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Situational Specificity in Alpine-marmot Alarm Communication

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Abstract

We studied the degree to which alpine marmot (*Marmota marmota* L.) alarm calls function as communication about specific external stimuli. Alpine marmots emit variable alarm calls when they encounter humans, dogs, and several species of aerial predators. The first part of the study involved observations and manipulations designed to document contextual variation in alarm calls. Alarm calls varied along several acoustic parameters, but only along one that we examined, the number of notes per call, was significantly correlated with the type of external stimulus. Marmots were more likely to emit single-note alarm calls as their first or only call in response to an aerial stimulus, and multiple-note alarm calls when first calling to a terrestrial stimulus. This relationship was not without exceptions; there was considerable variation in the number of notes they emitted to both aerial and terrestrial stimuli, and a single stimulus type — humans — elicited a wide range of acoustic responses. The second part of the study involved playing back three types of alarm calls to marmots and observing their responses. Marmots did not have overtly different responses to the three types of played-back alarm calls. Our results are consistent with the hypotheses that: 1. Alarm calls do not refer to specific external stimuli; 2. Alarm calls function to communicate the degree of risk a caller experiences; and 3. Alarm calls require additional contextual cues to be properly interpreted by conspecifics.

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Introduction

For species that emit situationally variable alarm calls, two hypotheses have been invoked to explain the meaning of variable calls (review: MACEDONIA & EVANS 1993). Alarm calls may vary according to the 'response urgency', or imminence of predation, the caller faces (ROBINSON 1980; OWINGS & HENNESSY 1984). Short calls may be produced when predation is imminent, while longer calls may be produced when there is more time to assess and manage the risk of predation (OWINGS & HENNESSY 1984; MACEDONIA & EVANS 1993). Thus, calls

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may communicate the degree of risk the caller experiences and may be a function of the caller's arousal (MACEDONIA & EVANS 1993).

Alternatively, different alarm calls may denote different types of predators (e.g. aerial vs. terrestrial predators), or even the exact species of predator (SEYFARTH et al. 1980; CHENEY & SEYFARTH 1990; MARLER et al. 1992; MACEDONIA & EVANS 1993). These alarm calls have been called referentially specific in that the calls refer to specific external stimuli (MACEDONIA & EVANS 1993). In this paper, we report the results of a study designed to determine the degree to which situationally variable alpine-marmot (*Marmota marmota* L.) alarm calls were referentially specific.

Alpine marmots emit alarm calls in a variety of potentially threatening situations (MÜLLER-USING 1956; KOENIG 1957; HOFER & INGOLD 1984; LENTI BOERO 1992). Marmots have been reported to both vary their alarm calls according to their perception of predation risk (HOFER & INGOLD 1984), and to produce different alarm calls when confronted by different predators (LENTI BOERO 1992). HOFER & INGOLD (1984) studied the situation in which calls were produced and concluded that marmots vary the number of times they repeat a simple call in a way that is correlated with the degree of risk the caller is experiencing. They noted that single-note alarm calls are produced when marmots see an eagle or an attacking fox, and multiple-note calls when marmots see distant foxes. LENTI BOERO (1992) suggested that alpine marmot alarm calls may be referentially specific, since, in her study, eagles always elicited single-note calls and foxes always elicited multiple-note calls. To better interpret these results, we need information on how calls are perceived (MARLER et al. 1992; MACEDONIA & EVANS 1993; BLUMSTEIN 1995b). HOFER & INGOLD (1984) noted that marmots respond more 'strongly' to single-note calls, and LENTI BOERO (1992) noted that a type of multiple-note call (her 'brief multiple-note whistles') were 'more disturbing' than single-note calls. Surprisingly, neither study examined the spectral characteristics of the alarm calls (HOFER & INGOLD (1984) did, however, measure call duration) — another potential domain of situational variation — nor did either study conduct playback experiments to experimentally study marmot's responses to acoustic variants.

