Chapter 27 The Evolution of Alarm Communication in Rodents: Structure, Function, and the Puzzle of Apparently Altruistic Calling

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On a summer day a number of years ago I looked down from an arête high up on the Creststone Needle, a peak in southwestern Colorado, and watched, with awe, two golden eagles (*Aquila chrysaetos*) cooperatively hunting in a meadow filled with yellow-bellied marmots (*Marmota flaviventris*). One eagle circled slowly above the meadow, which then erupted in a cacophony of loud chirps that radiated up the rock face. Marmots scampered to their burrows and reared up to attention. Meanwhile the second eagle flew low, and using the contours of the glacial moraines as cover, tried to attack the marmots, who were focused on its companion. That day the marmots were lucky and, after several sorties, the eagles flew off. Why were these chirps given? Did they repel the eagles? How could such conspicuous signals evolve? What might they mean? This chapter discusses the adaptive significance of alarm signals in rodents. I focus mostly on airborne vocal signals, but also mention substrate-born seismic alarm signals such as foot drumming.

When alarmed by predators, individuals of many species emit loud vocalizations known as *alarm calls* (Klump and Shalter 1984). Calls may be directed to conspecifics to warn them about the presence of a predator (Sherman 1977; Blumstein and Armitage 1997a), or to create pandemonium (Neill and Cullen 1974; Sherman 1985), during which time the caller may escape. Calls that function in these contexts should occur in social species. Calls may also be directed to the predator and may function to discourage pursuit (Hasson 1991), or perhaps to attract other predators —which would create competition, or predation on one predator by another, thus allowing the prey to escape (Högstedt 1983).

Snake-elicited foot-drumming by banner-tailed kangaroo rats (*Dipodomys spectabilis*) is a pursuit deterrent signal that informs the snake that it has been detected (Randall and Matocq 1997). Similarly, California ground squirrels (*Spermophilus beecheyi;* Owings and Coss 1977), black-tailed prairie dogs (*Cynomys ludovicianus;* Loughry 1988; Owings and Loughry 1985), and the Formosan squirrel (*Callosciurus erythraeus thaiwanensis;* Tamura 1989) directly mob snakes, and their mobbing is associated with both vocal and visual displays. In these cases, animals obtain phenotypic (self-preserving) benefits from producing alarms. Such behavior requires no complex explanation. However, when signals are directed toward conspecifics, the very act of signaling may also alert the predator to the caller's presence. Thus, explaining why animals emit potentially costly alarm calls to help others has been a topic of considerable interest for some time (Maynard Smith 1965; Charnov and Krebs 1975; Sherman 1977; Blumstein et al. 1997).

The structure and function of alarm signals are interrelated. For instance, we expect signals that are directed to a predator to be obvious. Marler (1955) argued that mobbing calls of songbirds illustrate this in that they are broadband, rapidly repeated sounds that are easy to localize. In contrast, alarm calls of songbirds that are elicited by aerial predators are difficult to localize because they have a relatively narrow bandwidth and fade in and out (Marler 1955). Thus, a complementary line of research seeks to understand the adaptive significance of alarm signal structure.

Studies of rodents have been influential in developing a better understanding of both aspects of alarm communication.

Which Rodents Produce Alarm Calls?

First, an apology. Because most rodents are nocturnal, solitary, and semifossorial, they are generally difficult to study. To properly categorize a vocalization as an alarm call one must observe an individual interacting with a predator. For most nocturnal species, this has not been done. Some species are described as producing whines or squeals when held (e.g., Watts 1975; Verts and Kirkland 1988), but this by itself is not evidence of an alarm call. Thus any review of alarm calling in rodents is unavoidably biased towards diurnal, terrestrial, and social species.

Functionally, alarm calls would be most valuable to diurnal, social, or colonial species. Alarm calls are long-distance signals. If calling increases predation risk then such signals should be produced only if calls carry relatively long distances, callers can accurately assess their own vulnerability, and callers benefit from communicating alarm to someone. Calling in the dark, when a caller might not be able to evaluate risk or track predators accurately, or calling underground when sounds attenuate quickly, could expose callers to excessive risk with little benefit and might therefore be disfavored.

Of course, there are exceptions. For example, the plains viscacha (*Lagostomus maximus*) is a highly social, nocturnal species that has been referred to as especially 'loquacious' (Hudson 1872). It has a rich repertoire of vocalizations, including two types of alarm calls (Branch 1993). Moreover, naked mole-rats (*Heterocephalus glaber*), which are totally subterranean, have at least six different calls that are associated with predator avoidance or colony defense (Pepper et al. 1991). Although long-distance seismic communication is common in fossorial mammals (Francescoli 2000), these signals are more commonly used to communicate territorial ownership and dominance or submission rather than to signal alarm (Francescoli 2000; Randall 2001).

In fact, alarm calling seems to be most common in diurnal rodents: it has been reported in twenty rodent families, and has probably evolved multiple independent times (table 27.1). Ultrasonic alarm calls have been recently reported in laboratory rats (*Rattus norvegicus*; Brudzynski 2001), but given the lack of comparative data, it is difficult to know how common these signals are in other species. Moreover, because ultrasonic signals attenuate quickly (Bradbury and Vehrencamp 1998), the active space of these alarm calls must be relatively small. Alarm calling has been best studied in the sciurid rodents (particularly in ground squirrels, prairie dogs, and marmots). Tree squirrels in several genera give alarm calls in addition to territorial calls. Some social gerbils, and muroid rodents—voles, bamboo rats, and whistling rats – also give alarm calls. Brush-tailed porcupines reportedly shake their quills and stomp their feet in alarm, cane rats and kangaroo rats, jerboas, and gerbils foot drum in alarm, and beavers slap their tail in alarm, but none of these mammals has been reported to produce alarm vocalizations. Alarm calling has also been reported in many South American hystricognath rodents (Eisenberg 1974), but the details have been little studied. It would be particularly rewarding to do so because these animals represent a radiation of complex sociality (Ebensperger 1998c; Ebensperger and Cofré 2001) that is phylogenetically independent from the better-studied sciurid rodents. Thus further study can evaluate the generality of adaptive hypotheses developed in convergent social systems.

What Are the Costs of Calling or Responding to Calls?

Understanding the adaptive significance of alarm calling has often focused on investigating its costs. Like other behaviors, if calling has no costs, it is not difficult to envision its evolution. Calling may have three types of fitness costs: energy, opportunity, or predation.

No studies have been conducted on the energetic costs of alarm calling in any species of rodent. Because individual alarm calls often are brief (< 5 sec in duration), energetic costs of producing a single utterance are probably trivial. However, animals often engage in tonic bouts of alarm calling whereby calls are repeated over time (Schleidt 1973; Owings and Hennessy 1984). Tonic calls have been reported in several ground squirrels (e.g., Balph and Balph 1966; Leger et al. 1984; Loughry and McDonough 1988), prairie dogs (e.g., Smith et al. 1977), marmots (e.g., Waring 1966; Heard 1977; Barash 1989; Blumstein and Armitage 1997a; Blumstein 1999a), and tree squirrels (Emmons 1978). In some cases, tonic communication persists for long periods after a predator has apparently left the area (Owings and Hennessy 1984; Loughry and McDonough 1988). The energetic costs of these bouts of calling are likely to be slightly greater than emitting a single call.

Opportunity costs—the costs of not engaging in other important behaviors—are experienced by both the signaler and the receiver. From the signaler's perspective, alarm calling seems to preclude foraging and engaging in activities other than vigilance. While analyses of time budgets may be used to contrast the opportunity costs of calling (i.e., the cost of not engaging in an alternative behavior), the link between opportunity costs and fitness is unstudied. From the receiver's perspective, responding to calls modifies current

Table 27.1 Genera in which acoustic alarm communication has been reported

Family	Genus	Common name	Reference	Alarm calls	Other alarm signals[a]
Sciuridae	*Aethosciurus*	Tree squirrels	Emmons 1978[1]		
	Ammospermophilus	Ground squirrels	Bolles 1988	yes	
	Callosciurus	Tree squirrels	Tamura and Yong 1993	yes	
	Citellus	Ground squirrels	Nikolskii 1979	yes	
	Cynomys	Prairie dogs	Blumstein and Armitage 1997b; Hoogland 1995	yes	yes
	Epixerus	Tree squirrels	Emmons 1978	yes	
	Eutamias	Chipmunks	Smith 1978	yes	
	Euxerus	Ground squirrels	Haltenorth and Diller 1980	yes	
	Funambulus	Palm squirrel	Roberts 1977	yes	
	Funisciurus	Tree squirrels	Emmons 1978	yes	
	Heliosciurus	Tree squirrels	Emmons 1978	yes	
	Marmota	Marmots	Blumstein and Armitage 1997b; Roberts 1977	yes	yes
	Microsciurus	Tree squirrels	Emmons 1997	yes	
	Myosciurus	Tree squirrels	Emmons 1978	yes	
	Paraxerus	Bush squirrels	de Graaff 1981	yes	
	Petinomys	Flying squirrels	Medway 1978	yes	
	Protoxerus	Tree squirrels	Emmons 1978	yes	
	Ratufa	Giant squirrels	Nowak 1991	yes	
	Rhinosciurus	Tree squirrels	Medway 1978	yes	
	Sciurus	Tree squirrels	Lishak 1984; Farentinos 1974	yes	yes
	Spermophilus	Ground squirrels	Blumstein and Armitage 1997b	yes	
	Tamias	Chipmunks	Weary and Kramer 1995	yes	
	Tamiasciurus	Tree squirrels	Greene and Meagher 1998	yes	
	Xerus	Ground squirrels	Haltenorth and Diller 1980	yes	
Castoridae	*Castor*	Beavers	Hodgdon and Larson 1973		yes
Dipodidae	*Jaculus*	Jerboas	Randall 1994		yes
Muridae	*Clethrionomys*	Red-backed voles	Nowak 1991	yes	
	Dicrostonyx	Lemming	Brooks and Banks 1973	yes	
	Gerbillurus	Hairy-footed gerbils	Dempster et al. 1998		yes
	Lemmus	Lemming	Krebs 1984	yes	
	Meriones	Gerbils	Roberts 1977	yes	yes
	Microtus	Voles	Youngman 1975; Wolff 1980b; Nikolskii and Sukhanova 1992	yes	
	Neotoma	Woodrats	Randall 1994		yes
	Onychomys	Grasshopper mice	McCarty 1978	yes	
	Parotomys	Whistling rats	de Graaff 1981	yes	
	Peromyscus	Deer mice	Lackey et al. 1985; Johnson and Armstrong 1987	yes	yes
	Praomys	Multi-mammate mice	de Graaff 1981	yes	
	Rhizomys	Bamboo rats	Medway 1978	yes	
	Rhombomys	Gerbils	Randall et al. 2000; Randall and Rogovin 2002	yes	yes
	Spalax	Lesser mole rats	van der Brink 1968	yes	
Myoxidae	*Dryomys*	Dormice	Roberts 1977	yes	
Geomyidae	*Dipodomys*	Kangaroo rats	Randall 1994		yes
	Microdipodops	Kangaroo mice	O'Farrell and Blaustein 1974	yes	
Pedetidae	*Pedetes*	Spring hare	Haltenorth and Diller 1980	yes	
Ctenodactylidae	*Ctenodactylus*	Gundis	Haltenorth and Diller 1980	yes	
	Felovia		Nowak 1991	yes	yes
	Massouteria		Nowak 1991	yes	yes
	Pectinator	Pectinators	Nowak 1991	yes	
Hystricidae	*Atherurus* = *Hystrix*	Brush-tailed porcupines	Haltenorth and Diller 1980; Roberts 1977	yes	yes
Petromuridae	*Petromus*	Dassie rats	Nowak 1991	yes	
Thryonomyidae	*Thryonomys*	Cane rats	Haltenorth and Diller 1980; de Graaff 1981	yes	yes

