	27	18	12	5.58	< .025
Reproductive, with no known living relatives	24	5	11		
Reproductive, with their mother or at least one sister alive, but no living descendants	18	13	8	5.37	< .025
Reproductive, with no known living relatives	17	3	8		
Reproductive residents: known to have lived in the same area the previous year or years	168	64	56	4.90	< .05
Reproductive nonresidents: temporary invaders to an area (see text)	49	9	17		
Reproductive, with either their mother, a sister, or a descendant alive and present when a predatory animal appears	21	9	9	–	N.S.‡
Reproductive, with at least one relative alive but not present when a predatory mammal appears	11	6	6		
Reproductive, without their mother or any sisters, but with nursing young known to be alive	46	21	22	0.38	N.S.
Reproductive, without their mother or any sisters, and whose young were destroyed	16	4	3		

*G statistic, corrected for continuity, and level of significance are given. †"Reproductive" means pregnant, lactating, or living with postweaning young of the year. ‡Not significant.

rectly toward the advancing predator, thereby seemingly directing the attention of conspecifics toward it (*43*). Indeed, I could often locate the predator by following the gaze of several alerted animals, whether or not they were calling. I do not know whether ground squirrels also use this cue. However, in 11 instances a ground squirrel probably could not see an advancing predator because of the ground squirrel's position in a swale; on eight of these occasions (73 percent), the ground squirrel sat up and oriented itself in the same direction as a conspicuous, calling conspecific, thus toward the apparently unseen predator. Only one of nine times (11 percent) did a ground squirrel in the same swale orient toward an apparently unseen predator when no conspecific was calling. Thus, no evidence supports the hypothesis that the alarm call results in the diversion of predators' attention to other prey (that is, hypothesis 1).

Members of all five mammalian predator species appeared undeterred by ground squirrel alarm calls, suggesting that the call does not function to discourage predator pursuit (that is, hypothesis 2). Indeed, members of all five species stalked or chased alarm callers, suggesting that calling may in fact make alarmers more conspicuous. Three of six adult ground squirrels preyed upon during this study had called just prior to being attacked. Also, calling ground squirrels were stalked or chased by predators significantly more often than were noncallers. A marked ground squirrel was stalked or chased 22 times; 14 of 107 calling animals (13 percent) were so attacked, but only 8 of 168 noncallers (5 percent) were similarly attacked ($P < .025$, two-tailed G statistic, corrected for continuity). To test hypothesis 2 further, I considered the responses of coyotes to callers separately. Because coyotes sometimes hunted by remaining motionless or hidden near bushes for long periods as if the element of surprise were important to their success, and provided that the alarm call under consideration discourages predator pursuit by indicating that the advantage of surprise has been removed, coyotes in particular might be deterred by "it." A coyote caught a mountain vole (*Microtus montanus*) and behaved as if it were continuing to hunt this species or other prey on ten occasions; in these cases, 39 ground squirrels gave alarm calls and 41 were silent. Five of the 39 callers (13 percent) were apparently stalked or were chased by the predator, while only 3 of the 41 noncallers (7 percent) were similarly pursued (this difference is not significant at the $P < .05$ level, G statistic). Thus, coyotes do not turn away from calling ground squirrels; if anything they, like other predators, are attracted to callers. None of the predators seemed to be startled or confused by alarm calls. On the four occasions when we observed the behavior of a predatory mammal toward the ground squirrel that it had just killed, the predator consumed its victim, suggesting that Belding's ground squirrels are not distasteful (nor poisonous) and that, therefore, alarm calling is not an aposematic display. The abundance of noncallers and the male-bias among them (Fig. 3) do not support the second hypothesis, the lack of correspondence between the nearest ground squirrel to the predator (that is, the one likely to be in greatest proximate danger) and the first alarm caller, or the first one behaving as if it saw the predator (Table 3) and the first alarm caller also do not support the hypothesis that the alarm call functions to discourage predator pursuit (hypothesis 2).

Although this population of ground squirrels was not divided up into identifiable, physically isolated demes (*13*), females successfully raising young were relatively sedentary during 1974–76 (Table 1). Behaviors observed among these stable aggregations might have spread by a process of between-group selection [that is, hypothesis 4; see (*14, 15*)]. Because these aggregations are composed mainly of close relatives—mothers, daughters, sisters, cousins, and nieces—the "groups" are appropriately characterized as matrilineal kinship associations. The likelihood that female family members are consistently alerted by alarm calls and the apparent interdependence of kinship and calling (Table 2) make it impossible in this species to

Table 3. Behavior of Belding's ground squirrels toward predatory mammals or toward alarm calls from conspecifics. Data are from 102 ground squirrel–predator interactions (1974 to 1976).