Referential specificity implies both 'production-specificity' and 'perception-specificity' (MARLER et al. 1992; MACEDONIA & EVANS 1993). If only a single class of stimuli elicits a single class of responses, there is said to be a high degree of production specificity. If alpine marmots have referentially specific alarm calls, they should always produce a 'raptor call' in response to raptors, and a 'terrestrial-predator call' in response to terrestrial predators. If 'terrestrial-predator calls' are produced in response to raptors, this suggests that calls are not highly referentially specific (MARLER et al. 1992). Perception specificity means that the different acoustic variants (e.g. raptor and terrestrial-predator calls) should in themselves be able to elicit the appropriate response in a conspecific who hears the call in absence of the stimulus that normally elicits the response and without normal contextual cues associated with alarm calling (reviews: CHENEY & SEYFARTH 1990; MARLER et al. 1992; EVANS et al. 1993; MACEDONIA & EVANS 1993). Thus, when a marmot hears a 'raptor call', it should respond differently than when it hears a 'terrestrial-predator call'. Although several studies have conducted playback experiments to investigate the meaning of alarm-call variants (LEGER & OWINGS 1978; LEGER et al. 1979; SEYFARTH et al. 1980; SCHWAGMEYER & BROWN 1981; HARRIS et al. 1983; BROWN 1985; MACEDONIA 1990; STONE & TROST 1991; EVANS et al. 1993; BLUMSTEIN 1995b; WEARY & KRAMER 1995), it is still open to question whether acoustic variation always leads to qualitatively different responses (e.g. BLUMSTEIN 1995b; WEARY & KRAMER 1995).

If calls are highly referentially specific, then the following three predictions should be supported: 1. There should be a strong correlation between stimulus type and acoustic response; 2. A single stimulus should always elicit the same type of acoustic response; and 3. Perceivers should respond differently to the call types if presented in the absence of the stimulus that normally elicits those calls.

Part I: Production Specificity

Methods

We studied alpine marmots in the Berchtesgaden National Park, Germany, for 33 days (9 May–28 Aug.) in the summer of 1994. The study site and general methods by which marmots were trapped and individually identified has been described elsewhere (ARNOLD 1990). We focussed on marmots living in three meadows: 1. In and around Königsbachalm (seven groups of variable size, with about 26 yearling and adult marmots); 2. Büchsenalm (six groups: 22 yearling and adult marmots); and 3. Gotzentalalm (four groups: 20 yearling and adult marmots). Many marmot social groups were contiguous and marmots in one group could hear alarm calls from neighboring groups and neighboring meadows. Alarm calls were defined as one or more whistle-like vocalizations separated from a previous vocalization by more than 2 s and emitted in response to potentially threatening situations. We defined each whistle in an alarm call as a note. Alarm calls had various numbers of notes and multiple note calls were produced by simply repeating notes. A bout of alarm calling contained one or more alarm calls emitted by an individual in response to a stimulus (whether we identified the stimulus or not).

Observations and Experiments. A total of 141 h were spent observing the marmots and noting all occurrences (MARTIN & BATESON 1986) of marmot alarm calls that we (and presumably the marmots) heard. We sat in a conspicuous location — often beside a road or heavily used hiking trail — outside the core area of marmot groups while making these observations; marmots generally appeared to quickly get used to our presence. Preliminary analyses and personal observations suggested that some single-note calls sounded different than others. Later spectrographic analysis revealed that these calls started at a higher frequency than that at which they ended, and we refer to these as 'start-high' calls. We analysed the first, or, in some cases, the only alarm call emitted, since we assumed that the first call best reflects the caller's immediate perception of risk. Subsequent calls may serve different functions (e.g. to maintain vigilance: OWINGS & HENNESSY 1984; OWINGS et al. 1986; LOUGHRY & MCDONOUGH 1988). First calls were classified into three categories — start-high, 'normal', single-note and multiple-note — and we attempted to determine the stimulus that elicited each call. The main drawbacks of this sampling technique were that the identity of the caller was not always known, and that, for many calls, we were unable to infer a stimulus.

