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Inter- and Intraspecific Variation in the Acoustic Habitats of Three Marmot Species

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Abstract

Closely related species often have remarkably different vocalizations. Some of the variation in acoustic structure may result from species adapting their calls to maximize transmission through their acoustic environments. We document the relative magnitude of inter- and intraspecific variation in acoustic transmission properties of the habitats of three closely related marmot species to study the relative importance that the acoustic environment may have played in selecting for species-specific marmot alarm calls. We used spectrogram correlation to quantify the degree to which pure tones and alarm calls changed as they were broadcast through marmot home ranges to describe the acoustic habitats of golden (*M. caudata aurea*), yellow-bellied (*M. flaviventris*), and alpine (*M. marmota* L.) marmots. Species lived in quantifiably different acoustic habitats. One analysis partitioned variation between species and between marmot social groups (nested within species). We found significant interspecific variation in the acoustic transmission fidelity of the three species' habitats and insignificant intraspecific variation between social groups. Further analysis of a larger sample of alarm calls broadcast through golden marmot social groups found significant intraspecific variation. Interspecific variation greater than intraspecific variation suggests that variable acoustic habitats may be responsible for at least some of the interspecific variation in alarm call structure. This is the first study to use spectrogram correlation to describe habitat acoustics. We discuss aspects of the method that may be useful for others seeking to quantify habitat acoustics.

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Introduction

Closely related species often have remarkably different vocalizations. Some vocalizations may be important species-isolating mechanisms and we should therefore expect species-specific vocalizations (e.g. BECKER 1982). Another broad class of vocalizations are 'alarm calls'. These, often loud, vocalizations are typically emitted when individuals encounter predators. Alarm calls may function to warn conspecifics or discourage predators from continuing their attack (KLUMP & SHALTER 1984). Species may respond to the alarm calls of other species and several species may converge on similar calls to facilitate interspecific communication (KLUMP & SHALTER 1984). Convergent calls may also arise from selection on call structure for inconspicuousness (MARLER 1955). Thus, factors other than species identification may be important in the evolution of divergent alarm calls.

Communication requires the transmission of signals from a signaler to a receiver. Acoustic signals must be transmitted through a medium during which time they become modified (WILEY & RICHARDS 1978; DUSENBERY 1992; ENDLER 1992; FORREST 1994).

Over distance, biologically important sounds may attenuate (i.e. experience amplitude loss), degrade (i.e. change acoustic structure), and compete with background noise (WILEY & RICHARDS 1978, 1982). Thus, we might expect selection to modify the structure of long-distance signals, like alarm calls, to maximize transmission in different habitats – ‘the local adaptation hypothesis’ (e.g. MORTON 1975; reviewed in BROWN et al. 1995).

Marmots (*Marmota*, Sciuridae, Rodentia) are large ground-dwelling squirrels found throughout the Northern Hemisphere. Marmots produce a remarkable variety of loud alarm vocalizations that can be heard throughout their social group’s home range and often in neighboring social groups. Some species produce tonal whistles, other species have raspy chirps, some species package their vocalizations into multiple-note calls, and all repeat their vocalizations at various rates. If the acoustic environment is important for the evolution of divergent marmot alarm calls, we should expect significant interspecific variation in the acoustics of each species’ habitat. However, the local adaptation-hypothesis should also work within species: significant intraspecific variation in habitat acoustics should select for intraspecific variation in call structure (e.g. NOTTEBOHM 1975; HUNTER & KREBS 1979; GISH & MORTON 1981). In this paper we document the relative magnitude of inter- and intraspecific variation in the transmission fidelity of a pure tone and the alarm call of each species broadcast through its own habitat to estimate the potential importance of the acoustic environment in selecting for divergent marmot alarm calls.

Methods

Study Sites

We studied the transmission fidelity of a 3-kHz pure tone and marmot alarm calls in three marmot species. In 1993 we studied golden marmots (*Marmota caudata aurea*) in Khunjerab National Park (Sost, Northern Areas, Pakistan; complete site description in BLUMSTEIN 1994, 1995a). In 1994 and 1995 we studied yellow-bellied marmots (*M. flaviventris*) in and around the Rocky Mountain Biological Laboratory (Gothic, Colorado, USA; complete site description in ARMITAGE 1991) and alpine marmots (*M. marmota*) in Berchtesgaden National Park (Berchtesgaden, Bavaria, Germany; complete site description in ARNOLD 1990). In 1995 we studied yellow-bellied marmots in the Fruita area of Capitol Reef National Park (Torrey, Utah, USA). Golden marmots are a highly social species of Old World marmots found in the Hindu Kush, Tien Shen, and Karakoram mountains of central Asia (BLUMSTEIN 1995a). Golden marmots live exclusively above the timber line in high alpine meadows where they must communicate against a backdrop of wind, glacial streams, and falling debris. Alpine marmots are found in the Alps, the Pyrénées and Carpathian mountains of Europe (VAN DEN BRINK 1968). Most alpine marmots live above the timber line. We studied alpine marmots living in a subalpine area in the Berchtesgaden Alps where flowing water, dense forests, lush subalpine vegetation, and numerous songbirds provided an acoustic backdrop through which the marmots had to communicate. Yellow-bellied marmots are found in a variety of habitats throughout the western United States (FRASE & HOFFMANN 1980). We studied yellow-bellied marmots living in subalpine riparian habitats (two social groups), subalpine meadows (four social groups), alpine meadows (two social groups), and riparian high desert habitats (four social groups). Tall, lush vegetation, rushing water, a plethora of songbirds, other sciurids, and environmental noise such as rock fall characterized the habitats in which yellow-bellied marmots must communicate.

