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Golden-marmot Alarm Calls. I. The Production of Situationally Specific Vocalizations

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Abstract

Many species of animals produce alarm calls that vary according to the situation. There are at least three different ways to communicate variation in situation: 1. Produce acoustically different call types; 2. Vary the rate or number of times that a single call type is produced; and/or 3. Vary the overall intensity in a single call. Combinations of these three mechanisms are also possible. I studied the production of alarm calls in free-living golden marmots (*Marmota caudata aurea*). Marmots emitted alarm calls when they encountered predators and startling stimuli. In the field these calls did not appear associated with predator type, but, rather, varied according to the degree of risk the caller perceived when it vocalized. Marmots produced calls with fewer notes when in higher risk situations, and calls with more notes when in lower risk situations. Thus, by varying the number of repeated notes in a single call type, marmots produced situationally specific alarm vocalizations.

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Introduction

When alarmed by predators, many animals produce specific vocalizations that function to warn conspecifics. These vocalizations are called alarm calls (KLUMP & SHALTER 1984). Alarm-call production can vary according to degree to which it is correlated with specific external stimuli (MACEDONIA & EVANS 1993). An implicit assumption, for species with situationally specific alarm calls, is that production and perception of variable alarm calls is symmetrical: perceivers respond to variation produced by signalers (OWINGS 1994). In this paper, I report the results of a study designed to first document situational variation in golden marmot (*Marmota caudata aurea*) alarm calls, and, if present, to then determine

likely mechanism(s) signalers use to produce situationally specific calls. The companion paper (Part II: BLUMSTEIN 1995) will discuss whether perceivers respond differently to call variants.

There are at least three different mechanisms by which a species can communicate situation: 1. Produce acoustically different call types; 2. Vary the rate or number of times that a single call type is produced; and/or 3. Vary the overall intensity in a single call. Combinations of these three mechanisms may also be used. For instance, California ground squirrels (*Spermophilus beecheyi*) use at least three mechanisms to communicate variation in a situation. They have acoustically different call types: whistles versus chatters (OWINGS & VIRGINIA 1978). They vary the number of repetitions of their chat vocalization to produce a chatter (OWINGS & VIRGINIA 1978), and they are able to vary their call intensity; emitting louder calls to announce predators and softer calls in social situations (LEGER & OWINGS 1978).

In the remainder of this paper, I first illustrate that golden marmots produce alarm calls. I then describe the acoustic structure of golden-marmot alarm calls to search for acoustic variability which could potentially be associated with specific events or situations. Finally, I describe experiments used to study the way in which calling marmots encode situational variation.

Methods

Study Population

Golden marmots (*Marmota caudata aurea*), 3–5 kg in weight, hibernating Old World sciurid rodents found in the Hindu Kush and Karakoram mountains of Central Asia (ROBERTS 1977), were studied at Dhee Sar (36 ° 81 ′N, 74 ° 95 ′E, elevation 4100–4300 m), an uninhabited high alpine meadow in Pakistan's Khunjerab National Park. The study lasted 514 d in total and covered 5 marmot summer active seasons (25 Jul.–12 Sep. 1989; 111 d between 6 May and 15 Sep. 1990; 100 d between 2 May and 21 Aug. 1991; 128 d between 1 May and 5 Sep. 1992; 126 d between 2 May and 4 Sep. 1993). The study focussed on adult marmots to control for possible age-related effects on predation risk and alarm calling. Khunjerab marmots are eaten by a variety of terrestrial and aerial predators: Tibetan red foxes, *Vulpes vulpes montana*; wolves, *Canis lupus*; snow leopards, *Panthera uncia*; golden eagles, *Aquila chrysaetos*; and, possibly, bearded vultures, *Gypaetus barbatus* (BLUMSTEIN 1994; BLUMSTEIN & ROBERTSON 1995).

The following definitions and background information will be useful for understanding the remainder of this and the companion paper. Marmot calls consist of an initial chirp immediately followed by 0–20 subsequent chirps. I refer to each chirp as a note and to multiple chirps emitted within a few s as a call (see Results for more detailed descriptions of alarm-call structure). Marmots may call several times and vary the number of notes in a call. One or more individual calls are defined as a calling bout.