Since natural aerial predators (predominantly Golden Eagles (*Aquila chrysaetos*)), and, potentially, Goshawks (*Accipiter gentilis*) were less common than potential terrestrial predators (red foxes (*Vulpes vulpes*), domestic dogs, and humans), we simulated aerial predators in two ways: using a kite that resembled an eagle, and using a wooden silhouette that resembled an eagle. Another species of marmot, the hoary marmot (*M. caligata*), produced 'normal' alarm calls in response to model gliders (NOYES & HOLMES 1979). Our kite (0.74 × 1.40 m) was smaller than a real golden eagle but superficially resembled an immature golden eagle. We attempted to launch the kite in such a way as to make it suddenly appear over targeted marmots without the targets seeing the people flying the kite. One observer estimated the distance between the kite and marmots that called. The accuracy for our ground-distance estimates, tested by periodically measuring distances, was about ± 5 m for distances of 0–50 m, and 10–15 m for distances of 50–200 m. Distances to aerial objects were not calibrated, but we think that the estimates of distances to our low-flying models were as accurate as the ground estimates. Our raptor silhouette (0.88 × 2.44 m) was made of 0.006 m brown-painted plywood, had 'primary feathers' cut into the wood, and was flown on a 100-m nylon line. There were two potential sources of error in these experiments. Firstly, the person releasing the model generally failed to hide from the target marmot. Secondly, as the model glided along the nylon line, it made a slight whining sound. Thus, we ignored the responses of the marmot directly under the silhouette (these marmots always looked at the fast-approaching looming model and immediately disappeared), and instead focussed on marmots who could not have seen the person releasing the model and who probably heard little or none of the whining. Unfortunately, this meant that the identity of the caller was generally unknown, and the exact distance between the caller and the stimulus was only roughly estimated. All experiments were conducted before July, when pups emerge above ground.

To study the degree to which a single stimulus could elicit different responses and to obtain a larger sample size of high-quality tape recordings of alarm calls, a single observer walked at a constant speed towards marmots and elicited alarm calls; we refer to these experiments as 'predation probes' (BLUMSTEIN 1994). For marmots that called, we assumed that the distance between the caller and the marmot when the marmot called was an appropriate measure of risk (BLUMSTEIN 1995a), and we estimated that distance. This assumption seems valid since the probability of predation is a function of the distance to the predator, and the velocity at which a predator approaches (MORSE 1980; YDENBERG & DILL 1986; LIMA & DILL 1990).

Alarm Call Recording and Analysis. Calls were recorded using a Sennheiser ME-88 microphone encased in a Light Waves wind screen with a Sony TC-D5M cassette recorder using high bias 60-min tapes. All calls were pre-filtered to prevent frequency artefacts from digitizing (aliasing; TTE J83G-22K-6-720B filter), and were then sampled at 22 kHz using a MacRecorder 8-bit AD-DA board and SoundEdit Pro Software (MacroMind Paracomp Inc., San Francisco, CA, USA). 'Boxy' sound spectrograms were generated using 256-point short-time Fourier transformations with 50 % overlap, a hamming window, and − 120-dB clipping (CHARIF et al. 1993). Only 'clean' spectrograms were subsequently analysed (time resolution: 5.75 ms; frequency resolution: 68.93 Hz) using Canary software (CHARIF et al. 1993).

We measured the following seven variables from the first alarm call emitted in response to the different stimuli: 1. The number of notes in each call; 2. The time between each note within a call; 3. The duration of each note within a call; 4. The frequency, at peak amplitude, of the first note; 5. The frequency bandwidth of the first note; 6. The starting frequency of the first note of each call; and 7. The end frequency of the first note of each call. From these variables we calculated the following two descriptive statistics: 1. The difference between the starting frequency and the end frequency of the first note of each call — negative values started at lower frequencies than they ended; and 2. The call rate, i.e. the number of notes divided by the total duration of the call. In subsequent analyses we use these two variables, along with the number of notes per call, the duration of the first note, and the bandwidth, as independent variables.

Associations between call type and natural-stimulus type (aerial/terrestrial), and between the call type and the artificial-stimulus type (kite/model) were tested with Fisher's exact tests. Since the caller's identity was unknown, there may be unknown dependencies in this analysis. Additionally, we were unable to control for the age or sex of the caller.

