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# The Evolution, Function, and Meaning of Marmot Alarm Communication

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## I. Introduction

When strolling through your favorite habitat, it is not uncommon to hear birds or mammals emit alarm calls (Klump and Shalter, 1984), particularly if you're strolling with a domestic predator! These striking and often easily identified vocalizations are often loud and localizable (Hurd, 1996; Wood *et al.*, 2000) and may be directed to both predators and conspecifics. Because predators may be better able to locate a caller, emitting these calls creates an evolutionary paradox: why call if it increases the likelihood of a caller being detected by a predator and killed (Maynard Smith, 1965)? One solution to this paradox is that if, by calling, individuals save their relatives, kin selection can explain its adaptive utility (Keller and Reeve, 2002). Alarm calls are thus a system in which we can study the dynamics of altruism. Moreover, because alarm calls may be directed to conspecifics, we can study their meaning. By *meaning*, I refer here specifically to their information content (Halliday, 1983; Macedonia and Evans, 1993). Calls could contain potentially referential information about the specific type of predator, and/or calls could contain information about the degree of risk that the caller faces when calling (Evans, 1997; Macedonia and Evans, 1993). Alarm calling is thus a system in which we can study the evolution and adaptive utility of complex communication and referentiality—a necessary component of human language. Calls can also contain other information, such as the identity, sex, and age of the caller. Thus, alarm-calling systems may offer us some unique insights into the adaptive significance of individuality.

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In this chapter, I summarize two decades of work studying marmot alarm communication. Marmots are large, ground-dwelling sciurid rodents, and I have studied 8 of the 14 species. My work has been conducted in Canada (Vancouver Island marmots—*Marmota vancouverensis*), Berchtesgaden National Park, Germany (Alpine marmots—*M. marmota*); Khunjerab National Park, Pakistan (golden marmots—*M. caudata aurea*), The Chuvash Republic, Russia (steppe marmots—*M. bobak*), and the United States (Mt. Rainer National Park, hoary marmots—*M. caligata*; Olympic National Park, Olympic marmots—*M. olympus*; Kansas and Ohio, woodchucks—*M. monax*; Capital Reef National Park, Utah, The Rocky Mountain Biological Laboratory, Colorado, and around Boulder, Colorado, yellow-bellied marmots—*M. flaviventris*). Marmots are an outstanding model system to study alarm call function and meaning because they are diurnal, live in discrete locations, alarm call when they encounter a variety of predators, and, unlike some of their more distant sciurid relatives (Leger *et al.*, 1980), emitting alarm calls in nonpredator contexts is relatively rare. My work has focused on three of the four Tinbergian questions (Tinbergen, 1963): the evolution, adaptive utility, and meaning of alarm calls. I also have thought about the applied value of studying alarm communication; a type of question that I have suggested could be considered as a ''fifth question'' (Blumstein, 2007b).

## II. Evolution

Marmots produce a variety of whistles, chirps, and chucks. Figure 1 illustrates spectrograms from all 14 species. It is immediately obvious that some species produce multiple alarm call types, while others produce only a single type of call. Interestingly, and unlike sexually selected vocalizations or those involved in species identification, these alarm calls are used in a single context: signaling alarm. What explains this variation in alarm call structure?

Some variations in call structure might be explained by the intended recipient. Alarm calls can be directed both to predators and to conspecifics. Generally, calls may be directed to conspecifics to warn them about the presence of a predator (Blumstein and Armitage, 1997a; Sherman, 1977) 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) and may thus be a general case of detection signaling. They may also attract other predators—which would create competition or predation on one predator by another, thus allowing the prey to escape (Högstedt, 1983).

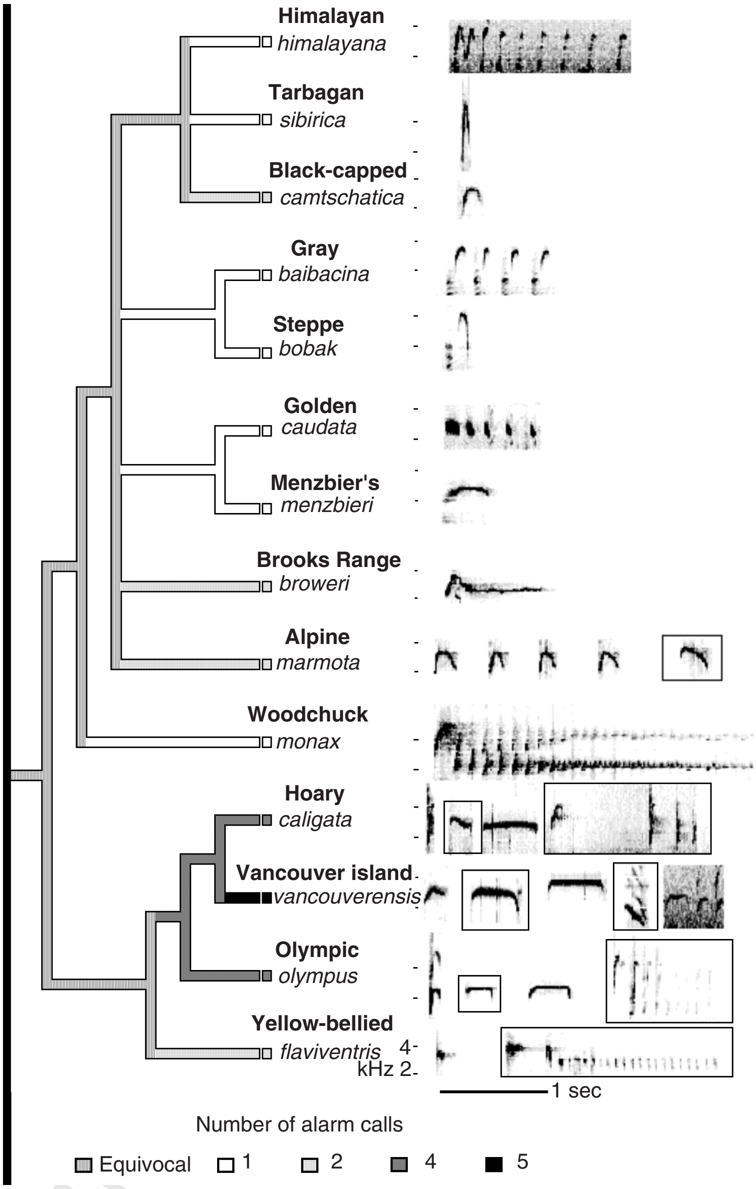

FIG. 1. Marmot phylogeny and spectrograms (256 point FFT, 50% overlap Canary spectrograms generating a frequency resolution of 5.75 ms × 86.93 Hz) of the alarm call repertoire of all 14 species along with hypothesized reconstruction of alarm call repertoire size. Reproduced with permission from Blumstein (2003). The partially resolved phylogeny is based on Kruckenhauser *et al.* (1999) and Steppan *et al.* (2000). For species with multiple call types, boxes separate adjacent call types.

