ALARM CALLING IN THREE SPECIES OF MARMOTS

by

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(Acc. 25-IV-1999)

Summary

Many species produce alarm calls that vary according to situation. Theoretically, alarm call structure could covary with predator type and could communicate potentially "referential" information, or calls could covary with the degree of risk a caller experienced when it emitted a call. Using similar methods, I studied the ways in which Olympic (*Marmota olympus*), hoary (*M. caligata*), and Vancouver Island marmots (*M. vancouverensis*) communicated situational variation. I observed both natural alarm calling, and I artificially elicited alarm

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[2] I thank: Janice Daniel for outstanding field assistance; Janice, Ken Armitage, Chris Evans, Joe Macedonia, and Alexander Nikol'skii for recent discussions about alarm communication; Martin Daly, John Hoogland, Marc Mangel, Jonathan Newman, and an anonymous reviewer for help streamlining the manuscript; the US National Park Service for permission to work in two spectacular parks (Olympic: Natural Resources Division Chief Cat Hawkins Hoffman; Mt. Rainier: Superintendent William Briggle and Gary Ahlstrand); and Jack Morrison and the crew at the Sunrise Visitor Center for logistical support. Work on Vancouver Island would not have been possible without the unflagging support of The Vancouver Island Marmot Recovery Team. I thank Andrew Bryant for extensive logistical support, background information, and hospitality, and Doug Janz, the 1997 Marmot Crew, and the B.C. Ministry of the Environment for additional logistical support while on Vancouver Island. Jim Hare loaned Bob the bobcat, and Mike DeLaronde allowed Ursa to participate in the dog experiment. I am grateful to Dave Barash for finding and sharing old alarm call recordings, for suggestions and information on potential study sites, and for sharing (over the years) his translations of Russian marmot papers. I thank Ed Blumstein for funding an unexpected but crucial computer repair. Major financial support was provided by NIH NRSA MH10793 and final manuscript preparation was supported by an Australian Research Council APD. Examples of marmot vocalizations can be found at The Marmot Burrow (*http://falcon.cc.ukans.edu/~marmota/marmotburrow.html*).

calls with simulated terrestrial and aerial predators. I used playback experiments to study marmots' responses to different alarm call variants. All three species produced four roughly similar but distinctive loud alarm vocalizations that could be categorized by their relative shape, duration, and whether calls were quickly repeated to create multi-note vocalizations. In addition, the Vancouver Island marmot produced a fifth loud alarm call-the kee-aw. Call micro-structure varied as a function of the distance the caller was from an alarming stimulus and the type of alarming stimulus. Two lines of evidence suggest that all three species had alarm calls associated with the caller's risk (*i.e.* they were not referential). First, marmots often changed call types within a calling bout: there were no unique stimulus-class specific vocalizations. Second, marmot responses to alarm calls were graded: marmots did not have unique responses to different call types. These three close taxonomic relatives with superficially similar calls, communicated risk differently.

Keywords: evolution of communication, alarm calls, referential communication, marmots.

Introduction

The structure of many species alarm vocalizations varies, in some way, with situational variables such as degree of risk or predator type (Klump & Shalter, 1984; Macedonia & Evans, 1993; Hauser, 1996). Situationally variable calls can be produced in at least three ways: by varying the rate or number of times a single call type is emitted, by varying the overall intensity of a call, or by producing acoustically distinctive calls. Acoustically distinct calls may be the precursor to predator-specific calls and predator-specific calls may be 'referential' (Blumstein & Armitage, 1997b). Referential communication is communication about objects in the environment (Evans, 1997) and has been the subject of considerable interdisciplinary research in part because it may require greater cognitive abilities than simply varying a call in relation to the degree of predation risk (Hauser, 1996; Evans, 1997). More importantly, in a variable environment with variable predators, precisely communicating the predator type may be the best way to warn offspring or other relatives about predation risk. Thus, understanding the evolution of the ways in which animals communicate predation risk, and specifically the evolution of multiple call types, may shed light on the evolution of referential communication.

As part of a larger study on the evolution of alarm communication in marmots (a monophyletic genus of large ground-dwelling sciurid rodents found throughout the northern hemisphere), I studied alarm communication in three closely-related North American species (Kruckenhauser *et al.*, 1999), the

Olympic marmot (*Marmota olympus*), the hoary marmot (*M. caligata*), and the critically endangered Vancouver Island marmot (*M. vancouverensis*). The 14 species of marmots emit from one to five species-specific alarm vocalizations (Nikolskii, 1984; Blumstein & Armitage, 1997b, Results). While all three species were previously reported to produce multiple alarm calls (Barash, 1973; Heard, 1977; Taulman, 1977), alarm communication was not studied in enough detail to determine the degree to which call types were referential, or to specify the ways in which each species communicated risk.

Several factors including social behavior, habitat type, predator type, and variation in escape strategies may be responsible for the evolution of divergent communicative abilities (Macedonia & Evans, 1993; Blumstein & Armitage, 1997b), but these three species are remarkably similar. They are found in patchy alpine environments living in social groups with multiple adults and offspring from previous years. All three species are exposed to similar sorts of aerial and terrestrial predators. In response to these predation risks, they employ similar antipredator strategies: they are more-or-less similarly vigilant, they return to burrows upon detecting danger, and they emit alarm calls to warn conspecifics (Blumstein *et al.*, in review). Thus, it seems reasonable to assume they should have similar communicative abilities. Given that previous evidence suggested that Olympic and hoary marmot calls communicate the degree of risk a caller experiences (Barash, 1973; Taulman, 1977) while Vancouver Island marmot calls were said to communicate predator type (Heard, 1977), a goal of this study was to determine, more critically, the degree to which the ways used to communicate situation also varied.

To determine the degree of referentiality in vocalizations, it is essential to study both production specificity and contextual independence (Marler *et al.*, 1992; Macedonia & Evans, 1993; Blumstein & Armitage, 1997a; Evans, 1997). If stimulus type uniquely covaries with the vocal response, there is a high degree of production specificity. Thus, if marmot alarm calls are highly referential, they should, for instance, have uniquely different raptor and canid calls that should only be produced in response to raptors and canids, respectively. Contextual independence means that acoustic variants (*e.g.* raptor calls versus canid calls) should elicit the appropriate response in a conspecific who hears the call in the absence of the stimulus that normally elicits the call and without other contextual cues associated with alarm calling (reviewed in: Cheney & Seyfarth, 1990; Marler *et al.*, 1992; Evans *et al.*, 1993; Macedonia & Evans, 1993; Evans, 1997).

In this paper I describe the means whereby the Olympic, hoary, and Vancouver Island marmot produce and perceive situationally specific alarm calls. I use a combination of natural observations and simple field experiments to study factors that influence alarm call production (part 1) and marmots' responses to alarm call variants (part 2). Throughout the paper I compare the ways in which these three close taxonomic relatives communicated situation.