General Methods of Collecting Background Information

Marmots were trapped in Tomahawk livetraps set in burrow entrances, then transferred to a canvas handling bag, processed (sexed, weighed, ear tagged, and marked or remarked with non-toxic Nyanzol dye), and released at the point of capture. Marmots were systematically observed with a combination of behavior, scan, and focal-animal sampling (MARTIN & BATESON 1986) during peak activity periods (0500–0930 h) on most days. Observers watched marmots from hides that were 100–500 m away from and above the marmots, using 15–45× spotting scopes and 7×, 8×, or 10× binoculars. In 1989, the inter-call interval between 22 naturally-occurring bouts of alarm calls was

timed. In 1991 and 1992, an attempt was made to note each bout of alarm calling heard in the study area throughout the day. In 1993, bouts were noted only when they occurred during morning observation periods. Unless otherwise noted, all analyses used the individual animal as the unit of analysis, and significance implies a two-tailed p < 0.05. Statistical analyses were conducted using StatView 4 and SuperAnova (ABACUS CONCEPTS Inc., Berkeley, CA, USA), and FASTSTAT (SYSTAT Inc., Evanston, IL, USA).

Alarm-eliciting Stimuli

The study of marmot responses to different species in their habitat provides an insight into the types of stimuli that alarm marmots and may explain how marmots communicate. Marmots spend 43 % of their time above ground engaged in vigilant activities (BLUMSTEIN 1994). Vigilant responses to stimuli were scored as any head movement not obviously associated with another behavior (e.g. foraging, self-grooming; BLUMSTEIN 1994).

Two responses of marmots to non-human animals were opportunistically recorded during morning observation periods. The two responses — look or alarm call — were mutually exclusive and independent of a subject's location in their home range and/or current behavior. I refer to these observations as interspecific interactions.

Responses were scored only when there was a clear line of sight between a focal marmot and the other species. Natural stimuli were classified into two categories: predators or non-predators. Subjects observed responding to the same type of stimulus (e.g. golden eagle, Tibetan red fox) more than once had a single randomly selected response to a given stimulus used in subsequent analyses.

Acoustic Structure of Alarm Calls

The acoustic structure of alarm calls was analyzed to search for acoustic variability which might communicate variation in predation risk. Calls were recorded with a Sennheiser MKH-816U directional microphone powered by a Sennheiser BP-2 battery pack (cut filter set to 1000 Hz) and a Sennheiser blimp windscreen onto a Marantz PMD-420 cassette deck, and copied to a Sony WM-D6C cassette deck onto TDK-SA or Maxell XLII-S 60- or 90-min tapes.

Initially I attempted to record naturally-occurring alarm calls, but, although I could easily count the number of notes/calls from these recordings, it was impossible to obtain high quality recordings for subsequent spectrographic analyses. I then attempted to record alarm calls elicited by humans walking towards marmots. These calls seemed to exhibit the natural range of variation elicited by aerial and terrestrial predators and other non-human threats. For each recorded call, the caller's identity and its distance from the eliciting human was noted.

To study acoustic structure, only human-elicited calls from identified adult marmots were used. Only the first call from multi-call bouts was analyzed because it was most likely to reflect the caller's immediate perception of risk. From these first calls, a single call per individual was selected randomly for subsequent analyses.

All calls were sampled at 22 kHz using a MacRecorder 8-bit AD-DA board and SoundEdit software (MacroMind Paracomp Inc., San Francisco, CA, USA) and, subsequently, bandpass filtered (1500–4200 kHz) using a 5-pole Butterworth filter in Signalyze (KELLER 1992) software (preliminary analyses suggested the fundamental frequency of all notes fall within this frequency range). Canary software (CHARIF et al. 1993) was used for all subsequent analyses. 'Boxy' sound spectrograms were generated using 256-point short-time Fourier transformations with a Hamming window and −140 dB clipping. Call notes were enlarged for measurement in Canary.

I counted the total number of notes in the first call on either the filtered waveform or on the sound spectrogram. Detailed acoustic measurements were made on the first four notes of the first call for the following reasons: 1. Most of the recorded calls contained at least four notes; 2. Preliminary visual inspection suggested that subsequent notes were similar to the fourth note; and 3. The calls were hypothesized to function to alert conspecifics immediately. Fig. 1 illustrates the measurements made on each of the first four notes of the first call.