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A comparative study sheds light on the ancestral function of alarm calling in rodents (Shelley and Blumstein, 2005). Erin Shelley and I focused on 209 species of rodents and noted whether or not they produced alarm calls. Social species should benefit from producing alarm calls, either by nepotistic or potentially reciprocal benefits. Thus, if calling evolved to have a conspecific alarming function, then we would expect that the evolution of sociality would precede the evolution of calling. We scored species as social if they were likely to live near kin; either because they lived in family groups or because they lived in colonies. However, producing alarm calls is a potentially risky behavior that may attract the attention of predators. If calling evolved to be directed towards predators, we assumed that individuals would only do so when they were relatively safe. Thus, producing them in the dark, where it is difficult to assess and manage predation risk, may be particularly risky. If calling evolved to be directed toward predators, we might expect that the evolution of diurnality would precede the evolution of calling. We noted whether they were predominantly active during the day or night, and whether they were never active at night (this reduced our sample size to 156 species for which we had sufficient data).

We used nonphylogenetic and phylogenetic techniques to study the evolution of calling in rodents using our 209 and 156 species data sets (Shelley and Blumstein, 2005). In nonphylogenetic logistic regressions, we found that more variation in the likelihood of calling was explained by diurnality (25–44%) than by sociality (7–8%). There was a weak relationship between sociality and diurnality (6–7% of the variation was explained). Phylogenetic analyses supported the hypothesis that calling was likely to evolve *following* the evolution of diurnality, but not following the evolution of sociality. These results are consistent with the hypothesis that the evolution of diurnality preceded the evolution of alarm calling. We inferred from this that calling may have initially evolved as a means to communicate with the predator, and we suggested that its initial function was detection signaling that was subsequently exapted (Gould and Vrba, 1982) to serve its conspecific warning function.

Call structure may also shed some light on the target. For instance, we expect signals that are directed to a predator to be ‘‘obvious.’’ Marler (1955) suggested that songbird mobbing calls illustrate this in that they are broadband, rapidly repeated sounds that are easy to localize. In contrast, songbird alarm calls elicited by aerial predators are difficult to localize because they have a relatively narrow bandwidth and fade in and out (Marler, 1955).

Unlike cockerels, which, when alarmed by terrestrial predators produce uniquely wide bandwidth, rapidly paced calls, and, when alarmed by aerial predators, produce high-frequency hard to hear faint whistles (Evans, 1997; Evans *et al.*, 1993); all marmot species I have studied do not have such production specificity. Rather, calls seemingly communicate the degree of risk a caller faces when calling (see the description later). Some marmot species emit calls that are less obvious as risk increases. Using a human as a threatening stimulus, I found that golden marmots, which have multinote calls, emit calls with fewer notes as risk increases (i.e., as a person gets closer to the caller) (Fig. 2). Alpine marmots repeat a simple note different number of times and emit calls with fewer repetitions as risk increases (Fig. 2). By contrast, other species make themselves more obvious as risk increases. Yellow-bellied marmots called more rapidly (Fig. 3) and emit more calls as risk increases, variables that influenced their responsiveness to playback (Fig. 3). Thus, even among congeners, mechanisms to potentially communicate risk vary, a theme that will be developed later.

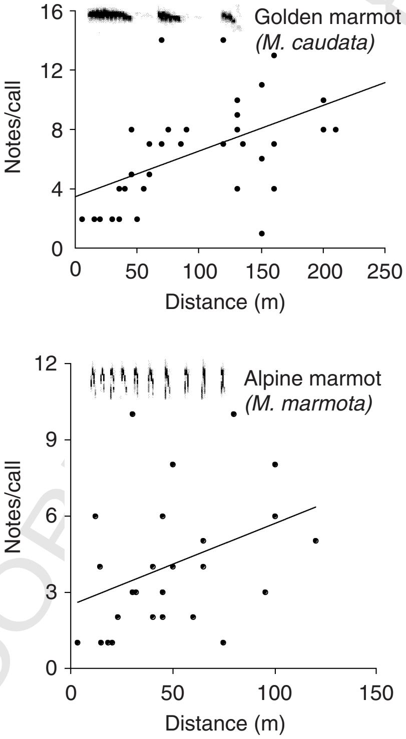

FIG. 2. Golden marmots produce first calls with fewer notes (adjusted $R^2 = 0.254, p < 0.001$), and alpine marmots produce first calls with fewer repeated notes (adjusted $R^2 = 0.10$, one-tailed $p = 0.031$), as the distance to an approaching human decreases. [Redrawn from Blumstein (1995a) and Blumstein and Arnold (1995), and used with permission from Blackwell Publishing; inset: alarm call spectrograms.]. A one-tailed *p*-value is reported for alpine marmots because of an *a priori* directional hypothesis.

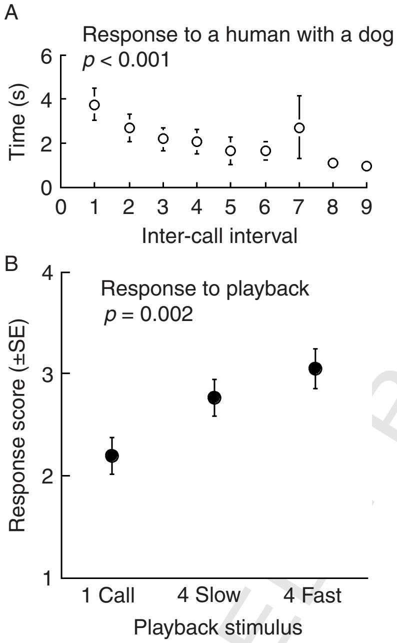

FIG. 3. (A) The response of yellow-bellied marmots to a human approaching with a dog. The intercall interval 1 = the time between the first and second call, intercall interval 2 = the time between the second and third call, and so forth. Intercall interval decreased significantly ($p < 0.01$) demonstrating that marmots emitted calls at a faster pace as risk increased. (B) Yellow-bellied marmots responded to both the number and rate of calls played back to them. Responses were scored: 0 = no response; 1 = stand and look, 2 = rear and look, 3 = rear-up on hind legs in upright position and look, and 4 = retreat to burrow. All calls were played back at 93 dB SPL.

Another factor that could explain variation in call structure is the acoustic habitat. The environment modifies the structure of all signals, often in predictable ways (Bradbury and Vehrencamp, 1998; Slabbekoorn, 2004). Attenuation is inevitable and many environments create ‘‘excess attenuation’’ (attenuation greater than −6 dB per doubling distance—Bradbury and Vehrencamp, 1998). There is also degradation—the inevitable loss of fidelity. Sounds that are transmitted through predictable habitats should lead to predictable attenuation and degradation (Naguib and Wiley, 2001). If animals can adapt their vocalizations to this challenge, the acoustic adaptation hypothesis predicts that a species' call should be best transmitted in its own habitat (Morton, 1975). This hypothesis was developed by ornithologists to explain the striking difference in birdsongs and birdcalls in dense forests (where they are frequently relatively tonal) as opposed to more open grasslands where they are more "buzzy." Support for the hypothesis comes from intraspecific studies of tits (Hunter and Krebs, 1979) and sparrows (Handford, 1988; Handford and Lougheed, 1991). Interspecific studies supporting the hypothesis (Wiley, 1991) have relied on large data sets of many species and have found that the strongest effects were from the most different habitat types (dense forests and grasslands) suggesting that smaller differences in environments may not have the same effect (Blumstein and Turner, 2005).