(continued)

Table 27.1 (continued)

Family	Genus	Common name	Reference	Alarm calls	Other alarm signals[a]
Bathyergidae	*Heterocephalus*	Naked mole rats	Pepper et al. 1991	yes	
Agoutidae	*Agouti*	Pacas	Eisenberg 1974	yes	yes
	Dasyprocta	Agouti	Emmons 1997	yes	yes
	Myoprocta	Acouchy	Emmons 1997	yes	yes
Dinomyidae	*Dinomys*	Pacarana	Eisenberg 1974	yes	yes
Caviidae	*Cavia*	Guinea pigs, cavies	Eisenberg 1974	yes	
	Dolichotis = Pediolagus	Maras	Eisenberg 1974	yes	yes
	Galea	Cuis	Eisenberg 1974	yes	yes
	Microcavia	Cavies	Eisenberg 1974	yes	yes
Hydrochaeridae	*Hydrochaeris*	Capybara	Emmons 1997	yes	
Octodontidae	*Ctenomys*	Tucu-tucus	Eisenberg 1974	yes	
	Octodon	Degus	Eisenberg 1974	yes	yes
	Octodontomys	Long-tailed octodons	Eisenberg 1974	yes	
	Spalacopus	Cururos	Eisenberg 1974	yes	yes
Echimyidae	*Hoplomys*	Armored rat	Emmons 1997	yes	
	Dactylomys	Bamboo rats	Emmons 1997	yes	
	Kannabateomys	Southern bamboo rats	Redford and Eisenberg 1992	yes	
	Proechimys	Spiny rats	Emmons 1997	yes	yes
Capromyidae	*Capromys*	Hutias	Eisenberg 1974	yes	yes
	Geocapromys	Ground hutias	Eisenberg 1974	yes	
	Plagiodontia	Hispaniolan hutias	Eisenberg 1974		yes
Chinchillidae	*Chinchilla*	Chinchillas	Eisenberg 1974	yes	
	Lagidium	Mountain viscachas	Eisenberg 1974	yes	yes
	Lagostomus	Vizcachas	Eisenberg 1974	yes	yes

NOTES: This summary is inevitably incomplete and has a number of intrinsic biases (see text). Nonetheless, it does illustrate that alarm communication has been reported in 20 of the 53 families of rodents.
[a]Other signals include tooth chattering, quill-shaking, tail-slapping, foot-thumping.

behavior (Baack and Switzer 2000). Typically, individuals immediately increase vigilance but, over time, receivers habituate to tonic signals (i.e., individuals assess that the danger has passed and return to what they were doing previously: Loughry and McDonough 1988; Nikolskii 2000; Hare and Atkins 2001; Blumstein and Daniel 2004). Again, the fitness consequences of this opportunity cost have not been investigated in any species of rodent. However, as long as there is some opportunity cost, there is a selective pressure on receivers to evaluate the reliability of callers.

If a caller calls when no predator is present, it is an unreliable informant. Caller reliability can be evaluated in two ways: receivers could either assess characteristics of reliable and unreliable *classes* of callers, or they could discriminate among *individuals*. For instance, if calls from juveniles were on average less reliable than calls from adults, and if juveniles had acoustically distinctive calls (as has been demonstrated in California ground squirrels; Hanson and Coss 2001b) and steppe marmots (Nesterova 1996), then receivers might "de-value" the calls from juveniles.

Individually distinctive acoustic signals do occur in rodents. For example, banner-tailed kangaroo rats (*Dipodomys spectabilis*) have individually distinctive foot drumming signatures that are used as territorial advertisements (Randall 1989a). The postcopulatory chirps of male Belding's ground squirrels are individually distinctive (Leger et al. 1984). However, individually distinctive alarm calls are relatively unstudied. Juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) were the first rodent (Hare 1998b), and the second mammal (the first being vervet monkeys: Cheney and Seyfarth 1980) in which discrimination among individual alarm callers has been inferred. Hare and Atkins (2001) selectively manipulated the reliability of Richardson's ground squirrel callers by either pairing playbacks of calls from an individual with the appearance of a stuffed badger (thus creating "reliable" callers) or broadcasting the calls without a badger present (thus creating "unreliable" callers). When the calls from reliable or unreliable individuals were later played back, reliable calls elicited a higher level of response.

Subsequently, using a habituation-recovery playback design (Evans 1997), yearling and adult yellow-bellied marmots discriminated among individuals as well as some age-sex classes (Blumstein and Daniel 2004). In this study, marmots were first habituated, with repeated playback, to different exemplars of calls from an individual that was

not a member of their social group. Subjects were then "probed" with either a novel call from the same individual or a novel call from a different individual nongroup member. Marmots increased vigilance and suppressed foraging in response to the call from the novel individual. Additional playbacks of calls from different age-sex classes demonstrated that these marmots were particularly responsive to calls from young (Blumstein and Daniel 2004), which is interesting because calls from young were initially hypothesized to be less reliable than calls from adults. In contrast, calls from young (which are demonstrably less reliable) were less evocative in both California ground squirrels (Hanson and Coss 1997, 2001b) and steppe marmots (*Marmota bobak;* Nesterova 1996). For yellow-bellied marmots, something other than reliability must favor individual discrimination abilities; an alternative nepotistic explanation is discussed as follows.

If, by calling, individuals exposed themselves to a greater risk of predation than noncallers, then calling behavior would be a phenotypically altruistic behavior (Alexander 1974). How such behaviors are maintained by natural selection is an interesting puzzle.

Is alarm calling in fact a risky behavior? Unfortunately, evidence for predation costs of calling is difficult to obtain. Most people who study alarm communication use these vocalizations to help locate individual callers (e.g., Gurnell 1987; Barash 1989). An obvious inference is that predators can do this as well. However, predation events are rare and hard to observe, and unlike studies in birds (e.g., Klump et al. 1986; Wood et al. 2000), there have been no experimental studies focusing on predator's responses to sciurid alarm calls (Lima 2002).

However, there have been studies of predators' responses to foot thumps by banner-tailed kangaroo rats (Randall and Matcoq 1997). Randall and Matcoq reported that hungry snakes were attracted to territorial foot drumming whereas recently fed snakes were repelled by foot drumming. Since snakes did not differentiate between the antipredator and territorial foot drumming, foot drumming may be costly.

Sherman (1977) found that when a terrestrial predator appeared, Belding's ground squirrels emitting calls were tracked and killed more often than noncallers, whereas calling in response to an aerial predator enhanced an individual's likelihood of escape over that of noncallers (who probably were unaware of the raptor's presence; Sherman 1985). Other researchers also have observed diurnal sciurids being attacked and killed by predators (e.g., Armitage 1982; Barash 1989; Murie 1992), but I am aware of no studies other than Sherman's, which simultaneously compared the fate of callers with noncallers. For instance, in 18 years of fieldwork, Barash observed thirteen cases of predation, but in none of these cases was a calling animal observed to be killed (Barash 1989).

Belding's ground squirrels sit up in place and call when they detect a terrestrial predator, whereas they scurry for cover before or while calling when closely pursued by a rapidly moving (aerial) predator (Sherman 1985). Likewise, Columbian ground squirrels (*Spermophilus columbianus*) modify their calling behavior as a function of predation risk (MacWhirter 1992). When suddenly surprised by a simulated aerial predator attack (a flying disk thrown directly at them), individuals bolted into the nearest burrow. In contrast, upon sighting a distant flying disk, or a taxidermically mounted badger from a distance—individuals gave repeated calls, often while running to their burrow. In some other species individuals that call only do so after they have sought cover. For instance, great gerbils (*Rhombomys opimus;* Randall et al. 2000), black-tailed prairie dogs (Hoogland 1996b), and yellow-bellied marmots (Blumstein and Armitage 1997a) generally call from burrow entrances, while taiga voles (*Microtus xanthognathus*) may stop calling if a predator comes too close and, following release from capture, call only after they have reached safety (Wolff 1980b).