Part 1. Alarm call production

Studying both alarm call production and responses to alarm calls is required for a complete understanding of the ways in which a species communicated risk. While neither alone is definitive, studying alarm call production is crucial in order to design playback experiments and to interpret their results. The aim of this part of the study was to determine the degree to which the structure of alarm calls was influenced by stimulus type and/or by the distance to the alarming stimulus. Substantial variation in call structure explained by the type of the alarming stimulus (*e.g.* terrestrial *vs* aerial), would suggest the opportunity for potentially referential communication. However, playback experiments (part 2) would still be required to determine the degree of contextual independence, and thus the degree to which calls actually communicated potentially referential information.

Methods

Study sites and subjects

Marmots are large (3-5+ kg), obligately hibernating, moderately to highly social, ground-dwelling sciurid rodents (Barash, 1989; Bibikow, 1996). An assistant and I studied alarm communication during their summer active seasons in 1996 and 1997 in the United States and in Canada (Table 1). Each population had pups emerge above ground during our study. Hoary and Olympic marmots individuals were easily distinguished by pelage variation and location. Vancouver Island marmots were ear-tagged as part of an on-going study of their population dynamics (Bryant & Janz, 1996), but they too were often individually variable enough for individual discrimination.

Alarm call production

All species were previously reported to produce multiple alarm and non-alarm vocalizations (Barash, 1973; Heard, 1977; Taulman, 1977; see Results). All three species often repeated their alarm vocalizations-whistles of various durations and 'shapes.' In this paper I use 'call'

TABLE 1. *Study sites and subjects*

	Study				Subjects		
	Dates	Days	Hr.	Group-hr.	N	N groups	Group size
Olympic[1]	3 June- 2 July 1996	22	215	263 $\bar{x} \pm$ SD = 43.8 ± 6.8 range: 34-51	22	6	mode = 3 $\bar{x} \pm$ SD = 3.7 ± 1.5 range = 2-6
Hoary[2]	5 July- 13 August 1996	25	210	615 $\bar{x} \pm$ SD = 76.8 ± 28.0 range: 31-106	33	8	mode = 4 $\bar{x} \pm$ SD = 4.1 ± 1.8 range = 2-8
Vancouver Island[3]	30 May- 27 July 1997	42	328	328 80-100 hr for 4 groups; 1.25 and 11.25 hr for 2 other groups	32[4]	6	mode = 4 $\bar{x} \pm$ SD = 5.3 ± 3.7 range = 1-12

[1] Studied at Hurricane Ridge, Olympic National Park (47°57′N, 123°30′W) — see also Barash (1973).

[2] Studied in the Sunrise area, Mt. Rainier National Park (46°55′N, 121°40′W) — see also Barash (1975).

[3] Studied outside Nanaimo, British Columbia (49°05′N, 124°20′W) — see also Bryant and Janz (1996).

[4] Represented over 33% of the 80-95 non-pups estimated to be alive in 1997.

to refer to a single vocalization as well as one type of multi-note vocalization — a trill. A bout of alarm calling contained one or more calls. Analysis was confined to alarm calls from identified non-pup callers.

Focal group observations were used to simultaneously monitor the location of all individuals in a social group and note all bouts of alarm calling and all predator visits. Observers sat in obvious view of the marmots at distances that appeared to not overtly influence their behavior. Observations were made throughout the day. When a marmot called, observers noted the caller's identity, the eliciting stimulus, the distance of the caller to the stimulus, the distance of the caller to the nearest burrow, the response of other marmots, the total number of alarm calls, and the duration of multi-call bouts.

Predators and alarm calling were uncommon. Using standard techniques (Blumstein, 1995a; Blumstein & Arnold, 1995; Blumstein & Armitage, 1997a), predator attacks were simulated in several ways to experimentally induce alarm calls and to increase our sample of alarm responses to known stimuli. If responses were not stimulus-specific, then I would infer that marmot alarm calls may not be highly referential.

The first manipulation involved walking towards marmots at a constant rate (*ca* 1m/s) and noting whether subjects called (Table 2). Most species of marmots alarm call in response to humans and there is a long history of human predation on marmots (Bibikow, 1996; Formozov

TABLE 2. *Details of experiments (number of experiments, number of different marmots, number/subject, number of alarm calls emitted) to elicit alarm calls from Olympic, hoary, and Vancouver Island marmots*

	Predation Probes				Terrestrial Stimuli[1]				Aerial Stimuli[2]			
	N	*N* ID	*N*/Subject $\bar{x} \pm$ SD	*N* AC	*N*	*N* ID	*N*/Subject $\bar{x} \pm$ SD	*N* AC[3]	*N*	*N* ID	*N*/Subject $\bar{x} \pm$ SD	*N* AC
Olympic	34	16	2.1 ± 1.4	2	badger: 13	12	1.7 ± 1.4	4 (2)	RC glider: 16	16	1.9 ± 1.0	8 (7)
Hoary	22	15	1.5 ± 0.7	1	badger: 14	14	1.4 ± 0.8	4	kite: 5	4	1.8 ± 0.5	0
									RC glider: 1	1	1.0	1
									glider: 21	14	2.0 ± 1.4	6 (5)
Vancouver Island	72[4]	19[5]	2.9 ± 2.0	2	bobcat: 8	8	1	3	glider: 18	13	1.6 ± 0.8	10 (6)
					dog: 1	3	1	0				

[1] The badger and bobcat were taxidermic mounts; the dog was alive and under leash and voice control.

[2] Models included a brown radio controlled Thunder Tiger Windstar sailplane (1.15 × 2.0 m), a brown Flying Eagle sailplane (0.88 × 1.38 m), brown Sky Rider gliders (0.88 × 1.38 m), and a 'frameless' nylon kite.

[3] Number of calls = number of subjects, if not, the number of subjects in parentheses.

[4] 56 probes to positively ID'd and distinguishable marmots.

[5] Positively ID'd.

et al., 1996; Nagorsen *et al.*, 1996). These ‘predation probe’ experiments (*e.g.* Blumstein & Armitage, 1997a) were largely unsuccessful at eliciting alarm calls in these three species.

The second manipulation simulated the presence of a terrestrial predator (Table 2). For both Olympic and hoary marmots I used a stuffed badger (*Taxidea taxus*) mounted on a radio controlled chassis. Because Vancouver Island does not have badgers and because I was unable to import the badger into Canada, I used a stuffed bobcat (*Lynx rufus*) mounted on a sled and a live well-controlled dog (*Canis familiaris*) to simulate a terrestrial predator moving through a Vancouver Island marmot colony. Marmots typically responded to models by retreating to burrows, orienting towards the models, and occasionally calling in response to the model’s presence. If a marmot called, the distance between the model and the marmot was measured.