Janice Daniel and I tested the hypothesis that a marmot species' alarm call is best transmitted in its own habitat (Daniel and Blumstein, 1998). First, we broadcast and rerecorded 3 kHz pure tones (chosen because this is the dominant frequency of marmot alarm calls) as well as a species' own calls through a number of social groups within a species' habitat. Calls were broadcast and rerecorded at 1, 10, 20, 30, and 40 m from the speaker. We used spectrogram correlation (Clark *et al.*, 1987), a technique that compares the structure of two spectrograms, to quantify change in the original signal (i.e., that rerecorded at 1 m) when transmitted 10, 20, 30, or 40 m through the environment. We found significant intraspecific variation in the acoustic transmission properties of the habitats of the three species studied (golden marmots, Alpine marmots, and yellow-bellied marmots—Blumstein and Daniel, 1997). Subsequent analyses have found significant variation in eight species' habitats (Fig. 4). For pure tones, interspecific variation was greater than intraspecific variation in habitat transmission fidelity (Blumstein and Daniel, 1997).

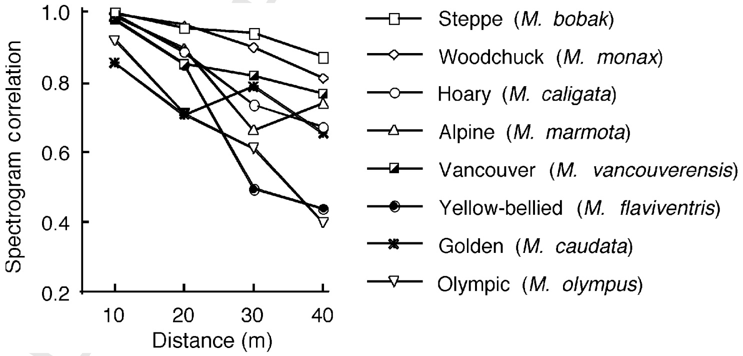

FIG. 4. Average spectrogram correlation values for 3-kHz pure tones broadcast through eight marmot species' habitats illustrating significant differences in the transmission fidelity of the different habitats.

To directly test the acoustic adaptation hypothesis, we systematically broadcast four different species' calls (hoary, Olympic, woodchucks, and yellow-bellied) in the four different species' habitats (Daniel and Blumstein, 1998). If the acoustic adaptation hypothesis explained the variation in the structure of these species' calls, we expected that each species call would be best transmitted in its own habitat. A significant interaction between habitat and call type in spectrogram correlation values would provide support for the acoustic adaptation hypothesis. Using MANOVA, we found significant habitat and species effects, but there was no significant interaction: a species' call is not best transmitted in its own habitat. Importantly, the effect size of the call (partial $\eta^2 = 0.80$) was larger than the effect size of the habitat (partial $\eta^2 = 0.31$) and this was much larger than the effect size of the interaction (partial $\eta^2 = 0.08$). Together, the results suggest that there are some calls that transmit well and some that transmit poorly, and that there is substantial variation in the transmissibility of habitats, but that the habitat has little effect on the evolution of differences in call microstructure.

By examining acoustic variation in isolated populations, among phylogenetically close relatives, and by examining the results of studies where sciurids have been isolated on islands, it is possible to hypothesize that drift, not selection, may be responsible for microstructural changes in call structure (Blumstein, 1999a; Daniel and Blumstein, 1998). For instance, long-tailed marmot calls (the golden marmots that I studied are a named subspecies of the long-tailed marmot) are geographically variable and this variation seems to be associated with a pattern of isolation by glaciation (Nikol'skii *et al.*, 1999). Sibling species, such as the hoary and Olympic marmot, have acoustically similar calls as do the closely related steppe marmot, black-capped marmot (*M. baibacina*), and tarbagan (*M. sibirica*). Finally, the structure of squirrel alarm calls, isolated by sea level changes on islands, has begun to diverge in as few as 7500 years (Nikolsky, 1981). Given the potential importance of drift, it is surprising that we found no geographic variation in yellow-bellied marmot alarm calls studied at three locations in Utah and Colorado (Blumstein and Armitage, 1997a). However, recent molecular evidence found substantial gene flow even between isolated populations, perhaps providing the solution to this puzzle (Floyd *et al.*, 2005).

If drift explains variation in the call microstructure, what explains variation in repertoire size? I studied three factors that could influence repertoire size: the acoustic environment, home range size, and sociality.

I ranked the acoustic transmission characteristics for eight species by summing the spectrogram correlation values at 10, 20, 30, and 40 m. I hypothesized that species living in acoustic environments that better allowed the transmission of 3-kHz pure tones could potentially communicate more complex information and thus should have larger call repertoire sizes. In these and the following analyses, I fitted regressions on raw data and on phylogenetically independent contrasts; results were similar. Either way analyzed, there was no relationship between the transmission fidelity of a habitat and the number of alarm call types (Fig. 5).

I collected home range size estimates from the literature and hypothesized that species living in larger home ranges would need to communicate more precise information and thus might have larger call repertoires. This might be expected because when distances between signalers and receivers are large, there is likely to be greater uncertainty about the true risk. If we assume that callers directing calls to conspecifics would benefit by the reduced ambiguity of using acoustically different calls, then we would expect that species with larger home ranges would have a larger call repertoire. In the raw data, there was a weak positive relationship between home range size and call repertoire size (Fig. 5). However, when results were examined in a contrast-based analysis, this relationship disappeared. The conservative interpretation is thus that there was no relationship between home range size and call repertoire size.

I used the Blumstein and Armitage (1997b, 1998) social complexity metric to quantify sociality. This metric focuses on the demographic roles present in a social group (adult males/females, 2-year-old males/females, yearling males/females, and pups) and uses information theory to quantify the variation in social structure. This acknowledges that social complexity requires some description of the number of roles and the number of individuals, and it acknowledges that social complexity emerges from variable social situations. Because species also vary in the time to natal dispersal, and thus social groups vary in the degree of relatedness within them, the number emerging from the information theory analysis is multiplied by the time to natal dispersal. By doing so, the metric assumes that kin groups are more socially complex than nonkin groups. In both analyses of species values and in contrast-based analyses, I found that more socially complex species produce more alarm call types (Blumstein, 2003).