Examination of the bivariate correlation matrix of the acoustic variables showed that some variables were highly correlated with each other. Principal components analysis (PCA — varimax extraction, orthogonal rotation) was used to reduce these correlated independent variables to fewer factors for
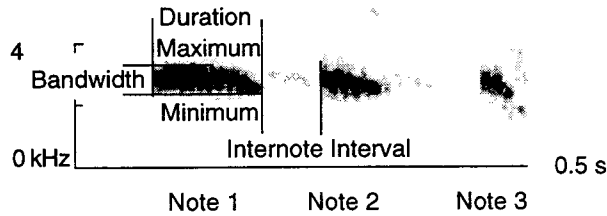
Fig. 1:   Acoustic measurements made on the first four notes of marmot alarm calls. For clarity, only the first note's measurements are shown. Subsequent notes resembled the third note more than the first two notes

subsequent statistical tests. I used coefficients from the PCA to compute factor scores from standardized variables (NORUSIS 1988).

Although the human-elicited calls sounded similar to naturally elicited calls, I wanted a more rigorous comparison. In 1990, a high-quality recording of the first alarm call given by an adult marmot in response to a fox was recorded. Acoustic measurements of this multi-note call were used to compute factor scores which were then compared with factor scores from human-elicited calls (t-value equation 9.5; SOKAL & ROHLF 1981). High quality recordings of calls in response to aerial predators were unavailable for similar analysis, but calls elicited by aerial predators sounded similar to human-elicited calls.

The Relationship between Alarm-call Variability and Predation Risk

Situationally specific calls are those where alarm call variants are associated with either the type of predator, or another identifiable external factor or situation (sensu MACEDONIA & EVANS 1993). Spectrographic analysis of first calls suggested that the number of notes per call was quite variable (see Results). Local shepherds, assistants, and I walked through the study site daily. Over the years, marmots may have habituated slightly to our presence, yet individuals still routinely called to humans. Hence, I attempted to elicit alarm calls by walking towards marmots.

I walked at a constant speed toward identified adult marmots and recorded the following information. For those identified marmots that called, I counted the number of notes in their call(s), the distance between the marmot and me each time the marmot called, and the date of the experiment. These experiments are termed predation probes. For marmots that called in 1991 and 1992 (154 calling events/287 predation probes), I randomly selected a single observation from each individual for subsequent analysis. The final data set consisted of the first calls from 36 different adult marmots (20 males, 16 females). A backward-stepping algorithm was used to delete variables with non-significant ($p > 0.1$) F-ratios. The distance to the calling marmot, the caller's sex, and the date were initially entered as independent variables. The resulting model with only significant variables is called the original model.

Data collected in 1993 were used to test the efficacy of the original model in explaining variation in another data set. Using coefficients generated from the original model, I calculated root mean square errors (root MSE) which reflect the goodness of fit of a model (BOWERMAN & O'CONNELL 1990). Root MSEs calculated from the 1991–1992 data provided a frame of reference for interpreting the 1993 root MSE.

Marmots with four or more predation probes conducted on them in 1991 were used in the next analysis, which considered the importance of marmot identity in explaining variation in the number of notes per call. Distance to the calling marmot was regressed against the number of notes in the first alarm call. Marmot identity was then entered as a second independent variable, causing the regression to become an ANCOVA. Strictly speaking, this analysis does not permit inferences beyond the studied individuals.

All previous analyses focused on the marmot's first call following a predation probe. However, if the number of notes per call was related to predation risk, then calls should change dynamically as risk increases or decreases. For those marmots whose calling bouts had more than a single call, I noted

Table 1: Response of marmots (alarm call, look) to other animals in their environment (predators, non-predators). Marmots were more likely to alarm call to predators than to non-predators (Fisher exact p < 0.0001)