The third manipulation simulated the presence of an aerial predator (Table 2). I flew a brown radio controlled model glider, a frameless kite, or brown styrofoam gliders over and around focal marmots to simulate aerial predators. I used diverse stimuli because it was impossible to keep the radio controlled glider intact in rocky and tree-filled habitat.

Models and simulated predators have been successfully used to elicit the full gamut of antipredator behavior, including alarm calling, in many species (*e.g.* Curio, 1993; Evans *et al.,* 1993; Greene & Meagher, 1998). The common assumption in all studies where models are used is that models contain enough salient features to elicit responses qualitatively similar to natural predators.

Alarm call structure

Calls were recorded onto high bias 60-min tapes using Sennheiser ME-67 or ME-88 microphones encased in ‘blimp’ windscreens with Sony TC-D5M cassette recorders. All calls were pre-filtered to prevent frequency digitizing artifacts (aliasing; TTE J83G-22K-6-720B filter) and were then sampled at 22 kHz using a MacRecorder 8-bit AD-DA board and SoundEdit software (MacroMind-Paracomp Inc., 1990). ‘Boxy’ sound spectrograms were generated using 512-point short-time Fourier transformations with 50% overlap, a Hamming window, and − 110 dB clipping (Charif *et al.*, 1995). Because attenuation, degradation and background noise modify the structure of sounds as they are transmitted through space (Wiley & Richards, 1978; Blumstein & Daniel, 1997), I analyzed only spectrograms without extensive background noise and excessive reverberation from minimally attenuated recordings using Canary 1.2 software (time resolution 5.8 ms; frequency resolution 43.5 Hz).

I focused on the first call, or in some cases the only call, an individual emitted in response to a stimulus because I assumed that the first call reflected a subject’s immediate perception of risk: subsequent calls in a calling bout may serve different functions (*e.g.* to maintain vigilance-Owings & Hennessy, 1984; Owings *et al.*, 1986; Loughry & McDonough, 1988). In some cases, several individuals called to the same stimulus; for these analyses I treated these responses as independent. If alarm calls referred to specific predator types, I expected that all individuals who alarm-called should produce roughly the same call. While marmot identity may influence call structure (*e.g.* Blumstein & Armitage, 1997a), acoustic variables that covary with identity may not covary with predator type or degree of risk.

I measured the following variables from the fundamental component of an individual’s first call: duration, minimum frequency, maximum frequency, frequency at peak amplitude, lowest frequency when the call began and lowest frequency when the call ended. From these measurements, I calculated the bandwidth (maximum-minimum frequency), the difference between the starting and ending frequency (a rough approximation of call shape), and the relative amount of change between the ending and starting frequency (end/start). In addition to these microstructural call characteristics, I counted the total number of alarm calls that each subject emitted to a stimulus, recorded the total time of the calling bout, measured the intervals between the first and second call, calculated the rate at which each subject called in a bout of calls (*N* calls/total time calling-in min), and counted the number of calls each caller made in the first 60 s of a calling bout in response to a stimulus.

Data reduction and statistical analyses

I randomly selected a single first call per subject to each of the following call-eliciting stimuli: humans; artificial terrestrial predators; natural terrestrial predators; model aerial predators; natural and potential aerial predators. The final data set contained 20 Olympic marmot calls from 14 subjects, 36 hoary marmot calls from 21 subjects, and 29 Vancouver Island marmot calls from 24 subjects. Because this level of subdivision generated categories represented by few individuals, I combined eliciting stimuli into two categories-aerial and terrestrial. This level of aggregation is defensible both because I do not necessarily expect exact stimulus-specific specification, and because aerial and terrestrial predators may produce qualitatively different risks.

I used contingency table analyses to study the association of a call type with stimulus classes. I used ANCOVA to study the independent effects of stimulus type (aerial/terrestrial) and distance to the stimulus on call structure. Finally, I used a Friedman non-parametric repeated measures ANOVA to study how the duration and intercall interval varied during a calling bout. Descriptive and non-parametric statistics were calculated using StatView (Abacus Concepts Inc., 1993). Parametric linear models were fitted with SuperAnova (Abacus Concepts Inc., 1991).

Results

All species called in response to apparently threatening visual stimuli and to ungulates and suddenly-appearing birds (Table 3); Olympic marmots also called in response to hearing conspecific alarm calls. Alarm calls were occasionally, but rarely, used in social situations. Alarm calls were emitted during one Olympic, and four hoary marmot fights. In addition to social alarm calls, all species growled and emitted other vocalizations associated with chases, fights, and play.

During the study Olympic marmots emitted only 52 bouts of alarm calls (31 of these were in response to our manipulations), Vancouver Island marmots emitted only 77 bouts of alarm calls (33 in response to our manipulations or to other humans), and hoary marmots emitted 179 bouts of alarm calls (45 in response to our manipulations or to other humans).

Olympic, hoary and Vancouver Island marmots produced four structurally distinctive loud alarm calls: ascending, flat, descending, and multiple-note trills (Fig. 1). In addition, Vancouver Island marmots produced a loud, low

TABLE 3. *Number of alarm calls/number of exposures of marmots to predators and potential predators*[1]

	Olympic	Hoary	Vancouver Island
Aerial predators and potential predators			
Golden eagle, *Aquila chrysaetos*	0/3		1/6
Bald eagle, *Haliaeetus leucocephalus*	0/2	1/1	4/8
Northern harrier, *Circus cyaneus*	0/1		
Cooper's hawk, *Accipiter cooperii*		0/3	
Rough-legged hawk, *Buteo lagopus*		0/1	
American Kestrel, *Falco sparverius*	0/3		1/4
Merlin, *Falco columbarius*			0/1
Unidentified falcons, *Falco* spp.		0/2	
Raven, *Corvus corax*	2/42	9/32	2/5
Terrestrial predators and potential predators			
Black bear, *Ursus americanus*	1/18		⩾ 1/13
Weasel, *Mustela frenata*		0/2	
Coyote, *Canis latrans*	2/2		
Gray wolf, *Canis lupus*			0/2
Red fox, *Vulpes fulva*		⩾ 1/ ⩾ 1	
Mountain lion, *Felis concolor*			0/1[2]

[1] In addition to predators and potential predators, hoary marmots called in response to elk (*Cervus canadensis*), and Olympic and hoary marmots called in response to deer (*Odocoileus hemionus*). Vancouver Island marmots called in response to the sudden flushing of band-tailed pigeons (*Columba flavirostris*).