We analysed recorded calls in more detail to search for potential acoustic correlates with external stimuli or the degree of risk. All analyses focussed on the first call. For naturally elicited alarm calls for which we had an estimate of the distance to the stimulus ($n = 5$ to dogs, $n = 3$ to raptors), each of the five independent variables was linearly modelled as a function of estimated distance to the stimulus (a measure of risk), and the stimulus category.

We used human-elicited calls to study the degree to which a single stimulus produced variable calls. We selected a single observation per identified individual ($n = 26$ marmots) and regressed the estimated distance to the human when the marmot first called against each of the five acoustic parameters.

Descriptive statistics were calculated with StatView 4.01 (ABACUS CONCEPTS 1992). Linear models were fitted in SuperAnova (ABACUS CONCEPTS 1991). Unless otherwise noted, significance implies a two-tailed $p < 0.05$.

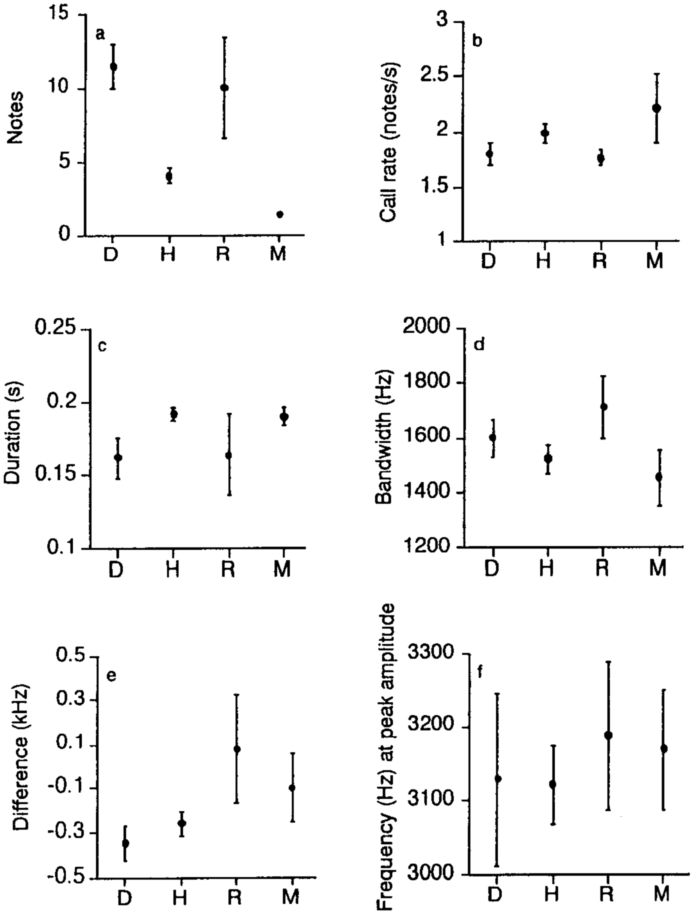

Fig. 1: Effect of stimulus type on acoustic structure ($\bar{X} \pm SE$) of alpine-marmot alarm calls: a. Notes per call; b. Call rate; c. Duration of the first note; d. Bandwidth of first note; e. Difference between starting and end frequency of the first note; f. Frequency at peak amplitude of the first note. On all graphs: D = dog; H = human; R = raptor; M = model aerial stimuli. Sample sizes for all variables (except call rate) were: D = 7; H = 26; R = 6; M = 9. Because multiple-note calls were not always produced, call-rate sample sizes were: D = 7; H = 21; R = 5; M = 3

Results

Alpine marmots often alarm called when encountering dogs, humans, raptors, and our model aerial predators. During our observations we never observed natural predation. However, foxes and golden eagles occur in typical densities on the study site and both predators have occasionally been observed to kill marmots (W. ARNOLD unpubl. data). Additionally, marmots sometimes alarm called to ravens (*Corvus corax*), smaller birds, and occasionally to a paraglider.