One reason that evidence may be equivocal about the cost of calling is that callers may also be communicating with the predator, and there may be variation between species in the value of such communication. Thus while the alarm calls of some ground squirrels (Sherman 1985) and marmots become more cryptic as risk increases (Blumstein 1995a; Blumstein and Arnold 1995), some other rodents call more, and at greater rates, as risk increases (e.g., Harris et al. 1983; Nikolskii and Nesterova 1989, 1990; Nikol'skii and Pereladova 1994; Nikol'skii et al. 1994; Nikol'skii 2000; Blumstein and Armitage 1997a; Randall and Rogovin 2002). For instance, yellow-bellied marmots produce more calls and calls at a faster rate as a human approaches them (Blumstein and Armitage 1997a). Making one's self more obvious as risk increases is consistent with the hypothesis that calls are directed to the predator. Thus, calls may simultaneously have a pursuit-deterrent function while they also communicate relative risk to conspecifics. Identifying the relative importance of both of these factors is a worthy goal for future research.

What Are the Benefits of Calling?

There are several possible solutions to the problem of phenotypically altruistic acts. I believe that we gain insight into the workings of evolution by decomposing inclusive fitness benefits into direct and indirect components (Brown 1987). Others (e.g., Hauber and Sherman 1998) question the use

of "direct" and "indirect" to describe fitness gains through descendents or nondescendents because, once appropriately weighted by relatedness, the Hamiltonian logic (Hamilton 1964) of inclusive fitness is agnostic about its source. Nonetheless, by calling, individuals may warn descendent or nondescendent kin, or both. Paths to obtaining direct fitness include reciprocity and directly increasing the probability of their own survival by calling, or the survival of their descendent kin (Sherman 1977, 1985).

Individuals could conceivably engage in reciprocal calling (Trivers 1971), whereby individual A might call one time and individual B might call another time. Without defectors, such a strategy might explain costly alarm calling. All such reciprocal arrangements rely on individual recognition and memory (Wilkinson 2002). Some ground squirrels and marmots have such abilities (Hare 1998b; Blumstein and Daniel 2004; Blumstein et al. 2004). Using olfactory cues, Belding's ground squirrels can remember individuals for at least 9 months (Mateo and Johnston 2000). However, there is no evidence from any rodent that callers "take turns," or that when surrounded by unreliable callers, other individuals cease calling. Moreover, alarm calls are unlikely to be reciprocal because they are broadcast widely. This means that eavesdropping "cheaters" can hear and benefit from calls but not take their turn at calling. Moreover, there is no way for a caller to select its audience so as to not warn cheaters if calls are loud and have a large active space. Reciprocity only works when there is a direct transfer of benefits from individual A to B and vice versa; if eavesdropping individuals C, D, and E also benefit, reciprocity is destabilized. (I thank Paul Sherman for clearly articulating this important point.)

If callers are in fact communicating to predators, then calling should reduce individuals' predation risk. Differentiating the degree to which callers are communicating to the predator or to conspecifics is difficult. Imagine a coyote or a mountain lion walking through a colony of prairie dogs or plains viscachas. As the predator passes through, multiple individuals may call (e.g., Branch 1993; Hoogland 1995). Calls evoke escape and heightened vigilance in conspecifics, and the predator walks on and leaves the colony. Is each caller calling to encourage the predator to move on? Is this a form of collective defense? Or, because individuals may be in different social groups, could each caller be calling to warn their family members? In this case we would see multiple callers, because many individuals have kin nearby.

Callers may obtain indirect fitness benefits by increasing the survival of collateral kin. There is some controversy over the relative importance of warning descendent versus collateral kin for explaining the adaptive significance of alarm calling. Sherman (1977) and Dunford (1977a) independently reported that by calling, individual Belding's and round-tailed ground squirrels (*Spermophilus tereticaudus*) respectively, were alerting descendent and nondescendent kin. Callers therefore received nepotistic fitness benefits from calling. Calling to increase indirect fitness has subsequently been reported to occur in chipmunks (Smith 1978; Burke da Silva et al. 2002), prairie dogs (Hoogland 1995, 1996a), as well as in several other ground squirrels (e.g., Schwagmeyer 1980; Davis 1984a; MacWhirter 1992). Sherman's (1977) study quantified the frequency of calling when animals were surrounded by different audiences (*sensu* Gyger 1990), but many other studies did not, and evidence for kin-selected benefits from calling often is based on a caller being surrounded by relatives.

There have been several suggestions (Shields 1980; Blumstein et al. 1997; Blumstein and Armitage 1998a) that such evidence of kin-selection *sensu lato* fails to clarify the relative importance of indirect fitness in explaining the evolution of alarm-calling behavior. On one hand, fitness is fitness however it is obtained, and indirect fitness should not be considered a special type of fitness (Dawkins 1979; Sherman 1980b; Hauber and Sherman 1998). On the other hand, viewing calling as a behavior that functions solely to protect descendents (which may have evolved as a form of parental care) is different from hypothesizing that alarm calling behavior functions solely to protect nondescendents. Admittedly, most researchers do not make this strong dichotomy; rather, they point out that calling is nepotistic and then determine which relatives are beneficiaries. Sherman (1977), studying Belding's ground squirrels, and my colleagues and myself, studying yellow-bellied marmots, found that adult females with emergent (and vulnerable) young-of-the-year are the age/sex class most likely to call. In the ground squirrels, females with older offspring (or more collateral relatives around) called at higher frequencies than females with fewer nearby relatives. However, in the marmots, numbers of adult kin did not affect calling frequencies. These differences suggest that nepotism in the form of alarm calling extends to descendent and collateral kin in Belding's ground squirrels, but only to descendents in marmots. Sherman (1980a, 1981a) discussed how demography (dispersal and mortality) affect the limits of nepotism. Demographic differences between marmots and Belding's ground squirrels may affect the different limits of nepotism, as evidenced by alarm calling in these two species.

A recent experiment suggests that both male and female marmots pay attention to vulnerable young (Blumstein and Daniel 2004). Following experimental playbacks of alarm calls from different age/sex classes, yellow-bellied marmots suppressed foraging the most after hearing calls from young. We inferred from this that marmots are particularly attuned to the status of vulnerable young. Note, this finding is inconsistent with the hypothesis that young callers were

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There have been several suggestions (Shields 1980; Blumstein et al. 1997; Blumstein and Armitage 1998a) that such evidence of kin-selection *sensu lato* fails to clarify the relative importance of indirect fitness in explaining the evolution of alarm-calling behavior. On one hand, fitness is fitness however it is obtained, and indirect fitness should not be considered a special type of fitness (Dawkins 1979; Sherman 1980b; Hauber and Sherman 1998). On the other hand, viewing calling as a behavior that functions solely to protect descendents (which may have evolved as a form of parental care) is different from hypothesizing that alarm calling behavior functions solely to protect nondescendents. Admittedly, most researchers do not make this strong dichotomy; rather, they point out that calling is nepotistic and then determine which relatives are beneficiaries. Sherman (1977), studying Belding's ground squirrels, and my colleagues and myself, studying yellow-bellied marmots, found that adult females with emergent (and vulnerable) young-of-the-year are the age/sex class most likely to call. In the ground squirrels, females with older offspring (or more collateral relatives around) called at higher frequencies than females with fewer nearby relatives. However, in the marmots, numbers of adult kin did not affect calling frequencies. These differences suggest that nepotism in the form of alarm calling extends to descendent and collateral kin in Belding's ground squirrels, but only to descendents in marmots. Sherman (1980a, 1981a) discussed how demography (dispersal and mortality) affect the limits of nepotism. Demographic differences between marmots and Belding's ground squirrels may affect the different limits of nepotism, as evidenced by alarm calling in these two species.

A recent experiment suggests that both male and female marmots pay attention to vulnerable young (Blumstein and Daniel 2004). Following experimental playbacks of alarm calls from different age/sex classes, yellow-bellied marmots suppressed foraging the most after hearing calls from young. We inferred from this that marmots are particularly attuned to the status of vulnerable young. Note, this finding is inconsistent with the hypothesis that young callers were

less reliable, and that calls from young should therefore communicate less risk than calls from adults. This finding is consistent with Sherman's (1980a, 1981a) limits of nepotism framework because adult yellow-bellied marmots are likely to be surrounded primarily by their offspring and by offspring from female relatives. Compared to Belding's ground squirrels, yellow-bellied marmots may limit their nepotistic behavior toward offspring because they evolved in a patchier habitat and live in a matrilineal group structure. In contrast, ground squirrels live in relatively higher-density meadows and many more relatives are likely to be within earshot of an alarm call. These demographic differences may help explain interspecific variation in the evolution and adaptive utility of alarm communication.

How Does the Acoustic Environment Affect Communication?

All signals must be transmitted from the signaler to the receiver, during which time they may degrade (i.e., lose fidelity) and attenuate (i.e., lose amplitude—Bradbury and Vehrencamp 1998). It follows that the environment should favor certain types of vocalizations. Several predictions can be drawn from first principles about the structure of long-distance signals like rodent alarm calls.

First, forest-dwelling species should have lower frequency vocalizations than species in open habitats to maximize transmission distance, because low-frequency sounds travel around objects and attenuate less than high-frequency sounds. The fundamental and dominant frequencies of alarm calls of southern African tree squirrels (*Paraxerus* spp. and *Funisciurus congicus*) are as predicted: forest species have lower frequency calls than do savannah species (Viljoen 1983). Emmons (1978) studied nine species of West African rainforest squirrels and contrasted their vocalizations to temperate *Sciurus* and *Tamiasciurus* species living in more open habitats. She found that certain long-distance calls from rainforest species were lower in frequency than similar calls from temperate tree squirrels. Smith (1978) studied two species of *Tamiasciurus* tree squirrels and found that they also produced relatively low-frequency alarm calls. Perla and Slobodchikoff (2002) found that frequency components of Gunnison prairie dog (*Cynomys gunnisoni*) alarm calls varied seasonally in ways that were consistent with the hypothesis that calls were modified to be transmitted through different microhabitats, which themselves changed seasonally. And Le Roux et al. (2002) found that a forest-dwelling whistling rat (*Parotomys* sp.) had a lower-frequency alarm call than a sibling species living in more open habitat.

