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A test of the acoustic adaptation hypothesis in four species of marmots

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ABSTRACT

Acoustic signals must be transmitted from a signaller to a receiver during which time they become modified. The acoustic adaptation hypothesis suggests that selection should shape the structure of long-distance signals to maximize transmission through different habitats. A specific prediction of the acoustic adaptation hypothesis is that long-distance signals of animals in their native habitat are expected to change less during transmission than non-native signals within that habitat. This prediction was tested using the alarm calls of four species of marmots that live in acoustically different habitats and produce species-specific, long-distance alarm vocalizations: yellow-bellied marmot, *Marmota flaviventris*; Olympic marmot, *M. olympus*; hoary marmot, *M. caligata*; and woodchuck, *M. monax*. By doing so, we evaluated the relative importance the acoustic environment plays on selecting for divergent marmot alarm calls. Representative alarm calls of the four species were broadcast and rerecorded in each species' habitat at four distances from a source. Rerecorded, and therefore degraded alarm calls, were compared to undegraded calls using spectrogram correlation. If each species' alarm call was transmitted with less overall degradation in its own environment, a significant interaction between species' habitat and species' call type would be expected. Transmission fidelity at each of four distances was treated as a multivariate response and differences among habitat and call type were tested in a two-way MANOVA. Although significant overall differences in the transmission properties of the habitats were found, and significant overall differences in the transmission properties of the call types were found, there was no significant interaction between habitat and call type. Thus, the evidence did not support the acoustic adaptation hypothesis for these marmot species. Factors other than maximizing long-distance transmission through the environment may be important in the evolution of species-specific marmot alarm calls.

Animal communication requires signals to be transmitted from a signaller to a receiver. 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; Dusenbery 1992; Endler 1992; Forrest 1994). Thus, we might expect selection to modify the structure of long-distance acoustic signals to maximize their transmission in different habitats (the acoustic adaptation hypothesis: Morton 1975; Hansen 1979; Rothstein & Fleischer 1987).

A detailed review of bioacoustics can be found elsewhere (e.g. Bradbury & Vehrencamp 1998). Briefly, attenuation due to spherical spreading will affect all signals generated from a point source with an expected decrease of 6 dB per doubling of distance. Additional attenuation of a signal will result from temperature- and humidity-dependent molecular absorption, as well as from scattering, reflection, diffraction and refraction of sound in directions away from the receiver. In addition to attenuation, signals may degrade in at least three ways (see Morton 1986 for definition of degradation). First, frequency-dependent attenuation may change a signal's overall structure when some frequencies attenuate more rapidly than other frequencies within a signal. Second, reverberation may blur together components of a signal which experience different path lengths and thereby change a signal's overall structure. Reverberation is caused by reflected, refracted, diffracted or scattered portions of a signal later re-entering the main beam of sound propagation. Third, irregular amplitude fluctuations change the internal amplitude patterns of a signal. Specifically, heterogeneoustemperature and wind gradients differentially refract sound waves.

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The acoustic adaptation hypothesis assumes that structural differences between habitats will influence sound transmission (Morton 1975). For example, analyses of pure tones broadcast through open and forested areas have confirmed that sounds in forests are affected more by reverberation from leaves and tree trunks than those in open areas (Richards & Wiley 1980; Waser & Brown 1986). Sound transmission in open areas is predicted to be affected more by irregular amplitude fluctuations than that in forests due to a greater amount of air turbulence (Wiley & Richards 1978; Richards & Wiley 1980).

The acoustic adaptation hypothesis predicts that certain types of vocalizations will transmit with less overall degradation than others in a given environment (Morton 1975). Specifically, tonal whistles are predicted to minimize degradation in reverberant habitats, whereas rapid repetition of trill-like elements is predicted to minimize degradation in the face of irregular amplitude fluctuations (Wiley & Richards, 1978; Brown & Handford 1996). The best support for this hypothesis comes from the association of bird song structure with the general habitat (forested versus open areas) in which it is produced (Chappuis 1971; Morton 1975; Nottebohm 1975; Ryan & Brenowitz 1985; Sorjonen 1986b; Handford 1988; Wiley 1991). Tonal whistles are significantly more likely to be sung by birds occupying forests, whereas rapid amplitude and frequency modulated trills are more likely to be used by birds inhabiting open areas. Recent computer simulation results verify the effects of reverberation and amplitude fluctuation on signal structure (Brown & Handford 1996).

Transmitting vocalizations through native versus foreign habitats provides another way to assess the relative importance of the acoustic environment as a selective force upon signal design (Hunter & Krebs 1979; Gish & Morton 1981; Ryan et al. 1990; Brown et al. 1995). Each naturally occurring vocalization will potentially experience a unique combination of degradational effects characteristic of its native habitat. The acoustic adaptation hypothesis predicts that a long-distance vocalization should transmit with less attenuation and degradation through its native habitat than other non-native vocalizations within that same habitat, where non-native vocalizations come from either geographical variants of the same species or closely related species. In other words, if no other selective pressures other than the acoustic environment are present, and a vocalization is fully designed to maximize transmission distance, then no other vocalization type should transmit with less attenuation and degradation than the native signal. This prediction assumes that signals are intended for long-distance communication, that receivers benefit from an intact signal, and that selection has indeed occurred to reduce attenuation and degradation for these vocalizations.