Table 1: Results from linear models designed to explain variation in the call parameters as a function of the distance a marmot was from a human when it called. The direction of the relationship, p values, and adjusted R^2 values are given. Model sample sizes are n = 26 (call rate: n = 21)

Call parameter	Relationship	p-value	Adjusted R^2
Notes/call	+	0.031[1]	0.101
Call rate	−	0.124	0.074
Duration	−	0.681	−0.034
Bandwidth	−	0.093	0.076
Start-end frequency	+	0.783	−0.038
Frequency at peak amplitude	−	0.777	−0.038

[1] One-tailed p-value given HOFER & INGOLD's (1984) directional hypothesis

Alarm calls varied along all measured acoustic parameters (Fig. 1). Calls seemed to form a continuum from start-high one-note calls, to one-note calls, to multiple-note calls. The number of notes per call (Fig. 1a) and the duration of the first note (Fig. 1c) were more variable to dogs and raptors than to humans and model raptors. Aerial stimuli elicited calls with more variable starting- and end-frequency differences in the first note than did terrestrial stimuli (Fig. 1e). Variation in the call rate to the model raptors was much greater than in response to other stimuli (Fig. 1b).

While event recording, we heard 321 bouts of alarm calls (2.28 bouts/h); 50 of these bouts began with, or consisted of, a single-note call (0.35 bouts/h), the remainder began with multiple notes (1.92 bouts/h). Of these 321 bouts of calls, 111 were elicited by an identifiable stimulus. For these 111 calls, there was a significant association ($p < 0.001$) between the type of stimulus (aerial/terrestrial) and whether a call had one or multiple notes. Calls elicited by aerial stimuli were more likely to have one note than had been expected by chance: aerial stimuli elicited 12 one-note and 12 multiple-note calls, while terrestrial stimuli elicited 13 one-note calls and 74 multiple-note calls. There was no association between the stimulus category and the rough acoustic structure of single-note calls: two start-high calls and 11 normal one-note calls were elicited by terrestrial stimuli; five start-high calls and seven normal one-note calls were elicited by aerial stimuli (Fisher exact, $p = 0.202$).

We presented the kite and the eagle silhouette seven times each between 13 and 28 May. In response to these 14 presentations, we elicited 26 alarm calls: 17 one-note calls and nine multiple-note calls. There was no association between the artificial aerial-stimulus type and whether the first elicited call had one or multiple notes (Fisher exact, $p = 0.683$). Artificial aerial stimuli seemed more likely to elicit one-note calls than multiple-note calls (binomial one-side, $p = 0.085$). This difference between the frequency of emitting one-note calls to artificial and real aerial stimuli may be a function of the estimated distance to the stimulus: all nine marmots recorded calling to artificial stimuli were estimated to be up to 100 m from the stimulus, while 60 % of those recorded calling to real raptors were estimated to be over 100 m from the raptor (Fisher exact, $p = 0.028$).

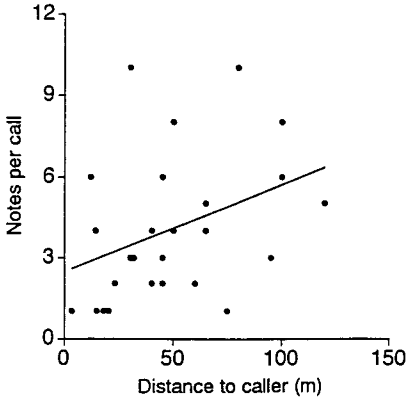

Fig. 2: Relationship between distance to a human and number of notes produced in the first alarm call. A linear regression explains 10 % of the variation in the number of notes per call (one-tailed, p = 0.031; n = 26 different marmots)

A total of 74 % of the variation in the number of notes per call in the data set of naturally elicited and recorded calls was explained by a linear model that included the stimulus category (aerial or terrestrial) and the estimated distance to the stimulus (adjusted $R^2 = 0.738$, model $p = 0.015$). However, only stimulus category significantly explained variation ($p = 0.006$); the distance covariate was not significant ($p = 0.266$). Although sample sizes were small, variation in no other measured call parameter was significantly explained by either of these two independent variables (model p-values, all > 0.2).