Second, low frequency calls are predicted in subterranean species, because of the rapid attenuation of high frequency sounds in earthen burrows. Studies of subterranean mammals generally (Francescoli 2000), and naked mole-rats particularly (Pepper et al. 1991; Judd and Sherman 1996), have shown that their alarm calls are indeed very low in frequency.

Third, dense forest habitat should select against rapid frequency modulation because rapidly paced calls would reverberate off trees and thus degrade. In the open we might expect selection to act against long pure tonal calls because they will be degraded by heat waves reflecting off the open ground. The antipredator vocalizations of antelope squirrels (*Ammospermophilus* spp.) vary with habitat, but not as predicted from first principles (Bolles 1988). Specifically, species in open desert habitats where we might expect selection against tonal calls have long-duration pure-toned trills. In contrast, those species in more closed, rocky/prairie habitats have shorter-duration harsh trills. Because habitat complexity and vertical relief might increase reverberation, selection should favor short and potentially redundant calls in such habitats. However, the opposite has been reported in two rodents. In Gunnison's prairie dogs (*Cynomys gunnisoni*), the number of syllables and the total call length are positively associated with habitat complexity (Slobodchikoff and Coast 1980). Populations in areas with more vegetative cover, rocks, and tree stumps emit longer calls and calls with more syllables than populations in more open country. Slobodchikoff and Coast (1980) suggested that these calls are longer and more complex in more structurally complex habitat, where callers might not be able to see other individuals, to ensure that kin are alerted to the presence of a predator. Nikol'skii (Nikol'skii 1974, 1984; Nikol'skii 1994; Nikol'skii et al. 2002) has found that marmot species (and populations) in habitats with greater relief have more rapidly paced alarm calls than species (and populations) in flatter terrain. If rapidly paced calls communicate greater risk (e.g., Blumstein and Armitage 1997a), then it is possible that habitat-specific perceptions of risk influence call structure. The relationship between habitat-specific predation risk and call complexity remains to be tested directly.

Studies on birds provide some support for the hypothesis that evolution has designed long-distance signals to maximize transmission through a species' habitat (e.g., Wiley 1991; Bradbury and Vehrencamp 1998). However, Daniel and Blumstein (1998) found no support for this acoustic adaptation hypothesis in marmots. While there was variation in how well marmot alarm calls were transmitted through habitats, and there was evidence that some habitats generally degraded calls more than other habitats, there was no statistical interaction between habitat and species. Thus, a species' own call was not transmitted best in its na-

tive habitat—an essential prediction of the acoustic adaptation hypothesis.

I found no support for the hypothesis that overall repertoire size is constrained by the acoustic transmission fidelity of the habitat. Blumstein (2003) broadcast and rerecorded pure tones through the habitats of eight marmot species, thus generating a metric of habitat transmission fidelity (Blumstein and Daniel 1997). No relationship occurred between habitat transmission fidelity and alarm call repertoire size. However, after removing variation in alarm call repertoire size explained by the acoustic environment, there was a relationship between social complexity and repertoire size (see also Blumstein and Armitage 1997b).

Taken together, we might generally expect the habitat to select for gross frequency characteristics of calls, whereas it might not have a direct effect on temporal characteristics or on microstructural differences. A recent comparative study (Blumstein and Turner 2005) drew similar conclusions for birdsong.

What Might Explain Variation in Call Microstructure?

Unlike birdsong (Catchpole and Slater 1995) or many of the calls of insects or anurans (Gerhardt and Huber 2002), alarm calls are not directly involved in species identification, territorial defense, or mate choice. And the diversity of alarm calls in rodents requires special explanation, especially because of the contrast to alarm calls in songbirds, which often are convergent (Marler 1955). What, other than gross habitat differences, might favor the calls of rodents to diverge?

Character displacement (Schulter 2002) has been suggested to be important among sympatric species. In three species of Townsend chipmunks (*Eutamias* spp.), alarm chirps were most distinctive and less variable in populations at species boundaries (Gannon and Lawlor 1989). Because character displacement results from resource competition, there should be a demonstrable cost to having less distinctive alarm calls in sympatry. While sympatric species may respond to each other's alarm calls (Blumstein and Armitage 1997a; Shriner 1998), it is likely that variation in reliability of heterospecific callers may select for divergence in sympatry. Specifically, if a small species has more predators than a larger species, the smaller species will be more likely to give alarm calls in situations that are not threatening to the larger species than vice versa. Thus, from the perspective of the larger species, calls from the smaller species are not reliable, but not vice versa. Selection within a species living in sympatry with alarm-calling heterospecifics might thus favor divergent calls. No data are currently available to evaluate this.

Genetic drift has been suggested to lead to call variation over time (Daniel and Blumstein 1998). Evidence of heritable genetic variation in call structure comes from studies of hybrids that have been reported to have calls of intermediate structure (Nikol'skiy et al. 1984; Nikol'skii and Starikov 1997), or structures that resemble one parent more than another (Koeppl et al. 1978). Sibling species have calls more similar to each other than more distant relatives (Hoffmann et al. 1979; Bibikow 1996; Nikol'skii 1996; Blumstein 1999a). Divergence of alarm calls may occur relatively rapidly once populations are isolated on islands or by glaciers (Nikol'skii et al. 1999). For instance, Nikolsky (1981) reported divergence in arctic ground squirrel alarm calls after 7,500 years of isolation on islands. Given the potential importance of drift, it is surprising that the alarm calls of geographically isolated populations of yellow-bellied marmots have not diverged (Blumstein and Armitage 1997a).

Finally, in at least one species (the yellow-bellied marmot), variation in temporal characteristics of calls seems to be important in communicating risk, while variation in the frequency structure of calls seems to be important for individual discrimination (Blumstein and Armitage 1997a). Selection for individual recognition systems can act on signalers, receivers, or both (Beecher and Stoddard 1990). For instance, if it is in the best interest of the signaler to indicate its identity, selection should favor signalers to produce distinctive calls. Such selection is likely to be common in territorial and nepotistic signaling systems. By contrast, there may be no particular benefit from producing individually specific variation, but there is a benefit to receivers for discriminating among callers. In this case, calls may not be distinctive, but receivers may nevertheless be able to discriminate among them.

Repertoire Size and the Evolution of Functional Reference

Human language is unquestionably unique relative to the diversity of nonhuman vocalizations (Hockett 1960; Pinker 1994). A comparative perspective allows us to gain novel insights into language evolution (Blumstein 1999b). A complementary line of research on alarm vocalizations in rodents has focused on the evolution of meaningful communication. While much has been written about avian repertoire size (Kroodsma 1982; Irwin 1990; Catchpole and Slater 1995), birdsong is hypothesized to only have one or two functions (mate choice and territory defense—Catchpole and Slater; 1995). Each song (or syllable) that a bird sings is not typically hypothesized to have a particular function per se. In contrast, alarm call variants of birds and mammals may in fact refer to external objects or events. Such functionally referential communication has been reported in fowl (Evans et al. 1993), in some nonhuman pri-

mates (e.g., Cheney and Seyfarth 1990; Zuberbühler 2000), and in a social mongoose (Manser 2001; Manser et al. 2001). Predator-specific, functionally referential calls have been reported in one study of Gunnison's prairie dogs (*Cynomys gunnisoni;* Slobodchikoff et al. 1991), but not in another (Fitzgerald and Lechleitner 1974), and in one study of alpine marmots (*M. marmota;* Lenti Boero 1992), but not another (Blumstein and Arnold 1995). Greene and Meagher (1998) reported that red squirrel (*Tamiasciurus hudsonicus*) alarm calls had a high degree of production specificity and were likely to be functionally referential. Functionally referential alarm calls may indicate specific types of predators (e.g., aerial or terrestrial), specific predatory species (e.g., snake, raptor, canid), or commands for recipients to follow (run away, stand alert, climb a tree). To study functional reference, two pieces of complementary evidence are required (Evans 1997).

First, there should be a strong association between a specific external object or event (e.g., the appearance of a coyote) and a particular call. This call should be different from calls elicited when, say, an eagle appears. Satisfying this condition means that calls have a high degree of "production specificity."

Second, calls should elicit unique behavioral responses. Communication can only be understood by studying the behavior of the signaler and the receiver; playback experiments help us understand meaning. Simply documenting variable alarm calls does not necessarily imply that individuals will respond differently to them (Blumstein 1995b). To demonstrate functional reference there must be predator-specific responses. Thus playback of a "coyote alarm call" or an "eagle alarm call" should evoke responses typically observed when the relevant predator is seen. If so, we can infer a high degree of response specificity.

Some support has been provided for the production specificity criterion, but less so for the response specificity criterion in rodent alarm communication. Greene and Meagher (1998) provide experimental evidence that red squirrels produced predator-class specific alarm calls. Slobodchikoff et al. (1991) and Ackers and Slobodchikoff (1999) simulated different predators by walking toward Gunnison's prairie dogs wearing different colored shirts. They reported that the animals modified the structure of their calls to potentially communicate information about the individual predator, as well as aspects of the size and shape of silhouette models of actual predators. Three species of Malaysian tree squirrels (*Callosciurus* spp.) reported to have a high degree of production specificity are also reported to vary their responses as a function of alarm call type (Tamura and Yong 1993). In none of these three cases were playback experiments conducted, so the degree to which calls alone can elicit unique responses is unknown.

