

Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls

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Abstract. Yellow-bellied marmots, *Marmota flaviventris*, were reported to produce qualitatively different alarm calls in response to different predators. To test this claim rigorously, yellow-bellied marmot alarm communication was studied at two study sites in Colorado and at one site in Utah. Natural alarm calls were observed and alarm calls were artificially elicited with trained dogs, a model badger, a radiocontrolled glider and by walking towards marmots. Marmots ‘whistled’, ‘chucked’ and ‘trilled’ in response to alarming stimuli. There was no evidence that either of the three call types, or the acoustic structure of whistles, the most common alarm call, uniquely covaried with predator type. Marmots primarily varied the rate, and potentially a few frequency characteristics, as a function of the risk the caller experienced. Playback experiments were conducted to determine the effects of call type (chucks versus whistles), whistle rate and whistle volume on marmot responsiveness. Playback results suggested that variation in whistle number/rate could communicate variation in risk. No evidence was found of intraspecific variation in the mechanism used to communicate risk: marmots at all study sites produced the same vocalizations and appeared to vary call rate as a function of risk. There was significant individual variation in call structure, but acoustic parameters that were individually variable were not used to communicate variation in risk.

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When alarmed by predators, many species produce specific vocalizations (Klump & Shalter 1984). Some species vary calls according to the type of predator detected (Seyfarth et al. 1980; Davis 1984; Sherman 1985; Cheney & Seyfarth 1990; Marler et al. 1992; Macedonia & Evans 1993), and others vary calls according to the degree of risk the caller experiences, perhaps according to the ‘response urgency’, or imminence of predation, that the caller faces (Robinson 1980; Owings & Hennessy 1984; Blumstein 1995a). The distinction is important, because it was generally assumed that only humans could communicate about events and stimuli external to themselves; non-humans supposedly only communicated about their internal states (reviewed in Marler 1985). Regardless of whether they are externally referential or not, both types of variable alarm calls are referred to as ‘situationally

specific’, in that call structure in some way varies according to situation.

Situationally specific calls can be produced several ways (Blumstein 1995a). Animals could (1) produce acoustically distinctive call types (an apparent precursor to externally referential communication), (2) vary the rate or number of times a single call type is produced, and/or (3) vary the overall intensity (i.e. volume) of a single call. Each of these ‘mechanisms’ could be used singularly or in combination. A general assumption is that each species uses a single mechanism or a single combination of mechanisms to communicate variation in situation.

To study the degree of situational specificity and to determine the degree of external referentiality in vocalizations, it is necessary to study both ‘production specificity’ and ‘perception specificity’ (Marler et al. 1992; Macedonia & Evans 1993; Blumstein & Arnold 1995). If stimulus type uniquely covaries with the vocal response, there is a high degree of production specificity. Thus, if yellow-bellied marmots have highly referential

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communication, they should, for instance, have uniquely different 'raptor' and 'canid' calls that should only be produced in response to raptors and canids, respectively. Perception specificity means that acoustic variants (e.g. raptor calls versus canid calls) should elicit the appropriate response in a conspecific who hears the call in 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).

There is some question about the degree to which yellow-bellied marmots produce externally referential alarm calls. Waring (1966) described the vocal repertoire of yellow-bellied marmots and published spectrograms of several of their vocalizations. He suggested that marmots varied the rate of their most common alarm call, their 'primary whistle motif', as a function of risk, not predator type. More recently, Davis (1991) performed a more detailed micro-structural analysis of yellow-bellied marmot alarm calls. Davis concluded, based on a multivariate discriminant function analysis, that yellow-bellied marmots had predator-specific calls. Of 23 variables he examined, the maximum frequency at peak amplitude was the variable best able to discriminate predator type (at best, discriminant functions were able to correctly classify only 37–65% of the calls to one of four eliciting stimuli). Davis did not point out that recorded peak amplitudes might covary with sound intensity (given that higher frequencies are more likely to attenuate) and may also vary with body size (larger animals produce lower frequency alarm calls). Intensity variation alone is not an ideal mechanism to encode information about predator type because perceived intensity, and therefore perhaps peak frequencies, would be influenced by the distance and relative orientation in space between the signaller and perceiver. Thus, perceivers at different distances from the caller might potentially draw different inferences about the type of predator present. Similarly, if frequency was a function of body size, marmots would have to know the identity of the signaller to properly assess the meaning of a signal. Recently, Blumstein & Daniel, in press noted that yellow-bellied marmots live in environments with particularly poor acoustics, and that micro-structural alarm-call variants might not be transmitted well enough to be differentiated by perceivers. Because

neither Waring nor Davis conducted playback experiments to experimentally document marmot responses to call variants, the question of how yellow-bellied marmots produce and perceive situationally specific vocalizations remains unclear.

In this paper, we describe the means whereby yellow-bellied marmots produce and perceive situationally specific alarm calls. We used 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, we address the fundamental assumption of whether intraspecific variation exists in the way a species encodes situational information.

PART 1: ALARM-CALL PRODUCTION

Methods

Study sites and subjects

Marmots (genus *Marmota*, ca 14 species) are large (3–5 kg), obligately hibernating, moderately to highly social, ground-dwelling sciurid rodents (Barash 1989; Bibikow 1996). We studied alarm communication by yellow-bellied marmots at three locations during most or parts of two summer active seasons for 745 h at three study locations. We studied marmots for 147 h in 1994 (29 June–20 July) and 415 h in 1995 (7 June–29 July) in and around the Rocky Mountain Biological Laboratory, Colorado, U.S.A. (RMBL; site description and marking and census methods in Armitage 1991); in 1995 we also studied marmots for 154 h (1–29 May 1995) in Capitol Reef National Park (Torrey, Utah, U.S.A.), and for 29 h (14–20 August 1995) in the City of Boulder Open Space Parks (Boulder, Colorado, U.S.A.). Unless otherwise indicated, quantitative results presented below excluded the Boulder observations.

At RMBL, we studied 60 different individually identified non-pup marmots (38 in 1994, 31 in 1995) from 11 different social groups in the sub-alpine East River Valley (7 groups in 1994, 6 groups in 1995), and about 17 unidentified individuals about 10 km away living in a higher alpine meadow (North Pole Basin). Yellow-bellied marmot habitat patches are typically described as 'colonial' or 'satellite' (Armitage 1991). Colonies consist of '... one or more males, resident

Table I. Known predator kills of yellow-bellied marmots in the East River valley (Gothic, Colorado, U.S.A.): 1962–1994

Predator	Young	Yearling	Adult	Total
Coyote, <i>Canis latrans</i>	1	18	21	40
Badger, <i>Taxidea taxus</i>	34	4	11	49
Eagle, <i>Aquila chrysaetos</i>		10	3	13
Bear, <i>Ursus americanus</i>		2	2	4
Marten, <i>Martes americana</i>		2	1	3
Long-tailed weasel, <i>Mustela frenata</i>	1	1		2
Red fox, <i>Vulpes vulpes</i>	2			2
Domestic dog, <i>Canis familiaris</i>	1			1

females, usually yearlings (animals one year old), and young (animals <4 months old) but satellite sites contain a single female with her offspring (Armitage 1991, page 381). Colonies contained one or more 'social groups'; i.e. a breeding female and her descendents and/or collateral kin who shared extensively overlapping home ranges, and 'satellite' patches contained a single social group. Virtually all identified RMBL marmots were from known genealogies. In Capitol Reef, we studied about 38 mostly unmarked but individually identifiable non-pup marmots living in at least seven different social groups; five groups were around the Fruita visitors' centre (elevation 1650 m), and two were around Pleasant Creek (elevation 1800 m). In Boulder, we studied seven or eight unmarked marmots (four or five of these were very large pups) in a single social group living on the Cunningham property (elevation 1650 m).

Yellow-bellied marmots are prey to a variety of raptors, canids, felids, mustelids and ursids (Andersen & Johns 1977; Armitage 1982; Zeveloff & Collett 1988; Blumstein 1989; Davis 1991; Van Vuren 1991; Van Vuren & Armitage 1994). From 1962 to 1995, 1 923 yellow-bellied marmots were trapped and tagged at RMBL. Predation is rarely directly observed (Andersen & Johns 1977; Armitage 1982), and most of the 114 instances of predation on yellow-bellied marmots at RMBL (Table I) were verified from kills of animals with radiotransmitters (Van Vuren 1990), or inferred from marmot skeletal remains found at a golden eagle, *Aquila chrysaetos*, nest, or from extensive digging at burrow sites by badgers, *Taxidea taxus*, followed by the failure of known residents to reappear (K. B. Armitage, unpublished data). Marmot remains were found in coyote scats in every month except during hibernation, and the

frequency of occurrences varied from 11 to 35% (Van Vuren 1991; R. A. Powell, unpublished data). For a cohort of yearling marmots implanted with radiotransmitters, coyotes, *Canis latrans*, and badgers were the major predators (Van Vuren & Armitage 1994). Such detailed data are unavailable for the other study sites, but raptors, canids, felids and mustelids occur in Capitol Reef National Park and in Boulder County. At Capitol Reef, golden eagle predation was observed twice (once on a yearling, once on an adult), and predation by other predators was inferred during three seasons of punctuated fieldwork (P. Hopkinson, personal communication).

Alarm-call production

Yellow-bellied marmots produce several vocalizations (Waring 1966; see Results). Their most common alarm vocalization is a brief, single-note whistle that may be repeated multiple times (Waring 1966; Davis 1991). A 'bout' of calling contains one or more whistles. When alarm calling, a marmot moves its mouth and its body visibly shakes; thus it is usually possible to identify callers (cf. Hoogland 1995). Alarm calls from pups were easily distinguished from older animals by their higher pitch. Because there was documented inter-individual variation in at least one alarm call acoustic parameter (fundamental frequency: Leger & Didrichsons 1994), and because some of this variation may be ontogenetic (relatively small pups produce higher-pitched calls; D. T. Blumstein & K. B. Armitage, unpublished data), all analyses focused on alarm calls from older animals. Pups at Boulder were very large, and their calls were not easily distinguishable from adults; thus we did not rigorously analyse most of these data and report most of it anecdotally.

We conducted focal group observations (where we simultaneously monitored the location of all individuals in a social group) and noted each bout of alarm calling and all predator visits. Observers sat in obvious view of the marmots at distances that appeared not to overtly influence their behaviour patterns. The distance between the observer and focal marmots varied greatly among social groups (range ca 15 m to over 150 m) and was a function of how accustomed marmots in the focal social group were to people. Observations were made throughout the day: 83% of our observations were made during the morning active period (0600–1200 hours). When we heard an alarm call, when possible, we noted the identity of the caller, the eliciting stimulus, the distance of the caller to the stimulus, the distance of the caller to the nearest refuge (yellow-bellied marmots exclusively use burrows as refugia) and the response of other marmots. When subjects produced bouts with more than a single alarm call, we counted the number of calls in a bout and timed the bout.