Distance between a caller and an approaching human significantly explained variation in only one of the measured call parameters (Table 1). HOFER & INGOLD (1984) predicted a positive relationship between distance and the number of notes per call; in fact distance significantly explained 10 % of the variation in the number of notes per call (one-sided $p = 0.031$; Fig. 2).

Part II: Perception Specificity

Methods

Playback Setup. We experimentally studied perception specificity by playing back alarm-call variants to free-living marmots and noting their responses. We questioned whether marmots have overtly different responses to played-back alarm-call variants to one-note calls, start-high calls, and 10-note calls (Fig. 3). We used four examples of each call type. While the one-note and start-high calls were 'natural', only one of the 10-note calls originally had 10 notes: two were originally nine-note calls, one was an eight-note call. Shorter calls had their last one or two notes duplicated (in SoundEdit Pro) to make 10-note calls. To test whether marmots responded to the calls or the playback apparatus, the song of a chaffinch (*Fringilla coelebs*) was selected as a 'control' sound.

All marmot calls were bandpass filtered (1.5–4.2 kHz 5 pole Butterworth filter) to remove background noise and harmonic structure (KELLER 1992). Calls were recorded onto high-bias cassette tape and played back on a Sony TC-D5M tape deck. The audio signal was split leaving the Sony headphone jack, sending the examplar directly to a video camera (Sony SP-7, video 8) and also through

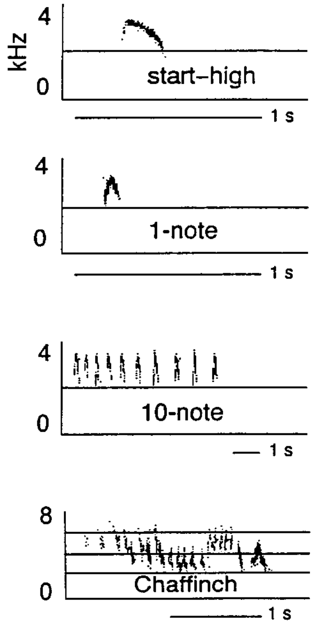

Fig. 3: Representative spectrograms (256 point Sound Edit) of stimuli used in playback experiments

an unbalanced-to-balanced line-conversion box (Countryman Type-85 Direct Box), across 132—264 m of balanced microphone cable, into a line amplifier (Sure FP11) that also converted the signal back to an unbalanced one, and, finally, to a Sony SRS-77G powered speaker with a relatively flat frequency response.

Speakers were placed out of the direct sight line of marmots at their burrows, and were camouflaged by natural vegetation and terrain. We sat over 100 m from the target marmot in plain sight. Marmots in our study site were very used to humans and, once they emerged from their burrows, appeared to habituate quickly to our presence.

Each experimental marmot (all ≥2-yr old, eight males, eight females) heard all four stimuli. To control for potential seasonal variation in responsiveness, we conducted all playback experiments over a 21-d period in Aug. Playback order was systematically varied in subsequent trials using different marmots. To minimize the probability of 'state-dependent' responses to the different test sounds (e.g. body condition: Bachman 1993), we conducted all playbacks to a focal individual in a single day. We waited at least 9 min after one playback before beginning the next playback. The average time between sets of four playbacks for each individual was 42.3 min (12.6 SE, range: 10–169 min). During the playback period, experimental marmots naturally heard, on average, 2.1 call bouts per h. Because the subject's behavior and, potentially, location can influence response to a playback (Blumstein 1994), we conducted all playbacks to 'relaxed' (i.e. not rapidly changing gaze direction) but vigilant marmots immediately in the vicinity of their main burrows ($\bar{X}$ distance to burrow = 0.03 m, 0.2 SE, range 0–1 m) and, because playback volume may influence responsiveness (Leger et al. 1979; Seyfarth et al. 1980; Harris et al. 1983; Blumstein 1994; but see Weary & Kramer 1995), line levels on the tape deck, line amplifier, and powered speaker were adjusted until the sound-pressure level, 0.1 m in front of the speaker, was about 100–104 dB (measured using a Realistic model 33–2050 sound-level meter). In fact, the average playback volume was 103.4 dB (0.30 SE, range 98–108 dB), and speakers were on average 21.7 m from the marmots (0.77 SE, range 13.0–33.0 m).