Most ground squirrels produce two different types of alarm calls (Blumstein and Armitage 1997b). The first, a short whistle, is often elicited by aerial predators, while the second, a longer trill, is often elicited by terrestrial predators. Ground squirrels also have predator-specific response differences: the sudden appearance of a raptor causes them to run to the nearest burrow, whereas they do not necessarily return to the nearest burrow after discovering a weasel (e.g., Turner 1973; Sherman 1985). However, closer examination typically reveals that "aerial" calls are actually elicited in high-risk situations (e.g., Robinson 1981; Owings and Hennessy 1984; Leger et al. 1984; Sherman 1985) and the production specificity is not high. Thus rather than communicating predator type, calls are likely to communicate degree of risk, which may reflect the time an individual has to escape the predator (e.g., Leger et al. 1979, 1984; Blumstein and Armitage 1997a; Robinson 1981; Sherman 1985) or may encode information about distance to the predator (Burke da Silva et al. 1994; Blumstein 1995a). Even when there is some degree of production specificity, playback experiments typically lead to graded responses, which are more indicative of risk, rather than information about a specific type of predator (e.g., Blumstein and Armitage 1997a; Blumstein 1999b).

Does Lack of Functional Reference Limit Complex Communication?

A reasonable question emerges from the observation that variable repertoires are not necessarily functionally referential: does a limited "vocabulary" prevent meaningful communication? At one level this question reveals an anthropocentric bias. Because humans have language, we classify language-like communication as especially complex. However, if we have learned anything by studying biological diversity, it is that there are multiple ways to solve a problem.

Rodents illustrate some of the ways in which animals can dynamically communicate the degree of risk. First, animals communicate risk by varying the number of calls emitted, or the rate at which they call, as seen in great gerbils (Randall and Rogovin 2002), yellow-bellied (Blumstein and Armitage 1997a), steppe (Nikol'skii 2000), and alpine marmots (Hofer and Ingold 1984; Blumstein and Arnold 1995), tassel-eared squirrels (*Sciurus aberti;* Farentinos 1974), chipmunks (Weary and Kramer 1995), and California (Leger et al. 1979) and Richardson's ground squirrels (Warkentin et al. 2001). Second, individuals can vary how they "package" calls into multi-note units, as seen in golden marmots (Blumstein 1995a). Third, individuals can vary the duration of a nonreferential whistle, as seen with Brant's whistling rats (*Parotomys brantsii*). Whistling rats produce longer whistles in lower-risk situations (a distant human or snake) and shorter whistles in higher-risk situations, which

are followed by disappearing into their burrows. Fourth, individuals can use different calls, as seen in yellow-bellied marmots (Blumstein and Armitage 1997a) and in the plains viscacha (Branch 1993). Or, combinations of calls may be used to dynamically communicate risk, as seen in Vancouver Island marmots (*Marmota vancouverensis;* Blumstein 1999a) and in great gerbils (Randall and Rogovin 2002). Fifth, call amplitude can communicate degree of risk, as seen in chipmunks (Weary and Kramer 1995), California (Leger et al. 1979) and Columbian ground squirrels (Harris et al. 1983), and yellow-bellied marmots (Blumstein and Armitage 1997a). Sixth, the existence of multiple callers rather than a single caller can communicate risk, as seen with chipmunks (Weary and Kramer 1995). Seventh, the duration of calling bouts may communicate degree of risk. For instance, snake-elicited antipredator behavior persists for longer periods of time when California ground squirrels are responding to a dangerous snake (large and warm) than to a less dangerous snake (small and cold; Swiasgood et al. 1999a, 1999b). Finally, some rodents have multichannel systems, such as the great gerbil (Randall et al. 2000) and the California ground squirrel (Owings and Hennessy 1984), which may have elements that both communicate risk to conspecifics and discourage attack by predators. Thus, while referential communication is a special case of alarm communication, it need not be viewed as the epitome of complex alarm communication. And, while complex communicative abilities may emerge from being able to produce different calls, they need not necessarily emerge from being able to produce different calls (Blumstein 1999b).

A Model for the Evolution of Alarm Communication in Rodents

Any model for the evolution of alarm communication must address three questions: (1) what factors influence whether a species produces alarm calls? (2) what is the function of alarm calling? and (3) what explains variation in call structure? I summarize the conclusions of this review schematically (fig. 27.1) and discuss them as follows.

Habitat, sociality, and behavior influence the evolution of alarm calling. Social, terrestrial, and diurnal species are those most likely to produce alarm calls, although there are some notable exceptions. Rodents produce alarm calls to increase personal, direct, and indirect fitness. We expect the degree of aggregation (sociality: e.g., Randall 1994; Randall 2001) and demography (Sherman 1980a, 1981a) to constrain the types of fitness benefits. For instance, solitary rodents, such as kangaroo rats (Randall and Matocq 1997), or a female ground squirrel with a snake in its reproductive burrow (Swaisgood, Owings, and Rowe 1999), produce alarm signals directed toward the predator to discourage it from hunting or to drive it away. By driving off a predator, individuals will save themselves as well as vulnerable offspring.

If solitary adult females are surrounded by mature offspring, or if animals live in more complex social groups formed by delayed dispersal and characterized by overlapping generations (Blumstein and Armitage 1998b, 1999), there exists the opportunity for animals to obtain indirect fitness benefits from calling. Enhancing this indirect fitness may be more important to some species than others, and not all species will have evolved alarm calling behavior the same way (e.g., Holmes 2001).

The evolution of call structure and repertoire size is influenced by a combination of environmental, social, and functional considerations. Available evidence suggests that a call's dominant frequency is influenced by the openness of the habitat; species living in closed, forested habitats have lower dominant frequencies than those in more open habitats. There remains, however, a need for studies to properly control for phylogeny and body size (e.g., Wiley 1991; Blumstein and Turner 2005) when testing for these effects. However, the acoustic environment seemingly has no other consistent influence on call structure. Interspecific variation may result from drift, although character displacement also is a possibility. In some cases, variation could result from advantages of communicating individual identity.

Functional considerations also influence the structure of alarm calls. More socially complex sciurid rodents emit more types of alarm calls (Blumstein and Armitage 1997b; Blumstein 2003) and there are indications of this in other taxa (e.g., naked mole-rats—Pepper et al. 1991). And while functionally referential communication is uncommon in rodents, modulating the number, rate, amplitude, and duration of alarm calls, using different calls or modalities, and manipulating call order are all ways rodents communicate degree of risk. Interestingly, in the species that are reported to have a high degree of production specificity (Gunnison's prairie dogs, red squirrels, and three species of Malaysian tree squirrels), complex and species-specific antipredator behavior is employed. Thus, the Macedonia and Evans' (1993) model for the evolution of functionally referential communication, which suggested that the need to communicate about different mutually exclusive escape strategies may have general, explanatory value for rodent alarm calls.

Diurnal, social rodents will continue to be an outstanding model system to study questions of the adaptive utility of alarm-calling behavior. New studies that test hypotheses generated from studies of sciurid rodents will increase our general understanding of factors responsible for the evolution and maintenance of alarm calling.

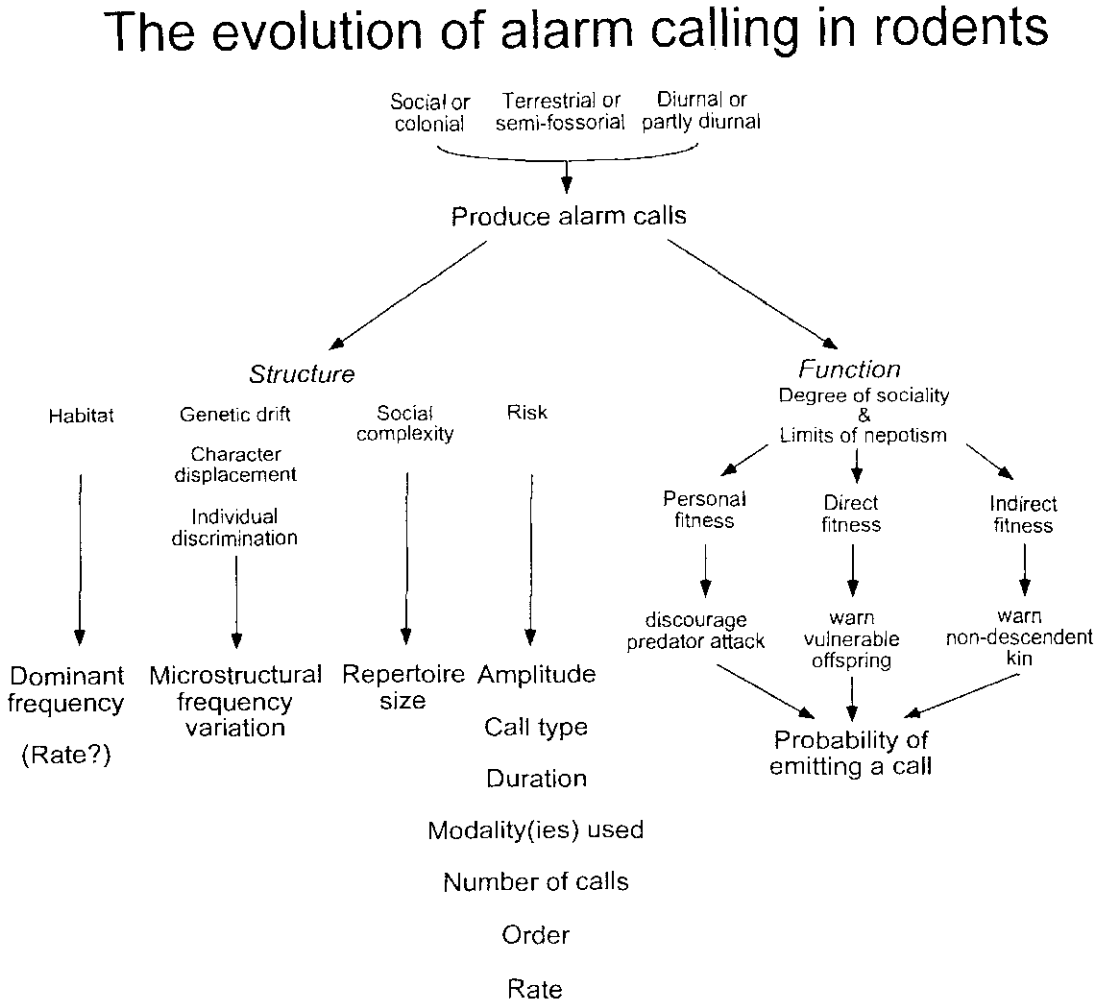

Figure 27.1 Summary of factors influencing the evolution of alarm calling in rodents. Alarm calling is most commonly reported in social or colonial species that are terrestrial or semifossorial, and are at least partly active by day. Various components of the structure of alarm calls are influenced by different factors. The dominant frequency of calls is higher in open habitats than closed habitats, and habitat complexity may influence calling rate via its effect on risk perception. Several factors influence microstructural frequency variation in calls. Social complexity influences repertoire size. Variation in risk influences the amplitude at which a call is emitted, call type, call duration, the modality or modalities used to communicate risk, the number of calls emitted, the rate at which calls are emitted, and the order in which calls are emitted. The probability of emitting an alarm call is a function of the benefits obtained, which are influenced by the degree of sociality. Highly social species, or species in which potential callers are surrounded by kin, may obtain indirect fitness by calling. Other species may obtain personal and direct fitness by calling.