Predators and alarm calling were uncommon. Thus we experimentally induced alarm calls to increase our sample of alarm responses to known stimuli by simulating predator attacks four ways: we walked towards marmots, we walked dogs towards marmots, we drove a radiocontrolled motorized badger towards marmots, and we flew a radiocontrolled model glider over marmots. All experiments were designed with the welfare of marmots in mind. Thus, we only used one type of living predator (leash-controlled or extremely well-trained dogs that exposed the marmot to no direct risk of predation) and used predator models or simulated predators (humans) to alarm marmots. Moreover, we minimized the number of experiments (generally \leq two manipulations per group per day; 1 social group/1 day = '1 group-day') to minimize the probability that we might habituate marmots to natural predators. One problem with using models and unnatural predators is that marmots may respond differently to our models than they did to natural predators. We discuss the naturalness of our simulations below. Nevertheless, the main goal of these manipulative experiments was to document the degree to which marmot alarm calls covaried with stimulus types that could be classified one of several ways (e.g. aerial/terrestrial and/or with respect to the exact stimulus used; see Results). If each alarming stimulus and/or type of stimulus elicited a range of

responses, and if responses were not stimulus-specific, then we would infer that marmot alarm calls did not have a high degree of external referentiality.

First, we walked towards focal marmots at a constant rate (ca 1 m/s) and noted whether subjects called. We refer to these experiments as 'predation probes' (Blumstein 1995a; Blumstein & Arnold 1995; cf. human experiment in Davis 1991). For this experiment, we selected a focal marmot (occasionally we could monitor multiple subjects) who was above-ground, identified it and noted the marmot's responses as we approached. If the focal marmot alarm called, we recorded the vocalization. If the bout had multiple calls, we recorded and counted them, and timed the bout length. We conducted this experiment 165 times to marmots living in 12 social groups at Capitol Reef and RMBL (1995 only). Fifty-two different marmots were experimentally 'probed' (median N exposures = 2.5, range = 1–21, total N exposures = 201). We elicited 50 alarm calls. The distance we began walking towards a focal marmot varied as a function of how accustomed marmots were to people: people could walk to as near as 5 m from some foraging marmots at the RMBL townsite or the Fruita area at Capitol Reef and elicit only a 'casual' look, but some subjects at sites outside the RMBL townsite returned to their burrow and looked and/or alarm called when people were over 100 m away (some *M. caudata aurea* in a very remote meadow in a Pakistani National Park began alarm calling at over 200 m: Blumstein 1995a). Although humans hunt yellow-bellied and other marmot species (Rue 1981; Bibikow 1996), human predation probably has not been a major selective factor influencing yellow-bellied marmot anti-predatory behaviour (cf. Slobodchikoff et al. 1991). None the less, marmots alarm call to humans, and we used humans as a reasonably standardized stimulus with which to elicit alarm calls. If there was considerable variation in the acoustic structure of alarm calls elicited by humans, one might question the degree to which alarm calls were highly referential (but see Slobodchikoff et al. 1991 for an example of calls that may covary with the human's identity).

For all human 'predation-probes' and all other predator simulation experiments, we did not control for the presence of other animals or the initial location of a focal marmot. Although the presence

of conspecifics (or specific conspecifics) might influence the probability of whether a subject called (e.g. Sherman 1977; Schwagmeyer 1980; Blumstein et al. 1997), we did not expect the presence of conspecifics to systematically influence the potential covariation between stimulus type and alarm call structure. Moreover, social groups were relatively large and topographic, and vegetative heterogeneity made it so that not all individuals in a social group could see the potentially alarming stimulus. Yellow-bellied marmots typically alarm called less than 5 m away from their main burrow (Blumstein et al. 1997; K. B. Armitage, unpublished observations), and individuals who were some distance away first returned to their burrow before calling. Thus we did not anticipate that distance to a burrow would influence the potential covariation between stimulus type and alarm-call structure. When we conducted more than one stimulus experiment in a given day in a given social group, we waited until focal marmots were neither alert nor vigilant (Armitage et al. 1996) and engaged in normal (pre-experiment) activities. Moreover, we often targeted different subjects in different parts of the social group's home range.

Second, at both RMBL (1995) and Capitol Reef, we walked well-trained or leash-controlled dogs around social groups to elicit alarm calls and noted those animals who called (cf. dog experiments in Owings & Leger 1980; Robinson 1980; Leger et al. 1984; Owings et al. 1986; Davis 1991). If a marmot began calling, we walked towards the marmot until she disappeared into her burrow. All animals in a social group could not always see the dog. We used three dogs at RMBL, and three different dogs at Capitol Reef. We conducted this experiment 23 times with marmots living in 8 social groups. Sixteen different marmots were exposed to dogs (median N exposures=2, range 1–6, N exposures=31). We elicited 22 alarm calls. If subjects called, we counted the number of calls in a bout, timed the bout and recorded alarm calls. Although patently unnatural (wild canids do not accompany people on a leash), the experiment did provide a way to present a canid in an ethical and more or less controlled fashion to marmots. Once again, if marmots produced a unique 'terrestrial predator' alarm call, we might expect a consistent type of call in response to the exposure of a living canid.

Third, we used a stuffed badger mounted on a radiocontrolled chassis ('RoboBadger') to simu-

late a terrestrial predator wandering through a marmot colony (cf. badger experiments in MacWhirter 1992; Hoogland 1995). Not all animals in a social group could see RoboBadger. We drove the stuffed badger from a hidden location towards focal marmots and noted all marmots that called. We conducted this experiment 31 times to marmots living in 12 different social groups at Capitol Reef and RMBL (1995 only). Thirty-four marmots were exposed to the stuffed badger (median N exposures=1, range 1–3, total N exposures=44). We elicited 17 alarm calls. If a marmot called, we recorded its vocalization, counted the number of calls in the bout, and timed the bout. The stuffed badger was driven at a reasonably slow speed (≤ 1 m/s), and generally meandered along a trail or dirt road. Live badgers moved slowly but determinedly when hunting marmots, and marmots responded to badgers by returning to their burrows, looking, and alarm calling (K. B. Armitage, personal observations). The model's radio receiver made a quiet, high pitched beeping sound, and the electric motor made a quiet humming sound. Under quiet conditions, we generally could not hear any artificial sound beyond 5–8 m of the model; if it was windy or there was substantial background noise (e.g. flowing water), the mechanical sounds did not travel more than a few metres. The starting distance between the model and focal marmots varied considerably as a function of suitable terrain and study site, but we generally started to drive the model towards a focal marmot at over 50 m. Because marmots often responded to the sight of the model over 50 m away, marmots appeared not to respond to the unavoidable sounds. As a control, we drove the radiocontrolled chassis around without the badger mount four times, through four social groups. Ten marmots saw the chassis, and four alarm called. Although marmots alarm called in response to the movement of the chassis alone, none 'trilled' to the chassis alone; marmots naturally alarm called to non-predatory objects moving along the ground (see Results).

Fourth, at Capitol Reef and at RMBL (in 1995) we flew a brown radiocontrolled model glider with a 2-m wing span over marmots to simulate an eagle attack and noted those animals that called (cf. aerial stimulus experiments in Noyes & Holmes 1979; Davis 1984; Sherman 1985; Davis 1991; MacWhirter 1992). We assumed that all animals in a social group could potentially see the

aerial model. We conducted this experiment 18 times with marmots living in eight social groups. Twenty-three marmots were exposed to the aerial model (median N exposures=2, range=1–4, total N exposures=49). We elicited 24 alarm calls. The radiocontrolled glider flew silently, and we launched it from a hillside above focal marmots. We generally flew it low and fast and in a reasonably straight line; sometimes we flew the model in a large arc in front of focal marmots. Most experiments ended with the model's crash, and flights were generally around 10–15 s. If subjects called, we counted the number of calls in a bout, timed the bout and recorded the alarm calls. Our model eagle appeared suddenly and elicited responses that appeared indistinguishable from attacks from real golden eagles: marmots bolted to their burrows, looked towards the plane, and some individuals alarm called (see also *Noyes & Holmes 1979*).

Alarm-call structure

Calls were recorded using Sennheiser ME-88 microphones encased in 'blimp' windscreens with either a Sony TC-D5M or a Marantz PMD-340 cassette recorder onto high-bias 60-min tapes. All calls were pre-filtered to prevent frequency digitizing artefacts (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 1990). 'Boxy' sound spectrograms were generated using 512-point short-time Fourier transformations with 50% overlap, a Hamming window, and -100 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*), we analysed only spectrograms without extensive background noise and excessive reverberation from high-quality (i.e. minimally attenuated) recordings using Canary 1.2 software (time resolution 2.88 ms; frequency resolution 43.47 Hz).

We focused on the first, or in many cases the only, whistle an individual emitted in response to a stimulus, because we assumed that the first whistle 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 and, for our analyses, we treated these responses as independent. If alarm calls referred to specific predator types, we would expect that all individuals who alarm called would produce roughly the same alarm call. We measured the following variables from an individual's first whistle: 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, we calculated the bandwidth (maximum minus minimum frequency), and the difference between the starting and ending frequency (a rough approximation of call shape). In addition to these 'micro-structural' call characteristics, we counted the total number of alarm calls that each subject emitted to a stimulus, 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.

Marmots also varied their call intensity. Call intensity was difficult to measure properly in the field, but our general impression was that many of the Capitol Reef alarm calls were quieter than many alarm calls heard elsewhere. In all locations, marmots sometimes varied call intensity within a calling bout.

Data reduction and statistical analyses

We recorded 267 non-pup alarm calls of sufficient quality to digitize and analyse. Some recordings were from unidentified subjects, some were of different bouts from the same subject and some were in response to unidentified stimuli. From this data set, we randomly selected at most a single call per subject to each of five stimuli (dogs, humans walking towards marmots, RoboBadger, eagles, model eagle) and used these observations to study how call structure was influenced by stimulus, distance to the stimulus and study site. The data set consisted of 76 observations from 45 subjects (25 adult females, 7 adult males, 4 yearling males, 2 yearling females, 7 unknown age/sex): 20 subjects appeared in a single stimulus category, 20 subjects appeared in two different stimulus categories, four subjects appeared in three different stimulus categories, and a single subject appeared in four stimulus categories. We assumed that if potential stimulus

effects systematically influenced call structure, our use of a single observation from a subject within a stimulus category would not bias our test for stimulus effects. Rather than creating a novel sub-sampled data set with its own unique numerical characteristics, we used the same data set to test for distance effects and acknowledge that the slightly unbalanced nature of the data set may bias our estimation of distance effects. Given significant inter-individual variation in the structure of calls (e.g. Leger & Didrichsons 1994; below and Results), an even more conservative approach would have been to sample each individual once. Using each individual a single time would have reduced the size of our data set and, because fewer calls would have been elicited from each stimulus, may have reduced potential stimulus-induced call variation. For all identified subjects recorded more than four times responding to the five stimuli, we constructed a data set containing all calls to the five stimuli and used this data set to study how marmot identity influenced call structure. The data set contained 71 observations from 12 adult female subjects: one subject appeared in one stimulus category; seven subjects appeared in two stimulus categories; three subjects appeared in three stimulus categories, and one subject appeared in four stimulus categories. Subjects contributed a median of 5 data points to this data set (range=4–11). For these 12 subjects, we added an additional 22 observations of calls elicited: from unknown stimuli ($N=12$), while in a trap ($N=2$), to a hare ($N=1$), to a raven ($N=1$), to humans on bicycles ($N=4$) and to deer ($N=2$). We used this data set with 93 observations in a discriminant function analysis; missing acoustic parameters from 5 of the calls left the final data set containing 88 observations on 12 subjects.