Class of animal	Observed responses							
	None	Sits up but does not change location	Runs toward					
			Conspecific	Rock	Bush	Mouth of any burrow other than home	Mouth of the home burrow	Defended area
Ground squirrels within the defended area surrounding the burrow								
Adult females (2 to 8 years)	6 (8%)	29 (37%)	3 (4%)	33 (43%)	1 (1%)	2 (3%)	3 (4%)	-
1-year females	2 (5%)	14 (37%)	2 (5%)	15 (40%)	0 (0%)	2 (5%)	3 (8%)	-
Juveniles of both sexes	2 (5%)	13 (33%)	3 (8%)	6 (15%)	1 (3%)	6 (15%)	8 (21%)	-
Total	10 (7%)	56 (36%)	8 (5%)	54 (35%)	2 (1%)	10 (7%)	14 (9%)	-
Ground squirrels not within the defended area surrounding the burrow								
Adult females	2 (3%)	12 (23%)	3 (5%)	15 (29%)	1 (2%)	1 (2%)	3 (5%)	16 (31%)
1-year females	1 (4%)	5 (22%)	0 (0%)	8 (35%)	0 (0%)	1 (4%)	2 (8%)	6 (26%)
Juveniles of both sexes	0 (0%)	2 (11%)	1 (6%)	6 (33%)	0 (0%)	4 (22%)	1 (6%)	4 (22%)
Total	3 (3%)	19 (20%)	4 (4%)	29 (31%)	1 (1%)	6 (6%)	6 (6%)	26 (29%)
Adult males (2 to 5 years)	5 (11%)	16 (35%)	4 (9%)	17 (37%)	1 (2%)	1 (2%)	2 (4%)	*
1-year males	3 (11%)	9 (32%)	2 (7%)	13 (46%)	0 (0%)	0 (0%)	1 (4%)	*
Total	8 (11%)	25 (34%)	6 (8%)	30 (41%)	1 (1%)	1 (1%)	3 (4%)	

*Males do not defend areas surrounding burrows as do females.

support between-group selection over kin selection (that is, hypothesis 3) [*16, 17*); but see (*18*)]. With a dog, I visited six Sierra Nevada populations of Belding's ground squirrels other than the primary population under study; all visited populations were greater than 0.5 km but less than 23 km from Tioga Pass Meadow. At least one alarm call, usually many, was heard at each soon after the dog was released. Thus I have no evidence that noncalling groups or populations of ground squirrels occur in the vicinity of Tioga Pass Meadow. These data are obviously inadequate to determine whether there are between-group or between-population differences in the percentages of alarm callers. Because I found no noncalling populations of Belding's ground squirrels and because aggregations of related females do not predictably break up, emigrate from their natal area, and reassemble with alarm callers not sharing common ancestry, however, the most important prerequisites (*13–15*) for the operation of between-group selection (that is, hypothesis 4) are seemingly absent.

Because female ground squirrels are more sedentary than are males (Table 1), females might be more frequently in jeopardy than males if predators return to hunt near sites of previous successful kills. Females also give alarm calls more frequently than do males (Fig. 3). Taken together, these observations suggest that the alarm call might function to reduce the likelihood of later attacks by the same predator (that is, hypothesis 5). However, mammalian predators at Tioga Pass Meadow do not preferentially return to sites of previous successes. For seven diurnal predations by coyotes and long-tailed weasels, the time between visits by a member of the successful species to a ground squirrel's defended area contiguous to one on which a kill had been made, 20.9 ± 6.2 days, was not different from ($P \geq .10$, Mann-Whitney U tests) the time between visits to seven randomly chosen defended areas, 18.9 ± 8.4 days, on which ground squirrels had never been captured [this comparison was made five times with seven different, randomly chosen defended areas each time; in no case were any significant differences found]. If predators did return to hunt near sites of previous successes, under hypothesis 5 young females should give alarm calls more frequently than older females; because the probability of dying increases with increasing female age in this species (*36*), young females would be in jeopardy from returning predators more often in their lifetimes than would older females [but see (*41*)]. Contrary to the prediction of decreases in calling with increases in female age, tendencies to give alarm calls increase with increasing female age. Discrimination among alarm-call-evoking situations, apparently on the basis of kinship with individuals likely to be alerted (Table 2), is also not predicted by hypothesis 5, but this observed discrimination does support the hypothesis that one function of the alarm call is to warn relatives (that is, hypothesis 3).

Because aggregations of (closely related) female Belding's ground squirrels are more stable through time than are male-male or male-female associations (Table 1), reciprocity (*20*) might be more likely to occur among females than among males. Therefore, the sexual dimorphism in probability of giving an alarm call (Fig. 3) could indicate that the call functions to warn conspecifics likely to reciprocate (that is, hypothesis 6). If so, the "reciprocators" are also family members, and reciprocation might therefore benefit callers genotypically as well as phenotypically (*21*). Because reciprocity, as Trivers (*20*) formulated the hypothesis, refers only to an exchange of phenotypic benefits, circumstances (*20*, p. 35) ". . . when the recipient is so distantly related to the organism performing the altruistic act that kin selection can be ruled out," the alarm call under discussion does not function only in the context described by hypothesis 6. The degree to which alarm callers discriminate against distantly related or unrelated individuals known not to call might indicate the degree to which the alarm call functions to warn phenotypic reciprocators (*20, 22*). Limited evidence suggests that the presence of certain kinds of noncallers at least does not deter females with living relatives from calling. Using data from 28 encounters between predatory mammals and reproductive females whose mothers or at least one sister or daughter were alive, I compared the time between the moment a human observer first saw a predator and the first alarm call and the percentage of callers versus noncallers under two circumstances: when no noncallers were present, and when at least one unrelated male, temporary female "invader," or one nonreproductive female not known to be related to any of the residents in a study plot was present. In neither of these comparisons did callers' responses differ significantly on the basis of the presence of noncallers ($P \geq .2$ for each comparison, Mann-Whitney U tests). In assessing the importance of this apparent lack of a difference, note that discrimination on the basis of whether certain relatives are alive does occur (Table 2). In other words, females call more frequently when relatives might be alerted; they refrain from calling when no kin are alive despite being surrounded by (unrelated) females, members of the sex that calls. Although reciprocation might occur between related ground squirrels with reciprocators benefiting genotypically as well as phenotypically (*15*)—because nonreciprocators are not obviously discriminated against when rather subtle discrimination on the basis of relatedness apparently occurs—it is not possible to support the phenotypic reciprocity hypothesis [that is, hypothesis 6 (*20*)] apart from the nepotism hypothesis (that is, hypothesis 3).