	Alarm call	Look
Predator[1]	28	11
Non-predator[2]	26	62

[1] Predators and potential predators adult marmots were observed to interact with: Tibetan red fox (*Vulpes vulpes montana*), bearded vulture (*Gypaetus barbatus*), golden eagle (*Aquila chrysaetos*).
[2] Non-predators adult marmots were observed to interact with: ungulates (*Capra ibex, Bos grunniens, Capra* sp., *Ovis* sp.), mustelids (*Mustela erminea, M. altica*), lagomorphs (*Ochotona macrotis, Lepus capensis*), Himalayan griffon vulture (*Gyps himalayensis*), snow pigeon (*Columba leuconota*), corvids (*Corvus corax, Pyrrhocorax pyrrhocorax, P. graculus*), passerines, Himalayan snowcock (*Tetraogallus himalayensis*), kestrels (*Falco tinnunculus, F. naumanni*).

the number of notes in the second call produced when I approached the marmots. Unfortunately I could not determine if calls had more notes as risk decreased. Preliminary trials found it was not possible to elicit alarm calls when I turned around and began walking away from previously calling marmots: marmots either disappeared or stopped calling as I walked away from them.

Results

Background Information

Between 94 and 188 marmots ($\bar{X} = 120$) were studied annually: some individuals were studied each year while others contributed to only a single year's data. Marmots alarm called from safe locations; if surprised by a predator or a human, they would almost always return and stand next to a burrow before vocalizing. In 1991 and 1992, marmots produced between 6.1 (May) and 22.3 (Jul.) bouts of alarm calls per d. In 1993, there were 0.98 bouts per h during morning observation periods. The average interval between the first and second call in a calling bout was 17 s. Bouts occasionally lasted up to 30 min, but generally were much briefer.

Alarm-eliciting Stimuli

Marmots alarm called more to predators than to non-predators (Table 1). When they called in response to non-predators, those species resembled predators. For instance, marmots sometimes alarm called to Himalayan snowcocks (*Tetraogallus himalayensis*) that suddenly appeared in the air above them, but also apparently ignored quietly foraging snowcock. Marmots emitted alarm calls to humans in about half the predation-probe experiments. When marmots did alarm-call to predators or threatening stimuli, calls were not identical. The most obvious difference among calls was the number of notes per call.

Acoustic Structure of Alarm Calls

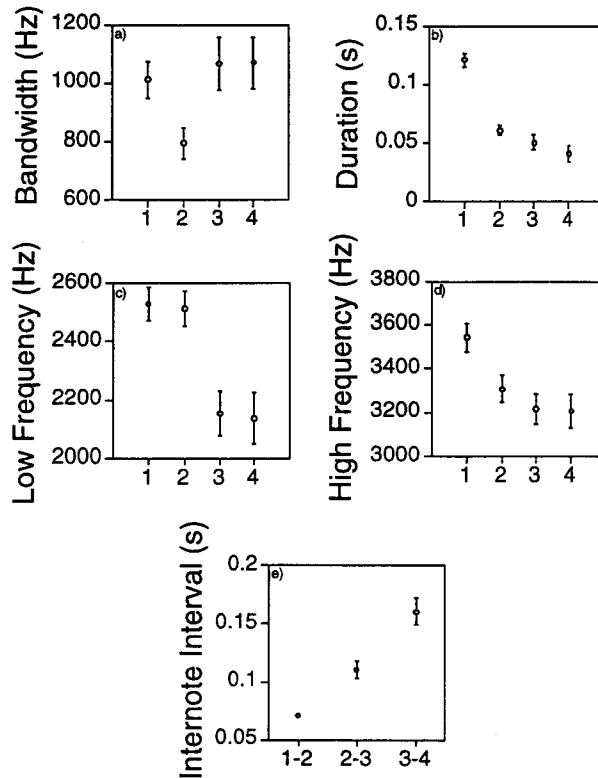Golden-marmot alarm calls exhibited sufficient variation to warrant further