The playback situation mimicked the situation of a distant marmot alarm calling. Depending on the exact location of the speaker, the hypothetical 'caller' could have been from the same or an adjacent

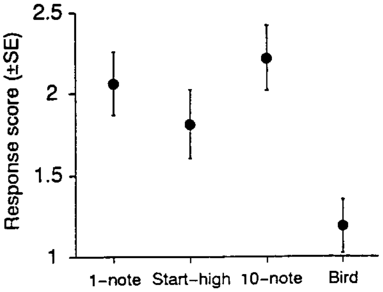

Fig. 4: Response scores to playbacks ($\bar{X}$ ± SE; see text for an explanation of categories). There was an overall significant treatment effect ($p = 0.011$). However, reactions to alarm calls did not differ significantly ($p = 0.575$)

social group. Marmots routinely responded to natural alarm calls from neighboring groups and to calls from distant parts of home groups.

Playback Analysis. Marmots responded to natural predators and to alarm calls by returning to their burrows (if away from their burrows) and looking around, and/or by disappearing into their burrows. We classified responses into four increasing levels of hypothesized arousal and scored the highest level response in the first 5 s following playback. This time interval was chosen because marmots periodically looked around and we asssumed that if a focal marmot did not look around in the 5 s following the playback, it had not responded to the playback. Possible response scores 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.

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, it was scored as 'look' rather than 'rear-up and look'. A Friedman non-parametric ANOVA was used to test for differences in responsiveness to the acoustic stimuli while blocking by individual.

Results

Marmots responded to the played-back alarm calls in the same way they responded to natural calls: they looked around, reared up and looked, disappeared into a burrow, or did not change their overt behavior. Marmots also 'responded' to the bird song by looking and rearing-up and looking. Unfortunately, chaffinches were silent in August (the recording came from May when they were one of the most commonly heard songbirds). However, in contrast to alarm calls, marmots appeared to respond to the chaffinch song in an inquisitive, rather than an alarming way, i.e. if they looked, they looked slowly, and were generally not startled into a look.

There was an overall significant treatment effect (Fig. 4, $p = 0.011$). Marmots did not respond differently in the first 5 s following playback to the three alarm-call variants ($p = 0.575$). Pairwise post-hoc comparisons revealed that 10-note calls were responded to differently from bird song ($p < 0.05$). Responses to other alarm calls, while not significantly different from bird song, were nevertheless in the expected direction (i.e. more responsiveness to the alarm calls).

Discussion

Alpine marmots at Berchtesgaden did not emit alarm calls with a high degree of referential specificity. Marmots tended to produce one-note alarm calls when they encountered aerial stimuli and multiple-note alarm calls when they encountered terrestrial stimuli. A considerable amount of the variation in the number of notes per call was explained by the broad stimulus class (aerial/terrestrial). No other measured acoustic parameters varied systematically according to the type of stimulus. However, marmots produced variable calls to the same type of stimulus: marmot's responses to humans were a continuous function of the distance a human was from the caller. Thus, the degree of production-specificity seems limited.

Theory predicts that species with a single escape strategy should not have strongly referentially specific alarm calls (MACEDONIA & EVANS 1993). Vervet monkeys (*Cercopithecus aethiops*) have markedly different responses and alarm calls to different predators (SEYFARTH et al. 1980). Alpine marmots have a reasonably simple escape strategy: upon detecting a predator or hearing an alarm call alpine marmots return to a burrow and increase vigilance. Alpine marmots have not been observed using trees or bushes as refuges, nor do they have identifiable refuges other than burrows.