Acoustical Analyses

We played back a 3-kHz pure tone and a representative natural alarm call from each species within marmot home ranges (Fig. 1). The 2.56 s 3-kHz pure tone was synthesized using SoundEdit software (MACROMIND · PARACOMP INC. 1990). We chose a 3 kHz pure tone because the fundamental frequency of all marmot alarm calls is \approx 3 kHz and a 2.56 s duration because that was the length of the broadcast alarm calls. The single

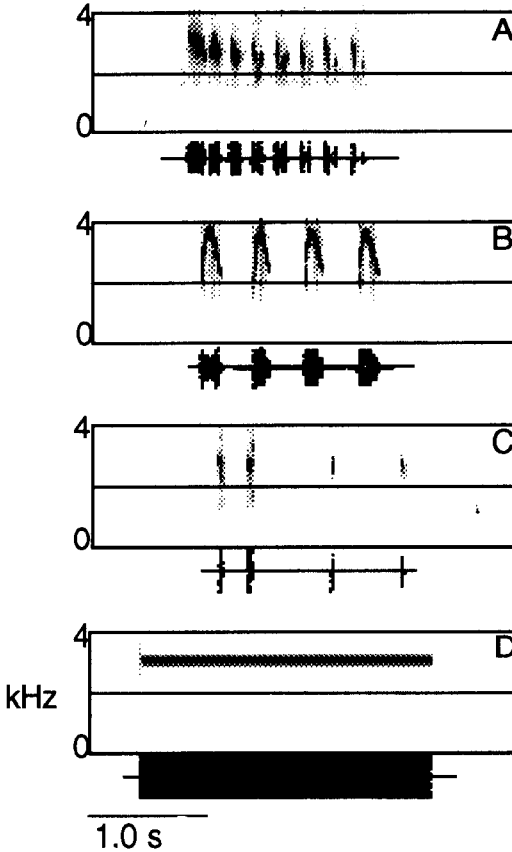


Fig. 1: Sound spectrograms (MacRecorder 256 point) and waveforms of the three alarm calls, A = golden marmot; B = alpine marmot; C = yellow-bellied marmot) and the 3-kHz pure tone (D) used for describing habitat acoustics

high-quality recording of each species was made during other studies (BLUMSTEIN 1994, 1995b,c; BLUMSTEIN & ARNOLD 1995; BLUMSTEIN & ARMITAGE 1997).

While aware of the controversy over pseudoreplication in playback design (MCGREGOR et al. 1992), we chose a single, representative exemplar of the only or most common call type for each species to estimate precisely how each stimulus was transmitted. Many environmental factors influence sound transmission (see Discussion) and it was our primary goal to describe the combined effect of these factors. Variation within a call type might not be differentiable at a distance (see Appendix), and, for our goals, a single exemplar of a call type was appropriate (see also BROWN et al. 1995).

Alarm calls were filtered to prevent aliasing (the appearance of spurious frequencies resulting from the digitizing process) using a TTE J83G-22K-6—720B filter. Calls were then sampled at 22 kHz using a MacRecorder 8-bit AD-DA board and SoundEdit Software. We removed ambient noise and overtones by filtering all calls with a five-pole Butterworth bandpass filter (1.5–4.0 kHz) using Signalize software (KELLER 1992).

All three species of marmots lived in obvious social groups. Each social group's acoustics was characterized by sampling nine locations in each habitat. The nine locations were chosen to include the home range area used by marmots; we used a main sleeping burrow as the center and set up a recording array around that burrow (Fig. 2). Four, 100 m long perpendicular lines extended from the main burrow. Along each line a 40 m recording transect was randomly oriented at 50 and 100 m. A ninth 40 m recording transect was randomly positioned at the main burrow.