In general, we used factor analysis to study the pattern of relationships between measured acoustic parameters. Rather than computing factor scores or choosing a single variable to represent each factor, we analysed each acoustic variable independently to better understand how each acoustic parameter varied with situation, distance, study site and caller identity. Because we conducted multiple analyses on certain data sets, we report P -values to four significant figures; readers may choose to interpret our exact P -values differently. If we calculated multiple comparisons, we specify the test statistic with each result. We used

linear models (ANCOVA, ANOVA, linear regression) to study the significance of and amount of variation in each acoustic parameter explained by the stimulus and the distance to the stimulus. We used ANOVA to test for the significance of study location (Capitol Reef versus RMBL), and/or marmot identity in explaining variation in measured acoustic parameters. We used stepwise discriminant function analysis to determine which, if any, measured acoustic parameters were uniquely associated with individual marmots and/or eliciting stimuli. Finally, we used a Friedman non-parametric repeated measures ANOVA to study how the rate of alarm whistles covaried with risk.

Descriptive statistics were calculated using StatView (Abacus Systems 1993). ANOVA and ANCOVA were modelled in SuperAnova (Abacus Systems 1991), and regressions were fitted with StatView. Principal components (varimax extraction, orthogonal rotation) were extracted using StatView. Discriminant functions (variable selection criteria: Wilks' lambda) were extracted in SPSS for Windows (Norusis 1994). Data were transformed when required to meet assumptions of analyses; exact transformations are noted on graphs and on tables.

Results

Alarm-call production

Marmots produced three acoustically distinct alarm vocalizations (Fig. 1): whistles ('primary whistle motif': Waring 1966), trills ('accelerando whistles': Waring 1966) and chucks (possibly Waring 1966's 'quiet whistles'). We heard 537 bouts of naturally elicited (79%) and artificially elicited (21%) alarm calls (56 at RMBL in 1994; 247 at RMBL in 1995; 234 at Capitol Reef). This total includes multiple calls from identified subjects and calls from unidentified subjects but excludes calls produced by pups. Naturally elicited calls included some calls to humans and to dogs, but these calls were not elicited by us under experimental conditions (e.g., marmots 'naturally' called to hikers with and without dogs, etc.). All three vocalizations were heard at all three study areas. Whistles were by far the most common alarm vocalization: 518 of the 537 observed bouts of alarm calls contained only whistles. Whistles were repeated from one to over 100 times: 61% of 480 bouts where we counted the number of

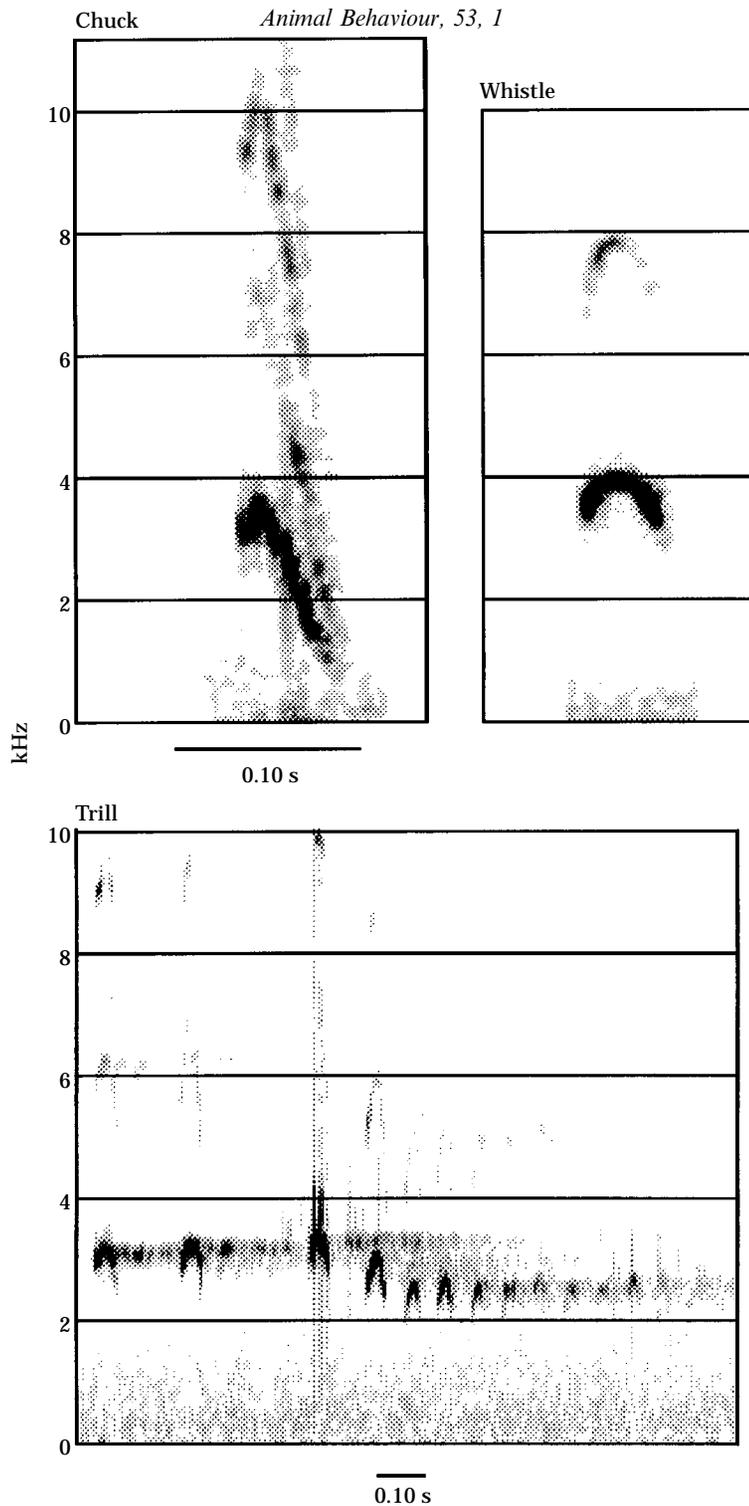


Figure 1. Spectrograms (256 point SoundEdit) of yellow-bellied marmot alarm vocalizations. Whistles were the most common alarm calls (97% of all bouts contained only whistles) and were often repeated multiple times and at different rates. Whistle structure varied, but never included the lower, descending frequencies heard in chucks. About 2% of calling bouts contained trills, and 1% contained chucks. Trills began with rapidly repeated whistles before the pace quickened and the frequency began to waver.

whistles contained a single whistle, 24% contained 2–5 whistles, 3% contained 6–9 whistles, and 12% contained at least 10 whistles. Marmots whistled in response to aerial predators (golden eagles) and terrestrial predators (red foxes, *Vulpes vulpes*, and although not observed during this study, coyote and badgers), the eagle model, the badger model, quickly approaching large birds (turkey vultures, *Cathartes aura* and ravens, *Corvus corax*), lagomorphs (hares, *Lepus* spp. and pikas, *Ochotona princeps*), humans (walking, in cars and on bicycles), ungulates (mule deer, *Odocoileus hemionus* at RMBL but despite a large population, not at Capitol Reef) and occasionally rain. Only 2.6% of 270 calling bouts from identified marmots appeared to be in response to a social stimulus. Of the 537 total observed bouts of alarm vocalizations, 14 contained trills and five contained chucks. Trills were always preceded by ‘normal’ whistles; marmots trilled by increasing their whistle rate and then modulating the fundamental frequency of their whistles. We heard 14 trills from 11 different subjects. Marmots trilled as they disappeared into their burrows after being pursued by a dog ($N=6$), when suddenly surprised by a human ($N=2$), in response to RoboBadger ($N=1$), and in response to an unidentified stimulus ($N=1$). Trills were also heard in social situations ($N=4$); during aggressive interactions a fleeing marmot sometimes trilled (also see Burke da Silva et al. 1994). Marmots also trill when fleeing from live badgers and unrestrained dogs (K. B. Armitage, unpublished observations). In the field, we heard five chucks from five subjects. Marmots chucked after alarm calling in response to our aerial model and following its crash landing ($N=3$), in social situations ($N=1$), at humans ($N=1$, the marmot chucked once, whistled once and chucked once). We also heard chucks apparently in response to our sitting in a marmot’s home range when we were not directly observing and quantifying marmot behaviour. Chucks were produced by marmots who appeared to be minimally alarmed and, in the field, inevitably followed whistles. Captive marmots sometimes chucked in live traps without whistling.

Alarm-call structure

Alarm whistles varied along all measured acoustic parameters (Fig. 2). Measured acoustic variables of calls elicited by dogs often, but not

always, differed from calls elicited from other stimuli (detailed analysis below). Acoustic structure of whistles elicited by other stimuli tended not to uniquely covary with stimulus type.

Four factors explained 83% of total variance in alarm whistles’ acoustic parameters (Table II). We defined factors based on an examination of factor scores of at least 0.71 (discussion in Tabachnick & Fidell 1986). We interpreted orthogonally rotated factors as (1) a frequency factor, (2) a number/rate of calling factor, (3) a shape of call factor and (4) a bandwidth factor. Call rate and duration did not load highly on any factor. Nevertheless, the factor analysis illustrates that micro-structural and temporal aspects of alarm calling are generally unrelated.

Does distance from the stimulus or stimulus type explain variation in whistle structure?

Distance explained about 10% of variation in the difference between the starting and ending frequency: marmots’ began their whistles at slightly higher frequencies than they ended them as an increasing function of stimulus distance (Table III). Distance explained no significant variation in any of the other examined variables. When each stimulus was analysed separately for distance effects, only five variables had significant or moderately significant relationships. For whistles to eagles, the starting frequency increased with distance ($R=0.86$; $P=0.06$) and the difference between the starting and ending frequency increased with distance ($R=0.89$; $P=0.04$). For whistles to RoboBadger, bandwidth declined as a function of distance to the model ($R=-0.48$; $P=0.07$), as did both the maximum ($R=-0.51$; $P=0.05$) and peak frequency ($R=-0.48$; $P=0.07$).