[2] The mountain lion was seen about 1-2 km and several hundred m below the nearest marmot colony.

frequency kee-aw vocalization (Heard, 1977). The first three call types were emitted singly and their length varied more or less continuously. They were acoustically distinguishable by the degree to which the starting and ending frequencies varied. I subjectively defined flat calls as those whose starting and ending frequencies differed by no more than ± 10%, ascending calls as those which ended at a frequency > 10% higher than they started, and descending calls as those which ended at a frequency > 10% lower than they started. Human observers could easily distinguish extreme examples of ascending and descending calls. Ultimately, playback experiments would reveal if these different 'shaped' calls were perceptually meaningful to marmots.

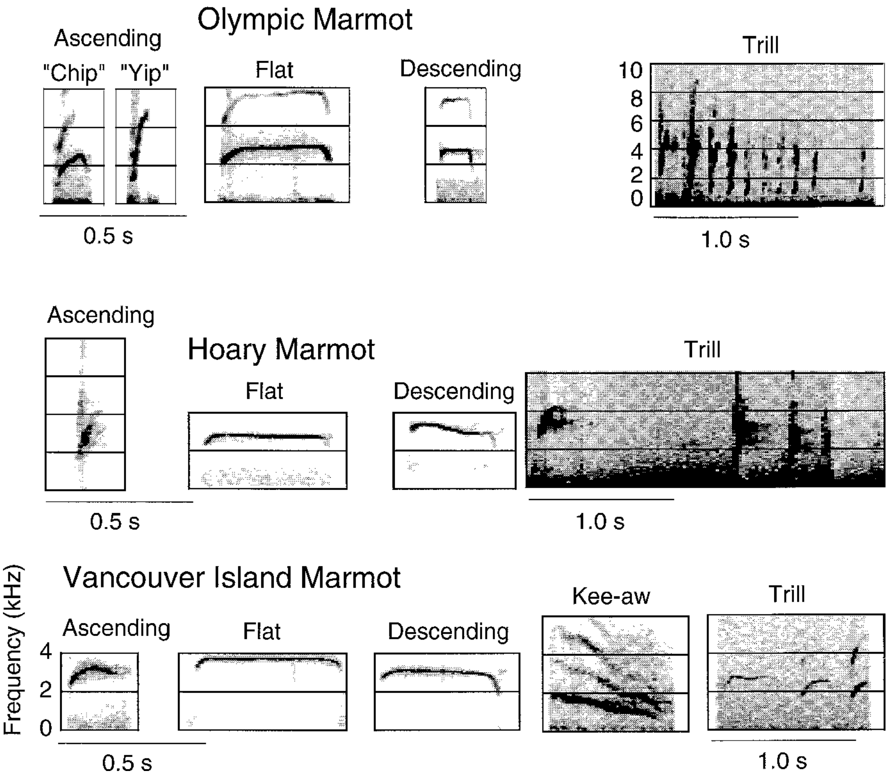

Fig. 1. Spectrograms (512 point SoundEdit) of alarm call repertoires of Olympic, hoary, and Vancouver Island marmots. Ascending calls ended at a frequency at least 10% higher than they began. Flat calls began and ended at approximately (*i.e.* ± 10%) the same frequency than they began. Descending calls ended at a frequency at least 10% lower than they began. Trills contained a series of ascending calls that were rapidly uttered to create multi-note call. The kee-aw is a unique loud vocalization produced by Vancouver Island marmots. All calls except trills are plotted on the same time axis.

In contrast to this classification scheme, Barash (1973, p. 182-184) described Olympic marmot calls varying only along their temporal domain-both his long and short calls ascended. Marmots emitted Barash's yip calls in alarming situations and it appears that yips may be combined to create a trill. I define a trill as the packaging of multiple short calls into a very quickly paced multiple-note vocalization. Taulman (1977), following Waring (1966), called these accelerating chirps. I prefer trill because of its potential homology with similar vocalizations in *Spermophilus* ground squirrels and in woodchucks (*Marmota monax*-although Lloyd, 1972 referred to the woodchuck vocalization as a warble). I heard hoary marmots trill only twice, and the only trill that I recorded was very degraded. Additionally, hoary and Olympic marmots occasionally 'chucked' (*sensu* Blumstein & Armitage, 1997a) when they emitted very low intensity and low frequency vocalizations in seemingly disturbing situations. Also in contrast to this classification scheme, Taulman (1977) reported that hoary marmots had long calls and descending calls (he did not specify the frequency difference used to classify calls), and Heard (1977) reported that Vancouver Island marmots had long, medium, and short duration calls in addition to the 'two-syllable' kee-aw — acoustically similar to the black-tailed prairie dog's (*Cynomys ludovicianus*) 'jump-yip' (Smith *et al.*, 1976). I used the same classification for all species to clarify comparisons and highlight differences.

Alarm call and bout structure

All species' calls varied along all measured acoustic parameters. In response to alarming stimuli, all species typically called once, but sometimes called hundreds of times (Olympic median = 20, mode = 1, range = 1-1,188; hoary median = 2, mode = 2, range = 1-391; Vancouver Island median = 2, mode = 1, range = 1-507). In bouts containing multiple calls, the duration and interval between calls of the first nine or ten notes did not vary for hoary (duration $p = 0.18$; interval $p = 0.11$) or Vancouver Island marmots (duration $p = 0.59$; interval $p = 0.12$). Olympic marmots were an exception. While the duration of their calls did not change ($p = 0.19$), the pace of their calls quickened (*i.e.* the interval between calls decreased) as the calling bout proceeded, but ultimately slowed as the calling bout ended ($p < 0.001$).

Only Vancouver Island marmots produced call types that co-varied with stimulus type (Table 4). Vancouver Island marmots produced more flat calls than expected by chance in response to terrestrial stimuli, and more descending calls to aerial stimuli. Trills rarely were the first call, and were thus excluded from this analysis. Individuals of all three species that trilled appeared highly agitated, and they trilled as they disappeared into their burrows.

Does distance to the stimulus or stimulus type explain variation in call structure?

Species differed in how they varied call and bout structure as a function of the distance to the stimulus and stimulus type (*i.e.* aerial/terrestrial; Table 5).

TABLE 4. *Alarm call types elicited by aerial and terrestrial stimuli*

Olympic				
	Ascending	Flat	Descending	
Aerial	2	3	1	
Terrestrial	7	3	1	
$X^2, p = 0.49$				
Hoary				
	Ascending	Flat	Descending	
Aerial	2	3	3	
Terrestrial	3	16	4	
$X^2, p = 0.27$				
Vancouver Island				
	Ascending	Flat[1]	Descending[1]	Kee-aw
Aerial	1	1	8	4
Terrestrial	4	9	0	1
$X^2, p < 0.001$				

[1] cell $X^2, p < 0.001$.