Comparing transmission fidelity in native versus foreign habitats is particularly appropriate for examining divergence between vocalizations of closely related species (Sorjonen 1986a; Fotheringham et al. 1997), or between populations of one species (Hunter & Krebs 1979; Gish & Morton 1981). Presumably, there could always be some sound, drawn from all possible sounds, that will transmit with less attenuation and degradation than a native vocalization in a habitat. Restricting the set of possible non-native vocalizations to closely related species, or geographical variants of the same species, should minimize but not completely eliminate this problem.

Marmots are large ground-dwelling squirrels (Order: Rodentia; Family: Sciuridae; Genus: *Marmota*, ca. 14 species) that possess a wide variety of species-specific alarm calls and inhabit a number of different habitats (Barash 1989; Bibikow 1996; Nikol'skii 1996). Marmots generally inhabit open meadow-like areas but use forest edge zones where they exist. The type of terrain varies by the degree of vertical relief, the vegetation type and height, and by the percentage of the area covered by either lush meadow-like vegetation, trees, boulder fields, talus slopes or permanent snow. Background noise differs to some degree between species' habitats: not all species live near running water, and each species is exposed to a unique combination of heterospecific vocalizations. Sound transmission differed between the habitats of three marmot species; specifically, 3-kHz pure tones, representing the approximate dominant frequency of most marmot alarm calls, degraded differently between species' habitats (Blumstein & Daniel 1997). Thus, marmots live in quantifiably different acoustic environments.

Selection by the acoustic environment might potentially play a role in the divergence of species-specific marmot alarm calls. Marmot alarm calls presumably function as long-distance signals either to warn conspecifics or to discourage predators from continuing their attack (Klump & Shalter 1984; Blumstein et al. 1997). Given that marmot alarm calls work over long distances, and that differences exist between the species' acoustic environments, then divergence between species-specific call structures could function to maximize transmission distance within each species' respective environment.

Previous studies examining the influence of the environment upon marmot alarm calls for several Eurasian species found that alarm-calling rate was associated with a habitat's relative topographical relief, where relief was used as a metric of relative sight line distance (Nikol'skii 1984; Nikol'skii 1994, 1996). Although the spectral (frequency) characteristics of these alarm calls are species-specific, marmots inhabiting the most mountainous environments (high relief with limited visibility) called with characteristically faster rates than species living in less mountainous (medium relief) habitats. Marmot species inhabiting the steppe (low relief with high visibility) called at the slowest rates. This association held for both inter- and intraspecific differences in calling rate. In contrast to Nikol'skii's work, we focus on overall call structure and try to understand variation in spectral characteristics.

We test the acoustic adaptation hypothesis in four species of marmots: the yellow-bellied marmot, *Marmota flaviventris*, the Olympic marmot, *M. olympus*, the hoary marmot, *M. caligata*, and the woodchuck, *M. monax*. We broadcast alarm calls of the four species in each of their habitats and compared the transmission fidelity of the calls (overall call degradation) when broadcast through native and foreign habitats. We predicted that if selection by the acoustic environment played an important role in the divergence of these alarm calls, then the call of each species should transmit with less degradation than any of the calls of the other three species within its native habitat. We therefore predicted a significant interaction between species' habitat and species' alarm call type.

METHODS

Study Sites

We broadcast calls in yellow-bellied marmot habitat at Grand Coulee National Recreation Area, Washington, at sites near the Fort Spokane Visitor Center (47°54′ N, 118°18′ W; elevation: 400–450 m) on 30 and 31 May 1996. Yellow-bellied marmots inhabit a variety of habitats ranging from alpine and subalpine meadows to riparian high desert habitats (Frase & Hoffmann 1980). The Grand Coulee National Recreation Area is typical of high desert habitat and is remarkably similar to yellow-bellied marmot habitat on the front range of the Rocky Mountains. The area is composed of relatively dry grassy meadows bordered by stands of ponderosa pine, *Pinus ponderosa*. Vegetation averaged between 0.15 and 0.20 m high, with scattered sages that were up to 0.40 m high. Wind, bird song and calling insects provided substantial background noise. For this species' habitat, and all subsequent species' habitats, we attempted to broadcast calls when transient background noise was at a minimum.

We broadcast calls in Olympic marmot habitat on Hurricane Ridge in Olympic National Park, Washington (47°58′ N, 123°33′ W; elevation: 1500–1750 m) on 19 and 20 June 1996. Olympic marmots are an endemic species found exclusively in subalpine and alpine regions of the Olympic Peninsula (Barash 1973). Sites studied were typical Olympic marmot habitat: subalpine meadow surrounded by small stands of subalpine fir, *Abies lasiocarpa*. Meadow vegetation height was between 0.05 and 0.15 m on average (see Barash 1973 for more complete description of vegetation composition). The sites studied did not contain flowing water or water-related noise. Background noise included bird song and wind.