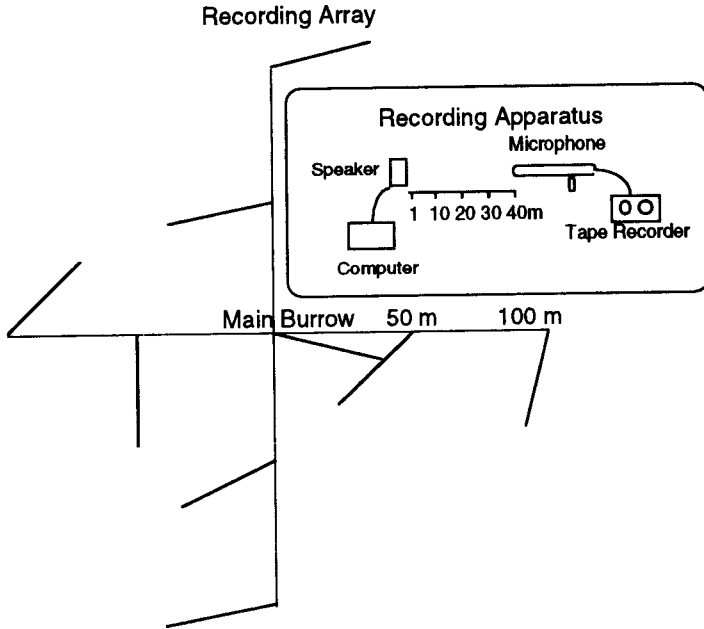


Fig. 2: The recording array and apparatus used to quantify a marmot group's acoustic habitat. Each array was centered on a marmot social group's main sleeping burrow. Four, 100 m long perpendicular lines extended from the main burrow. Along each line, a 40 m recording transect was randomly oriented at 50 and 100 m. A ninth 40 m recording transect was randomly positioned at the main burrow

Alarm calls and pure tones were played back from a Macintosh PowerBook 100 and broadcast through a Sony SRS-77G powered speaker elevated 0.3 m above ground (which corresponded roughly to the height of a marmot rearing up bipedally on its hind legs and calling). The single speaker was directional and had a relatively flat frequency response for the played back exemplars. We adjusted the sound pressure level to ≈ 95 dB at 1 m from the speaker (golden mean = 94.8 dB, SD = 0.46, n = 18; alpine mean = 94.9 dB, SD = 0.12, n = 8; yellow-bellied mean = 95.8 dB, SD = 1.73, n = 12) using a Realistic model 33-2050 sound level meter. Although exact call intensities were difficult to measure in the field, all species of marmots emitted alarm calls within this range (D. T. BLUMSTEIN & J. C. DANIEL unpubl. data). Sounds were re-recorded at 1 m (the 'reference' distance) and 10 m, 20 m, 30 m, and 40 m (the 'experimental distances') using Sennheiser directional microphones (an MKH-816 in 1993; an ME-88 in 1994 and 1995), high-quality cassette tape recorders (a Marantz PMD-420 cassette deck or a Sony WM-D6C in 1993; a Sony TC-D5M in 1994 and 1995) with fresh alkaline batteries (to minimize tape speed fluctuations), and high bias cassette tape. We chose 1 m as the reference distance instead of the original exemplar because all speakers produce some degradation and we assumed there was negligible habitat-induced degradation at 1 m. Moreover, 1 m was outside the distance of near-field effects for our sounds (≈ 0.08 – 0.12 m; – e.g. DUSENBERY 1992). The directional microphone was pointed towards the speaker and was parallel with and 0.15 m above the ground (corresponding roughly to the height of a quadrupedally standing and foraging marmot's ears). The numbers of social groups studied varied between species (n = 18 golden marmot social groups; n = eight alpine marmot social groups; n = eight yellow-bellied marmot social groups in and around RMBL; and n = four yellow-bellied marmot social groups at Capitol Reef).

Recordings of pure tones and alarm calls were digitized at 22 kHz using a MacRecorder and SoundEdit, and we calculated spectrogram correlations using Canary (CHARIF et al. 1993). Spectrogram correlation compares the overall three-dimensional 'shape' (frequency \times time \times amplitude) of two sound spectrograms (e.g. the original sound and a sound recorded some distance from a source) by shifting two spectrograms along their temporal and/or frequency axes to calculate a number representing the maximum overall similarity (Canary's algorithm shifts spectrograms along their temporal axis and thus is a 'one-dimensional' spectrogram correlation). Spec-

rogram correlations range from 0 (no similarity) to 1.0 (identical sounds). The main benefit of using spectrogram correlation is that results are not dependent on the set of measured variables; the method assesses overall similarity (see Discussion).