Distance explained variation in only two of the 14 measured parameters for Olympic marmots, one for hoary marmots, and three for Vancouver Island marmots. In contrast, stimulus type did not explain any variation in the microstructure of Olympic marmot calls. Stimulus type explained variation in four of the parameters for hoary marmots: they produced longer, higher-pitched, and narrower bandwidth calls to terrestrial stimuli than to aerial stimuli. Stimulus type explained variation in five of the parameters for Vancouver Island marmots: they produced higher frequency, narrower bandwidth calls that ended at a higher frequency than they started, and changed relatively little in their starting and ending frequency to terrestrial stimuli than to aerial stimuli.

Despite the presence of significant stimulus effects explaining variation in the microstructure of hoary and Vancouver Island marmot alarm calls, production specificity was not high. Distance to the stimulus also explained variation one of hoary marmot parameters that also had a significant stimulus effect, and one of the Vancouver Island marmot parameters that also had a significant stimulus effect. In addition to microstructural variation not being uniquely associated with stimulus type, 8-24% of the bouts containing multiple calls, also contained multiple call types (Olympic = 4/35; hoary = 8/97; Vancouver Island = 9/37) — further evidence that production speci-

TABLE 5. *Significant results ($p < 0.05$) from ANCOVA that modeled microstructural call characteristics as a function of stimulus type and distance to the stimulus*

Species	Stimulus type (aerial/terrestrial)	Distance to stimulus (m)
Olympic marmot		Minimum frequency, start frequency.
Hoary marmot	Call rate, duration of first call, minimum frequency, bandwidth.	Duration of first call.
Vancouver Island marmot	Minimum frequency, bandwidth, end frequency, end-start frequency, relative change in frequency.	Duration of first call, interval between call 1 and call 2, bandwidth.

See methods for a complete list of all parameters measured.

ficity was not high. This was most apparent in Vancouver Island marmots who often mixed kee-aws with other types of calls. Vancouver Island marmots often kee-awed after first emitting longer duration whistles; when the first call was a kee-aw (Table 4), the stimulus had already passed out of sight.

Part 2. Response to alarm calls

Communication requires perceivers to respond to signal variation (Hauser, 1996). All three species produced different types of vocalizations and situationally varied the structure of their vocalizations. In this section I present results from a series of playback experiments designed to study how marmots responded to different vocalizations.

Methods

High-quality recordings of calls and other sounds were sampled with 8-bit resolution at 22 kHz with a Macintosh PowerBook 180 or using an external MacRecorder (AD-DA) board and a Macintosh PowerBook 100. Some experiments (details below) required a single vocalization; others required multiple vocalizations. I used SoundEdit software (MacroMind-Paracomp Inc., 1990) to construct multiple playback stimuli for each call type.

All stimuli were played back directly via a Macintosh PowerBook 100 or 180 computer through either a Sony SRG-77G or an Acoustic Research 570 'Powered Partner' speaker. Both speakers produced realistic sounding calls at the playback distances used. Speakers were typically camouflaged using vegetation, rocks and logs 30-200 m from the computer operator. Unless otherwise noted, the volume of played-back stimuli was adjusted to approximately 100 ± 5 dB measured 0.2 m in front of the speaker with a Realistic model 33-2050 sound level meter-a typical sound pressure level for all species. The playback situation was designed to mimic an unseen marmot alarm calling from within the social group's home range.

Factors including behavior patterns (Blumstein, 1998), presence of neighbors (Nesterova & Nikol'skii, 1991), distance to burrow (Blumstein, 1998), age (Nesterova, 1996; Schwagmeyer & Brown, 1981), and body condition (Bachman, 1993) may influence responsiveness to playback. To control for as many potentially confounding factors as possible, I did not conduct playbacks to pups, and I attempted to conduct all playbacks to marmots standing or sitting and looking within 10-15 m of the hidden speaker and within 2 m of their burrow. Marmot behavior varies throughout the day and the motivation to resume normal activity after hearing an alarm call may change throughout the day (*e.g.* a satiated animal may not need to resume foraging for several hours, or once alarmed into a burrow, may remain in the burrow for many hours). To control for motivational changes, for each experiment I tried to expose a subject to the set of playback stimuli within a 30 min interval to minimize variation induced by body condition and motivation-induced variation (see Hauser, 1996).

Habituation to the experimental protocol is always a potential problem of playback experiments (Weary, 1992). To minimize the likelihood that marmots habituated to our experimental protocol, I waited until subjects resumed their normal activity before playing back subsequent stimuli, I systematically varied the order in which I played back stimuli, and I changed the location of the speaker during playback periods. Despite these precautions, there may still be effects from playback order. I tested for order effects using Friedman non-parametric ANOVAs where I blocked by subject. I found and report only one significant order effect (see below).

To eliminate the chance that marmots responded to something about the playback protocol or equipment, for each species I played back and noted the response to a gray jay (*Perisoreus canadensis*) contact call. I used the single contact call recorded in Colorado used in a previous playback experiment (Blumstein & Armitage, 1997a) and played it back at 85 ± 5 dB (measured 2 m from the speaker), a volume that made it sound like a nearby jay emitting a contact call. Jays lived in all species habitats. In almost all cases (see below), playback of contact calls was either ignored by marmots, or elicited slow head turning.

Quantifying response to playback is difficult and should in part be based on normal antipredator behavior. Marmots responded to natural predators and alarm calls (both naturally produced and played back) by returning to their burrows (if not already there), looking around, rearing up on their hind legs and bipedally looking around, and/or by disappearing into their burrows. I saw no obvious differences in gaze direction in response to playback (*i.e.* look up versus look around; *e.g.* Cheney & Seyfarth, 1990; Evans *et al.*, 1993). Additionally, some Olympic marmots alarm called in response to played back alarm calls.

I classified responses to playback into four increasing levels of hypothesized arousal and scored the highest level response in the first 5 s following playback (Blumstein & Arnold, 1995; Blumstein & Armitage, 1997a; *cf.* Nikol'skii *et al.*, 1994). I chose 5 s because marmots spend much of their time engaged in vigilance behaviors and therefore routinely looked around (Barash, 1973; Holmes, 1984; personal observations). I assumed that if a focal marmot did not look around in the first 5 s, she had not responded to the playback. Possible response scores (following Blumstein & Arnold, 1995) were:

1. no response: the marmot did not obviously change its orientation in the first 5 s following playback.
2. look: the marmot moved its head in response to playback and appeared to look around. Body posture remained fixed.
3. rear-up and look: the marmot changed its body posture by rearing up on its hind legs and looking around. By rearing up, a full-sized marmot could elevate its head about 15 - 20 cm higher than a standing-and-looking marmot.
4. out-of-sight: the marmot disappeared into its burrow in response to the playback.