We broadcast calls in hoary marmot habitat around the Sunrise Visitor Center in Mt Rainier National Park, Washington (46°55′ N, 121°40′ W; elevation: 1900–2200 m) on 23 and 24 July 1996. Hoary marmots typically inhabit high elevation, or high latitude, alpine habitats characterized by rocky outcrops and talus slopes (Barash 1989). The sites that we studied comprised a combination of subalpine meadow, talus slopes, cliffs and krummholz vegetation. Meadow vegetation was composed of lush grasses and alpine wildflowers averaging between 0.05 and 0.30 m in height. Rushing water, wind and bird song provided background noise. At the time of the study, one of the sites was partially snow-covered.

We broadcast calls in woodchuck habitat near Lawrence, Kansas (38°58′ N, 95°14′ W; elevation: 250 m) on 5 and 7 September 1996. Sites were located near Perry and Lone Star lakes. Woodchucks typically inhabit low-elevation, forest edge habitats within riparian areas of deciduous woodland (Barash 1989). The vegetation height at our sites averaged between 0.20 and 0.40 m near the ground. All sites were composed of a combination of both open field and wooded areas, which is typical of woodchuck forest edge habitat. A myriad of calling insects, birds and wind provided abundant background noise.

Acoustic Stimuli

Pure tones

We synthesized 0.5-s pure tones at 2, 3 and 4 kHz using SoundEdit software (MacroMind-Paracomp Inc. 1990) to provide standardized nonalarm call stimuli to compare the differences in transmission properties among habitats. Frequencies of 2, 3 and 4 kHz approximate the range of fundamental frequencies of the alarm calls used by the four marmot species. The alarm calls we used varied between 0.05 and 1.5 s in duration. We used pure tones of 0.5 s because this duration represented a rough average of the particular alarm calls broadcast.

Alarm calls

Marmots produce a variety of alarm calls ranging from tonal whistles to raspy chirps. Some species possess only one call type, whereas other species possess several call types (Blumstein & Armitage 1997b). For example, the woodchuck has one call type: a two-part call composed of a loud whistle followed by a series of rapidly repeated trill-like notes (Lloyd 1972). The yellow-bellied marmot has two call types: one call is a single, short, loud whistle and the other call is a multinote trill (Waring 1966; Blumstein & Armitage 1997a). Both hoary and Olympic marmots produce four call types that include flat, ascending, and descending calls, and multinote trills (Barash 1973; Taulman 1977; D. T. Blumstein, unpublished data). Each species, except for perhaps the woodchuck, repeat their alarm calls at various rates (in >100 h studying woodchucks, D. T. Blumstein did not hear a single woodchuck vocalization).

For this study, we broadcast two hoary marmot alarm call types (flat and ascending), two Olympic marmot alarm call types (flat and ascending), one yellow-bellied marmot alarm call type (single whistle), and a woodchuck alarm call (Fig. 1). The hoary flat call, the Olympic flat call, and the yellow-bellied whistle are the most frequently used call types of each marmot species (Blumstein & Armitage 1997a; D. T. Blumstein, unpublished data). Hoary and Olympic ascending calls are less commonly uttered but none the less represent an integral part of both species' repertoires (D. T. Blumstein, unpublished data). Not much is known about the woodchuck's calling behaviour; it is possible that the initial whistle in the two-part call is also used independently of the second trill-like part.

Because there may be some individual variation in alarm call structure (Blumstein & Armitage 1997a), and