Summary

Alarm calls are signals elicited by predators that may be directed to predators, most likely to discourage attack, or to conspecifics to warn them about the presence of a predator. Social, terrestrial, and diurnal species are those most likely to produce alarm calls, although there are some notable exceptions. The evolution of call structure and repertoire size is influenced by a combination of environmental, social, and functional considerations. More socially complex sciurid rodents emit more types of alarm calls. If solitary adult females are surrounded by mature offspring, or if animals live in more complex social groups formed by delayed dispersal and characterized by overlapping generations, there exists the opportunity for animals to obtain indirect fitness benefits from calling. Overall, rodents may receive both personal, direct, and indirect benefits from calling. Enhancing indirect fitness may be more important to some species than others, and not all species will have evolved alarm-calling behavior the same way. Diurnal social rodents will continue to be an outstanding model system to study questions of the adaptive utility of alarm calling behavior.

Acknowledgments
I thank Alexander Nikol'skii for introducing me to the Russian literature on alarm communication and Luis Ebensberger for an introduction to South American rodents; neither is responsible for anticipated omissions. I thank Janice Daniel, Kim Pollard and my reviewers--Jan Randall and Ron Swaisgood--for constructive comments on previous versions, and Erin Shelly who found reports of genera of alarm calling rodents that I originally missed. I am *extremely* grateful to Paul Sherman who went out of his way to improve the clarity of this chapter, and to remind me of the importance of the 'limits of nepotism'—an hypothesis which is likely to explain interspecific variation in the adaptive utility of alarm communication and other nepotistic behaviors.

Literature Cited

Ackers, S. H., and C. N. Slobodchikoff. 1999. Communication of stimulus size and shape in alarm calls of Gunnison's prairie dogs, *Cynomys gunnisoni*. Ethology 105:149-162.

Armitage, K. B. 1982. Marmots and coyotes: behavior of prey and predator. Journal of Mammalogy 63:503-505.

Baack, J. K., and P. V. Switzer. 2000. Alarm calls affect foraging behavior in Eastern chipmunks (*Tamias striatus*, Rodentia: Sciuridae). Ethology 106:1057-1066.

Balph, D. M., and D. F. Balph. 1966. Sound communication of Uinta ground squirrels. Journal of Mammalogy 47:440-450.

Barash, D. P. 1989. Marmots: social behavior and ecology. Stanford, Stanford University Press.

Beecher, M. D., and P. K. Stoddard. 1990. The role of bird song and calls in individual recognition: contrasting field and laboratory perspectives, Pages 375-408 *in* M. Berkley, and W. C. Stebbins, eds. Comparative perception-vol. II: complex sounds. New York, Wiley.

Bibikow, D. I. 1996, Die murmeltiere der welt: Die Neue Brehm-Bucherei Bd. 388. Heidelberg, Spektrum Akademischer Verlag.

Blumstein, D. T. 1995. Golden-marmot alarm calls: I. The production of situationally specific vocalizations. Ethology 100:113-125.

Blumstein, D. T. 1995. Golden-marmot alarm calls: II. Asymmetrical production and perception of situationally specific vocalizations? Ethology 101:25-32.

Blumstein, D. T. 1999. Alarm calling in three species of marmots. Behaviour 136:731-757.

Blumstein, D. T. 1999. The evolution of functionally referential alarm communication: multiple adaptations; multiple constraints. Evolution of Communication 3:135-147.

Blumstein, D. T. 2003. Social complexity but not the acoustic environment is responsible for the evolution of complex alarm communication / La complexité sociale est responsable de l'évolution de la communication d'alarme complexe, non le milieu acoustique, Pages 41-49 *in* R. Ramousse, D. Allainé, and M. Le Berre, eds. Adaptative strategies and diversity in marmots / Stratégies adaptatives et diversité chez les marmottes. Lyon, International Marmot Network.

Blumstein, D. T., and K. B. Armitage. 1997. Alarm calling in yellow-bellied marmots: I. The meaning of situationally-specific calls. Animal Behaviour 53:143-171.

Blumstein, D. T., and K. B. Armitage. 1997. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. American Naturalist 150:179-200.

Blumstein, D. T., and K. B. Armitage. 1998. Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. Behavioral Ecology 9:8-19.

Blumstein, D. T., and K. B. Armitage. 1998. Why do yellow-bellied marmots call? Animal Behaviour 56:1053-1055.

Blumstein, D. T., and W. Arnold. 1995. Situational-specificity in alpine-marmot alarm communication. Ethology 100:1-13.

Blumstein, D. T., and J. C. Daniel. 1997. Inter- and intraspecific variation in the acoustic habitats of three marmot species. Ethology 103:325-338.

Blumstein, D. T., and J. C. Daniel. in review. Yellow-bellied marmots discriminate among the alarm calls of individuals and are more responsive to the calls from juveniles. Animal Behaviour

Blumstein, D. T., J. Steinmetz, K. B. Armitage, and J. C. Daniel. 1997. Alarm calling in yellow-bellied marmots: II. Kin selection or parental care? Animal Behaviour 53:173-184.

Blumstein, D. T., and A. C. Turner. in review. Can the acoustic adaptation hypothesis predict the structure of Australian birdsong? The Auk.

Bolles, K. 1988. Evolution and variation of antipredator vocalisations of Antelope squirrels, *Ammospermophilus* (Rodentia: Sciuridae). Zeitschrift für Säugetierkunde 53:129-147.

Bradbury, J. W., and S. L. Vehrencamp. 1998. Principles of animal communication. Sunderland, MA, Sinnauer.

Branch, L. C. 1993. Social organization and mating system of the plains viscacha (*Lagostomus maximus*). Journal of Zoology (London) 229:473-491.

Brooks, R. J., and E. M. Banks. 1973. Behavioural biology of the collard lemming [*Dicrostonyx groenlandians* (Trail)]: an analysis of acoustic communication. Animal Behaviour Monogr. 6:1-83.

Brown, J. L. 1987. Helping and communal breeding in birds. Princeton, Princeton University Press.

Brudzynski, S. M. 2001. Pharmacological and behavioral characteristics of 22 kHz alarm calls in rats.

Neuroscience and Biobehavioral Reviews 25:611-617.
Burke da Silva, K., D. L. Kramer, and D. M. Weary. 1994. Context-specific alarm calls of the eastern chipmunk, *Tamias striatus*. Canadian Journal of Zoology 72:1087-1092.
Burke da Silva, K., C. Mahan, and J. da Silva. 2002. The trill of the chase: eastern chipmunks call to warn kin. Journal of Mammalogy 83:546-552.
Catchpole, C., and P. J. B. Slater. 1995. Bird song: biological themes and variations. Cambridge, Cambridge University Press.
Charnov, E. L., and J. R. Krebs. 1975. The evolution of alarm calls: altruism or manipulation? American Naturalist 109:107-112.
Cheney, D. L., and R. M. Seyfarth. 1980. Vocal recognition in free-ranging vervet monkeys. Animal Behaviour 28:362-367.
Cheney, D. L., and R. M. Seyfarth. 1990, How monkeys see the world. Chicago, University of Chicago Press.
Daly, M., and S. Daly. 1975. Socio-ecology of Saharan gerbils, especially *Meriones libycus*. Mammalia 39:289-311.
Daniel, J. C., and D. T. Blumstein. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. Animal Behaviour 56:1517-1528.
Davis, L. S. 1984. Alarm calling in Richardson's ground squirrels (*Spermophilus richardsonii*). Zeitschrift für Tierpsychologie 66:152-164.
Dawkins, R. 1979. Twelve misunderstandings of kin selection. Zeitschrift für Tierpsychologie 51:184-200.
de Graaff, G. 1981. The rodents of Southern Africa: Notes on their identification, distribution, ecology and taxonomy. Durban, Butterworths.
Dempster, E. R., M. R. Perrin, C. T. Downs, and M. Griffin. 1998. *Gerbillurus setzeri*. Mammalian Species 598:1-4.
Dunford, C. 1977. Kin selection for ground squirrel alarm calls. American Naturalist 111:782-785.
Ebensperger, L. A. 1998. Sociality in rodents: the New World fossorial hystricognaths as a study model. Rev. Chilena Hist. Nat. 71:65-77.
Ebensperger, L. A., and H. Cofré. 2001. On the evolution of group-living in New World cursorial hystricognath rodents. Behavioral Ecology 12:227-236.
Eisenberg, J. F. 1974. The function and motivational basis of Hystricomorph vocalizations. Symposium Zoological Society of London 34:211-247.
Emmons, L. H. 1978. Sound communication among African rainforest squirrels. Zeitschrift für Tierpsychologie 47:1-49.
Emmons, L. H. 1997. Neotropical rainforest mammals: a field guide, 2nd ed. Chicago, University of Chicago Press.
Evans, C. S. 1997. Referential communication. Persp. Ethol. 12:99-143.
Evans, C. S., L. Evans, and P. Marler. 1993. On the meaning of alarm calls: functional reference in an avian vocal system. Animal Behaviour 46:23-38.
Farentinos, R. C. 1974. Social communication of the tassel-eared squirrel (*Sciurus aberti*): a descriptive analysis. Zeitschrift für Tierpsychologie 34:441-458.
Fitzgerald, J. P., and R. R. Lechleitner. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. American Midland Naturalist 92:146-163.
Francescoli, G. 2000. Sensory capabilities and communication in subterranean rodents, Pages 111-144 *in* E. A. Lacey, J. L. Patton, and G. N. Cameron, eds. Life underground: the biology of subterranean rodents. Chicago, University of Chicago Press.
Gannon, W. L., and T. E. Lawlor. 1989. Variation of the chip vocalization of three species of Townsend chipmunks (Genus *Eutamias*). Journal of Mammalogy 70:740-753.
Gerhardt, H. C., and F. Huber. 2002, Acoustic communication in insects and anurans. Chicago, University of Chicago Press.
Greene, E., and T. Meagher. 1998. Red squirrels, *Tamiasciurus hudsonicus*, produce predator-class specific alarm calls. Animal Behaviour 55:511-518.
Gurnell, J. 1987. The natural history of squirrels. New York, Facts on File Publications.
Gyger, M. 1990. Audience effects on alarm calling. Ethology, Ecology and Evolution 2:227-232.
Haltenorth, T., and H. Diller. 1980. A field guide to the mammals of African including Madagascar. London, Collins.
Hanson, M. T., and R. G. Coss. 1997. Age differences in the response of California ground squirrels