In an analysis of independent contrasts that controlled for variation in alarm call repertoire size explained by transmission fidelity (one-tailed $p = 0.49$), 57% of the variation in repertoire size was explained by social complexity (one-tailed $p = 0.04$). Similarly, after accounting for nonsignificant variation explained by home range size (one-tailed $p = 0.37$), 59% of the variation in repertoire size was explained by social complexity (one-tailed $p = 0.05$). Thus, it seems that social complexity is relatively more important than either the acoustic habitat or the home range size in explaining variation in alarm call repertoire size in the marmots studied

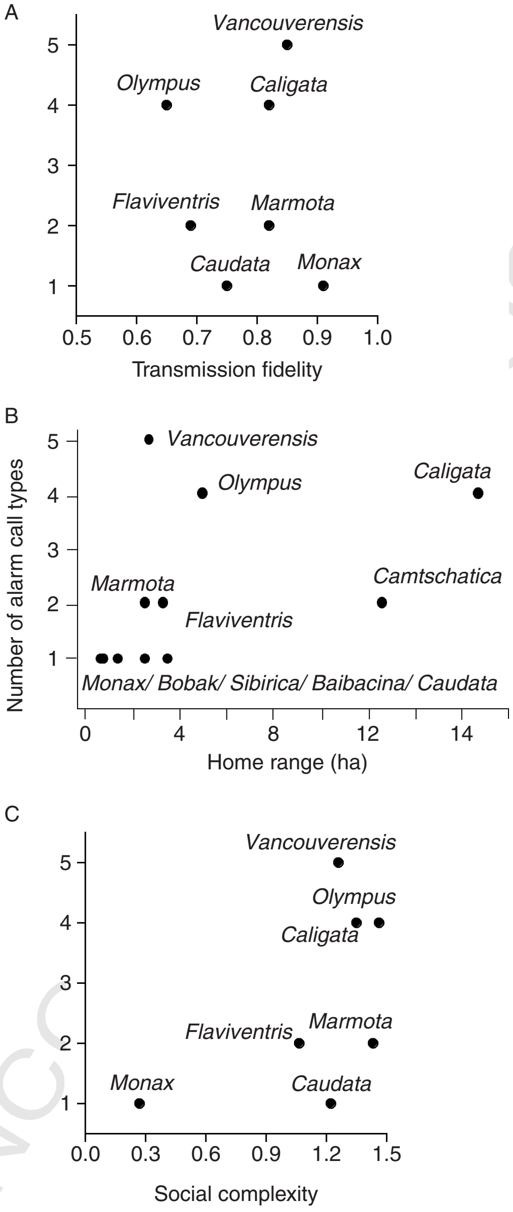

FIG. 5. Bivariate relationships between (A) habitat transmission fidelity, (B) home range size, or (C) social complexity and alarm call repertoire size (number of alarm calls) in marmots. [Modified in part with permission from Blumstein (2003).] Species values are plotted. In an analysis of independent contrasts that controlled for variation in alarm call repertoire size

to date. These results suggest that social complexity (see also Blumstein and Armitage, 1997b), not simply the need to communicate over long distances, selects for complex communication.

In summary, alarm calling seems to have initially evolved as a means of detection signaling to predators. Conspecific warning functions are thus an exaptation, the adaptive utility of which will be discussed in the next section. Because some species make themselves more obvious as predation risk increases, there is likely a dual function of alarm calling. The structure of alarm calls is variable and this variation is likely to reflect drift processes, rather than selection from the acoustic environment. Marmots produce different numbers of alarm call types and a significant amount of variation in repertoire size is explained by sociality.

## III. FUNCTION

The apparent paradox I discussed in the introduction, as to why animals should produce potentially costly vocalizations that warn others, will be discussed here. I confess at the outset that I have not demonstrated that emitting calls increase predation risk (in thousands of hours watching marmots, I have only seen one complete predation event, and in many more thousands of hours, my assistants have only seen a few successful predatory episodes on adults), nor did I specifically document other costs of calling. In theory, alarm calls could have an energetic cost, but even studies of birdsong do not always quantify substantial energetic costs (Ward *et al.*, 2003), and alarm calls are relatively rare events and thus should be even less costly. For instance, in yellow-bellied marmots, we document a bout of calling every 2.1 h of observations (between 2002 and 2006, we noted 1677 bouts of calling in 3553 h of direct observation). However, individuals that call remain vigilant and reduce time allocated to other activities when they call. Individuals that respond to calls trade-off foraging and other activities with antipredator vigilance. Au3

Thus, if we assume that calling (and responding to calls) has some opportunity cost (Blumstein, 2007a), let us now focus on potential benefits from calling. I previously discussed potential benefits from calls directed to *predators*. Most species of marmots do not engage in contagious calling where the calls of one individual elicit calls from other individuals (e.g., as

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found in some primates—Zuberbühler, 2001). Contagious calling is consistent with the hypothesis that callers were signaling detection and were thus directing their calls at the predator where each individual benefits (Zuberbühler *et al*., 1999). The one exception is the Olympic marmot, which in response to playback sometimes called (Blumstein, 1999a). In all species I have studied, it is not uncommon to only hear one or a few individuals' alarm calls as a predator passes through an area. But marmots do respond to the calls of other marmots by increasing their vigilance and retreating to their burrows. Here, I focus on the adaptive utility of calls directed to *conspecifics* while acknowledging that calls could simultaneously function to deter pursuit (Caro, 2005).

Reciprocal altruism (Trivers, 1971) appears to be unimportant in alarm-calling systems. There is no evidence from any sciurid rodent alarm-calling system that individuals engage in reciprocal bouts of calling (Blumstein, 2007a). In some respects, this is puzzling because calls are often sufficiently individually identifiable (see the description later), animals are able to remember important attributes associated with callers (see the description later), and because such a system would limit the cost to any given caller. In other respects, this is not puzzling because calling is a relatively rare and important thing to do, and because there is no guarantee that a recipient today will be around to warn an actor tomorrow. Moreover, reciprocity works best when there is a direct transfer of benefits between two individuals; eavesdropping by multiple recipients destabilizes the process (Blumstein, 2007a). Finally, the legacy of calls being directed to predators may constrain calling when there is a direct benefit from doing so.

That said, the sight of a predator does not inevitably elicit calling. In all the species of marmots I have studied, not all individuals call when a predator is within sight. It seems that individuals do not emit alarm calls unless they themselves are safe. This is in contrast to what has been reported in Belding's ground squirrels (Sherman, 1985), other mammals (Caro, 2005), and some birds (Cresswell, 1993) which may call while being pursued by particularly threatening predators. By contrast, marmots do not call first and then run to safety. Rather, they retreat to safety, increase their vigilance, and then decide whether or not to emit an alarm call. So what influences the probability of calling?