Fig. 2: Acoustic measurements ($\bar{X} \pm$ SE) on the first four notes of human-elicited golden marmot alarm calls: a. Bandwidth (Hz); b. Duration (s); c. Low frequency (Hz); d. High frequency; e. Internote interval (s). Sample sizes are 28 for all first note, second note, and internote interval 1–2 measurements, 27 for third note and internote interval 2–3 measurements, and 24 for fourth note and internote 3–4 measurements

analysis of situational specificity. Alarm calls from 28 different marmots were tape-recorded; 211 of the tape-recorded calls were of sufficient quality for subsequent acoustic analysis. A single call from each individual was used for descriptive analysis (Fig. 2). Acoustic variability appeared to increase with each subsequent note and internote interval. The mean duration of the internote interval tended to increase ($r_s = 1$, $p = 0.157$, $n = 3$ intervals), while the duration of each note, and the low and high frequencies, decreased with subsequent notes (all $r_s = 1$, $p = 0.083$, $n = 4$ notes). The first, third, and fourth notes had a greater bandwidth than the second note ($U_{note\ 2,1} = 221.5$, $p = 0.013$; $U_{note\ 2,3} = 240.5$, $p = 0.049$; $U_{note\ 2,4} = 177.5$, $p = 0.010$).

Four factors explained 84 % of total variance (Table 2). I interpreted orthogonally rotated loadings as: 1. A temporal factor; 2. A factor representing the frequency of the calls; 3. A factor representing the number of notes per call; and 4. A factor representing the bandwidth of the calls. Thus, the number of notes

Table 2: Rotated factor scores calculated from the 23 alarm calls with four or more notes and the percentage of total variance explained by each factor

	Temporal Factor	Frequency Factor	Notes Factor	Bandwidth Factor
Duration-3	0.871	0.225	0.117	0.155
Duration-2	0.855	− 0.067	− 0.123	0.264
Internote-1-2	− 0.818	0.154	0.129	− 0.265
Bandwidth-3	0.805	0.362	0.187	0.158
Duration-4	0.785	0.051	0.100	0.031
Internote-2-3	− 0.776	0.015	0.420	− 0.326
Low frequency-3	− 0.775	0.325	− 0.339	0.079
Internote-3-4	− 0.749	− 0.312	0.445	− 0.188
Bandwidth-4	0.742	0.192	0.034	0.461
Low frequency-4	− 0.678	0.594	− 0.021	− 0.094
Duration-1	0.529	− 0.171	0.550	0.273
Low frequency-2	− 0.064	0.903	− 0.128	− 0.321
High frequency-2	0.246	0.878	− 0.020	0.308
High frequency-4	0.101	0.845	0.016	0.410
High frequency-3	0.292	0.842	− 0.107	0.300
Low frequency-1	− 0.285	0.805	− 0.180	− 0.295
High frequency-1	− 0.023	0.803	− 0.071	0.524
Notes/call	0.067	0.126	− 0.917	− 0.105
Bandwidth-1	0.244	0.161	0.090	0.884
Bandwidth-2	0.406	0.131	0.122	0.790
Variance	34.6	26	9.1	14.3

per call appeared to be independent of the finer microstructural variation of alarm calls.

The four factor scores from the fox-elicited call were statistically indistinguishable from factor scores from human-elicited calls. Furthermore, temporal and frequency characteristics of unrecorded fox calls seemed to fall within the range of variation of human-elicited marmot calls.

The Relationship between Alarm-call Variability and Predation Risk

The distance between the human and a calling marmot significantly accounted for 25 % of the variation in the number of notes per call (Fig. 3). For the 36 calls used to develop this 'original model', the mean number of notes per call was 6.5 (± 0.58 SE), and the mean human-marmot distance was 99.4 m (± 9.93 SE). Date and sex had non-significant F-ratios and were deleted in the backward-stepping procedure.

In a novel data set collected in 1993, a model with distance alone predicted the number of notes per call to within about four notes per call. The first calls of 18 different subjects, selected from 1993 predation probes, had a root MSE of 3.86. By comparison, the root MSE for the original model was 2.93.