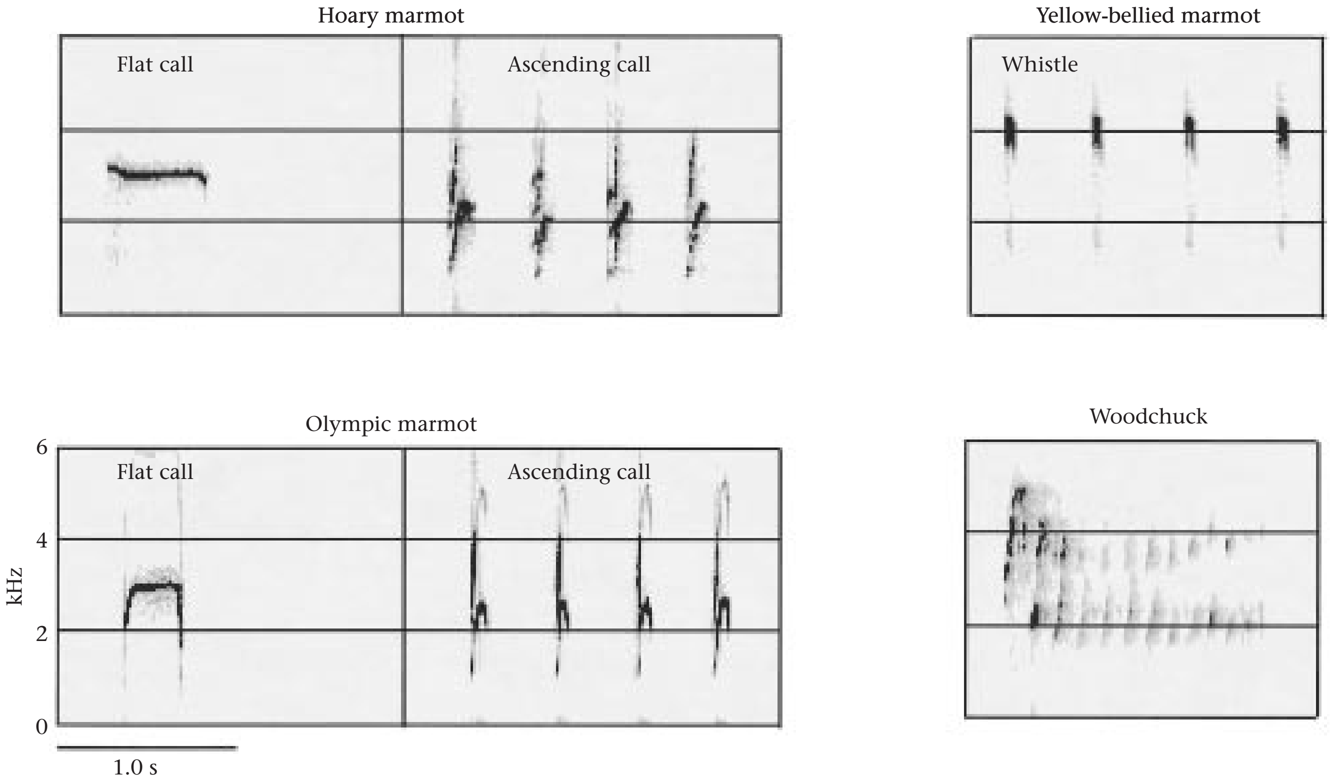

Figure 1. Sound spectrograms (256 point SoundEdit) of the alarm calls of the four species of marmots used in this study. Only one exemplar of each call type is shown.

because we wanted to be able to generalize to the call type (McGregor et al. 1992), we broadcast two exemplars of each call type. The number of exemplars of each call type was limited by the availability of high-quality recordings while designing the study. The two exemplars of the woodchuck call, the yellow-bellied whistle and the Olympic flat call were recorded from different individuals. The exemplars of the hoary flat call, the hoary ascending call and the Olympic ascending call were recorded from the same individual calling at different times. We obtained high-quality marmot alarm call recordings from sound libraries and personal collections (details in Daniel 1998).

All alarm calls were prefiltered to prevent aliasing (the appearance of spurious frequencies due to a low sampling rate during 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. The fundamental frequencies of these marmot alarm calls vary between 1.0 and 4.5 kHz. We removed ambient noise and overtones by filtering all calls with a 5-pole Butterworth bandpass filter (1.0–4.5 kHz) using Signalize software (Keller 1992).

For each alarm call exemplar, we created a 2-s stimulus. Because the hoary flat call, Olympic flat call and woodchuck call have relatively long durations and are generally repeated at a slow rate, we included only a single vocalization per 2-s interval; the remainder of each 2-s interval contained silence. Because the yellow-bellied whistle, hoary ascending call and Olympic ascending call are relatively short in duration and may be repeated at a fast rate, we included four identical vocalizations of each call type within the 2-s interval. Each pure tone included only one tone per 2-s interval.

Stimulus Transmission

Yellow-bellied, Olympic and hoary marmots live in obvious social groups, whereas woodchucks are generally solitary (Blumstein & Armitage 1997b). Average home range size occupied by a group (or a single individual in the case of woodchucks) varies between and within species (Barash 1973; Holmes 1979; Ferron & Ouellet 1989; Armitage 1988). For each species, we broadcast all alarm calls through the habitat of three social groups to quantify transmission fidelity. For each social group, we sampled nine locations. The nine locations were chosen to include the most frequently used areas within the home ranges of marmots. As described in more detail in a previous study, we chose a main sleeping burrow as the centre of each recording array set-up around that burrow (Blumstein & Daniel 1997). The recording array comprised four 100-m lines extending in each of four perpendicular directions from the main burrow. The orientation of the recording array around the main burrow was chosen randomly. We broadcast pure tones and alarm calls from the main burrow, and from eight additional locations at the 50-m and 100-m points along each of the four perpendicular lines. The direction of broadcast at each of these nine locations was chosen randomly (see figure 2 in Blumstein & Daniel 1997). At each broadcast location, we rerecorded pure tones and alarm calls at 1 m (the reference distance: see Acoustical Analysis), 10 m, 20 m, 30 m and 40 m (the experimental distances). Natural marmot alarm calls can usually be heard at distances greater than 40 m; however, we recorded no further than 40 m to ensure a sufficient signal-to-noise ratio for subsequent digital analysis.