One factor that may influence the probability of calling is the caller's endocrine state. We used a ''trap-calling assay'' where we noted whether individuals called when we approached them in traps. Importantly, subjects who are more likely to call when in a trap are more likely to call when approached or when they encounter a predator (Blumstein *et al*., 1997). We amassed a data set of 29 breeding-age females who called on one occasion, but not on another, and we compared fecal glucocorticoid levels on these

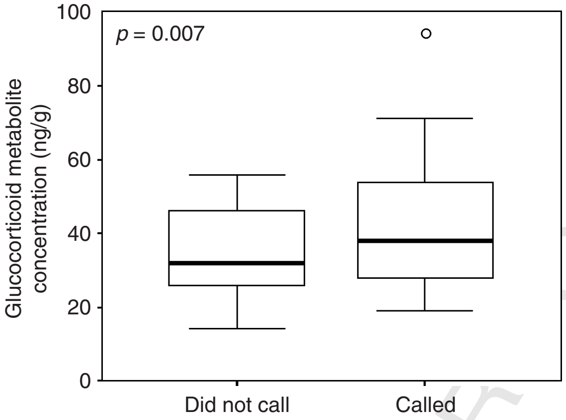

FIG. 6. Fecal corticosteroid metabolites in adult female yellow-bellied marmots on an occasion when they emitted a call and on another occasion when they did not emit a call. [Modified from Blumstein *et al.* (2006a) and used with permission from the Royal Society.]

two occasions (Fig. 6). Our results were not confounded by some factors known to influence glucocorticoid levels, including time of day, age, breeding status, and time of season. We found that fecal glucocorticoid metabolites in individuals that emitted calls on one day but not on another had systematically higher levels of this "stress" hormone on days when they called (Blumstein *et al.* 2006a). State, specifically stress level (as estimated by glucocorticoid metabolites), thus provides a mechanism that could explain why some individuals are more likely to call when particular relatives are within earshot (see the description later). State also provides a plausible mechanism that could influence caller reliability (discussed later).

Building on excellent studies from Sherman (1977) and Hoogland (1995) that showed that Belding's ground squirrels and black-tailed prairie dogs are exquisitely sensitive to their audience and modify call production based on the presence or absence of both direct and indirect kin, we (Blumstein *et al.*, 1997) asked whether and how yellow-bellied marmot call production is sensitive to the presence of indirect kin within earshot. In a series of analyses that looked at how the propensity of calling was influenced by the presence, absence, or number of conspecifics, we found that female yellow-bellied marmots substantially, significantly, and somewhat uniquely increased the rate of calling after they had emergent young (Table I). Our observations do not support the hypothesis that the presence of indirect kin influenced either the rate of calling or the likelihood of calling [e.g., only mothers increased calling in response to the presence of vulnerable pups in

TABLE I

Calling Rates Before and After Pup Emergence

| | Adult female (mother) | Adult females | Adult males | Yearling females | Yearling males |
|---|---|---|---|---|---|
| 1995 | $N = 4$ | $N = 10$ | $N = 3$ | $N = 6$ | $N = 5$ |
| Rate < | **0.05 (±0.04)** | 0.08 (±0.05) | 0.06 (±0.05) | 0.03 (±0.02) | 0.05 (±0.02) |
| Rate > | **0.31 (±0.12)** | 0.04 (±0.08) | 0.01 (±0.01) | 0.00 (±0.00) | 0.07 (±0.06) |
| Rate (total) | 0.18 (±0.07) | 0.06 (±0.06) | 0.03 (±0.02) | 0.01 (±0.01) | 0.06 (±0.03) |
| 1980, 1985, 1991 | $N = 20$ | $N = 9$ | $N = 6$ | $N = 14$ | $N = 12$ |
| Rate < | **0.02 (±0.05)** | 0.04 (±0.03) | 0.05 (±0.07) | 0.02 (±0.04) | 0.01 (±0.02) |
| Rate > | **0.08 (±0.10)** | 0.003 (±0.01) | 0.02 (±0.03) | 0.04 (±0.11) | 0.02 (±0.04) |
| Rate (total) | 0.05 (±0.08) | 0.01 (±0.02) | 0.03 (±0.04) | 0.02 (±0.03) | 0.01 (±0.02) |

Table from Blumstein *et al.* (1997) and used with permission from Elsevier.

Alarm-calling rates (bouts of alarm calls/h ± SD) before pups emerged above ground (rate <), after pups emerged above ground (rate >), and the overall seasonal average (total rate during the two periods over which marmot alarm calling was quantified: 1995 summer only, and the composite of 1980, 1985, and 1991). Note the substantial (and significant) increase in calling by adult females (bold type) after pups emerged.

the social group; the number of other group members (likely to be relatives) had no effect on calling rate, etc.]. Taken together, these results suggest that calling is nepotistic (Sherman, 1980a,b). However, unlike other systems where calling is nepotistically directed to collateral kin, in yellow-bellied marmots, nepotistic behavior is directed to vulnerable young (Blumstein *et al.*, 1997). It is possible that the general patchiness of yellow-bellied marmot colonies and their relatively limited size provides fewer opportunities for nepotism. By contrast, prairie dogs and Belding's ground squirrels often live in much denser populations. Ultimately, it seems that these demographic differences may explain interspecific variation in the adaptive utility of alarm communication (Blumstein, 2007a).

Of course individuals other than mothers produce alarm calls, albeit less frequently. What is their function? Some of it could be detection signaling to predators. These calls also function to warn conspecifics because conspecifics clearly respond to callers (Blumstein and Daniel, 2004). Ultimately, teasing apart the variation explained by these audiences is a fundamentally important question that remains unanswered in any calling species.

In summary, alarm calling appears to have limited costs but some benefits. A primary function of yellow-bellied marmot alarm calling is for mothers to warn vulnerable young; calling by them is a form of parental care. Elevated basal glucocorticoid levels in mothers with young may provide a proximate mechanism underlying this pattern. This hypothesis remains to be formally tested, and experiments must be conducted to properly identify causality. The adaptive significance of calling by non-mothers may be different, and identifying the relative importance of conspecific and heterospecific audiences remains to be clarified.

## IV. MEANING

Alarm calls could potentially contain information about: the species producing the call, the predator type eliciting the call, the risk a caller experiences when it calls, and caller's age, sex, condition, and identity. My interests in alarm calling originally stemmed from a desire to study the evolution of complex communication and language (Cheney and Seyfarth, 1990; Evans and Marler, 1995; Snowdon, 1993). I adopted a trait-based view of language evolution and focused on referential ability (Blumstein, 1999b). Human language is notable in the degree to which we can assign arbitrary acoustic labels to types of stimuli (Hockett, 1960) and the ability to communicate referential information is amenable to comparative study if one studies more than a single species. Referential signals communicate information about environmental events, objects, or perhaps actions (Evans, 1997). Marler *et al.* (1992) coined the term ''functional reference'' to focus specifically on animals' abilities and to avoid any connotation of higher-level representational cognitive abilities. I believe this distinction is important because it is theoretically possible to have referential abilities without having the ability to form representations, and the methods to study representations are more rigorous than those that can be used to study functional reference (Evans, 1997). Like human speech, it is important to realize that referentiality is one type of information that could be encoded in an alarm signal; other types include the degree of risk or an individuals' arousal (Manser *et al.*, 2002).

To study functional reference, we must document two things (Marler *et al.*, 1992): the degree of a call's production specificity and a call's contextual independence (or ''perception specificity''). A call with a high degree of production specificity is one that is elicited by a narrow range of stimuli. Because some marmot species were said to have predator-specific calls (Heard, 1977; Lenti Boero, 1992), while others did not, marmots seemed to be an ideal system to study the evolution of referential abilities. However, the second criterion is essential to demonstrate functional reference: calls, divorced from other contextual information, should reliably elicit the appropriate response to a particular referent.