'Boxy' sound spectrograms were generated using 256-point short-time Fourier transformations (0% overlap for pure tones, 50% overlap for alarm calls), a Hamming window, and -110 dB clipping (CHARIF et al. 1993). Using Canary, we calculated normalized spectrogram correlations between the sounds recorded at 1 m and 10, 20, 30, and 40 m. Normalized spectrogram correlations are insensitive to amplitude variation: if two signals are identical but for their relative amplitude, the peak cross-correlation would still be 1.0 (normalizing algorithm and detailed discussion in CHARIF et al. 1993). We used normalized spectrogram correlations because we assumed that partially attenuated calls, that still retained their overall frequency \times time 'structure', would still be interpretable by marmots, but fully attenuated calls (or parts of calls) would be less interpretable. We set the filter bandwidth to 2.9–3.1 kHz for the pure tones (to filter out most extraneous noise) and to 1.5–3.8 kHz for the alarm calls (approximately the maximum observed bandwidth of alarm calls). The wider bandwidth used for alarm calls permitted a better assessment of the effects of background noise.

Statistical Analyses

Descriptive statistics were calculated in StatView (ABACUS CONCEPTS INC. 1993); linear models were fitted using SuperANOVA (ABACUS CONCEPTS INC. 1991) and SAS (SAS INSTITUTE INC. 1990). For all models we computed Type III sums of squares; for the second and third models we calculated all Bonferroni/Dunn pairwise post-hoc comparisons and report adjusted R^2 values. Specifically, we fitted three models to the spectrogram correlations.

The first model, a two-factor nested MANOVA, estimated the variation in pure tone transmission explained by species and by social groups (nested within species). The model was

$$Y_{10}, Y_{20}, Y_{30}, Y_{40} = s + g(s) + e, \quad (\text{eqn 1})$$

where $Y_{10}, Y_{20}, Y_{30}, Y_{40}$ = the spectrogram correlation at 10 m, 20 m, 30 m, and 40 m from the speaker; g = the social group nested within s = the species of marmot; and e = error. To balance the model, we selected eight social groups from the golden and yellow-bellied marmot data that were missing few measurements and that represented the variety of microhabitats. We estimated variation explained by both species and group nested within species by subtracting significant λ 's from 1 (TABACHNICK & FIDELL 1989).

We fitted the second linear model to pure tone and alarm call results to test for species differences in transmission characteristics after controlling for the effect of distance and the interaction of distance and species. The model was

$$y = d + s + d*s + e, \quad (\text{eqn 2})$$

where y = the spectrogram correlation; d = the distance from the speaker; s = the species of marmot (categorically coded); $d*s$ = the interaction between distance and species; and e = error. Strictly, the pure tone results permit us to compare species' habitats because the pure tones were identical signals transmitted through different habitats. We provide the alarm call results for comparison. All re-recorded alarm calls and pure tones were analyzed for all species but the golden marmot. For golden marmots, we analyzed all alarm calls but randomly selected 10 social groups for pure-tone analysis.

The third linear model was fitted to all the golden marmot alarm call results to test for significant intraspecific variation in alarm call transmission properties. The model was

$$y = d + g + d*g + e, \quad (\text{eqn 3})$$

where y = the spectrogram correlation; d = the distance from the speaker; g = the marmot social group (categorically coded); $d*g$ = the interaction between distance and group; and e = error. This model tested for social group differences after controlling for the effect of distance and the interaction of distance and social group. For this analysis, we only studied golden marmots, since it was the single largest data set.

Results

The three species of marmots lived in quantifiably different acoustic habitats. A total of 11% of the variation in pure tone transmission was significantly explained by 'species'

($\lambda = 0.890$, $p = 0.009$); no significant variation was explained by social group nested within species ($p = 0.105$). Significant variation in pure tone transmission was explained by either or both of these factors at 10 m and 30 m; no significant variation was explained at 20 m or 40 m (Table 1).

A total of 39% of explained variation in pure tone transmission was explained by species ($p = 0.001$) and distance ($p < 0.001$): the interaction term was not significant ($p = 0.783$). Post-hoc pairwise comparisons suggested that while pure tone transmission did not significantly differ between yellow-bellied marmots and golden marmots ($p = 0.945$), all other pairwise comparisons were significantly different (yellow-bellied vs. alpine $p = 0.001$, golden vs. alpine $p = 0.001$: see – Fig. 3).

Alpine marmot alarm calls changed (i.e. were attenuated, degraded, and otherwise interfered with) less than other species' as they were transmitted through their home ranges, whereas yellow-bellied marmot calls changed the most (Fig. 3). Both species ($p < 0.001$) and distance ($p < 0.001$) significantly explained 65% of the variation in the alarm call cross-correlation; the interaction term was not significant ($p = 0.396$). For the alarm calls, all post-hoc pairwise comparisons were significantly different ($p < 0.001$).