Although marmots alarm called to the five stimuli at significantly different distances ($F_{4,67}=4.454$, $P=0.0030$), there appeared to be sufficient variation in those distances to potentially explain variation in signal parameters. Marmots first called to eagles at significantly greater distances ($\bar{X} \pm \text{SD}=166 \pm 114.4$ m, range=3–600 m, $N=5$; significance calculated by Fisher post-hoc LSD) than to humans (32 ± 37.6 m, range=3–90 m, $N=25$), the model plane (54 ± 24.2 m, range=15–90 m, $N=11$), and RoboBadger (28 ± 32.9 m, range=2–130 m, $N=15$). Marmots first called to dogs (97 ± 87.5 m,

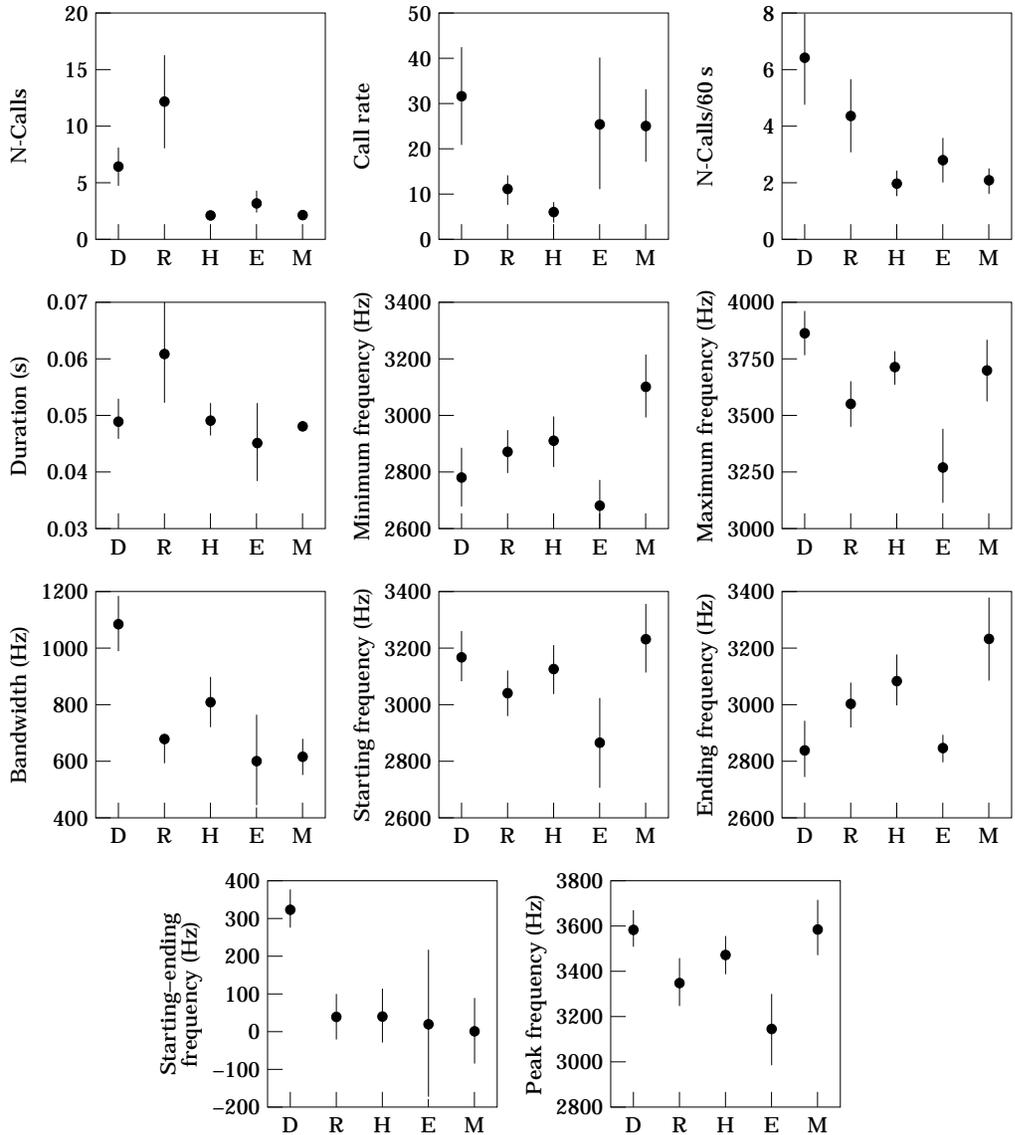


Figure 2. Average \pm SE effect of stimulus type on acoustic structure of yellow-bellied marmot alarm calls. On all graphs: D=dog; R=RoboBadger; H=human; E=golden eagle; M=model eagle. Sample sizes: D=18 for all; R=15 for all but N-calls/60 s ($N=11$); H=26 for all; E=5 for all; M=12 for all.

range=2–250 m, $N=16$) at significantly greater distances than to humans or the model badger.

The way we classified stimuli influenced the amount of variation explained by stimulus type (Table III). When stimuli were classified into five categories (dogs, humans, RoboBadger, eagles, model eagle: Table III), stimulus type explained 8–11% of the variation in the number of calls,

calling rate, the number of calls in the first 60 s, the maximum frequency, the bandwidth and the difference between the starting and ending frequency. Post-hoc Fisher's Protected LSD tests suggested that responses to dogs were important in accounting for significance in the analysis of five categories (Table IV). Most (16/21) of the significant post hoc pair-wise differences were

Table II. Rotated factor scores calculated from measured whistle parameters and the percentage of total variance explained (bold) by each factor ($N=72$ whistles with complete data)

	Frequency factor*	Number of calls factor	Shape factor	Bandwidth factor
Starting frequency	<i>0.954</i>	-0.049	0.056	-0.097
Peak frequency	<i>0.937</i>	0.139	0.033	0.261
Minimum frequency	<i>0.846</i>	-0.082	-0.252	-0.414
Maximum frequency	<i>0.816</i>	0.268	0.078	0.406
Ending frequency	<i>0.740</i>	0.063	-0.553	-0.266
N calls/60 s†	0.085	<i>0.949</i>	-0.118	0.033
N calls†	0.054	<i>0.925</i>	-0.133	0.053
Starting–ending	0.144	-0.145	<i>0.812</i>	0.243
Bandwidth	-0.012	0.347	0.324	<i>0.807</i>
Duration	0.0004	-0.409	-0.372	0.589
Call rate†	-0.127	-0.064	0.576	-0.086
Variance	35.9	20.4	17.2	9.6

*Factor scores ≥ 0.71 are italicized and defined each factor.

†Transformation = $[\sin(x^{0.5})]^{-1}$.

between dogs and the other four stimuli. We also classified stimuli into two categories according to their risk. Wild canids (coyotes) were the major predator on yearling and adult marmots during the long-term studies at RMBL, and marmots called frequently to dogs and wild canids. We classified canids as ‘high-risk’ stimuli and all other stimuli as ‘lower-risk’. Marmots called to dogs at least 67% of the time and to each other stimulus class 0–66% of the time. When classified according to ‘risk’, stimulus type explained 4–15% of the variation in the number of calls, number of calls in the first 60 s, the maximum frequency, the bandwidth, the ending frequency and the difference between the starting and ending frequency (Table III). Classifying stimuli according to their ‘location’, i.e. whether they were aerial or terrestrial stimuli (Table III), explained significant variation for only whistle bandwidth.

Does whistle structure vary geographically?

Yellow-bellied marmots sounded similar and had similar call parameters in all three study sites and in Waring’s (1966) recordings. We analysed the Capitol Reef and the RMBL calls in more detail in a two-way ANOVA to test for variation explained by study site after controlling for variation explained by stimulus and in a one-way ANOVA to test for study-site effects alone. Whether marmots were recorded at Capitol Reef or RMBL explained some (7–13%) of the vari-

ation in maximum frequency, bandwidth and the frequency at peak amplitude but none in the other measured acoustic variables (Table V).

Does marmot identity influence whistle structure?

Marmot identity explained substantial variation in those acoustic parameters that did not covary with situation (Table VI). Identity alone significantly explained 18–35% of the variation in whistle duration, minimum frequency, maximum frequency, frequency at peak amplitude and starting and ending frequencies, but stimulus type explained no significant variation in any of the variables.

Discriminant function analysis strengthened this conclusion: those variables that covaried with individual were not used to communicate situation. Of all measured acoustic parameters from the 12 marmot’s recorded calls (all were adult females), only duration and maximum frequency were extracted in a step-wise discriminant analysis. Given the number of individuals, we would have expected discriminant functions by chance to classify 7.3% of the calls to individual (Tabachnick & Fidell 1989, page 544). In fact, 25.8% were correctly classified (Table VII).

Does whistle structure uniquely covary with stimulus type?

The eight micro-structural variables and the three transformed number of whistles/whistle rate

Table III. *P*-values and explained variation from ANCOVAs, ANOVAs and linear regressions for the 11 dependent variables* as a function of stimulus classification scheme and distance

	<i>N</i> call†	Rate‡	<i>N</i> /60 s‡	Duration	Min.	Max.	Bandwidth	Peak	Start	End	Start-end
Five-stimuli											
Five-stimuli‡	0.0397	0.0570	0.0501	0.3500	0.2633	0.0249	0.0035	0.0957	0.2444	0.2531	0.0277
Distance	0.9202	0.8239	0.7832	0.7710	0.8735	0.8830	0.9885	0.5533	0.1606	0.6334	0.0111
Model	0.0718	0.0920	0.0846	0.4194	0.3579	0.0469	0.0069	0.1513	0.2624	0.2412	0.0018
Adj. <i>R</i> ²	0.074	0.065	0.072	0.001	0.008	0.089	0.151	0.046	0.023	0.026	0.191
Five-stimuli (only)											
Adj. <i>R</i> ²	0.0177	0.0479	0.0217	0.2394	0.1903	0.0362	0.0054	0.1214	0.3771	0.1097	0.0129
Distance (only)	0.105	0.075	0.105	0.021	0.030	0.084	0.139	0.045	0.004	0.049	0.114
Adj. <i>R</i> ²	0.9435	0.6275	0.7131	0.4726	0.6326	0.9729	0.6588	0.7001	0.3121	0.2394	0.0036
Adj. <i>R</i> ²	-0.014	-0.011	-0.013	-0.007	-0.011	-0.014	-0.011	-0.012	0.001	0.006	0.102
Risk stimuli											
Risk stimuli§	0.0130	0.7172	0.0137	0.8906	0.2936	0.0204	0.0004	0.1178	0.5545	0.1170	0.0020
Distance	0.5916	0.7028	0.8137	0.4683	0.8319	0.5487	0.6736	0.9999	0.4028	0.4356	0.0221
Model	0.0446	0.8328	0.0437	0.7668	0.5122	0.0667	0.0017	0.2711	0.5050	0.1460	0.0001
Adj. <i>R</i> ²	0.060	-0.024	0.064	-0.021	-0.009	0.049	0.145	0.009	-0.009	0.027	0.207
Risk stimuli (only)	0.0053	0.5812	0.0044	0.5670	0.1988	0.0370	0.0006	0.1654	0.5325	0.0459	0.0004
Adj. <i>R</i> ²	0.088	-0.009	0.097	-0.009	0.009	0.045	0.138	0.013	-0.008	0.040	0.148
Location stimuli											
Location stimuli**	0.1840	0.1055	0.1848	0.3261	0.2728	0.2130	0.0157	0.6701	0.8647	0.2303	0.0504
Distance	0.7459	0.8638	0.5378	0.6042	0.4973	0.8379	0.3598	0.6478	0.3088	0.1664	0.0011
Model	0.4101	0.2377	0.3855	0.4763	0.4872	0.4577	0.0481	0.8478	0.5934	0.2441	0.0022
Adj. <i>R</i> ²	-0.003	0.013	-0.001	-0.007	-0.008	-0.006	0.058	-0.024	-0.014	0.012	0.138
Location stimuli (only)	0.1607	0.1085	0.1749	0.3550	0.2856	0.2383	0.0241	0.8329	0.9539	0.2824	0.1632
Adj. <i>R</i> ²	0.013	0.021	0.012	-0.002	0.002	0.005	0.054	-0.013	-0.013	0.002	0.013

*Dependent variables are defined as: *N* calls=number of alarm whistles; Rate=number of calls/total bout length (=1 if only a single alarm whistle); *N*/60 s=number of calls in the first 60 s of calling; Duration=length of the alarm call; Min.=the minimum frequency of the alarm call; Max.=the maximum frequency of the alarm call; Bandwidth=maximum frequency - minimum frequency; Peak=the frequency at peak amplitude; Start=the lowest frequency at the beginning of the alarm call; End=the lowest frequency at the end of the alarm call; Start-end=a rough index of shape calculated by subtracting the ending frequency from the starting frequency. *P*-values for significant main effects are highlighted in bold. Sample sizes range from 68 to 76 depending upon model.