As I systematically elicited calls from a variety of species and conducted playback experiments to determine the degree to which uniquely different calls could elicit different responses, I discovered that none of the marmots I studied had functionally referential calls (Blumstein, 1995a,b, 1999a,b; Blumstein and Armitage, 1997a; Blumstein and Arnold, 1995). None of the species had sufficiently high production specificity to suggest that calls were functionally referential. However, I also learned that marmots used a variety of mechanisms to communicate risk (Table II). Such response urgency or risk-based communication is well known from ground-dwelling sciurid rodents (Owings and Hennessy, 1984; Robinson, 1981; Sloan and Hare, 2004; Warkentin *et al*., 2001). Golden and alpine marmots packaged calls into multinote signals that covaried with the degree of risk a caller experienced. Olympic, hoary, and Vancouver Island marmots had different call types, some of which covaried with the stimulus class (aerial or terrestrial) that elicited the calls. Most species responded to call type variation, while some did not (Blumstein, 1995b). None of the species responded in a way that suggested that unique calls elicited unique responses. And, I discovered things that I did not expect. Vancouver Island marmots appeared to have a simple form of syntax: the order in which different call types were produced influenced response (Blumstein, 1999a).

Discovering this remarkable variation in mechanism suggested two important things. First, as studied so well in some insect and anuran systems (Gerhardt and Huber, 2002), communication mechanisms can evolve quickly: closely related species may have different mechanisms as illustrated by contrasting yellow-bellied marmots (two call types, rated-based

TABLE II

DIVERSITY OF MECHANISMS USED BY MARMOTS TO COMMUNICATE RISK

| Species | No. calls | Mechanism | References |
|---|---|---|---|
| *M. monax* | 1 | [a] | Unpublished observation |
| *M. bobak* | 1 | Rate | Unpublished observation, Nikol'skii *et al*., 1994 |
| *M. caudata aurea* | 1 | Package | Blumstein, 1995a,b |
| *M. flaviventris* | 2 | Number/rate | Blumstein and Armitage, 1997a |
| *M. marmota* | 2 | Package (number?) | Blumstein and Arnold, 1995 |
| *M. olympus* | 4 | Number/rate & call type | Blumstein, 1999a |
| *M. caligata* | 4 | Rate? | Blumstein, 1999a |
| *M. vancouverensis* | 5 | Call duration and bout composition | Blumstein, 1999a |

[a] *M. monax* rarely emit alarm calls and I was unable to conduct playbacks to study mechanism.

mechanism) and Olympic marmots (four call types, rate-based mechanism). Second, it is perhaps more profitable to study what and how animals communicate, rather than trying to force a human construct into a nonhuman system. This is an important lesson that still is not fully appreciated by those searching for ‘‘word’’ analogs in nonhuman signals. The signal may be an utterance, or the signal may have a longer time course. We must let the species under study tell us where to look for meaning. While I value teasing apart the information contained in signals, to do so we may have to look beyond word-like analogies.

In general, we should expect different attributes of signals to contain information about different things (Lambrechts and Dhondt, 1995; Marler, 1960), and the marmot alarm calls illustrate this nicely. By making a number of acoustic measurements, we found that in addition to predation risk, yellow-bellied marmot alarm calls also contain potential information about caller’s age, sex, and identity (Blumstein and Armitage, 1997a; Blumstein and Munos, 2005). Interestingly, these attributes are encoded differently. Risk is communicated by varying the rate and number of calls produced (Blumstein and Armitage, 1997a). Microstructural differences encode sex, age, and identity (Blumstein and Armitage, 1997a; Blumstein and Munos, 2005). In a large data set containing multiple calls recorded from individuals on different occasions, stepwise discriminant function analysis classified over 62% of calls correctly to individual, compared with a less than 1% randomly expected classification (Blumstein and Munos, 2005). By broadcasting and rerecording calls through marmot habitat, Olivier Munos and I also discovered that the acoustic characteristics that encode identity degrade less than a randomly selected set of acoustic characteristics (Blumstein and Munos, 2005). This result provides some suggestion that there has been selection to encode individuality rather than it simply being an unselected by-product of laryngeal morphology (Fitch and Hauser, 1995, 2003; see the description later).

Surprisingly, there have been no studies that have focused strictly on sexual selection in marmots. It is conceivable that alarm calls can be used in mate choice decisions. Cockerels that emit risky aerial alarm calls have higher reproductive success than cockerels that emit fewer risky aerial alarm calls (C. S. Evans, unpublished data). As with other species (Clutton-Brock and Albon, 1979; Davies and Halliday, 1978), it is conceivable that the acoustic characteristics of marmot alarm calls may reflect body condition or size, or simply emitting calls indicate good condition. These are areas open for exploration.

Moving away from marmots, we can ask the broader question of what selects for different alarm call types. One hypothesis is that the need to communicate about mutually incompatible escape options may be important in selecting for functional reference (Macedonia and Evans, 1993). Specifically, if the best escape strategy for evading one predator is to freeze and lay low, while the best escape strategy for another predator is to retreat into a burrow, and if signalers can benefit from communicating this to conspecifics, then we should expect different alarm call types. We see this in fowl: cockerels produce aerial alarm calls, which are relatively cryptic, are associated with the signaler freezing, and also cause recipients to freeze upon hearing them, and terrestrial alarm calls, which are associated with the signaler making himself conspicuous once in a safe location and also cause recipients to flee to safe locations (Evans *et al.*, 1993). The mutually incompatible response hypothesis also explains differences in lemur species that may or may not produce functionally referential calls (Macedonia and Evans, 1993) and seemingly explains why vervet monkeys, some other primates (Cheney and Seyfarth, 1990; Zuberbühler, 2000), a prairie dog (Kiriazis and Slobodchikoff, 2006), a social mongoose (Manser, 2001; Manser *et al.*, 2001, 2002), and a tree squirrel (Greene and Meagher, 1998) have functionally referential calls. I suggest that a comprehensive hypothesis about the evolution of functional reference will combine sociality (which demonstrably is associated with alarm call repertoire size in sciurid rodents) and the mutually incompatible response hypothesis. Such a hypothesis will also have to explicitly acknowledge the two-step process of evolving production specificity and contextual independence (Blumstein, 1999b).

In summary, marmots encode the relative predation risk a caller faces when they call; there is limited referential information contained in their calls. Marmots communicate risk using a variety of mechanisms. Some of these mechanisms potentially communicate risk immediately (producing different call types) while others require a longer time frame for a receiver to extract information about risk (varying the number or rate of calls). In addition to risk, other potentially useful information is also contained in marmot alarm calls. Identifying the potential information in calls and the mechanisms by which it is encoded should lead to a rich understanding of communication.