Golden marmot home range significantly explained variation in alarm call transmission (Fig. 4; adjusted $R^2 = 0.41$, group $p < 0.001$, distance $p < 0.001$, group*distance $p = 0.872$). Of the pairwise group comparisons (40/153 Bonferroni/Dunn post-hoc pairwise comparisons, p -critical = 0.0003), 26% were significantly different. An additional 33 had p -values between 0.0003 and 0.05.

Discussion

Marmot Habitat Acoustics

There were significant interspecific differences in the marmot acoustic environments. All three marmot species produce alarm calls that potentially encode situationally specific information about the degree of risk a caller experiences (WARING 1966; BLUMSTEIN 1995b,c; BLUMSTEIN & ARNOLD 1995; BLUMSTEIN & ARMITAGE 1997). Interestingly, each species used a different mechanism to encode situationally specific information. Alpine marmots had two different loud alarm calls: a 'normal' whistle and the subtly different 'start-hi' call (BLUMSTEIN & ARNOLD 1995). Yellow-bellied marmots had a

Table 1: MANOVA results specifying the significance of species and group nested within species towards explaining variation (R^2) in pure transmission. Overall, species significantly explained 11% of the variation in pure tone transmission ($p = 0.009$); no significant variation was explained by social group nested within species ($p = 0.105$)

Distance	Model p	Species p	Group (species) p	R^2
10 m	0.002	0.006	0.019	0.22
20 m	0.302	0.072	0.444	0.13
30 m	0.019	0.019	0.053	0.19
40 m	0.730	0.551	0.722	0.09

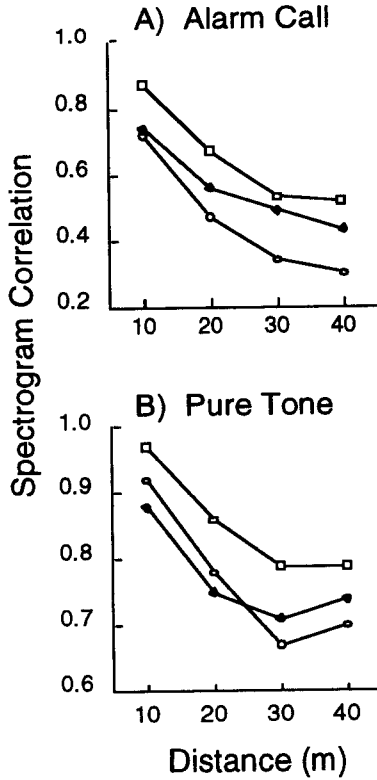


Fig. 3: Average normalized spectrogram correlations of alarm calls (A) and pure tones (B) as a function of distance from the speaker in three habitats of three marmot species: □ alpine, ◆ golden, and ○ yellow-bellied. Averages were calculated from each of the social group's mean correlation (see text for sample sizes and CHARIF et al. 1993 for spectrogram correlation algorithms)

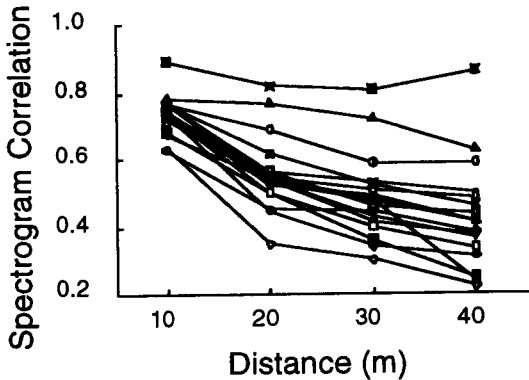


Fig. 4: Golden marmot group's average alarm call spectrogram correlation × distance from the speaker. Generally nine different measurements were used to calculate the mean for each distance for each social group. All Bonferroni/Dunn post-hoc pairwise comparisons were calculated (p-critical = 0.0003); 26% (40/153) were significantly different (0.0003 < p < 0.05 for 33 additional pairwise comparisons)

single-note 'whistle' and the rarely given 'trill' (WARING 1966; BLUMSTEIN & ARMITAGE 1997). Golden marmots produced a raspy chirp when alarmed that was repeated a variable number of times (BLUMSTEIN 1995b). Both alpine marmots and golden marmots varied the number of 'notes' they 'packaged' together in an alarm call (BLUMSTEIN 1995b; BLUMSTEIN & ARNOLD 1995). Yellow-bellied marmots primarily communicated situational variation by varying the rate at which calls were produced and rarely 'packaged' their alarm calls into 'trills' (WARING 1966; BLUMSTEIN & ARMITAGE 1997).