†Transformation= $[\sin(x^{0.5})]^{-1}$.

‡Five-stimuli=dogs, humans, RoboBadger, eagles, model eagle.

§Risk stimuli=high risk: canids (=dogs), and lower risk: all other stimuli.

**Location stimuli=aerial stimuli (eagles, model eagle), terrestrial stimuli (dogs, human, RoboBadger).

Table IV. Stimulus type, classified into five categories (human, dog, RoboBadger, eagle, and model eagle), explains significant variation in six of 11 measured alarm-call acoustic parameters (Table III)*

	Human	Dog	RoboBadger	Eagle	Model
Human		<i>N</i> /60 s Bandwidth Start–end	<i>N</i> calls Rate	Max.	
Dog			<i>N</i> calls Rate <i>N</i> /60 s Max. Bandwidth Start–end	<i>N</i> calls <i>N</i> /60 s Max. Bandwidth Start–end	Bandwidth Start–end
RoboBadger				Rate	Rate
Eagle					Max.

*Summarized here are the significant post hoc pair-wise comparisons for each ANOVA calculated using Fisher's Protected LSD. Variables defined as in Table III.

variables had little ability to discriminate calls to stimulus. Only one variable, the number of calls, was extracted from the step-wise discriminant procedure. The number of calls had limited predictive ability, however: only 25% of stimuli were correctly classified versus an expected 15.2% correct classifications by chance alone (Table VIII). When calls in response to dogs, humans and RoboBadger were mis-classified, virtually all incorrect classifications were to the eagle and model eagle categories. Perhaps these mis-classifications were a result of the variation in the number of calls dogs, humans and RoboBadger elicited. When stimulus was coded as 'high-risk' (dogs) or 'lower-risk' (all other stimuli), and the analysis re-run, 79% were classified to stimulus (80% correctly to 'high-risk', 78% correctly to 'lower-risk'). This 'risk' model used two variables to classify calls to stimulus: starting–ending frequency and the number of calls in 60 s. When stimulus was coded as 'aerial' or 'terrestrial' and the analysis re-run, no discriminant functions were extracted.

Does the tempo of alarm calling change with distance?

Nine marmots alarm called to dogs with bouts containing at least 10 whistles. For these marmots, the interval between alarm calls significantly decreased as subsequent calls were given (test calculated on first nine inter-call intervals; Friedman $\chi^2_r=25.66$, $P=0.001$; Fig. 3). Because we walked dogs towards marmots (closer

distance=higher presumed risk), the interval between calls decreased as risk increased. Thus, calling rate increased with risk. This result may not generalize to potentially less 'risky' stimuli. Seven marmots called at least 10 times to RoboBadger, which also approached marmots. Marmots called at a significantly slower rate (Mann–Whitney: $z=-3.02$, $P=0.003$) to the badger than to living dogs. The interval between calls also did not decrease as distance decreased (Fig. 3; test calculated on first seven inter-call intervals: $\chi^2_r=1.95$, $P=0.92$). Marmots tended not to call repeatedly to our human predation probes, eagles or the model eagle, and we were unable to make similar comparisons.

PART 2: RESPONSE TO ALARM CALLS

Results from part 1 illustrate that the number and rate of alarm whistles appear related to the degree of risk a caller experiences: marmots called faster when risk was apparently greater. Specifically, marmots produced quickly paced repeated whistles to dogs and increased their calling rate as dogs approached. Eagles, which generally appeared quickly but also disappeared quickly, elicited a few quickly-paced whistles. Chucks appeared to be produced when marmots were 'disturbed' rather than 'alarmed': they chucked after risk seemed to decrease. Although results suggested that several acoustic factors covaried with stimulus type and with apparent risk, there

Table V. *P*-values and explained variation from ANOVAs for the 11 dependent variables as a function of study site (Capitol Reef, $N=36$, or RMBL, $N=40$) and stimulus*

	<i>N</i> calls	Rate	<i>N</i> /60 s	Duration	Min.	Max.	Bandwidth	Peak	Start	End	Start-end
Study site	0.1403	0.2296	0.1871	0.7529	0.3886	0.0037	0.0369	0.0204	0.3857	0.1874	0.4623
Five-stimuli	0.0083	0.0128	0.0605	0.2561	0.1825	0.1096	0.0157	0.1817	0.4438	0.0944	0.0112
Model	0.0150	0.0246	0.0455	0.3507	0.2327	0.0020	0.0019	0.0257	0.4203	0.0984	0.0219
Adj. <i>R</i> ²	0.120	0.111	0.085	0.009	0.026	0.177	0.179	0.104	0.067	0.059	0.109
Study site	0.5861	0.7909	0.1302	0.6418	0.4451	0.0007	0.0085	0.0098	0.2651	0.2473	0.8243
Adj. <i>R</i> ²	-0.009	-0.013	0.018	-0.011	-0.006	0.134	0.078	0.074	0.003	0.005	-0.013

*Significant main effects *P*-values are highlighted in bold. Sample sizes range from 68 to 76 depending upon exact model. Variables are defined and transformed as in Table III.

Table VI. *P*-values and explained variation from ANOVAs for the 11 dependent variables as a function of marmot identity ($N=12$ marmots responding 4–11 times to 1–4 different stimuli) and stimulus*

	<i>N</i> calls	Rate	<i>N</i> /60 s	Duration	Min.	Max.	Bandwidth	Peak	Start	End	Start–end
ID	0.4912	0.6222	0.5752	0.0018	0.0160	0.0001	0.4052	0.0001	0.0012	0.0022	0.3541
Five-stimuli	0.9730	0.2047	0.9860	0.6588	0.2535	0.1319	0.7035	0.1341	0.4400	0.3233	0.9484
Model	0.6659	0.5738	0.7277	0.0007	0.0181	0.0001	0.3641	0.0001	0.0025	0.0041	0.6117
Adj. <i>R</i> ²	–0.043	–0.024	–0.060	0.327	0.203	0.380	0.024	0.383	0.282	0.264	–0.031
ID	0.3621	0.7894	0.4142	0.0001	0.0146	0.0001	0.2127	0.0001	0.0008	0.0020	0.3270
Adj. <i>R</i> ²	0.019	–0.062	0.009	0.345	0.183	0.344	0.055	0.348	0.284	0.254	0.026
Five-stimuli	0.8212	0.3452	0.7962	0.0574	0.2852	0.2779	0.3008	0.2848	0.4859	0.4359	0.9827
Adj. <i>R</i> ²	–0.037	0.008	–0.036	0.075	0.016	0.017	0.014	0.016	–0.007	–0.002	–0.054

*Significant main effects *P*-values are highlighted in bold. Sample sizes range from 68 to 71 depending upon model. Variables are defined and transformed as in Table III.

Table VII. Classification table (percentage classified to each category) of the results of the 12-individual discriminant function analysis

Individual	N	Predicted individual*											
		1	2	3	4	5	6	7	8	9	10	11	12
1	6	33.3	33.3	0	33.3	0	0	0	0	0	0	0	0
2	5	0	20	0	0	20	40	0	0	0	0	0	0
3	5	0	20	40	0	0	0	0	0	0	0	0	0
4	6	0	0	0	25	0	12.5	0	0	0	0	0	0
5	8	12.5	0	12.5	0	50	0	0	0	0	0	0	0
6	5	40	20	0	0	0	40	0	0	0	0	0	0
7	9	0	9.1	0	0	0	0	0	18.2	9.1	27.3	18.2	9.1
8	8	0	0	0	0	11.1	0	11.1	55.6	0	0	0	22.2
9	15	13.3	0	13.3	20	20	0	0	20	6.7	6.7	0	0
10	8	0	12.5	12.5	12.5	37.5	0	0	0	12.5	0	0	12.5
11	7	0	0	14.3	0	0	14.3	0	0	0	0	71.4	0
12	6	0	16.7	16.7	0	0	0	16.7	33.3	0	16.7	0	0

*All subjects were adult females: subjects 1–6 lived at Capitol Reef; subjects 7–12 lived at RMBL. Percentage of cases correctly classified to proper individual=26%.

Table VIII. Classification table (percentage classified to each category) of the results of the 5-stimulus discriminant function analysis

Group	N	Predicted group*				
		Dog	Human	RoboBadger	Eagle	Model eagle
Dog	18	39	0	0	17	44
Human	26	8	0	0	8	85
RoboBadger	15	13	0	0	47	40
Eagle	5	0	0	0	60	40
Model eagle	12	8	0	0	17	75

*Percentage of cases correctly classified to proper group=25%.

was substantial variation in calls elicited by all stimuli. The following playback studies focused on the temporal variables (whistle rate and number) for four reasons. First, temporal variables were related to stimulus type and risk (Table III) and were unrelated to other micro-structural variants (Table II). Second, it was easy to experimentally manipulate the rate and number of calls to create playback stimuli and conduct playback experiments. Third, even though whistle structure covaried with stimulus type, results from another study (Blumstein & Daniel, in press) suggest that micro-structural variants may not be transmitted with high fidelity through yellow-bellied marmot habitats. Fourth, some micro-structural variation may be associated with individual recognition (Table VII).

In this section, we present results from a series of playback experiments designed to study how marmots responded to different vocalizations. These experiments addressed the following questions. First, do marmots respond to conspecific alarm whistles and/or whistles from other species? Second, do marmots respond differently to chucks versus whistles? Third, does the rate, number and/or volume of alarm whistles influence marmot response? Fourth, how consistent are playback results over time and between locations?

Methods

High-quality recordings of whistles, chucks and other sounds were sampled with 16-bit resolution at 48 kHz with a NuMedia-2 AD-DA board (Spectral Innovations, Inc., Portland, Oregon) on a Macintosh IIsi. We selected eight very high-fidelity recordings of alarm whistles (Fig. 1) from eight subjects (six adult females recorded at

Capitol Reef, and one adult female and one yearling female, recorded at RMBL) elicited in a variety of situations (three in response to humans, two in response to dogs, one in response to RoboBadger and one produced in a social encounter). Some experiments (details below) required a single whistle; others required multiple whistles. Using SoundEdit Pro software, we constructed playback stimuli from four of the Capitol Reef whistles. Specifically we made four playback stimuli that contained a whistle repeated four times with a 0.5-s interval between whistles ('four-fast'), four playback stimuli that contained a whistle repeated four times with a 4.0-s interval between whistles ('four-slow'), and four playback stimuli containing a single whistle ('single'). The other four whistles were always played back singly. Chucks (Fig. 1) were extremely quiet vocalizations that attenuated and degraded quickly; we obtained no high fidelity recordings in the field. The two highest fidelity chucks we recorded were from two pups: one unsexed and one female. Both chucks were in response to people; one was recorded while the pup was in a live trap awaiting routine processing, the other was from a pup 'chucking' from a burrow entrance. Although we could not rigorously compare their acoustic structure to adult chucks recorded under more natural conditions, they resembled adult chucks heard in the field and those occasionally produced by captive adults temporarily brought into the laboratory for other studies. We had no high-quality recordings of trills (Fig. 1) and therefore could not use them in playback experiments. We also selected two whistles from two different rock squirrels, *Spermophilus variegatus* and one contact call from a chukar, *Alectoris chukar* (both recorded at

Table IX. Mean response scores (\pm SE) for the three alarm call variants: a single whistle (one call), four whistles separated by 4 s (four-slow), four whistles separated by 0.5 s (four-fast), and directional pair-wise comparisons (four-slow > one, etc.)