Inaccessible terrain, such as a cliff or large body of water, occasionally prevented us from broadcasting and rerecording at all nine locations per group. Because at least six broadcast locations were available per group, we randomly chose six of the nine broadcast locations from the three social groups of each species' habitat (N=18 broadcast locations per habitat) for subsequent analysis.

We broadcast the pure tones and alarm calls from a Macintosh PowerBook 100 through a Sony SRS-77G-powered directional speaker situated 0.3 m above the ground (which corresponded roughly to the height of a marmot rearing up bipedally on its hind legs and calling). The speaker had a relatively flat frequency response from 2 to 4 kHz. We adjusted the sound pressure level of the pure tones and alarm calls so that the output was 90.6 ± 2.7 dB at 1 m with a SPER Scientific 840029 digital sound metre (accuracy ± 0.7 dB; weighting=A, peak response). While this sound pressure level was slightly less than that uttered by most calling marmots, we used it to minimize distortion of the broadcast calls. Sounds were rerecorded onto high-bias cassette tape using a Sennheiser directional microphone (ME-88) encased in a 'blimp' windscreen and a high-quality cassette tape recorder (Sony TC-D5M). Fresh alkaline batteries were used at each recording session (each group) to minimize fluctuations in tape speed between groups. 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 marmot's ears when it is standing quadrupedally and foraging).

Acoustical Analysis

We digitized pure tones and alarm calls rerecorded at each broadcast location. All sounds were prefiltered to prevent aliasing and were then sampled at 22 kHz using a MacRecorder 8-bit AD/DA board and SoundEdit software. Each pure tone and alarm call exemplar was edited into a separate 2-s sound file for subsequent analysis.

Using Canary (Charif et al. 1995), we calculated normalized spectrogram correlations between the sounds recorded at the reference distance of 1 m and the experimental distances of 10, 20, 30 and 40 m. Normalized spectrogram correlation compares the overall two-dimensional shape of two spectrograms (frequency × time) but ignores amplitude differences between the two sounds being compared. Two spectrograms are shifted along their temporal axis until a peak correlation value is reached. The peak correlation value represents the maximum overall similarity between the two sounds. Normalized spectrogram correlations range from 0 (no similarity) to 1.0 (identical sounds). If two sounds are identical except for their relative amplitude, the peak correlation value would be 1.0 (see Charif et al. 1995).

We generated 'boxy' sound spectrograms using 256-point short-time Fourier transformation (50% overlap), a Hamming window and a − 110-dB clipping level (Charif et al. 1995). We set the filter bandwidth to 1.0–4.5 kHz for the pure tones and alarm calls as this range of frequencies encompasses the frequency bandwidth used by the marmots studied. Differences in spectrogram parameters affect the absolute correlation values obtained. Thus, absolute correlation values may be directly compared only when all parameters are identical (see Khanna et al. 1997). In a previous study we used slightly different parameters to make spectrograms of the 3-kHz pure tones: 0% overlap, and a filter bandwidth of 2.9–3.1 kHz, and therefore results are not exactly comparable (Blumstein & Daniel 1997).

Statistical Analyses

Pure tones

We examined differences in pure tone transmission within the four species' habitats using the following two-way MANOVA:

$$y_{10}, y_{20}, y_{30}, y_{40}=h+f+h*f+\varepsilon, \qquad (1)$$

where y_{10}, y_{20}, y_{30}, y_{40} are the spectrogram correlation values at 10, 20, 30 and 40 m from the speaker, h is the habitat, f is the frequency of the pure tone, $h*f$ is the interaction between habitat and frequency, and ε is the error. This and other MANOVA models were fitted using PROC GLM in SAS (SAS Institute 1990).

A previous study (Blumstein & Daniel 1997) reported significant, but relatively weak effects of marmot social groups upon degradation of 3-kHz pure tones. Thus, there was slight intraspecific variation (among social groups) in transmission fidelity. Because intraspecific variation was minimal, we ignored intraspecific variation for this and subsequent MANOVA analyses, and treated each broadcast location (N=18) as an independent sampling unit to describe the species habitat.

We report the strength of association for each MANOVA effect as η^2 ('eta-squared'), which is calculated by subtracting Wilk's λ from 1.0. Because the sum of η^2s for all effects in a MANOVA may be greater than 1.0, η^2 does not necessarily reflect the true proportion of variance accounted for by each effect; rather, we interpret η^2 to be a measure of the relative importance of each effect (Tabachnick & Fidell 1996). We report significance at the 5% level for all MANOVA effects.

We calculated multivariate post hoc comparisons with Hotelling's T^2 tests (using the CANDISC procedure of SAS). We adjusted for multiple comparisons using a sequential Bonferroni procedure after setting our experimentwise significance level at 5% (Rice 1989).

Alarm calls

The acoustic adaptation hypothesis predicts a significant interaction between the habitat and the call type for the following two-way MANOVA:

$$y_{10}, y_{20}, y_{30}, y_{40}=h+c+h*c+\varepsilon, \tag{2}$$

where y_{10}, y_{20}, y_{30}, y_{40} are the spectrogram correlation values at 10, 20, 30 and 40 m from the speaker, h is the habitat, c is the call type, $h*c$ is the interaction between habitat and call type, and ε is the error.