I used Friedman non-parametric ANOVAs to test for differences in responsiveness to the acoustic stimuli while blocking by individual. Wilcoxon tests were used for post-hoc comparisons. I report unadjusted p-values; the p-critical value after a Bonferroni correction is 0.017 for the 3 stimulus tests (0.05/3) and 0.013 for the 4 stimulus tests (0.05/4).

Playback experiments and results

Specific playback experiments were designed based both on preliminary data collected in the field and on suggestions from previous authors about alarm call meaning. Experimental details are summarized in Table 6. Below I review each experiment and its results.

Olympic marmots

I conducted four playback experiments to study the meaning of Olympic marmot alarm calls. Despite little variation in measured acoustic parameters being explained by either distance or by stimulus type, Olympic marmots produced acoustically different calls of different durations, that were repeated different numbers of times and at different rates.

Two experiments, Call Type and Call Duration (Table 6) were designed to determine the salience of variation in call shape and duration. Results suggest that while variation in call duration does not elicit different levels of arousal, variation in call shape does (Fig. 2). Different types of ascending calls tended to elicit different levels of arousal in perceivers (post-hoc Wilcoxon $z = -2.070$, $p = 0.038$).

Two experiments, Number/Rate and Tonic (Table 6) were designed to determine the salience of variation in the number or rate of alarm calls immediately and over a longer time scale. Marmots tended to respond more intensively to four calls than they did to a single call in the time immediately following playback (post-hoc Wilcoxon $z = -2.000$, $p = 0.046$ for both comparisons against the single call).

TABLE 6. *Details of playback experiments*[1]

	Dates	*N* exemplars	*N* subjects	*N* social groups	Interval between playbacks (min) $\bar{x} \pm$ SD (range)
Olympic					
Call Type	24, 25 June 1996	4 × 0.4 s ‘flatish’ 2 × chip 2 × yip	3 AF, 2 AM, 3 non-pups	3	18 ± 11 (10-38)
Call Duration	26 June 1996	4 × 0.2 s 4 × 0.4 s 4 × 0.6 s	1 AF, 1 F, 4 non-pups	2	13 ± 9 (8-31)
Number/Rate	25 June 1996	4 × 0.4 s played 1× 4 × 0.4 s played 4× with intervals of 4 s silence 4 × 0.4 s played 4× with intervals of 0.5 s silence	2 AF, 1 AM, 1 F, 1 M, 1 non-pup	2	19 ± 13 (10-43)
Tonic	28 June 1996	4 × 0.4 s played 1× 4 × 0.4 s played 1 call/s for 99×[2]	3 AF, 2 AM, 1 M, 2 non-pups	2	10 ± 1 (10-12)
Hoary					
Call Type	28, 29 July 1996	4 × 0.8 s ‘flatish’ 2 × ascending 2 × descending	3 AF, 1 AM, 4 non-pups	3	11 ± 2 (8-17)
Call Duration	29, 30 July 1996	4 × 0.3 s 4 × 0.8 s 4 × 1.3 s	2 AF, 6 non-pups	4	12 ± 3 (9-20)
Number/Rate	30 July 1996	4 × 0.8 s ‘flatish’ 4 × 0.8 s played 3 × with intervals of 11 s silence[3] 4 × 0.8 s played 3 × with intervals of 2 s silence[4]	1 AF, 1 AM, 8 non-pups	4	20 ± 23 (6-81)

TABLE 6. *(Continued)*

	Dates	*N* exemplars	*N* subjects	*N* social groups	Interval between playbacks (min) $\bar{x} \pm$ SD (range)
Vancouver Island					
Call Duration/Type	25-27 June and 3-4 July 1997	2 × 0.16 s 2 × 0.57 s 2 × Kee-aw	4 AF, 2 YM, 4 Y	3	10 ± 14 (5-51)
Call Shape	28, 30 June and 1 July 1997	2 × ascending 2 × descending 2 × 'flatish'	3 AF, 2 AM, 1 YM, 4 Y	3	6 ± 2 (4-10)
Bout Composition	6, 7, 9 July 1997	2 × long played 4 × with intervals of 9 s silence 2 × long + 3 kee-aws with intervals of 9 s silence 2 × kee-aws played 4 × with intervals of 9 s silence	5 AF, 1 AM, 1 YM, 3 Y	2	19 ± 24 (9-85)

[1] For each experiment, individuals heard one exemplar of each stimulus played back in a predetermined order. Analyses (2-way Friedman non-parametric ANOVA) blocked by individual. For all but the Olympic tonic experiment, the dependent variable was the highest level of response in the first 5 s following the end of the experiment (see text).

[2] While Olympic marmots typically did not begin a calling bout by calling 1 call/s, at times they emitted 1 call/s.

[3] In a preliminary analysis, 11 s was the average interval between calls elicited by terrestrial stimuli.

[4] In a preliminary analysis, 2 s was the average interval between calls elicited by aerial stimuli.