Subjects*	One call ($\bar{X} \pm$ SE)	Four-slow	Four-fast	χ^2 †	P †	Four-slow >One‡	Four-fast >One‡	Four-fast >Four-slow‡
CR ($N=9$)	1.78 (0.22)	2.56 (0.18)	2.67 (0.29)	7.280	0.0263	0.0098	0.0197	0.3695
CR+RMBL-1 ($N=21$)	2.19 (0.18)	2.76 (0.18)	3.05 (0.19)	13.069	0.0015	0.0025	0.0011	0.0921
CR+RMBL-2 ($N=21$)	2.05 (0.19)	2.48 (0.13)	2.67 (0.17)	9.745	0.0077	0.0101	0.0030	0.1425
RMBL-1 ($N=12$)	2.50 (0.23)	2.92 (0.29)	3.33 (0.23)	6.727	0.0346	0.0478	0.0099	0.0799
RMBL-1-Town ($N=6$)	2.17 (0.31)	3.00 (0.45)	3.67 (0.33)	9.333	0.0094	0.0294	0.0122	0.0787
RMBL-1-River ($N=6$)	2.83 (0.31)	2.83 (0.40)	3.00 (0.26)	0.400	0.8187	0.5000	0.2819	0.3274
RMBL-2 ($N=12$)	2.25 (0.28)	2.42 (0.19)	2.67 (0.23)	3.909	0.1416	0.2071	0.0294	0.0899
RMBL-2-Town ($N=6$)	1.67 (0.33)	2.00 (0.00)	2.33 (0.21)	3.846	0.1462	0.1587	0.0513	0.0787
RMBL-2-River ($N=6$)	2.83 (0.31)	2.83 (0.31)	3.00 (0.37)	0.667	0.7165	0.5000	§	0.2819

*Subjects lived in different geographical locations and were from different matriline within a geographical location: CR=Capital Reef National Park; RMBL=Rocky Mountain Biological Laboratory; RMBL-1=RMBL playbacks conducted in June; RMBL-2=RMBL playbacks conducted in July; 'Town' refers to Gothic townsite locations; 'River' refers to subjects living down-valley along the East River.

† χ^2 and P -value from Friedman non-parametric ANOVA.

‡One-tailed P -values from Wilcoxon signed-rank tests. Because we calculated three pseudo-independent comparisons, a more conservative critical P -value may be 0.0167 (=0.05/3 comparisons).

§Impossible to calculate significance; all but one comparison were ties.

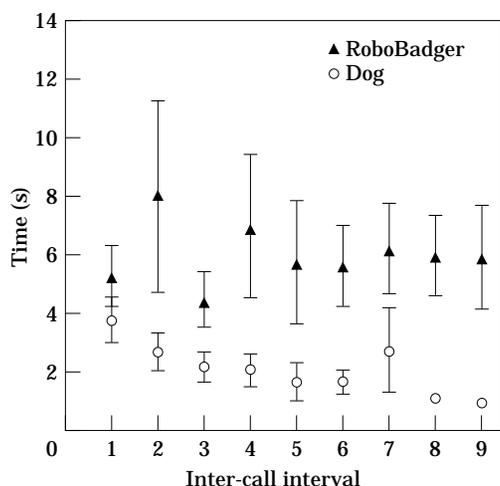


Figure 3. Average \pm SE time (s) between alarm calls for calling bouts that contained at least 10 calls ($N=9$ for dogs, $N=7$ for RoboBadger). Inter-call interval 1=the time interval between the first and the second alarm call, inter-call interval 2=the interval between the second and third calls, etc. Dog: $P<0.01$ ($\chi^2_r=25.66$, calculated on the first 9 intervals); RoboBadger: $P=0.92$ ($\chi^2_r=1.95$, calculated on first 7 intervals).

Capitol Reef), and one gray jay, *Perisoreus canadensis*, contact call (recorded at RMBL; Fig. 4). Each of these vocalizations was played back singly.

Stimuli were either played back directly via a Macintosh PowerBook 180 computer (8-bit resolution), or were recorded from the 16-bit board onto hi-bias cassette tape and played back via a Marantz PMD-340 cassette deck. In both cases, calls were played back through a single AR 570 speaker (Acoustic Research, Canton, Massachusetts). Both playback methods produced realistic-sounding calls at the playback distances used. Unless otherwise noted, we adjusted the volume of played-back stimuli to approximately 92–93 dB measured 0.1 m in front of the speaker with a Realistic model 33-2050 sound level meter. It was difficult to accurately measure the sound pressure level of the extremely brief alarm whistles in the field, but obvious variation in whistle intensity occurred both within and between calling bouts. Non-systematic samples of calling marmots at close ranges (and of marmots calling from live traps) suggested that 93 dB was a typical sound pressure level for yellow-bellied marmot alarm

whistles. The playback situation was designed to mimic an unseen marmot alarm calling from within the social group's home range.

Factors including behaviour patterns (Blumstein 1994), distance to burrow (Blumstein 1994), age (Schwagmeyer & Brown 1981), and body condition (Bachman 1993) may influence responsiveness to playback. To control for as many potentially confounding factors as possible, we did not conduct playbacks to pups, we 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. For each experiment, we tried to expose a subject to the set of playback stimuli within a 2-h interval to minimize body condition and motivation-induced variation (each experiment took 1–3 days).

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, we waited until subjects resumed their normal activity before playing back subsequent stimuli, we systematically varied the order we played back stimuli, and we changed the location of the speaker during playback periods.

Because we wished to generalize our results to the type (or 'class') of acoustic stimulus (e.g., 'single' whistles, 'four-fast' whistles, etc.), we used multiple exemplars that were not necessarily elicited in the context in which we played them back. Thus, some of our 'four-fast' stimuli were created from a whistle that was originally not repeated. This playback protocol is justified because our hypotheses about number and rate of whistles are indifferent to micro-structural variation (see experiment 3). We also made no attempt to playback vocalizations recorded from other social group members (e.g. Cheney & Seyfarth 1990) because our sample of very high-fidelity alarm calls was small and because we wanted to be able to generalize to the broadest possible 'class' of acoustic stimuli.

Quantifying response to playback is difficult and should in part be based on normal anti-predator behaviours. 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. On three occasions (twice at Capitol

Reef, once at RMBL), we observed marmots freeze when spotting a human (twice) and/or RoboBadger (once). We never observed marmots freeze in response to naturally produced or played-back alarm calls. Marmots climbed trees to look around (all sites) and to forage on leaves (Boulder), but we never saw marmots flee up a tree following alarm calls, as might be predicted if different calls elicited different escape strategies (Macedonia & Evans 1991). We saw no obvious differences in gaze direction (i.e. look up versus look around; e.g. Cheney & Seyfarth 1990) in response to playback.

Other studies of the meaning of sciurid alarm calls used changes in vigilance behaviour to quantify responsiveness (e.g. Leger et al. 1979; Harris et al. 1983), but such vigilance measures may not work well for quantifying marmot responsiveness. Marmots spend much more time engaged in vigilant activities than ground squirrels (Armitage et al. 1996: Table 11), and this 'normal' vigilance makes it difficult to detect a slight change in vigilance following playback. In a playback study on the meaning of bobac marmot, *M. bobac*, alarm calls, Nikol'skii et al. (1994) found that alert duration drops dramatically after the first 20 s following playback. In a playback study on the meaning of golden marmot, *M. caudata aurea*, alarm calls, Blumstein (1995b) found no significant differences in the vigilance of marmots following different playbacks (two different alarm-call variants and a bird-song control) on a medium time scale (14 s following playback, the average interval between subsequent alarm calls), or a longer time scale (60 s following playback). Only two variables associated with vigilance on a shorter time scale (the duration of the first look and the response delay to playback) differed significantly between alarm-call exemplars and the control bird song.

We 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; cf. Nikol'skii et al. 1994). We chose 5 s because marmots spend much of their time engaged in vigilance behaviours and therefore routinely looked around (Armitage & Chiesura Corona 1994; Armitage et al. 1996). We 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 as follows.

- 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.

Response scores were adjusted based on what the marmot was doing immediately before it heard the playback. For instance, if a marmot was already rearing up and looking, and it looked in response to the playback, we scored look rather than rear up and look (this happened only twice). We used Friedman non-parametric ANOVAs to test for differences in responsiveness to the acoustic stimuli while blocking by individual.

Experiment 1: Do Marmots Respond to Alarm Whistles?

Marmots live in sympatry with other alarm-calling mammals. At Capitol Reef, marmots lived around rock squirrels, white-tailed antelope ground squirrels, *Ammospermophilus leucurus*, and Colorado chipmunks, *Tamias quadrivittatus*. At RMBL, marmots lived around golden-mantled ground squirrels, *Spermophilus lateralis*, least chipmunks, *Tamias minimus*, and the occasional pika. Of these, rock squirrels produced a call that closely resembled a marmot whistle.