We broadcast two exemplars of each call type at every location. Because the spectrogram correlation values obtained for the two exemplars at every location were paired observations, we tested for exemplar-specific differences with a Wilcoxon signed-ranks test, using StatView 4.0 (Abacus Concepts 1993). These comparisons were made for each of the four distances separately across all habitats (N=72 comparisons per distance for each call type). Exemplars differed significantly in degradation from one another (P<0.005). Because the goal of the study was to test for differences between species and not to study exemplar-specific variation per se (McGregor et al. 1992), we averaged the two exemplar values at each distance at a broadcast location for this and all subsequent analyses.

Residuals from this and the previous MANOVA were not normally distributed (Wilk–Shapiro: W=0.786 for alarm calls, P<0.05; W=0.570 for pure tones, P<0.05). Additionally, the variance-covariance matrices were not homogeneous (Bartlett's likelihood ratio: χ^2_{230}=711.4, P<0.05, for alarm calls; χ^2_{110}=321.6, P<0.05, for pure tones). A variety of transformations did not substantially improve residual distribution, nor did they modify our results or conclusions. We therefore report results based on untransformed data.

We calculated multivariate post hoc comparisons with Hotelling's T^2 tests, and adjusted results for multiple comparisons.

RESULTS

Pure Tones

Results of the two-way MANOVA indicate that there was a significant habitat effect (approximate $F_{12,524}$=7.11, P<0.0001) and a significant frequency effect (approximate $F_{8,396}$=2.20, P=0.03) for the three pure tones, with habitat having a larger effect (η^2=0.33) than frequency (η^2=0.08). The overall interaction term was not significant (η^2=0.05, approximate $F_{24,692}$=0.45, P=0.99). Thus, although some habitats may transmit all three frequencies with less degradation than other habitats, and some of the frequencies may transmit with less degradation than other frequencies within any habitat, habitats do not differentially transmit one frequency with less degradation than another frequency.

There was no difference in pure tone transmission fidelity between the hoary marmot and woodchuck habitats, and there was no difference in pure tone transmission fidelity between the Olympic marmot and yellow-bellied marmot habitats (Fig. 2). However, after correcting for multiple comparisons, there was a tendency (some comparisons were significant, whereas others were not) for the two groups to differ from one another in pure tone transmission (Fig. 2). Post hoc

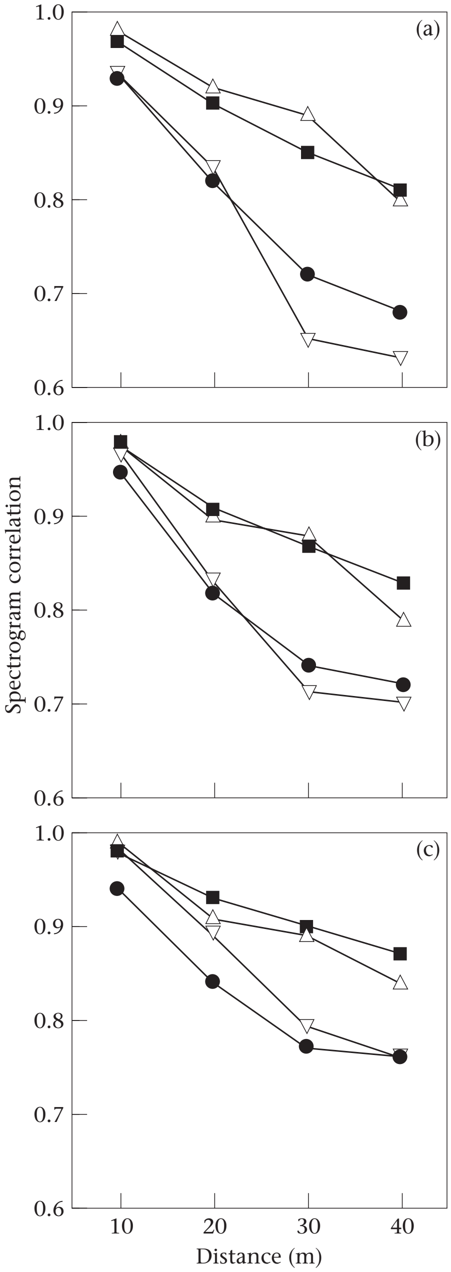

Figure 2. Average normalized spectrogram correlations of (a) 2-kHz, (b) 3-kHz and (c) 4-kHz pure tones as a function of transmission distance for the four species' habitats. Post hoc comparisons between habitats (■: hoary; △: woodchuck; ●: Olympic; ▽: yellow-bellied) which, after correction for multiple comparisons, were significant at the 5% experimentwise level are as follows: 2-kHz pure tone: hoary and Olympic, hoary and yellow-bellied, woodchuck and Olympic, woodchuck and yellow-bellied; 3-kHz pure tone: woodchuck and yellow-bellied. All other comparisons between habitats were statistically indistinguishable.

comparisons significant at the experimentwise 5% level are specified in the figure legend (Fig. 2).