## V. Individuality and Reliability

Why should alarm calls be individually specific? From a proximate standpoint, laryngeal variation will inevitably lead to some acoustic variation (Fitch and Hauser, 1995, 2003). Is this acoustic variation useful? Individual-specific contact calls (Rendall *et al.*, 1996; Wanker and Fischer, 2001) maintain group stability, while the individual-specific calls that creching birds and mammals produce (Insley, 2000; Jouventin *et al*., 1999; Leonard *et al*., 1997) function to allow parents to reunite with their offspring. In these signaling systems, we should expect there to be selection on both the signaler and the receiver (Searcy and Nowicki, 2005). Selection on the signaler will lead to more distinctive vocalizations, while selection on the receiver will lead to an ability to discriminate among them.

Alarm calls are a bit different because while it is easy to hypothesize the benefits of calling, and of responding to a call, it is more difficult to think about why selection should select for signalers to make distinctive calls when the desired response is to simply warn a vulnerable conspecific or tell a predator that it is been detected (Blumstein, 2007a; Blumstein *et al*., 2004). To address this problem, let us consider both the signaler and the receiver in more detail, and let us assume that individuals differ in the reliability with which they emit calls. Variation in caller reliability is easy to envision if we acknowledge that experience or endocrine state may influence the likelihood of calling. Consider a naïve individual that calls to many stimuli; with experience, fewer stimuli potentiate calls (Cheney and Seyfarth, 1990). If stress levels potentiate calling, and if individuals vary in their stress levels, some are more or less likely to call in any given situation. If stress is unrelated to the true risk of predation, then we can easily envision that stressed subjects may call when there is no risk of predation. In this circumstance, from the receivers' perspective, discriminating reliable callers from unreliable callers is essential so as not to waste time responding to false alarms.

From the signalers' perspective, we still need to know what benefits they might obtain by emitting individually distinctive calls. Several lines of evidence suggest that there has been selection on signalers to make distinctive calls. First, acoustic characteristics that allow us to statistically discriminate between individuals degrade less than a randomly selected set of characteristics (Blumstein and Munos, 2005). Second, as I will discuss later, receivers can discriminate among individuals (Blumstein and Daniel, 2004). Third, more social species seem to have more information content about individuality contained in their calls than less social species (K. Pollard and D. Blumstein, unpublished data). Using information theory, Beecher derived a method to calculate the number of bits of information about individuality contained in a signal (Beecher, 1989a,b). Using these ''Beecher statistics,'' Oliver Munos and I found that there were about 3.4 bits of information about the individual contained in yellow-bellied marmot alarm calls (Blumstein and Munos, 2005). Importantly, this information content would allow marmots to distinguish a maximum of 10 individuals (i.e., $2^{3.4} = 10.5$ individuals)—a number that is consistent with the number of permanent residents in yellow-bellied marmot groups. Working with the more social Olympic marmot, we discovered that these marmots have about 5.6 bits of information about individuality contained in their calls (K. Pollard, S. Cox Griffin, and D. T. Blumstein, unpublished data). Future comparative work will formally test the hypothesis that the evolution of sociality is correlated with the evolution of information contained about individuality; preliminary results are encouraging. Finally, Kim Pollard has developed a stochastic dynamic model suggesting that if callers are surrounded by relatives, and if individuals vary in their reliability, kin selection could select for greater individual distinctiveness (K. Pollard, unpublished data).

Yellow-bellied marmots are able to discriminate individuals solely on the basis of their reliability (Blumstein *et al.*, 2004). To demonstrate this, we conducted a habituation-recovery experiment (Evans, 1997), where we associated the calls of one individual with a threatening stimulus (and thus created a reliable caller) and the calls of another subject with no threatening stimulus (and thus created an unreliable caller). The threatening stimulus was a taxidermic mount of a badger (a marmot predator), and the unthreatening stimulus was the badger covered with a tarp. The habituation series consisted of 10 min of rapidly paced calling with or without the badger present. For such learning experiments, it is essential for pretest and posttest subjects to different exemplars of the habituation series. The key comparison is how a subject's response to calls from the reliable and unreliable callers changes as a function of the habituation series. Thus, it is a before-after treatment-control within-subjects design. Our assay for all these experiments was the amount of time subjects continued to forage on a handful of bait. When not foraging, marmots looked around; in some cases they disappeared into their burrow.

We found that marmots are exquisitely good at detecting variation in caller reliability. A single 10-min exposure to an unreliable caller (a subject whose calls were broadcast while the badger was covered with a tarp) was sufficient for marmots to respond differently (Fig. 7). What was particularly extraordinary was how marmots responded. We expected that yellow-bellied marmots, like some primates (Cheney and Seyfarth, 1988, 1990; Gouzoules *et al.*, 1996; Ramakrishnan and Coss, 2000) and other sciurid rodents (Hanson and Coss, 2001; Hare and Atkins, 2001; Nesterova, 1996) would follow the ''crying wolf'' phenomenon: unreliable individuals would elicit reduced vigilance because marmots had learned that they are unreliable. What we found was the exact opposite. Unreliable callers elicited more vigilance. Results from a second experiment were consistent with this finding: marmots hearing degraded calls (which presumably provided less reliable information about the true risk of predation), suppressed foraging and were more vigilant (Blumstein *et al.*, 2004).

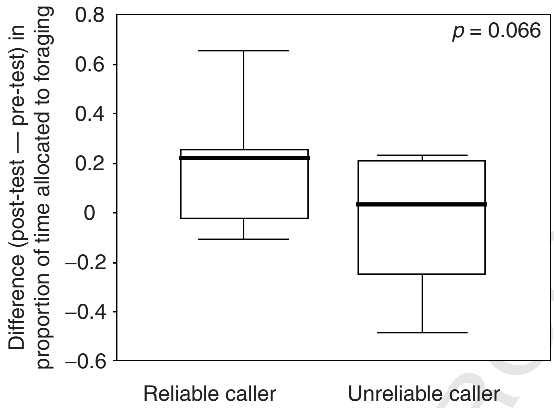

FIG. 7. Response of yellow-bellied marmots (posttraining—pretraining) to a reliable caller and an unreliable caller. [Modified from Blumstein *et al.* (2004) and used with permission from the Royal Society.] Note: Because of the potentially disturbing nature of this experiment, for ethical reasons the sample size was limited and we (*a priori*) set our alpha to 0.1.

I interpret these results as being an alternative way of dealing with uncertainty—when unsure, allocate more time to independent investigation. Unreliable individuals are unreliable specifically because they do not communicate the true risk of predation. Why then would a reliable individual elicit a shorter bout of investigation? Perhaps because looking around a bit was sufficient to know that they must have made a mistake. The overall conclusion parallels lessons from insects and anurans (Gerhardt and Huber, 2002): mechanisms of perception may evolve rapidly and are likely to be as variable as mechanisms of production.

In summary, yellow-bellied marmots and other sciurids produce individually distinctive alarm calls. Individuality seems to correlate with social complexity: the calls of species that are more social contain more bits of information about individuality within them. One function of individually distinctive alarm calls is to allow recipients to differentiate subjects based on their reliability. Surprisingly, yellow-bellied marmots illustrate a unique way by which animals may respond to unreliable subjects. Rather than reducing responsiveness to unreliable callers, they increase responsiveness. Thus, in addition to discovering a novel mechanism to respond to reliability, these results illustrate that, as in insects and anurans, the mechanisms by which individuals respond to signals are somewhat plastic.