To test whether marmots responded to conspecific alarm calls and/or just whistle-like vocalizations, we compared the marmot's responses to single-note whistles versus single-note rock squirrel calls at both Capitol Reef (where there were rock squirrels) and RMBL (where there were no rock squirrels). We played back two marmot recordings and two rock squirrel recordings and control sounds to six non-pup marmots (3 females, 3 unknown) at Capitol Reef (9–10 May 1995) and six non-pup marmots (4 females, 2 males) at RMBL (13 June 1995). We used contact calls from common sympatric birds as a control

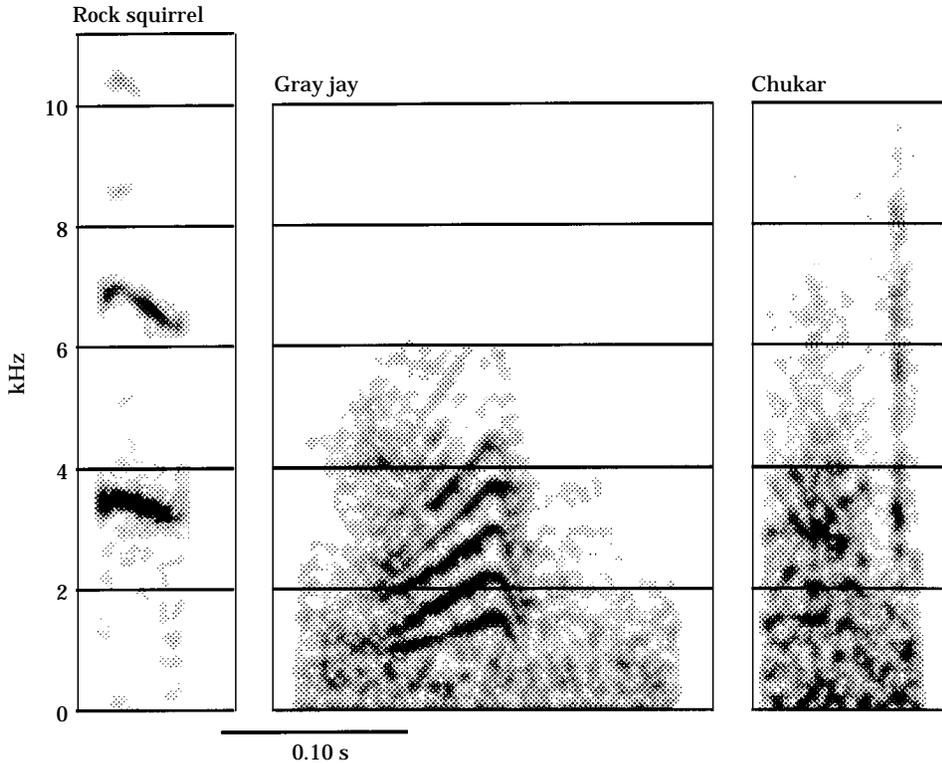


Figure 4. Spectrograms (256 point SoundEdit) of non-marmot vocalizations used in playback experiments. Rock squirrels produced several vocalizations; the single whistle was the most common alarm vocalization.

sound. At Capitol Reef we used a chukar, and at RMBL we used a gray jay contact call. Because bird calls and rock squirrel calls were generally produced at a lower volume than marmot alarm calls, we played back all stimuli at 82 dB, a volume that all species naturally produced. Each subject had an interval of at least 1 min between the different sounds (Capitol Reef: \bar{X} =4.5 min, range=1–13 min; RMBL: \bar{X} =2.3 min, range=1–5 min). Although intervals between playbacks were short, marmots resumed their previous activities quickly after the relatively quiet sounds; no playbacks were conducted until subjects had resumed previous activity. We hypothesized that marmots would respond most to their own whistles and least to bird contact calls.

Results

Most subjects (11/12) responded to the squirrel and marmot calls; only three responded to the bird call. At each location, and when results from

both locations were pooled, marmots responded more intensively to alarm calls than they did to non-alarm bird calls (pooled results: overall treatment $P=0.0012$; marmot whistle versus bird call, $P<0.05$; rock squirrel call versus bird call $P\approx 0.05$; Fig. 5). In the pooled data set, marmots responded similarly to calls from rock squirrel and marmot (Wilcoxon $z = -0.816$, $P=0.41$); because of ties, sample sizes were too small to test each set separately. There was a non-significant tendency (Mann–Whitney $z = -1.687$, two-tailed $P=0.092$) for marmots at Capitol Reef to respond more strongly than RMBL marmots to rock squirrel calls.

Experiment 2: Do Marmots Respond Similarly to Chucks and Whistles?

To test whether marmots responded differently to alarm whistles versus chucks, we played back alarm whistles (two exemplars) and chucks (two exemplars) to six non-pup marmots (2 female, 4

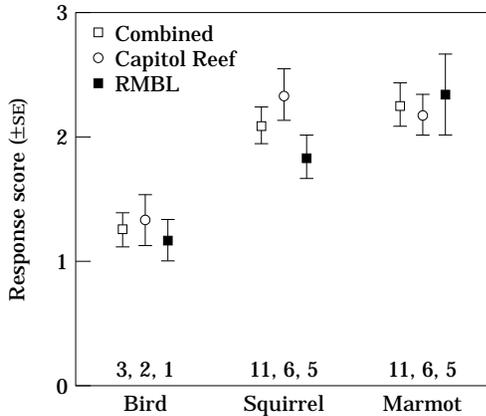


Figure 5. Average \pm SE marmot response scores to sympatric bird contact calls, a rock squirrel alarm call and a single marmot whistle. Means are from six subjects at Capitol Reef and six subjects at the RMBL-townsite. Combined means are the grand means of both sites. All vocalizations were played back at 83 dB. The number of responses to the played-back stimuli are noted at the bottom.

male) on 26 June 1995. Subjects had at least a 5-min interval between hearing each stimulus (\bar{X} =8.9 min, range=5–13 min); once again, marmots had to resume normal activity prior to subsequent playbacks. Playback volume for whistles was set to 92 dB. Since chucks were naturally produced at a lower sound intensity than whistles, we played back chucks at two intensities; a more natural-sounding 87 dB (Lo-C), and an artificially loud 95 dB (Hi-C). We hypothesized that whistles would elicit higher levels of responsiveness than chucks and that sound pressure level would not influence responsiveness to chucks. To test our a priori directional pair-wise hypotheses, we used Wilcoxon signed-rank tests after ANOVA.

Results

All six subjects responded to alarm whistles, four responded to the loud chuck (Hi-C), and only a single subject responded to the quiet chuck (Lo-C). Marmots responded more intensively to whistles than they did to either loud chucks (Wilcoxon $z = -2.236$, one-tailed $P = 0.013$) or soft chucks (Wilcoxon $z = -2.271$, one-tailed $P = 0.012$; Fig. 6). There was a tendency for loud chucks to elicit higher level responses than soft chucks (Wilcoxon $z = 1.732$, two-tailed $P = 0.083$).

Experiment 3: How do Marmots Respond to Different Numbers, Rates and Volumes of Whistles?

We compared marmot's responses to three types of played-back calls (four exemplars of each call): a single note alarm call, four slow alarm calls (four calls each separated by 4 s; four-slow), and four fast calls (four calls each separated by 0.5 s; four-fast). We predicted increasing levels of responsiveness with increasing number and call rate and used one-tailed Wilcoxon signed-rank tests to test pair-wise differences following ANOVA. At Capitol Reef, 9 subjects (6 females, 3 unknown) heard the alarm calls on 14 and 15 May. Experiments at RMBL were conducted on 19 and 20 June with 12 subjects (9 females, 3 males). There was at least a 5-min interval between the time a subject heard each stimulus (\bar{X} =29.1 min, range=5–187 min).

To determine whether a single alarm call elicited consistent responses when played back at different volumes, we pooled results from three sets of experiments conducted at the RMBL town site. Single-note alarm calls were played back to six subjects at 82 dB in experiment 1, to six subjects at 92 dB in experiment 2, and to six subjects at 93 dB in experiment 3. Only one subject heard all three volumes, 6 heard two volumes, and two heard a single volume. Because we could not block by subject, we tested for differences using a Kruskal–Wallis non-parametric ANOVA.

Results

Most (17/21) subjects responded to the single alarm whistle, and all subjects responded to both four-call playbacks. Number and rate of whistles significantly affected responsiveness (Fig. 7, Friedman $\chi^2_r = 13.069$, $P = 0.002$). Marmots responded more to four calls than they did to single calls (Table IX). Marmots did not respond significantly more to four fast calls than to four slow calls, although the trend was in the predicted direction (Table IX). Playback volume did not influence responsiveness to a single note alarm call ($P = 0.74$; Fig. 8, '1 AC').

Experiment 4: How Consistent are Playback Results Over Time and Between Locations?

We conducted a second set of 'single–four–fast–four–slow playbacks' (see above) to 12 marmots at

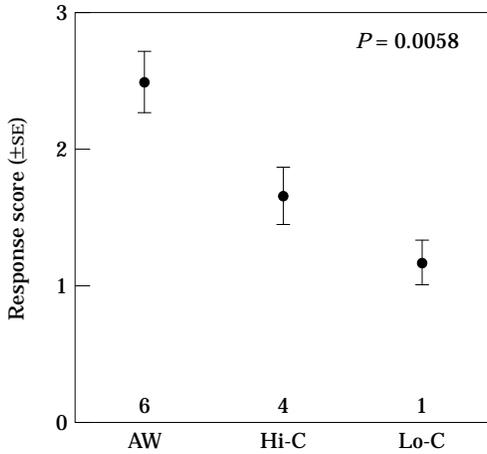


Figure 6. Average \pm SE marmot response scores to a single alarm whistle (AW; played at 93 dB), and to single chucks played back at two volumes (95 dB=Hi-C, 87 dB=Lo-C). Results are from six subjects at the RMBL-townsite. The number of responses to the played-back stimuli are noted at the bottom.

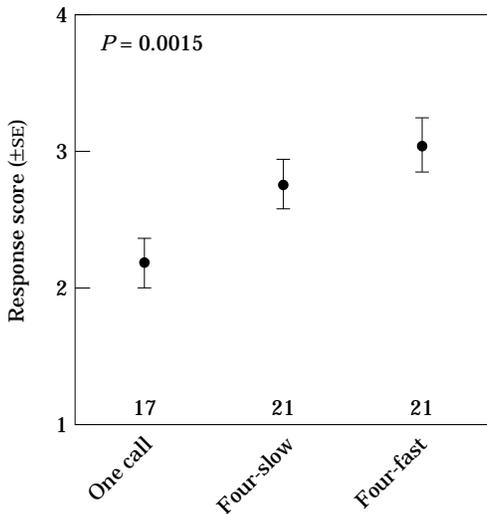


Figure 7. Average \pm SE marmot response scores to whistles: one call=a single whistle; four-slow=four whistles separated by 4 s; four-fast=four whistles separated by 0.5 s. All calls were played back at 93 dB. Data are from 21 subjects: nine at Capitol Reef, six at RMBL-Town, and six at RMBL-River. The number of responses to the played-back stimuli are noted at the bottom.

RMBL between 17 and 21 July (8 females, 4 males). Some subjects were used in both the June (hereafter RMBL-1) and July (hereafter RMBL-2)

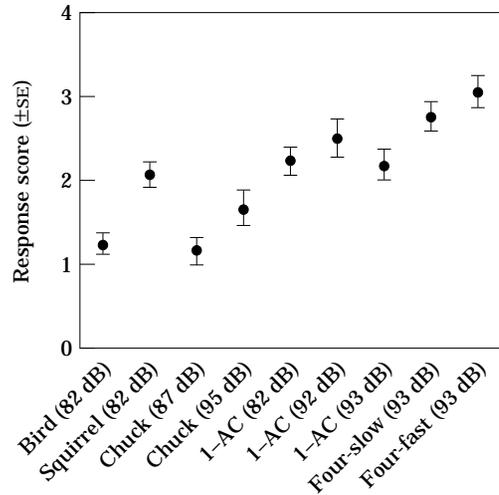


Figure 8. Marmot responsiveness to playback of recorded sounds and acoustic variants.

playbacks. For both playbacks, at least 5 min separated each stimulus playback (\bar{X} =12.7 min, range=5–27 min). All playbacks in Capitol Reef were in areas where marmots had considerable contact with humans. At RMBL, some marmots lived around human dwellings while others lived in areas with less human contact. For each of our RMBL playbacks, half were to subjects living around dwellings (RMBL-Town), and half were to subjects not around dwellings (RMBL-River). We analysed the three locations separately (Capitol Reef, RMBL-Town, RMBL-River) to see whether disturbance influences response to playback. We analysed both sets of data separately to check for consistency.