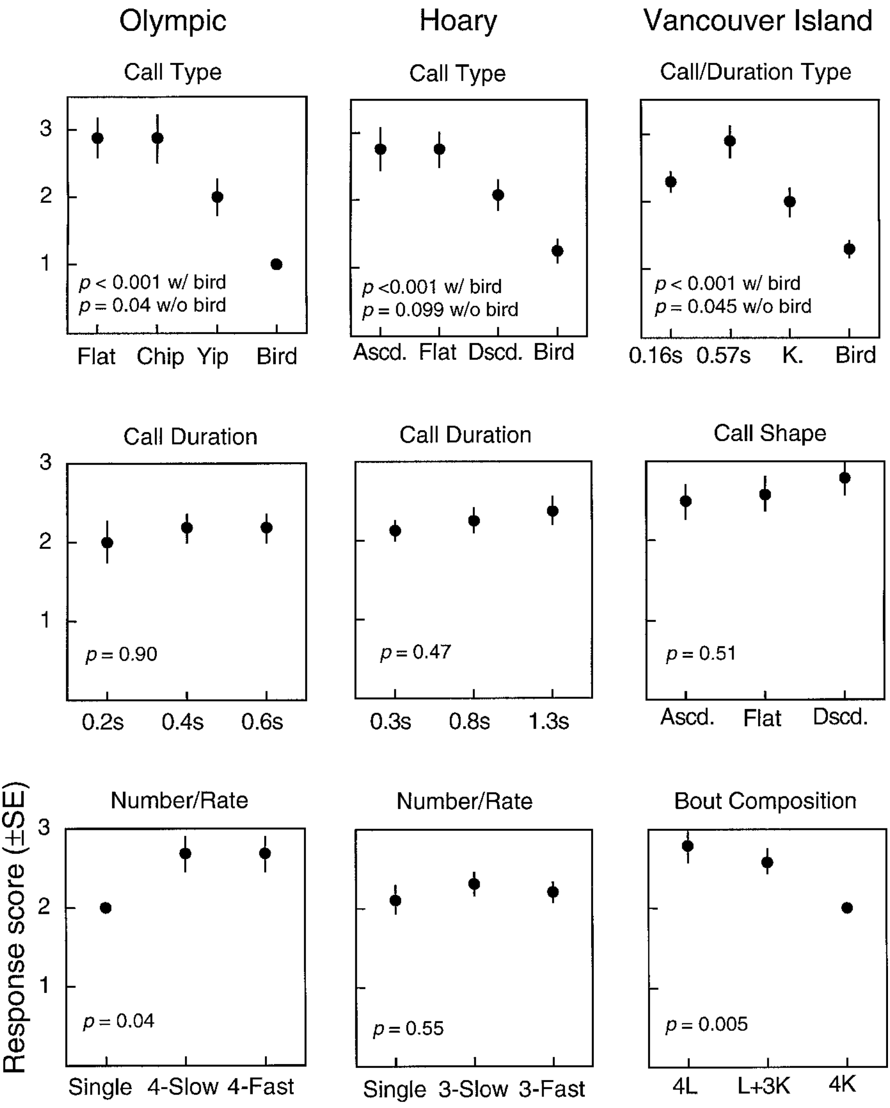

Fig. 2. Average ± SE response scores to playback stimuli. Each graph plots the results of one playback experiment (see text for details). Playback stimulus abbreviations as follows: Ascd. = ascending call; Dscd. = descending call; K. = kee-aw; 4L = 4 'long' calls; L+3K = 1 'long' call + 3 kee-aws; 4K = 4 kee-aw calls. p-values are from Friedman non-parametric ANOVA blocking by individual.

Calls may serve other purposes than to immediately alert conspecifics; they may be used to maintain vigilance (Owings & Hennessy, 1984; Loughry & McDonough, 1988). Two remarkable characteristics of Olympic marmot alarm calls were the high variance in the number of calls per bout and the bout length. Some of this variation may be because there are different functions of short calling bouts versus longer calling bouts (*e.g.* Owings & Hennessy, 1984; Loughry & McDonough, 1988; Hersek & Owings, 1993). Schleidt (1973) first suggested that repeated 'tonic' signals may be used specifically to influence the behavior of perceivers on a longer time scale. The objective of the Tonic experiment was to determine whether repeated Olympic marmot alarm calls maintained vigilance in perceivers.

The Tonic experiment compared the response of marmots hearing a single call to those hearing one call per second for 99 seconds. I quantified the total amount of time during which subjects heightened their vigilance (specifically, the time spent rearing or rearing-up and looking) for 240 s following the start of the playback.

One subject responded to the 99 call playback by going out of sight into its burrow for 192 s. I excluded this subject from the analysis. The remaining seven subjects spent significantly (Wilcoxon $z = -2.366$, $p = 0.018$) less time in heightened vigilance following the single call playback ($\bar{x} \pm \mathrm{SD} = 13 \pm 0.24$ s) than they did following the 99 call playback (143 ± 96.4 s).

Hoary marmots

I conducted three experiments to study the meaning of hoary marmot alarm calls. Variation in both temporal and frequency characteristics was explained by both stimulus type and the distance to the stimulus type. Was variation in call structure and tempo meaningful to marmots?

Two experiments, Call Type and Call Duration (Table 6) were designed to determine the salience of variation in call type and duration. Results suggest a tendency for call type, but not call duration to influence responsiveness (Fig. 2). Ascending calls tended to elicit a slightly higher response than descending calls (post-hoc Wilcoxon $z = -1.890$, $p = 0.059$). Both ascending and flat calls caused subjects to go out of sight into their burrows.

The third experiment used the inter-call interval estimated from preliminary data to study the effect of multiple calls and the pace of multiple calls.

Marmots did not respond differently to the played back stimuli (Fig. 2). However, this was the only experiment with a significant order effect (Friedman $X_r^2 = 7.600$, df = 2, $p = 0.022$).

Vancouver Island marmots

I conducted three playback experiments to study the meaning of Vancouver Island marmot alarm calls. Preliminary analyses (Table 5) suggested that both frequency and temporal characteristics may be salient.

Because Heard (1977) classified marmot calls by their duration and because he recognized the kee-aw as a unique call, the first experiment, Call Duration/Type (Table 6), was designed to study the salience of call duration and type. Long calls (the 0.57s calls) tended to elicit the highest level response and kee-aws the lowest level response (Fig. 4; Wilcoxon $z = -2.460$, $p = 0.014$). Marmots tended to respond more to long calls than short calls (Fig. 2; Wilcoxon $z = -2.121$, $p = 0.034$). Short calls (the 0.16s calls) and kee-aws did not elicit different levels of responsiveness (Wilcoxon $z = -1.732$, $p = 0.083$).

The second experiment, Call Shape, focused on the salience of the variation in the shape of non kee-aw calls (Table 6). Marmots typically responded by looking or rearing up and looking but they did not respond differently to playbacks of ascending, flat, or descending calls (Fig. 2).

Vancouver Island marmots were notable because calling bouts often included multiple types of calls. The Bout Composition experiment (Table 6) was designed to determine the salience of calling bouts with different call types. Both bouts that included long calls elicited significantly higher levels of response than bouts consisting of only kee-aws (4 long *vs* 4 kee-aws, Wilcoxon $z = -2.530$, $p = 0.011$; long + 3 kee-aws *vs* 4 kee-aws, Wilcoxon $z = -2.449$, $p = 0.014$). In addition to the highest level of response, I recorded the total time spent in the highest level of response in the 30 s following the playback. Results were identical to those seen by quantifying the highest level of response.

Combined results

All three marmot species produced four distinctive loud alarm vocalizations that could be categorized by their relative shape, and whether calls were packaged into multi-note vocalizations or not (Fig. 1). In addition, Vancouver Island marmots produced a loud, lower frequency kee-aw vocalization. Alarm vocalizations were rarely emitted in response to conspecific aggression, but Olympic marmots occasionally alarm called in response to hearing conspecific alarm calls.