(*Spermophilus beecheyi*) to avian and mammalian predators. Journal of Comparative Psychology 111:174-184.
Hanson, M. T., and R. G. Coss. 2001. Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. Ethology 107:259-275.
Hare, J. F. 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. Animal Behaviour 55:451-460.
Hare, J. F., and B. A. Atkins. 2001. The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). Behavioral Ecology and Sociobiology 51:108-112.
Harris, M. A., J. O. Murie, and J. A. Duncan. 1983. Responses of Columbian ground squirrels to playback of recorded calls. Zeitschrift für Tierpsychologie 63:318-330.
Hasson, O. 1991. Pursuit-deterrent signals: communication between prey and predators. Trends in Ecology and Evolution 6:325-329.
Hauber, M. E., and P. W. Sherman. 1998. Nepotism and marmot alarm calling. Animal Behaviour 56:1049-1052.
Heard, D. C. 1977. The behaviour of Vancouver Island marmots, *Marmota vancouverensis*. M.S. thesis, University of British Columbia.
Hockett, C. F. 1960. The origin of speech. Scientific American 203(3):89-96.
Hofer, S., and P. Ingold. 1984. Die pfiffe des alpenmurmeltiers. Form und auftreten im zusammenhang mit der feindvermeidung. Review Suisse Zoology 91:861-865.
Hoffmann, R. S., J. W. Koeppl, and C. F. Nadler. 1979. The relationships of the amphiberingian marmots (Mammalia: Sciuridae). University of Kansas, Occasional Papers of the Museum of Natural History 83:1-56.
Holmes, W. G. 2001. The development and function of nepotism: why kinship matters in social relationships, Pages 281-316 *in* E. Blass, ed. Developmental Psychobiology, Volume 13 of Handbook of Behavioral Neurobiology. New York, Plenum Publishers.
Hoogland, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. Chicago, University of Chicago Press.
Hoogland, J. L. 1996. Why do Gunnison's prairie dogs give anti-predator calls? Animal Behaviour 51:871-880.
Hudson, W. H. 1872. On the habits of the vizcacha (*Lagostomus trichodactylus*). Proceedings of the Zoological Society of London 1872:822-833.
Irwin, R. E. 1990. Directional sexual selection cannot explain variation in song repertoire size in the New World blackbirds (Icterinae). Ethology 85:212-224.
Johnson, D. W., and D. P. Armstrong. 1987. *Peromyscus crinitus.* Mammalian Species 287:1-8.
Judd, T. M., and P. W. Sherman. 1996. Naked mole-rats recruit colony mates to food sources. Animal Behaviour 52:957-969.
Klump, G. M., E. Kretzschmar, and E. Curio. 1986. The hearing of an avian predator and its avian prey. Behavioral Ecology and Sociobiology 18:317-323.
Klump, G. M., and M. D. Shalter. 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. Zeitschrift für Tierpsychologie 66:189-226.
Koeppl, J. W., R. S. Hoffmann, and C. F. Nadler. 1978. Pattern analysis of acoustical behavior in four species of ground squirrels. Journal of Mammalogy 59:677-696.
Krebs, C. J. 1984. Voles and lemmings, Pages 651-655 *in* D. W. MacDonald, ed. The encyclopedia of mammals. New York, Facts on File.
Kroodsma, D. E. 1982. Song repertoires: problems in their definition and use, Pages 125-146 Acoustic communication in birds. New York, Academic Press.
Lacher, T. E., Jr. 1981. The comparative social behavior of *Kerodon rupestris* and *Galea spixii* and the evolution of behavior in the caviidae. Bulletin of the Carnegie Museum of Natural History 17:1-71.
Lackey, J. A., D. G. Huckaby, and B. G. Ormiston. 1985. *Peromyscus leucopus.* Mammalian Species 247:1-10.
Le Roux, A., T. P. Jackson, and M. I. Cherry. 2001. Does Brants' whistling rat (*Parotomys brantsii*) use an urgency-based alarm system in reaction to aerial and terrestrial predators? Behaviour 138:757-773.
Le Roux, A., T. P. Jackson, and M. I. Cherry. 2002. Differences in alarm vocalizations of sympatric populations of the whistling rats, *Parotomys brantsii* and *P. littledalei* (Rodentia: Muridae). Journal of

Zoology (London) 257:189-194.
Leger, D. W., S. D. Berney-Key, and P. W. Sherman. 1984. Vocalizations of Belding's ground squirrels (*Spermophilus beldingi*). Animal Behaviour 32:753-764.
Leger, D. W., D. H. Owings, and L. M. Boal. 1979. Contextual information and differential responses to alarm whistles in California ground squirrels. Zeitschrift für Tierpsychologie 49:142-155.
Lenti Boero, D. 1992. Alarm calling in Alpine marmot (*Marmota marmota* L.): evidence for semantic communication. Ethology, Ecology and Evolution 4:125-138.
Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology and Evolution 17:70-75.
Lishak, R. S. 1984. Alarm vocalizations of adult gray squirrels. Journal of Mammalogy 65:681-684.
Loughry, W. J., and C. M. McDonough. 1988. Calling and vigilance in California ground squirrels: a test of the tonic communication hypothesis. Animal Behaviour 36:1533-1540.
Macedonia, J. M., and C. S. Evans. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 93:177-197.
MacWhirter, R. B. 1992. Vocal and escape responses of Colombian ground squirrels to simulated terrestrial and aerial predator attacks. Ethology 91:311-325.
Manser, M. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. Proceedings of the Royal Society of London, Series B 268:2315-2324.
Manser, M. B., M. B. Bell, and L. B. Fletcher. 2001. The information receivers extract from alarm calls in suricates. Proceedings of the Royal Society of London, Series B 268:2485-2491.
Marler, P. 1955. Characteristics of some animal calls. Nature 176:6-8.
Mateo, J. M., and R. E. Johnston. 2000. Retention of social recognition after hibernation in Belding's ground squirrels. Animal Behaviour 59:491-499.
Maynard Smith, J. 1965. The evolution of alarm calls. American Naturalist 99:59-63.
McCarty, R. 1978. *Onychomys leucogaster*. Mammalian Species 87:1-6.
Medway, L. 1978. The wild mammals of Malaya (Peninsular Malaysia) and Singapore, 2nd ed. Kuala Lumpur, Oxford University Press.
Murie, J. O. 1992. Predation by badgers on Columbian ground squirrels. Journal of Mammalogy 73:385-394.
Neill, S. R. S. J., and J. M. Cullen. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. Journal of Zoology (London) 172:549-569.
Nesterova, N. L. 1996. Age-dependent alarm behaviour and response to alarm call in bobac marmots (*Marmota bobac* Müll.), Pages 181-186 *in* M. Le Berre, R. Rmousse, and L. Le Guelte, eds. Biodiversity in marmots. Moscow-Lyon, International Network on Marmots.
Nikol'skii, A. A. 1994. Geographical variability of the alarm call rhythmical structure in *Marmota baibacina*, Pages 111-126 *in* V. Y. Rumiantsev, ed. Actual problems of marmots investigation. Moscow, ABF.
Nikol'skii, A. A. 1996. Species specificity and interspecies parallelisms of alarm call in eurasian marmots, Pages 187-192 *in* M. Le Berre, R. Ramousse, and L. Le Guelte, eds. Biodiversity in marmots. Moscow-Lyon, International Network on Marmots.
Nikol'skii, A. A. 2000. Influence of spatial and temporal factors on vocal activity of the steppe marmot, *Marmota bobak*. Zoologicheskii Zhurnal 79:338-347.
Nikol'skii, A. A., V. M. Kotlyakov, and D. T. Blumstein. 1999. Glaciation as a factor of geographic variation in the long-tailed marmot (bioacoustical analysis). Doklady Biological Sciences 368:509-513.
Nikol'skii, A. A., N. L. Nesterova, and M. V. Suchanova. 1994. Situational variations of spectral structure in *Marmota bobac* Müll. alarm signal, Pages 127-148 *in* V. Y. Rumiantsev, ed. Actual problems of marmots investigation. Moscow, ABF Publishing House.
Nikol'skii, A. A., and O. B. Pereladova. 1994. An alarm call of Menzbier's marmot (*Marmota menzbieri* Kaschk., 1925), Pages 149-168 *in* V. Y. Rumiantsev, ed. Actual problems of marmots investigation. Moscow, ABF Publishing House.
Nikol'skii, A. A., E. E. Roschina, and O. V. Soroka. 2002. New conformation of correlation between the relief's desmemberment and the alarm call's temporal organiszton (on instance of *Marmota bobac*) *in* K. B. Armitage, and V. Y. Rumiantsev, eds. Holarctic Marmots as a Factor of Biodiversity-Proceedings of the 3d International Conference on Marmots, Cheboksary , Russia, 25-30 August 1997. Moscow, ABF Publishing House.
Nikol'skii, A. A., and V. P. Starikov. 1997. Variation in the alarm call in ground squirrels *Spermophilus*