Alpine marmot habitats had the highest fidelity for both pure tones and alarm call transmission. Although we studied the transmission properties of the only, or the most common type, of alarm call in golden, alpine, and yellow-bellied marmots, we suspect that other acoustic variants in the same frequency bandwidth are similarly transmitted (see Appendix for a discussion of microstructural variation in yellow-bellied marmot alarm calls). Thus we see a superficial relationship between the way in which species communicate situational specificity (or at least encode potential situational information) and the acoustic environment. The acoustic environment with the highest transmission fidelity was associated with subtly different loud alarm calls while the acoustic environment with the lowest transmission fidelity was associated with a 'rate-based' alarm communication mechanism. This conclusion must be considered preliminary: the relationship between habitat acoustics and alarm repertoire size and 'complexity' in the entire genus (≈ 14 species) is currently under study.

Although significantly less intraspecific variation was explained than interspecific variation, for at least golden marmots there was significant intraspecific variation in habitat-induced transmission fidelity. The local -adaptation hypothesis predicts that both individuals and species will alter their vocalizations to maximize signal transmission. BLUMSTEIN & ARMITAGE (1997) found no evidence of location-specific intraspecific variation in yellow-bellied marmot alarm calls. While not specifically studied, BLUMSTEIN (1995b,c) found no evidence of systematic variation in golden marmot alarm calls around Dhee Sar. However, NIKOLSKII & ORLENEV (1980) reported significant and substantial intraspecific variation in the *M. caudata* calls studied elsewhere (some of this variation may 'become' interspecific if *M. caudata aurea* is classified as a unique species). Other reports have also described intraspecific variation in marmot alarm call structure (*M. camtschatica*, NIKOLSKY et al. 1991; *M. baibacina*, NIKOL'SKII 1994). Thus, although there is intraspecific variation in the habitat acoustics of alpine, golden and yellow-bellied marmots, there seems to be relatively less intraspecific variation than interspecific variation in alarm calls: one would never mistake an alpine marmot alarm call for a yellow-bellied marmot alarm call.

A variety of factors may influence habitat acoustics and we did our best to control for these effects when quantifying marmot habitat acoustics. We feel that the significant home range and species differences reflect the effects of significantly different acoustic habitats, and are not measurement artifacts. For instance, time of day, weather, other animals, season (with associated vegetational differences), and environmental noise may influence acoustic transmission (WILEY & RICHARDS 1978; DUSENBERY 1992). Acoustic measurements in all but four of the 38 marmot home ranges were made during the height of the growing season in each species' habitat. Thus, our results may reflect a relatively bad time of year to communicate (particularly in those locations where the vegetation was taller than marmots), but all are somewhat standardized. An exception was the four yellow-

bellied marmot home ranges studied at Capitol Reef National Park; these were studied in a climatologically aberrant year (May 1995) and vegetation in the home ranges was not at peak growth. Moreover, most measurements were made between 10.00 and 14.00 h to control for temporal variation, and it took us only about 2 h to complete all the field measurements on an array.

Spectrogram Correlation

This is the first time we are aware that spectrogram correlation has been used to describe the effects of the environment on signal transmission fidelity. Bioacoustic applications of spectrogram correlation were developed primarily by ornithologists to compare bird songs. Spectrogram correlation was used to study individual and sex differences (LESSELLS et al. 1995), to compare 'tutor tapes' with later crystallized bird song (CLARK et al. 1987; NELSON & MARLER 1994), and to sort and describe bird song units (THOMPSON et al. 1994).

We used spectrogram correlation to compare a sound, which has been broadcast some distance, to a reference sound. Previous quantitative techniques to compare sound spectrograms often relied on visual sorting or subjecting a series of temporal and spectral measurements to multivariate analyses (e.g. MARTINDALE 1980; CLARK 1982; SHACKELL et al. 1988; MITANI & BRANDT 1994). Results may in part be a function of the set of measured variables (MARTINDALE 1980; BROWN et al. 1995). Several techniques have been developed to compare or describe the overall 'shape' of spectrograms (e.g. BERTRAM 1970; MILLER 1979; PICKSTOCK et al. 1980; WILLIAMS 1993). Previous techniques have been tedious to calculate and none has been universally accepted by students of animal vocal communication. Furthermore, none has been applied to study how biological sounds change as they are transmitted through environments. Previous methods proposed to quantify overall change in sounds broadcast through the environment include GISH & MORTON's (1981) 'change index' and BROWN & WASER's (1988) 'distortion' method.

GISH & MORTON (1981) developed a technique to compare waveforms (not spectrograms) to quantify change in sounds transmitted through environments. By comparing the degree to which the shape of two amplitude traces of sounds recorded at various distances from a source differed, they generated a 'change index'. The technique has largely been ignored, but it and other work (e.g. BERTRAM 1970; MILLER 1979) was a precursor to bioacoustic applications of spectrogram correlation.