Olympic marmots did not emit alarm calls with a high degree of production specificity, but call variation could communicate relative predation risk. Aerial and terrestrial stimuli did not elicit unique alarm calls (Table 4), and after controlling for call variation explained by distance (a metric of relative risk), variation in stimulus type (aerial/terrestrial) did not significantly explain variation in any call attributes (Table 5). However, Olympic marmots increased the pace as a calling bout progressed. Olympic marmots typically responded to played back alarm calls by looking around, and playbacks of multiple calls elicited higher levels of response than single calls (Fig. 2). Upon hearing tonic bouts of calling, marmots maintained their heightened vigilance longer than they would upon hearing a single call. Playback experiments suggested that different types of ascending calls could elicit different responses: playbacks of chips elicited higher levels of response than playbacks of yips. Together, these results suggest that Olympic marmots did not have a referential alarm calling system. While call number and rate did not significantly covary with measures of risk, marmots responded to variation in the number/rate of calls, an observation consistent with a number/rate based way to communicate risk.

Hoary marmots emitted calls with a high degree of production specificity; playback results suggested that variation in call shape could communicate relative predation risk. Aerial and terrestrial stimuli did not elicit unique alarm call types (Table 4). While distance to the stimulus explained some variation in the microstructure of hoary marmot alarm calls, stimulus type (aerial/terrestrial) explained substantial variation in some of the call rate/duration parameters (Table 5). Hoary marmots called more and longer to terrestrial than aerial stimuli, and their calls were more quickly paced when they called in response to aerial stimuli. Hoary marmots responded to all alarm vocalizations by increasing their vigilance (Fig. 2). Playback experiments suggest that call microstructure may influence responsiveness: ascending calls elicited higher levels of response than descending calls. Other playback experiments were less revealing: call length, the number of calls, and the rate of calling did not influence response.

Vancouver Island marmots produced different types of alarm calls that could be used to communicate relative predation risk. While different stimuli did not elicit unique call types, marmots produced more flat calls in response to terrestrial stimuli and more descending calls in response to aerial stimuli than expected by chance (Table 4). Stimulus type explained significant variation in several frequency parameters while distance to the stimulus uniquely explained variation in the duration of the first call and interval between the first two calls (Table 5). Playback results suggested that longer calls elicited higher levels of response than shorter calls, and that kee-aws were relatively lower risk vocalizations that may function to maintain vigilance in perceivers (Fig. 2).

Discussion

Current evidence suggests that while these three close taxonomic relatives have the largest antipredator vocal repertoires reported in marmots (Nikol'skii, 1996; Blumstein & Armitage, 1997b), no species has a highly referential alarm communication system. All species produce multiple alarm calls, but similar calls are given in different circumstances and different calls are given in similar circumstances. Thus, there is not a high degree of production specificity in any species' alarm calling behavior. While playback experiments suggest that the degree of contextual independence differs between species, no species obviously responds in ways suggesting that calls refer to particular types of predators or specifically to predatory risks coming from different locations.

Unlike three Old World marmots (golden marmots-Blumstein, 1995a; alpine marmots-Blumstein & Arnold, 1995; and some populations of grey marmots (*M. baibacina*)-Nikol'skii, 1994), but similar to yellow-bellied marmots (another New World species-Blumstein & Armitage, 1997a), none of the three species packaged calls into commonly-used multiple note vocalizations. All three species did produce a rarely-used, but apparently very high-risk multiple-note vocalization, the trill. Interestingly, trills varied between species: Olympic marmot trills resembled the trills of yellow-bellied marmots and woodchucks in their rapid tempo, short note duration, and frequency modulation more than they resembled trills of hoary or Vancouver Island marmots (*cf.* Fig. 1 with Fig. 1 in Lloyd, 1972, and Fig. 1 in Blumstein

& Armitage, 1997a). The tempo and number of hoary and Vancouver Island marmot trills were more like the multiple-note calls emitted by highly aroused grey marmots (Nikol'skii, 1994) and steppe marmots (Nikolskii, 1984).

All three species produced low-frequency descending vocalizations. However, only the Vancouver Island marmot emitted it loudly enough to be classified as a loud alarm call. Heard (1977) suggested and I agree that what I refer to as chucks and Taulman (1977) referred to as low frequency calls, are homologous with the Vancouver Island marmot's kee-aw. Yellow-bellied (Blumstein & Armitage, 1997a), hoary, and Olympic marmots produce very low-intensity and low-frequency descending calls in contexts that suggest arousal rather than alarm. Chucks may precede or follow bouts of loud alarm calling. In yellow-bellied marmots, chucks arouse little response in other marmots. In contrast to chucks, Vancouver Island marmot's kee-aws typically elicited looks from conspecifics and kee-aws could modulate the meaning of longer-duration calling bouts.

From these results I conclude that all species use their calls to communicate relative predation risk, not predator type. Interestingly, the ways in which species communicated relative risk vary.

Olympic marmots appear to communicate risk by varying the number and rate of alarm calling, and their remarkably long bouts can maintain vigilance in perceivers. Calling bout length certainly helps a human observer locate alarming stimuli and it is likely that it also helps non-calling marmots locate alarming stimuli. However, I suspect this occurs by perceivers spending more time looking around rather than 'knowing' that long calling bouts are associated with a specific class of predators. Interestingly, some marmots alarm called in response to played back alarm calls. That they do this is consistent with a communication system designed to communicate risk and heighten vigilance in perceivers.

The way in which hoary marmots communicated situational variation is a bit less clear. Hoary marmot calling rate was significantly influenced by whether the stimulus was aerial or terrestrial: aerial stimuli tended to elicit quickly paced calls while terrestrial stimuli elicited longer calls uttered at a slow rate. Unfortunately, there was no evidence suggesting that calls played back at different rates elicited different responses. While hoary marmots appeared to encode situational variation by varying the rate of calling, perceivers did not differentiate different alarm call playbacks of different numbers and/or rates. A lack of responsiveness is not unknown for playbacks to marmots using more-or-less identical methods and equipment (Blumstein, 1995b; Blumstein & Arnold, 1995), or to other sciurids using other methods and equipment (Nikol'skii et al., 1994; Weary & Kramer, 1995).

Finally, while Vancouver Island marmots have a sophisticated alarm calling system, they still seem to communicate relative predation risk as opposed to stimulus-class specific, and therefore potentially referential information. Vancouver Island marmots vary call duration and bout composition to communicate risk and this is method of encoding risk that may operate on multiple time scales. A perceiver hearing a long call responds immediately by increasing its vigilance. On a longer time scale, kee-aws function to maintain vigilance in a way that their homologous chucks appear not to.

In conclusion, these three marmots emit superficially similar alarm calls that communicate the relative risk of predation. Although they are close taxonomic relatives, each species communicated risk a slightly different way. Geological evidence suggests the species became isolated 10-100,000 years ago (Hoffmann *et al.,* 1979; Rogers *et al.,* 1991). Nikolsky (1981) found that the alarm calls of arctic ground squirrels (*Spermophilus parryi*) isolated for 7,500 years began to diverge enough to be identifiably different. My results suggest that ways in which species communicate risk may evolve in as few as 10,000 years or as few as 2-3,000 generations.

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