major and *S. erythrogenys* (Rodentia, Sciuridae) in the contact zone in the Kurgan Oblast. Russian Journal of Zoology 1:340-351.
Nikolskii, A. 1974. Geographical variability of sound call rhythmic organization in marmots of the group Bobac (Rodentia, Sciuridae). Zoologicheskii Zhurnal 53:436-444.
Nikolskii, A. A. 1979. Species specificity of the alarm call in suslics (*Citellus*: Sciuridae) of Eurasia. Zoologicheskii Zhurnal 58:1183-1194.
Nikolskii, A. A. 1984. Sound signals of the mammals in the evolutionary process. Moscow, Nauka.
Nikolskii, A. A., and N. L. Nesterova. 1989. Responses of *Marmota baibacina* to con- and heterospecific vocalizations. Vest. Moscow Univ. 16(3):50-55.
Nikolskii, A. A., and N. L. Nesterova. 1990. Perception of acoustic signals by *Marmota caudata* (Sciuridae, Rodentia). Vest. Moscow Univ. 16(1):53-59.
Nikolskii, A. A., and M. V. Sukhanova. 1992. Situation dependent variations of a call emitted by great gerbil, *Rhombomys optimus* and by Brandt's vole, *Microtus brandti*, retreating to burrows. Zoologicheskii Zhurnal 71(12):125-132.
Nikolskiy, A. A., V. P. Denisov, T. G. Stojko, and N. A. Formosov. 1984. The alarm call in F1 hybrids *Citellus pygmaeus* x *C. suslica* (Sciuridae, Rodentia). Zoologicheskii Zhurnal 63:1216-1225.
Nowak, R. M. 1991. Walker's mammals of the world, 5th ed. Baltimore, Johns Hopkins Univ. Press.
O'Farrell, M. J., and A. R. Blaustein. 1974. *Microdipodops pallidus*. Mammalian Species 47:1-2.
Owings, D. H., and R. G. Coss. 1977. Snake mobbing by California ground squirrels: adaptive variation and ontogeny. Behaviour 62:50-68.
Owings, D. H., and D. F. Hennessy. 1984. The importance of variation in sciurid visual and vocal communication, Pages 169-200 *in* J. O. Murie, and G. R. Michener, eds. The biology of ground-dwelling squirrels. Lincoln, University of Nebraska Press.
Owings, D. H., and W. J. Loughry. 1985. Variation in snake-elicited jump-yipping by black-tailed prairie dogs: ontogeny and snake-specificity. Zeitschrift für Tierpsychologie 70:177-200.
Perla, B. S., and C. N. Slobodchikoff. 2002. Habitat structure and alarm call dialects in Gunnison's prairie dog (*Cynomys gunnisoni*). Behavioral Ecology 13:844-850.
Pepper, J. W., S. H. Baraude, E. A. Lacey, and P. W. Sherman. 1991. Vocalizations of the naked mole-rat, Pages 243-274 *in* P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander, eds. The biology of the naked mole-rat. Princeton, Princeton University Press.
Pinker, S. 1994. The language instinct. New York, William Morrow and Company, Inc.
Randall, J. A. 1989. Individual footdrumming signatures in banner-tailed kangaroo rats *Dipodomys spectabilis*. Animal Behaviour 38:620-630.
Randall, J. A. 1994. Convergences and divergences in communication and social organisation of desert rodents. Australian Journal of Zoology 42:405-433.
Randall, J. A. 2001. Evolution and function of drumming as communication in mammals. American Zoologist 41:1143-1156.
Randall, J. A., and M. D. Matocq. 1997. Why do kangaroo rats (*Dipodomys spectabilis*) footdrum at snakes? Behavioral Ecology 8:404-413.
Randall, J. A., and K. A. Rogovin. 2002. Variation in and meaning of alarm calls in a social desert rodent *Rhombomys opimus*. Ethology 108:513-527.
Randall, J. A., K. A. Rogovin, and D. M. Shier. 2000. Antipredator behavior of a social desert rodent: footdrumming and alarm calling in the great gerbil, *Rhombomys opiums*. Behavioral Ecology and Sociobiology 48:110-118.
Redford, K. H., and J. F. Eisenberg. 1992, Mammals of the neotropics. vol. 2: the southern cone. Chicago, University of Chicago Press.
Roberts, T. J. 1977. The mammals of Pakistan. London, Ernest Benn Ltd.
Schleidt, W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. Journal of Theoretical Biology 42:359-386.
Schluter, D. 2002. Character displacement, Pages 149-150 *in* M. Pagel, ed. Encyclopedia of evolution. New York, Oxford University Press.
Schwagmeyer, P. L. 1980. Alarm calling behavior of the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*. Behavioral Ecology and Sociobiology 7:195-200.
Shelley, E.L. and D.T. Blumstein. 2005. The evolution of vocal alarm communication in rodents. Behavioral Ecology 16:169-177.
Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. Science 197:1246-1253.

Sherman, P. W. 1980. The limits of ground squirrel nepotism, Pages 505-544 *in* G. W. Barlow, and J. Silverberg, eds. Sociobiology: beyond nature/nurture? Boulder, Westview Press.
Sherman, P. W. 1980. The meaning of nepotism. American Naturalist 116:604-606.
Sherman, P. W. 1981. Kinship, demography, and Belding's ground squirrel nepotism. Behavioral Ecology and Sociobiology 8:251-259.
Sherman, P. W. 1985. Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? Behavioral Ecology and Sociobiology 17:313-323.
Shields, W. M. 1980. Ground squirrel alarm calls: nepotism or parental care? American Naturalist 116:599-603.
Shriner, W. M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Animal Behaviour 55:529-536.
Slobodchikoff, C. N., and R. Coast. 1980. Dialects in the alarm calls of prairie dogs. Behavioral Ecology and Sociobiology 7:49-53.
Slobodchikoff, C. N., J. Kiriazis, C. Fischer, and E. Creef. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. Animal Behaviour 42:713-719.
Smith, C. C. 1978. Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). Journal of Mammalogy 59:793-808.
Smith, S. F. 1978. Alarm calls, their origin and use in *Eutamias sonomae*. Journal of Mammalogy 59:888-893.
Smith, W. J., S. L. Smith, E. C. Oppenheimer, and J. G. Devilla. 1977. Vocalizations of the black-tailed prairie dog, *Cynomys ludovicianus*. Animal Behaviour 25:152-164.
Swaisgood, R. R., D. H. Owings, and M. P. Rowe. 1999. Conflict and assessment in a predator-prey system: ground squirrels versus rattlesnakes. Animal Behaviour 57:1033-1044.
Swaisgood, R. R., M. P. Rowe, and D. H. Owings. 1999. Assessment of rattlesnake dangerousness by California ground squirrels: exploitation of cues from rattling sounds. Animal Behaviour 57:1301-1310.
Tamura, N. 1989. Snake-directed mobbing by the Formosan squirrel *Callosciurus erythraeus thaiwanensis*. Behavioral Ecology and Sociobiology 24:175-180.
Tamura, N., and H.-S. Yong. 1993. Vocalizations in response to predators in three species of Malaysian *Callosciurus* (Sciuridae). Journal of Mammalogy 74:703-714.
Trivers, R. L. 1971. The evolution of reciprocal altruism. Quarterly Review of Biology 46:35-57.
Turner, L. W. 1973. Vocal and escape responses of *Spermophilus beldingi* to predators. Journal of Mammalogy 54:990-993.
Van Den Brink, F. H. 1968, A field guide to the mammals of Britain and Europe. Boston, Houghton Mifflin Company.
Viljoen, S. 1983. Communicatory behaviour of southern African tree squirrels, *Paraxerus palliatus ornatus*, *P. p. tongensis*, *P. c. cepapi* and *Funisciurus congicus*. Mammalia 47:441-461.
Waring, G. H. 1966. Sounds and communications of the yellow-bellied marmot (*Marmota flaviventris*). Animal Behaviour 14:177-183.
Warkentin, K. J., A. T. H. Keeley, and J. F. Hare. 2001. Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. Canadian Journal of Zoology 79:569-573.
Weary, D. M., and D. L. Kramer. 1995. Response of eastern chipmunks to conspecific alarm calls. Animal Behaviour 49:81-93.
Wiley, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. American Naturalist 138:973-993.
Wilkinson, G. S. 2002. Reciprocal altruism, Pages 985-990 *in* M. Pagel, ed. Encyclopedia of evolution. New York, Oxford University Press.
Wilson, D. E., and D. M. Reeder. 1993. Mammal species of the world. Washington, D.C., Smithsonian Institution Press.
Wolff, J. O. 1980. Social organization of the taiga vole (*Microtus xanthognathus*). The Biologist 62:34-45.
Wood, S. R., K. J. Sanderson, and C. S. Evans. 2000. Perception of terrestrial and aerial alarm calls by honeyeaters and falcons. Australian Journal of Zoology 48:127-134.
Youngman, P. M. 1975, Mammals of the Yukon territory. Ottawa, National Museum of Canada.
Zuberbühler, K. 2000. Referential labelling in Diana monkeys. Animal Behaviour 59:917-927.