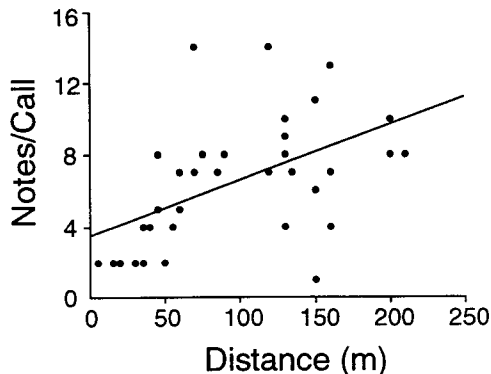Marmot identity significantly explained variation in the number of notes per

Fig. 3: Distance between a calling marmot and the human eliciting the call regressed against the number of notes in the marmot's first alarm call to that human. Distance significantly (p < 0.001) explained 25 % of the variation in the number of notes per call (adjusted R^2 = 0.254; regression equation: notes/call = 3.447 + distance × 0.031)

Table 3: Repeated observations of the responses of seven different marmots to the predation-probe experiment. ID = marmot identification number; n = number of observations; Distance = distance between the marmot and the human eliciting the call; Notes = number of notes in the human-elicited calls

ID	Sex	n	Distance $\bar{X}$ (SE)	Notes $\bar{X}$ (SE)
12	f	4	143.8 (44.03)	7.75 (1.93)
15	f	6	24.2 (5.23)	3.17 (0.91)
38	f	6	62.5 (14.30)	5.33 (1.23)
2	m	6	69.2 (17.44)	6.50 (0.89)
92	m	4	142.5 (13.62)	6.50 (1.55)
100	m	7	23.6 (2.73)	2.57 (0.43)
115	m	8	130.0 (13.36)	11.63 (0.53)

call. In 1991, seven marmots called four or more times in response to predation probes (Table 3). Distance alone, regressed against number of notes per call, significantly explained about 50 % of the variation in number of notes per call in this data set (adjusted R^2 = 0.498, model F = 40.679, df = 1, p = 0.0001). Marmot identity was a significant covariate (F = 5.196, df = 6, p = 0.001), and the model with distance and identity significantly explained about 70 % of the variation in the number of notes per call (adjusted multiple R^2 = 0.695; model F = 14.016, df = 7, p = 0.0001). Thus, a significant and substantial amount of the total variation in number of notes per call seems to be accounted for by the identity of the caller.

Marmots produced calls with fewer notes as a human continued to approach them. In the 1991–1992 predation-probe data set, 20 marmots alarm-called a second time as I continued to approach; the others ceased calling and disappeared

into their burrows. Of these second calls, 65 % (13/20) had fewer notes than the first call in that bout (sign test p = 0.007).

Discussion

Golden marmots emitted variable alarm calls when they encountered predators or alarming stimuli. Unlike many (but not all) avian species, that call prior to reaching a refuge (KLUMP & SHALTER 1984), golden marmots alarm called from apparently safe locations. This is in marked contrast to Belding's ground squirrels (*Spermophilus beldingi*), whose alarm calls to terrestrial predators were frequently emitted away from a refuge (SHERMAN 1985), but similar to Columbian ground squirrels (*S. columbianus*) who also returned to a burrow prior to calling (MACWHIRTER 1992).

Unlike other sciurids where a considerable proportion of 'alarm calls' were used in social situations (OWINGS & HENNESSY 1984), golden marmots rarely called in response to other marmots. The few instances of alarm calls in social contexts occurred during agonistic interactions, when, in a few cases, a marmot being chased by another marmot called while fleeing. This suggests that golden-marmot alarm calls may serve a function other than simply predator alarm. However, because 'social alarm calling' was very rare, studying its function would be difficult.

Golden-marmot alarm calls varied according to situation but not obviously according to predator type. Calls differed as a function of the distance between an approaching human and the caller. Marmots emitted calls with fewer notes when a human was close and calls with more notes when a human was farther away. In contrast to golden marmots, yellow-bellied marmots (*M. flaviventris*), a species suggested to have microstructural variation in their alarm calls (DAVIS 1991), increase the rate of calling as risk increases (WARING 1966). Other species of marmots have also been reported to increase call rate in proportion to risk (NIKOL'SKII et al. 1994). Columbian ground squirrels seemed to monitor a predator's movements and call rate increases as a function of predator movement (HARRIS et al. 1983). Calling rate also varies in Carolina wrens (*Thryothorus ludovicianus*): wren chit rates decline as they apparently habituate to a stationary predator, and increase if a stationary predator moves (MORTON & SHALTER 1977). In contrast to these species, and more like golden marmots, dwarf mongooses (*Helogale undulata*) decrease the number of pulses in both their panic twitters and their excitement twitters as predators close on callers (BEYNON & RASA 1989).