Differences in overall degradation between the three frequencies in any given habitat appeared to be minimal. Across all habitats, the 4-kHz pure tone generally tended to transmit with less overall degradation than the 3-kHz pure tone, whereas the 2-kHz pure tone generally tended to transmit with the most overall degradation; however, most of these comparisons were not significant.

Alarm Calls

The results of the two-way MANOVA examining the effects of habitat, call type and the interaction between habitat and call type, indicated that the overall interaction term was not significant ($\eta^2=0.08$, approximate $F_{60,1560}=0.56$, $P=0.99$). The effects of both habitat and call type were significant with call type having a substantially larger effect ($\eta^2=0.80$, approximate $F_{20,1324}=40.72$, $P<0.0001$) than habitat ($\eta^2=0.31$, approximate $F_{12,1056}=13.00$, $P<0.0001$). The acoustic adaptation hypothesis predicts a significant interaction effect between species' habitat and species' call type. The lack of a significant interaction indicates that habitats do not differentially transmit one call type with less overall degradation than another call type.

Consistent with a significant call type effect in the absence of a significant interaction effect, call types tended to maintain their relative rankings across all habitats (see Fig. 3; particularly at 30 and 40 m). A significant habitat effect in the absence of a significant interaction effect indicates that some habitats generally transmit calls with less degradation than other habitats (see Fig. 3).

Native call types did not transmit with less overall degradation than foreign call types within a given habitat (Fig. 4). Post hoc comparisons indicated that the woodchuck and hoary ascending calls both degraded significantly more than all other call types in their respective habitats. The Olympic ascending call degraded significantly more than the yellow-bellied call and its counterpart, the Olympic flat call in its native Olympic habitat, but degraded significantly less than the hoary ascending and woodchuck calls in the Olympic habitat. Although both the hoary flat and Olympic flat calls transmitted with relatively little degradation in their own habitats, neither were statistically distinguishable from several other call types that transmitted with comparable degradation in these habitats, such as the yellow-bellied whistle, the Olympic ascending call, and either the Olympic flat or hoary flat calls. Only the yellow-bellied whistle degraded significantly less than most other call types in its native habitat.

DISCUSSION

We found no evidence to support the acoustic adaptation hypothesis in these four marmot species. The interaction effect between species' habitat and species' call type was not significant (Fig. 3). Some species' habitats transmitted all calls with less overall degradation than other species' habitats (Fig. 3), whereas some calls consistently transmitted with less degradation than other calls regardless of habitat (Fig. 3). In general, native call types did not transmit with less degradation than foreign call types within a given habitat (Fig. 4).

We measured call degradation by calculating normalized spectrogram correlations. Normalized spectrogram correlations enabled us to describe the overall change (overall degradation) in the structure of the calls as they were transmitted over distance, but did not allow us to make comparisons of the specific parameters of degradation (reverberation, irregular amplitude fluctuations, frequency-dependent degradation) between habitats. Thus, a similar spectrogram correlation value indicates a similar amount of overall degradation between two calls, but it does not specify parameter-specific degradation; two calls degraded in very different ways may have the same correlation value (Khanna et al. 1997). We assumed that as calls degrade, they become less interpretable by marmots regardless of the specific features resulting in the overall structural change. It is possible that the results of Canary's correlation test may not represent 'degradation' as perceived by marmots. For example, marmots may cue exclusively on a particular feature of a call. Ultimately, we need more information on marmot perceptual abilities to evaluate this assumption.

In addition to degradation, overall alarm call attenuation may be important for marmot signal detection and discrimination (Blumstein 1998). We did not directly measure how alarm calls attenuated with distance but additional analyses measuring pure tone attenuation found no differences in frequency-dependent attenuation for 2-, 3- and 4-kHz pure tones broadcast through different habitats (Daniel 1998). This result suggests (but does not preclude) that overall attenuation of alarm calls does not vary among these four habitats. We therefore infer that degradation (rather than overall attenuation) is the parameter of interest. Playback experiments examining distance perception in songbirds have shown that territorial males discriminate between undegraded and degraded songs broadcast at the same amplitude (reviewed in McGregor 1994). To determine whether such degradation is perceptually salient to marmots, similar playback studies need to be conducted with marmots.

Both alarm call and pure tone degradation is influenced by habitat (see MANOVA results). There is thus a potential for the acoustic environment to select for divergent call structure between species. None the less, post hoc comparisons of pure tone and alarm call degradation between the four species' habitats indicated that differences between several of these habitats were not significant. Neither the Olympic and yellow-bellied habitats, nor the hoary and woodchuck habitats, differed significantly from one another in transmission of the three pure tones, nor for most alarm call types (except for the hoary ascending call). Thus, differences in transmission properties between several species' habitats may not be