## VI. Applied Relevance of Alarm-Calling Behavior

‘‘Conservation behavior’’ is the application of general principles and insights of behavioral biology to conservation biology (Blumstein and Fernández-Juricic, 2004). Previous applications of communication to conservation have focused on using individually discriminable vocalizations to help census populations (Baptista and Gaunt, 1997; McGregor *et al.*, 2000), estimate condition (McGregor *et al.*, 2000), identify population differences (McGregor *et al.*, 2000), and study the effects of anthropogenic noise (Brumm and Slabbekoorn, 2005; McGregor *et al.*, 2000). Clearly, the substantial individual-specific variability in the alarm calls of yellow-bellied marmots (Blumstein and Munos, 2005) and many other species (Davidson and Wilkinson, 2002; Hare, 1998; Nikol’skii and Suchanova, 1994; Rendall *et al.*, 1996; Semple, 2001) suggests that this indeed could be a useful tool to noninvasively census populations. While noninvasive censusing is important, there are other previously unappreciated conservation benefits from understanding alarm-calling behavior.

Fifty percent of marmot species are either IUCN red-listed or are otherwise of conservation interest. The Vancouver Island marmot is one of the most endangered species in the world; at the time of writing, fewer than 50 individuals remained in the wild and managers are using captive breeding and reintroduction to try to recover the population (Bryant, 2005; Bryant and Page, 2005). One early lesson from my Vancouver Island marmot work was that this species had a full repertoire of antipredator behavior, including the ability to produce more alarm call types than any other species (Blumstein *et al.*, 2001). More recent work found that calling and other antipredator behavior apparently persists in captivity (Blumstein *et al.*, 2006b). Thus, alarm calling, and the propensity to alarm call, is a behavior that can be used to understand whether behavior has changed in the relaxed selection induced by some captive breeding programs.

The observation that calls initially evolved as a form of detection signaling has an important conservation message: range expansions by novel predators could have deleterious consequences because novel predators may not have evolved to play the same games (Hugie, 2003) as alarm-calling species. We know that species’ ranges change naturally (Kirkpatrick and Barton, 1997), and unnaturally (through anthropogenic habitat changes and deliberate and accidental translocation—Long, 2003; Low, 1999). We also know that there are likely to be deleterious consequences for prey species when predators change their ranges (Berger *et al.*, 2001; Low, 1999). We should be wary of ritualized interactions that prey may have with their predators, particularly when predators did not evolve with them. Thus, alarm-calling species may be especially vulnerable to the introduction of novel predators. This counterintuitive suggestion requires proper study.

The fecal glucocortioid metabolite results have at least two implications for conservation. First, if calling is a risky behavior in that it exposes animals to predators, we must be very careful about stressing free-living animals—it could increase their exposure. Second, calling may be an indicator of stress (see also Bercovitch *et al.*, 1995; Boinski *et al.*, 1999; Norcross and Newman, 1999) that can be used in both captivity and in the wild. And, if stress is associated with reproductive failure (Abbott *et al.*, 1997; Wasser, 1999), calling in captivity may be a noninvasive indicator that individuals are stressed. In the wild, sudden increases in calling behavior may help identify anthropogenic stressors. Of course, such relationships will be more easily detected in longer term studies of individually identified subjects.

Finally, by studying marmot alarm-calling behavior, we can gain insights into national defense (Blumstein, in press). This may seem far-fetched, but in 2005, I participated in an interdisciplinary workshop on Darwinian Security hosted by the National Center for Ecological Analysis and Synthesis. An edited volume (Sagarin and Taylor, in press) emerged from our working group. The book develops connections between behavior, ecology, and evolutionary biology and national defense. In the context of defense, we need to know how to respond to unreliable sources of information (which may come from human intelligence or from signals from adversaries or interactants). A lesson from marmots is that unreliable sources should elicit independent investigation. Another lesson is that detection signaling is an effective mean of reducing risk. In the context of defense, we should announce the discovery of terrorist plots with the aim that this would force terrorists to change operational methods or targets.

Au4

Au5

In summary, a fundamental understanding of the proximate basis, evolutionary history, and function of calling has at least five important applied implications. First, it provides the tools for noninvasive population censuses. Second, it helps us evaluate a species' antipredator abilities. Third, it provides a warning about a possible negative outcome from predator range shifts. Fourth, it gives us methods to noninvasively measure stress in captivity and in the wild, and may thus provide information that can help identify a cause of reproductive failure. Finally, it has implications for national defense.

## VII. SUMMARY AND FUTURE WORK

I have adopted a Tinbergian route to study alarm communication in marmots. Alarm signals probably evolved as a means to signal detection to predators and have become exapted into a conspecific warning system.

Marmots have acoustically divergent alarm calls and this species produce between one and five alarm call types. The acoustic environment probably explains limited variation in call structure. Alarm call repertoire size is explained by social complexity; more social species produce more types of alarm calls. Much work has focused on yellow-bellied marmots. The current adaptive utility of yellow-bellied marmot calling seems to be to warn vulnerable offspring, although some additional variation in calling may be explained by signaling to the predator. Calls are individually distinctive and this distinctiveness allows marmots hearing calls to modify their response based on caller reliability. Glucocorticoids appear to potentiate calling: individuals that called on one occasion but not another had systematically higher fecal glucocorticoid levels when they called. My alarm calling results have implications for studying and managing threatened or endangered marmots: populations can be acoustically censused, antipredator abilities can be documented, and stress can be noninvasively measured in captivity and in the field.

While I have focused on alarm communication, marmots obtain other information about risk acoustically. Many species respond to the sounds which their predators make. A phylogenetic reconstruction of the ability to respond to the sound of predators predicts that yellow-bellied marmots should respond to predators. Recent playback experiments suggest that they do, and experiments further suggest that marmots have an innate ability to respond to the sounds of locally extinct predators (Blumstein *et al.*, 2007). Future work will focus on the specific acoustic cues that marmots use and which enable them to respond to novel predators.

Sometimes, when we handle a yellow-bellied marmot pup within about 10 days of emergence, it gives a long, disturbing scream. These screams are unique and structurally different from their alarm calls. Interestingly, these screams have noticeable nonlinearities. It has been hypothesized that vocalizations with nonlinearities may be more difficult to habituate to (Fitch *et al.*, 2002). Future work will directly test this hypothesis by adding nonlinearities to calls and studying habituation.

My past work has completely ignored an important Tinbergian dimension: the ontogeny of calling. All species I studied seem to be able to emit fully formed (although relatively higher frequency) calls about the time they first emerge from their natal burrows (i.e., by about the time they are a month old). The frequency, but not obviously the structure, changes as their body size increases. Thus, calls appear not to be learned. The context of calling, however, appears to be amenable to some degree of experience (Shriner, 1999). Future work may explore this.

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