Because alpine marmots failed to respond differently to played-back variants, their calls can not be said to be highly referentially specific (MARLER et al. 1992). Admittedly our responses were crudely scored (HAUSER 1994) and more detailed measures of response (RYDEN 1980; EVANS & GAIONI 1990) might detect differences in marmots' responses to alarm-call variants. Nevertheless, if calls were strongly referentially specific, we might expect different overt responses such as gaze direction (e.g. looking up to aerial calls as against looking around for terrestrial calls), or other different responses (e.g. disappearing vs. looking) to be obvious. If calls were not strongly referential then a priori predictions would be more difficult to make: in general we might expect different rates or types of vigilance, and/or disappearance probabilities. Since we found no evidence of different gaze directions, and because some marmots immediately disappeared into their burrows in response to the played-back alarm calls, we were unable to quantify gaze direction or differential vigilance. Marmots have a very wide-angle visual field. When we scored 'no response' marmots could have in fact scanned their visual field without moving their heads.

However, lack of responsiveness to alarm-call variants is not unknown in ground squirrels. Golden marmots (*M. caudata aurea*: BLUMSTEIN 1995b) and Eastern chipmunks (*Tamias striatus*: WEARY & KRAMER 1995) do not respond in qualitatively different ways to played-back alarm-call variants. Interestingly, while golden-marmot alarm calls were not obviously associated with predator type, chipmunks produced different alarm calls to different types of predators (BURKE DA SILVA et al. 1994).

Perhaps if playbacks were conducted with marmots engaged in a different behavior at the start of the playback, such as foraging, we might have seen more response variation (i.e. marmots could have returned to a burrow or not, but see WEARY & KRAMER (1995)). LENTI BOERO (1992) reported that alpine marmots hearing natural calls at burrows do not overtly modify their behavioral response. She focussed on the responses of foraging marmots to natural alarm calls. Unfortunately, factors such as the distance to the nearest refuge, hunger level, or other factors (YDENBERG & DILL 1986; BACHMAN 1993) may influence an individual's response to a potential threat. Marmots are difficult to bait and baiting them to distant foraging sites prior to conducting a playback (e.g. as has been done with seed-eating *Spermophilus* and *Tamias* squirrels and chipmunks) was deemed impractical, and would have created additional problems controlling for response motivation (YDENBERG & DILL 1986). Thus, we chose to control for behavior, location, and, potentially, the motivation to respond by playing back alarm calls to vigilant marmots at their main burrows.

Our observations are consistent with the hypothesis that acoustic variation may be a function of the degree of risk that callers experience. Calls with fewer notes were elicited when humans were closer, and one-note alarm calls were often elicited to close aerial stimuli. By producing fewer notes in higher-risk situations, alpine marmots may vary their calls in a way that reduces conspicuousness to predators (OWINGS & HENNESSY 1984). Golden marmots similarly reduced the number of notes in their calls as potential risk increased (BLUMSTEIN 1995a). Interestingly alpine marmots emitting one-note calls did not always disappear after calling: short calls were apparently not a function of time constraints imposed on the caller by the threatening stimulus (ROBINSON 1980; OWINGS & HENNESSY 1984). Inconsistent with a reduction-in-conspicuousness hypothesis are the observations of an insignificant tendency to increase call rate and bandwidth as a human approaches. Moreover, an alarmed marmot calling from its burrow may be quite safe from predation.

Playback results are not inconsistent with a degree-of-risk interpretation. Given that different individuals may have different perceptions of what is risky or have different reasons for calling (OWINGS & HENNESSY 1984), we would expect that additional contextual information would be required for a perceiver to properly interpret an alarm call. Contextual cues can embellish and add richness to communication and may be required when a signal has ambiguous external referents (LEGER 1993).

Our results suggest that alpine marmots do not emit calls with a high degree of production-specificity, nor do they respond in obviously different ways to calls divorced from other potentially salient cues. It thus seems premature to conclude that alpine marmots have referentially specific alarm calls (LENTI BOERO 1992). Well-controlled experiments (EVANS et al. 1993) on captive marmots would generate a more complete understanding of the relationship between alpine-marmot alarm calls and degree of risk. Results from a preliminary experiment we conducted with captive marmots suggest that habituation-dishabituation playback protocols (CHENEY & SEYFARTH 1990) may be a productive way to study marmot's perception of acoustic variants.

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