A more recent method to compare overall acoustic change required the calculation of two 'distortion' values: the first calculated in the temporal domain, the second calculated in the frequency domain (BROWN & WASER 1988; BROWN et al. 1995). Briefly, waveforms of sounds recorded at a certain distance from a source were 'averaged' (to remove background noise), the average waveforms were 'normalized' to a constant amplitude and then cross-correlated with a reference sound (one that experienced little or no degradation) to generate a distortion value in the temporal domain. Averaged spectral plots from sounds recorded at different distances were compared by subtracting the spectrum from a reference spectrum to calculate a distortion value in the frequency domain. Because these methods used averaged signals, effects of background noise were eliminated and a detailed study of

frequency-dependent attenuation was possible. However, these analyses were computationally intensive and required considerable time on a supercomputer. Moreover, the methods led to two distortion values that were not highly correlated (BROWN & WASER 1988).

There are some potential problems with, and particular characteristics of, spectrogram correlations and the algorithms used to correlate spectrograms that make them inappropriate for some uses. Moreover, the software user must select a variety of parameter values that may have potentially important ramifications. Our use of spectrogram correlation to quantify the combined effects of attenuation, degradation, and background noise avoided most of these problems.

One recognized problem of using spectrogram correlations to compare different sounds is that two identically shaped sounds at different frequencies may have little overlap and therefore a low correlation (CHARIF et al. 1993). For instance, if one were to correlate a hypothetical alarm call from a young and small marmot with an older and larger marmot, the calls may overlap little but otherwise have an identical shape. 'Two-dimensional' spectrogram cross-correlation (where spectrograms are shifted along both the temporal and frequency axis to locate the maximum overlap) would solve this problem. However, because we correlated a sound with itself after transmission, we did not need to use two-dimensional correlation: high correlations imply the sound changed little as it was transmitted across space, while low correlations imply relatively more change.

Spectrogram correlations can be influenced by the choice of clipping levels, spectrogram resolution, filter bandwidth, and other parameter values. Thus, the absolute correlations can only be compared with other correlations calculated identically. As suggested by CHARIF et al. (1993), we experimented with a variety of parameter values before selecting our final values. We used identical parameter values throughout. That the absolute value of the pure-tone spectrogram correlations were much higher than the alarm-call correlations was largely a function of filter bandwidth: greater bandwidth implies a greater opportunity for background noise to contaminate a recording. We felt this was a biologically reasonable assumption for the alarm-call correlations and selected a correspondingly wide filter bandwidth. For the pure tones, we wanted to study how that particular frequency was transmitted and consequently selected a narrow bandwidth.

Another potential limitation of correlations is that the coefficient has no probability value associated with it. This is particularly a problem when one wants to compare two sounds: a single correlation value alone is simply a comparison of two sounds. We avoided this potential pitfall by using the average of multiple replicates of the same exemplar broadcast in a marmot home range and testing for the significance of these averages.

Like other studies of signal production, spectrogram correlations tell us nothing about differential marmot perception. Spectrogram correlations simply quantify the relative amount that a sound has changed when traveling through space: identical values could result for sounds that changed different ways (see also BROWN et al. 1995). The exact nature of the change may or may not influence perceptual salience. If, for instance, marmots respond to any reasonably loud sound of a certain frequency and duration, then even heavily degraded alarm calls may have some perceptual salience. Presumably calls that were mostly attenuated would not have much salience. Nevertheless, playbacks of calls recorded from different distances are ultimately required to better understand their per-

ceptual salience (e.g. RICHARDS 1981; MCGREGOR & FALLS 1984; MCGREGOR & KREBS 1984).

Spectrogram correlation provides a relatively simple yet biologically salient way to describe the acoustic habitat. With reasonably good recording equipment and inexpensive microcomputers and software, any researcher can now more rigorously describe the acoustic habitat of their study organism. Quantifying how sounds change as they are transmitted through species' habitats will permit more quantitative studies of the relationship between the environment and the evolution of acoustic signals.

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Appendix

If slightly different exemplars have significantly different transmission properties, an experimental design should probably include multiple alarm-call exemplars. Using multiple exemplars would drastically increase the amount of time required for digitizing and editing signals and increase data analysis time (see also BROWN et al. 1995). To determine if subtly different acoustic variants are transmitted differently, we synthesized two yellow-bellied marmot alarm calls using SoundEdit (Fig. A1). Both sounds were identical in duration (0.06 s) and frequency bandwidth (2.4–3.6 kHz). Synthesizing them permitted us to match their amplitudes exactly. One sound resembled a yellow-bellied marmot alarm call that started and ended at approximately the same frequency (2.4 kHz) and peaked at 3.6 kHz; we refer to this as a 'normal' call. The other synthesized call began at a higher frequency than it ended (start 3.2 kHz, end 2.4 kHz) but peaked at the same frequency (3.6 kHz); we refer to this as a 'start-hi' call.