Alarm calls and other responses may have multiple targets, and predators might be a target of alarm calls (CARO 1986, 1988; HASSON 1991; HERSEK & OWINGS 1993). If predators, not marmots, were the primary target of the alarm calls, then the number of notes per call might be predicted to increase as risk increased to make the caller more conspicuous (HASSON 1991). Golden marmots decreased the number of notes per call as risk increased, suggesting that the predator was not the primary target, or, if the predator was the primary target, that calls were not designed to increase conspicuousness.

Predators, even if not the primary target of alarm calls, could still influence call structure. Marmots may have produced shorter calls to reduce their conspicuousness to predators (OWINGS & HENNESSY 1984). That the number of notes per call decreased as risk increased is consistent with the hypothesis that callers attempted to reduce their conspicuousness further while still trying to inform other marmots about the presence of a threat. Another prediction from this hypothesis is that the number of notes per call is related to acoustic characteristics associated with localizability (e.g. frequency, bandwidth). That the number of notes per call emerged as its own factor in the factor analysis provides evidence against this prediction: the number of notes per call was not correlated with other measured acoustic parameters.

The predation probe experiment assumed that the distance to a human was a suitable metric of predation risk. Furthermore, it assumed that marmots who first saw humans at relatively close distances perceived higher risks than marmots who first saw humans at greater distances. While other factors such as the distance a marmot was from a burrow, the distance the marmot first saw the human, the direction of the approaching human, and/or the marmots' current behavior (LENTI-BOERO 1992; BLUMSTEIN 1994) could also potentially influence an individual's perception of risk, the two assumptions seem valid. Predation risk, the probability of an animal being killed in the next moment, is a function of both the distance a predator is from its prey and the rate at which the predator approaches (MORSE 1980; YDENBERG & DILL 1986; LIMA & DILL 1990; BLUMSTEIN 1994). Interestingly, there were no significant associations between the number of notes per call and the distance at which the marmot first oriented towards me, returned to its burrow, or disappeared into its burrow. Evidence from other species suggests that the 'urgency' of alarm calls is a function of the distance and/ or the speed with which a predator approaches a caller (e.g. ROBINSON 1981; BEYNON & RASA 1989). That marmot-human distance alone explained a significant amount of variation in the number of notes per call emphasizes the importance of the distance to the alarming stimulus in the assessment of predation risk. Moreover, it also suggests that alarm calls vary according to marmots' perceptions of risk.

There is some debate as to the degree to which alarm calls are associated with external events or specific situations (review: MARLER et al. 1992; EVANS et al. 1993; MACEDONIA & EVANS 1993). In some species, alarm calls appear to be associated with specific predators or with the hunting strategy of different predators (LEGER & OWINGS 1978; KLUMP & SHALTER 1984; SHERMAN 1985; CHENEY & SEYFARTH 1990; MACEDONIA 1990; EVANS et al. 1993). Vocalizations associated with a specific type of predator have been called referentially specific because they contain sufficient encoded information to elicit the appropriate response in a conspecific who hears the call (review: CHENEY & SEYFARTH 1990; MARLER et al. 1992; EVANS et al. 1993; MACEDONIA & EVANS 1993). Other species produce alarm calls that vary, not necessarily according to predator species or type, but, rather, according to the degree of risk the caller experiences. In some cases, degree of risk may covary with predator type, but the correlation between predator type and alarm-call production is not as tight (MACEDONIA & EVANS 1993).

Golden-marmot alarm calls did not obviously vary according to predator type. To more rigorously study the relationship between call type and predator type, controlled laboratory experiments (EVANS et al. 1993) would have to be conducted. When marmots called to low-flying golden eagles, calls seemed louder than usual. Interestingly, the perceiver's ability to use amplitude cues to estimate distance to the caller (MORTON 1982; WILEY & RICHARDS 1982), or predation risk (LEGER & OWINGS 1978) diminishes if signalers vary their amplitude and perceivers are not always at a uniform distance from the signaler. Thus, while amplitude production could conceivably vary according to situation, perception of call variation might not always be expected to parallel production of call variation.

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