Results

All four-note playbacks elicited responses and most (26/33) single-note whistles elicited responses. Although P -values varied, in most subsets four fast calls elicited slightly higher responses than four slow calls, which in turn elicited higher responses than a single call (Table IX). A notable exception to this trend was the RMBL-River site, where marmot responses were relatively high (but see RMBL-1-Town) and unchanging with time (cf. RMBL-1 with RMBL-2, Table IX). RMBL-River was an area with limited human contact.

COMBINED RESULTS

Yellow-bellied marmots produced three distinctive alarm vocalizations: they whistled, chucked and trilled. Whistles were by far the most common alarm vocalization, and were virtually always the first call type given. We found no evidence that whistle structure systematically and uniquely varied as a function of stimulus type. Marmots whistled at different rates, and there was evidence that repetition rate increased with risk: marmots whistled faster as dogs approached. Marmots occasionally trilled by increasing whistle rate and modulating the fundamental frequency. Trills were uttered when the threatening stimulus was close, and thus trills seemed to be 'very high-risk' alarm vocalizations. In nature, marmots chucked following long bouts of calling and callers seemed more 'disturbed' as opposed to 'alarmed'. Thus, some aspects of alarm vocalizations seemed to be produced in a way that communicated the degree of risk a caller experienced.

Playback experiments supported this conclusion. Marmots responded most to fast-paced multiple-note whistles and least to chucks (Fig. 8). Marmots did not respond to playbacks of non-alarm calls from conspecific birds, but did respond to the playback of a similar-sounding squirrel alarm call, whether or not the squirrel was sympatric. Playback volume did not influence responsiveness to a normal single-note whistle. When we played back chucks at an artificially high volume, marmots responded more than when they were played back at a more natural volume. With the exception of RMBL-River, marmots at Capitol Reef and RMBL responded similarly to alarm calls.

We found no evidence of systematic differences between locations in the means used to communicate variation in risk. Moreover, with one exception (maximum frequency) those acoustic variables that covaried with subject tended not to be used to communicate situational variation (Tables II, V).

DISCUSSION

Yellow-bellied marmot alarm calls did not have a high degree of production specificity: marmots typically whistled to alarming stimuli and identical stimuli elicited a range of responses (Figs 2, 3). Marmots did respond differently, however, to

different alarm calls (Fig. 8). Thus, we conclude that although yellow-bellied marmots did not have highly externally referential alarm calls (Davis 1991), their calls did vary according to the degree of risk a caller experienced (Waring 1966). Marmots appeared to classify stimuli into categories of high-risk and lower-risk, because this categorization explained similar amounts of variation in call structure, as did a classification scheme that uniquely classified stimuli (dog, human, model badger, eagle, model eagle; Table III). Although some evidence suggests that some sciurids classify alarming stimuli according to whether they are aerial or terrestrial (e.g. Balph & Balph 1966; Melchior 1971; Owings & Leger 1980, 'chatters'; Davis 1984; Burke da Silva et al. 1994; Blumstein & Arnold 1995), yellow-bellied marmots apparently did not classify stimuli this way; an aerial/terrestrial classification scheme explained little variation in call characteristics otherwise associated with risk (Table III). Other sciurids produce similar calls to aerial and terrestrial stimuli, suggesting that they too may not classify stimuli as to whether they are aerial or terrestrial (e.g. Dunford 1977; single-note whistles: Leger et al. 1980; Schwagmeyer 1980).

Although situationally specific, yellow-bellied marmot alarm calls cannot be said to be highly referentially specific. For marmots to have referentially specific alarm calls using a number/rate-based mechanism of communicating situational variation, they would have had to produce a unique number or rate of calls for each stimulus type. For instance, marmots would have to whistle 10 times for a canid and five times for an eagle. That they did not, and that different stimuli induced similar numbers/rates of alarm calls, is further evidence against a highly referential communicative system. Moreover, we might not expect a number/rate mechanism to be used in a highly referential system because there would potentially be a great opportunity for perceptual errors (background noise or other callers might make it difficult for a perceiver to accurately count alarm calls).

Marmots would presumably benefit from the contextual independence of highly-referential alarm calls. Externally referential signals, by definition, do not require much additional contextual information (e.g. identity, location or age of caller; Leger 1993) to be properly interpreted (Marler et al. 1992). An individual hearing an

'eagle call' would realize that there was an eagle around and take appropriate precautions. In contrast, an individual hearing five quickly paced whistles would require additional information to optimally respond to a predatory threat. For instance, if there was individual variability in the number of calls typically produced, proper interpretation of the risk indicated by five quickly paced whistles would require the perceiver to know the caller's identity. Thus, perceivers would presumably benefit from more 'objective' information about the specific type of predatory threat. Several factors may contribute to the evolution of externally referential communication.

Macedonia & Evans (1993) pointed out that differing escape opportunities/strategies may be an important factor responsible for the evolution of highly referential alarm communication. Yellow-bellied marmots are somewhat arboreal (Garrott & Jenni 1978; this study), and are certainly more arboreal than golden marmots or alpine marmots, *M. marmota* L. (Blumstein & Arnold 1995), yet unlike woodchucks, *M. monax* (Swihart 1982), yellow-bellied marmots were never observed to flee up a tree. Yellow-bellied marmots occasionally froze in response to a threatening stimulus. Nevertheless, calls did not differ or obviously elicit overtly different escape strategies. In contrast, vervet monkeys produce predator-specific alarm calls and have predator-specific escape strategies (e.g. climb tree and move to outer branches when fleeing a leopard, bipedally stand and look around grass in response to a snake), and playbacks of these predator-specific alarm calls elicit the appropriate response (Cheney & Seyfarth 1990).

Degree of risk can be associated with response urgency or time constraints imposed by the potential predator's hunting mode (Robinson 1980). Canids eat marmots, and at RMBL, coyotes were inferred to be the major predator on yearling and adult marmots. Yellow-bellied marmots called at very high rates to dogs (another canid), and increased their calling rate as the dogs approached. That dogs elicited numerous calls may be a function of the relatively long duration that they were present: marmots could repeat their calls since dogs moved relatively slowly through callers' home ranges. Fast-moving, and therefore presumably high-risk stimuli (eagles and our eagle model) often elicited a few quickly paced whistles. Hunting raptors appeared and disappeared quickly, and callers were not exposed to the risky

stimulus for long periods of time; thus we might not expect bouts with many alarm calls. Alternatively, the time constraints imposed by a quickly approaching predator may have limited the number of calls (MacWhirter 1992). Presumably lower-risk stimuli, such as humans, elicited few whistles at slow rates. Other sciurids increased calling rate and/or responded more to fast-paced calls as risk increased (e.g. Harris et al. 1983; Nikolskii & Nesterova 1989; 1990; Nikol'skii & Pereladova 1994; Nikol'skii et al. 1994). That call rate varied as a function of risk suggests that yellow-bellied marmot's call structure covaries with motivational state. Such 'affective' vocalizations cannot be considered highly referential (Marler et al. 1992).

Leger et al. (1980) and MacWhirter (1992) noted that some predator attacks on ground squirrels were aborted following alarm calling. There is some evidence that yellow-bellied marmot alarm calls may be directed to the predator (see Hasson 1991 for a review of communication towards predators; Owings & Hennessy 1984). Yellow-bellied marmots increased their conspicuousness in relatively high-risk situations in two ways: they called faster, and calls appeared to have a larger bandwidth (Table III, Fig. 2). In contrast, both golden marmots (Blumstein 1995a) and alpine marmots (Blumstein & Arnold 1995) 'packaged' individual whistles together to create alarm vocalizations with variable numbers of whistles. For these two species, the number of whistles in each call decreased as risk increased. Thus, both golden and alpine marmots seemed to decrease conspicuousness as risk increased. We frequently observed marmots change location to keep a predator in sight while simultaneously alarm-calling (see also Armitage & Downhower 1974). Only if the predator (e.g. a dog) moved towards the marmot did the marmot enter its burrow. Typically the marmot called until the predator (e.g. a coyote or badger) moved out of sight. This pattern not only occurred for marmots living in a group, but also for marmots living singly.

A second line of evidence suggesting that calls may be directed to the predator stems from the different responses to aerial and terrestrial predators. Although aerial predators such as eagles can probably hear marmot alarm calls (Stebbins 1983; Brown & Amadon 1989), the benefits of calling repeatedly to aerial predators, owing to their

extremely fast attack speeds and limited presence, would presumably be less than calling to a relatively slow-moving canid. One potential function of signalling to predators is to 'encourage' them to 'move on' (Hasson 1991). Although not rigorously analysed, marmots sometimes called in response to deer (at RMBL but not at Capitol Reef). When they called to deer, they tended to call until the deer moved on and away from the caller (a response also predicted if marmots were calling to warn conspecifics).

We found no evidence that yellow-bellied marmots in different geographical locations used different mechanisms to communicate situational variation: yellow-bellied marmots sounded and responded like yellow-bellied marmots wherever they were studied. Geographical variation in alarm-call structure (but not mechanisms) was reported in long-tailed marmots (Nikolskii & Orlov 1980), black-capped marmots, *M. camtschatica* (Nikolsky et al. 1991) and in grey marmots, *M. baibacina* (Nikol'skii 1994). Subspecific differences in mechanisms of song acquisition were found in some birds (e.g. King & West 1983; Kroodsmas & Canady 1985; Nelson et al. 1995). Such intraspecific variation seems to be associated with different benefits from learning different numbers of songs, and/or benefits from learning songs at different times. Bird songs, however, are subject to different selective regimes (e.g. natural and sexual selection) and have different functions (e.g. territorial advertisement, mate assessment, species recognition) than marmot alarm calls. We envision strong stabilizing selection acting within a species on the way in which anti-predatory situational variation is communicated.

Bird songs have characteristics that allow perceivers to recognize species and often discriminate between individuals (reviewed in Lambrechts & Dhondt 1995). Thus several conflicting selection pressures may be acting on vocalization structure (Marler 1960). The need to discriminate species may select for certain 'invariant features' (Marler 1960), while individual recognition may select for variable acoustic characteristics. We are aware of no studies that have pointed out that a similar logic applies for situationally variable alarm calls. Specifically, acoustic parameters that vary according to situation should not vary much between individuals, and those acoustic parameters used for individual discrimination should not vary according to situation. Nikol'skii & Suchanova

(1994) found that the frequency modulation pattern of bobac marmots permits a high degree of discrimination between individuals (using discriminant function analysis), and Nikol'skii et al. (1994) emphasized the covariation between alarm calls' temporal characteristics and predation risk. Micro-structural variation permits individual discrimination in at least two pika species, *O. princeps* (Conner 1985) and *O. hyperborea* (Nikol'skii et al. 1990), and variation in the rate of calling covaries with situation (*O. princeps*: Ivins & Smith 1983). Different micro-structural characteristics of Belding's ground squirrel (*S. beldingi*) vocalizations statistically permit individual discrimination and situational discrimination (Leger et al. 1984). It appears that for yellow-bellied and bobac marmots, at least one pika, and at least one species of ground squirrel, those alarm-call characteristics that varied between individuals were not used to encode situational variation. We suspect that this pattern may prove to be common.

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