Conclusions

My observations suggest that it is possible to begin discriminating among theoretical alternative functions of alarm calls and other behaviors that, because they may be phenotypically hazardous, appear altruistic. Data and arguments deriving from them imply that, of the six hypothesized alternative benefits of giving alarm calls, warning relatives, hypothesis 3 (*2, 11*) is a likely function of the alarm call that Belding's ground squirrels give when terrestrial predators approach. Regarding the other possible functions of this alarm call, no evidence supports hypotheses 1 (diverting predators' attention), 2 (discouraging predator pursuit), or 5 (reducing the likelihood of later attacks by the same predator). That the alarm call may function to help the group (hypothesis 4) or to warn reciprocators (hypothesis 6) is possible; but when assumptions of the fourth and sixth hypotheses and predictions derived from them and from the hypothesis 3 that the call alerts relatives are contrasted and are compared with field observations of the ground squirrels' behavior, both appear to be at most less important functions than warning kin.

Among the sciurids in which males give little or no parental care and in which matrilineal kin groups are known or are appropriately suspected to be a basic population unit (*34*), there exist similarities in the form (*29–31*) and female sex- and age-specificity of alarm calls to terrestrial predators (*11, 29, 34, 44*). Further, in at least one sciurid in which males have harems and live with and probably protect their mates and their mates' offspring year-round, harem-males call most frequently (*45*). These observations suggest that warning kin might be a common function of sci-

urid alarm calls to predatory mammals and they imply that asymmetries in tendencies to call may be expressions of discriminative nepotism (*21*).

References and Notes

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39. Similarly, E. A. Carl [see (*38*)] noted that for a nonreproductive, transient or "refugee" population of *Spermophilus undulatus*, that included members of both sexes, "The population was singularly silent; only occasionally did I hear a squirrel vocalization, in sharp contrast to the barrage of alarm calls that greeted me whenever I walked across the study area" (*38*, p. 410).
40. The 1974 and 1975 breeding seasons were divided into three segments for each reproductive female considered in the analysis: (i) spring emergence-parturition, (ii) parturition-first appearance of young above ground, and (iii) first appearance of young-fall disappearance of the female (hibernation). The arc sine square root transformation was used to produce normality in the data analyzed. The data consist of the percentage of times that calls were given by females of each age class, 1 to 7+ years, when a predatory mammal appeared.
41. D. P. Barash (*1*) observed an apparently similar effect of age on tendency to give alarm calls among marmots. The effect that he and I observed might result if older, more experienced females either (i) are more familiar with routes of escape near their burrows, thus more able than less experienced females to evade predators once they have rendered themselves conspicuous by giving an alarm call, or (ii) are redirecting nepotism from current or future (expected) young to offspring or grandchildren that have reached reproductive age, or both (i) and (ii). Advantages of assisting descendants whose likelihood of future reproduction is higher than a female's own reproductive potential may favor increasing nepotism with advancing age among female mammals generally [a similar suggestion was made by S. B. Hrdy and D. B. Hrdy, *Science* **193**, 913 (1976)]. Menopause-like termination of reproduction coupled with extensive maternal care in, for example, elephants [R. M. Laws, I. S. C. Parker, R. C. B. Johnstone, *Elephants and Their Habits* (Clarendon, Oxford, 1975)] may suggest that nepotism is sometimes completely redirected toward relatives that have survived to reproductive age [see also (*21*)].
42. L. W. Turner (*25*, *31*) made similar observations on *Spermophilus beldingi*. E. R. Warren [*J. Mammal.* **5**, 265 (1924)] also reported single *S. armatus* chasing long-tailed weasels while conspecific ground squirrels looked on. Once K. Loehr [thesis, University of Nevada, Reno (1974), p. 22] observed ". . . several adult Belding Ground Squirrels . . ." chasing a weasel.
43. H. R. Melchior (*30*) and E. A. Carl (*38*) reported that *Spermophilus undulatus* behave similarly. R. C. Farentinos [*Z. Tierpsychol.* **34**, 441 (1974)] reports parallel observations for *Sciurus aberti*.
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