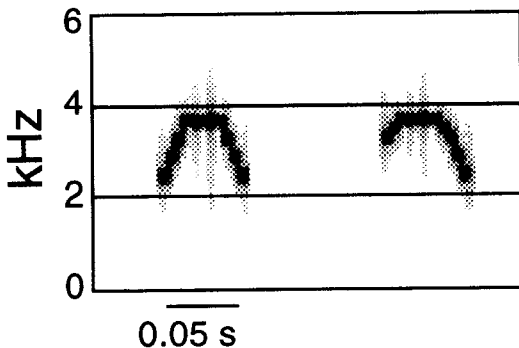


Fig. A1: Spectrograms (256 point SoundEdit) of the two synthesized alarm calls, the 'normal' alarm call, and the 'start-hi' alarm call

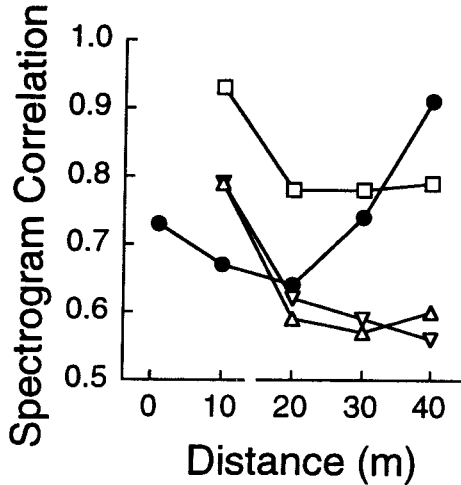


Fig. A2: Mean spectrogram correlations for the two synthesized alarm calls (∇ start-hi, \triangle normal) correlated against their own reference call (each call recorded at 1 m), and the correlation between the two calls at a given distance (\bullet). Correlations for the 3-kHz pure tone is given for reference (\square). In all cases, means were calculated from sounds recorded along 12 different recording transects

We played back and re-recorded the two synthesized alarm calls and a 3 kHz pure tone at 1, 10, 20, 30, and 40 m in eight different marmot home ranges at RMBL in Jul. 1995. Unlike the previous experiments, for this experiment we randomly located the 12 40-m recording transects (two large groups had two, and one very large group had three transects) within marmot home ranges across which we played back and re-recorded the three sounds. Spectrograms were generated using previously described parameters.

As before, we correlated spectrograms from each of the three sounds using that sound's 1 m spectrogram as a reference. Additionally, and for each distance (1, 10, 20, 30, and 40 m), we correlated spectrograms of the two different synthesized calls with each other. Thus, we correlated the 10 m recording of the start-hi call with the 10 m recording of the normal call, the 20 m recording of the start-hi call with the 20 m recording of the normal call, etc. We used two-way ANOVA to test if the 'normal \times start-hi' correlations differed from both the normal correlations and the start-hi correlations, after controlling for distance-induced variation in correlations.

The data show that the two synthesized alarm calls degraded similarly with distance (Fig. A2; Bonferroni/Dunn post-hoc $p = 0.920$, p -critical = 0.017) and became more alike (Bonferroni/Dunn post-hoc comparisons: 'normal' cf. 'normal \times start-hi' $p = 0.015$; 'start-hi' cf. 'normal \times start-hi' $p = 0.019$; p -critical = 0.017). The two synthesized alarm calls initially, at 1 m, had an average correlation of 0.73; at 40 m the average correlation increased to 0.91. That these two synthesized calls became more similar when re-recorded farther from the speaker raises two points: one analytical and one biological.

First, it suggests that using a single exemplar of an alarm call alarm-call type was an appropriate way to address our question about how a typical call type is transmitted through a species' habitat. The two different synthesized variants degraded similarly. Our question required us to make the best possible estimate of acoustic degradation. Given the plethora of factors that can influence transmission, we used a single exemplar to eliminate 'exemplar-related' variation. Other questions, such as studying transmission of different call types or studying individual or sex-related differences in call transmission, might require using multiple alarm call exemplars.

Second, a previous study of yellow-bellied marmot alarm communication found subtle micro-structural variation in the alarm call of the yellow-bellied marmot that co-varied with predator type (DAVIS 1991). Our results suggest that given the low transmission fidelity in yellow-bellied marmot habitats, perceivers might have difficulty distinguishing subtle differences in call structure from a distance. We believe that using spectrogram correlations to quantify habitat-induced signal degradation can be useful in defining the range of potentially salient acoustic variation. Ultimately, animals themselves will have to tell us what types of acoustic variants they find perceptually meaningful (e.g. NELSON & MARLER 1990).