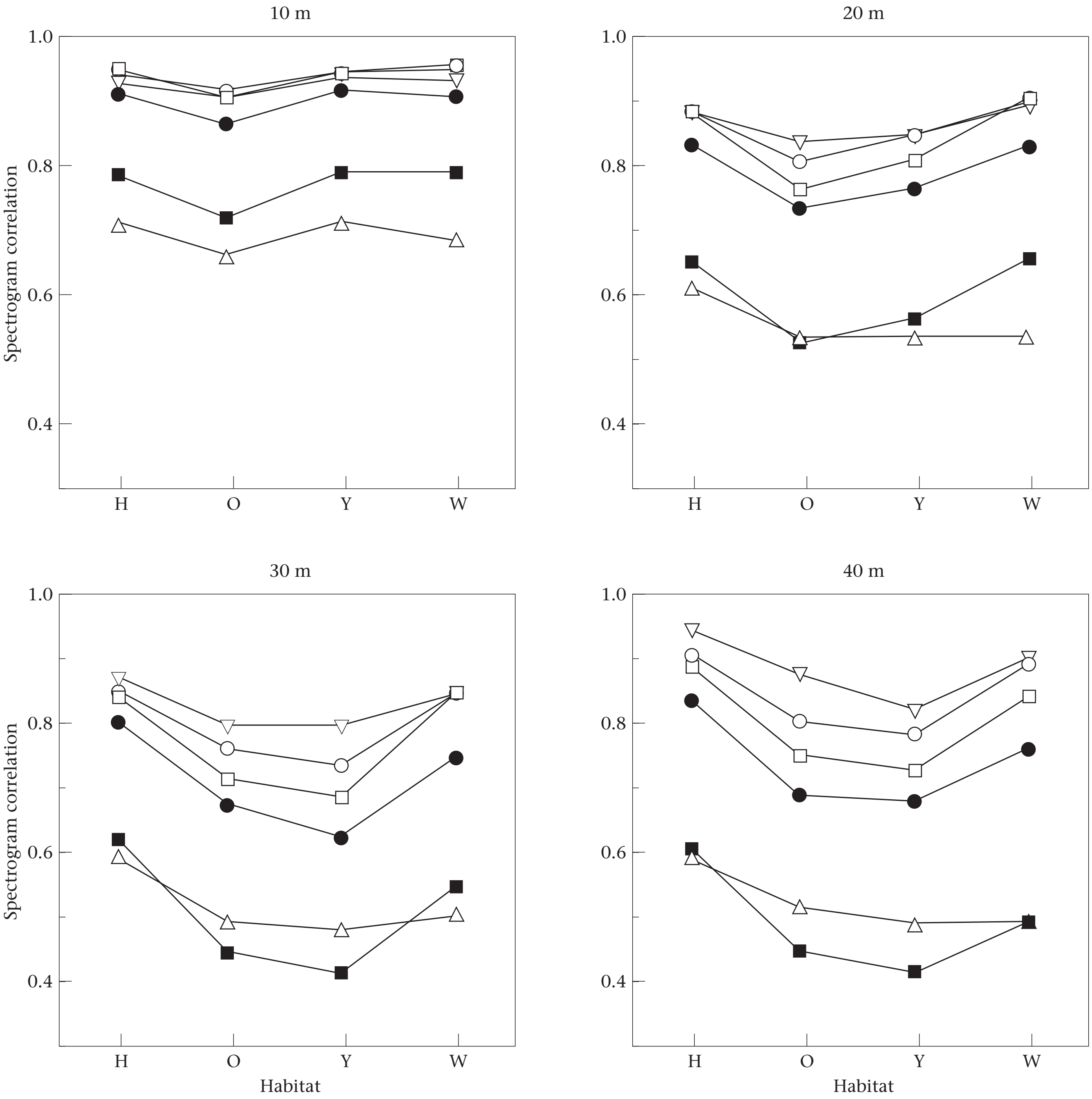

Figure 3. Average normalized spectrogram correlations for the six call types in the four species' habitats (hoary: habitat (H), flat call (□), ascending call (■); Olympic: habitat (O), flat call (○), ascending call (●); woodchuck: habitat (W), call (△); yellow-bellied: habitat (Y), call (▽)) at 10, 20, 30 and 40 m. The two exemplars of each call type are averaged for this figure, and for all subsequent figures. This figure graphically illustrates the MANOVA results. There was no interaction between call type and habitat (approximate $F_{60,1560}$=0.56, P=0.997). In general, some habitats transmitted calls with less overall degradation than other habitats, and call types maintained their relative rankings regardless of habitat.

sufficiently large to effectively select for differences in call structure.

Where habitat differences tend to exist between species, habitat differences do not necessarily parallel the acoustic variation seen between the respective species' call structures. For example, the hoary and Olympic calls are acoustically very similar (Fig. 1), but occur in habitats that tend to differ in the transmission of the three pure tones and most alarm calls (Figs 2 and 3). Acoustically more distinctive calls, such as the woodchuck call and the hoary flat call (Fig. 1), come from habitats with statistically indistinguishable transmission qualities (Figs 2 and 3). Thus, factors other than the acoustic environment must play a role in the evolution of species-specific alarm calls.

Marmots could be communicating directly to predators to discourage attack (Klump & Shalter 1984).

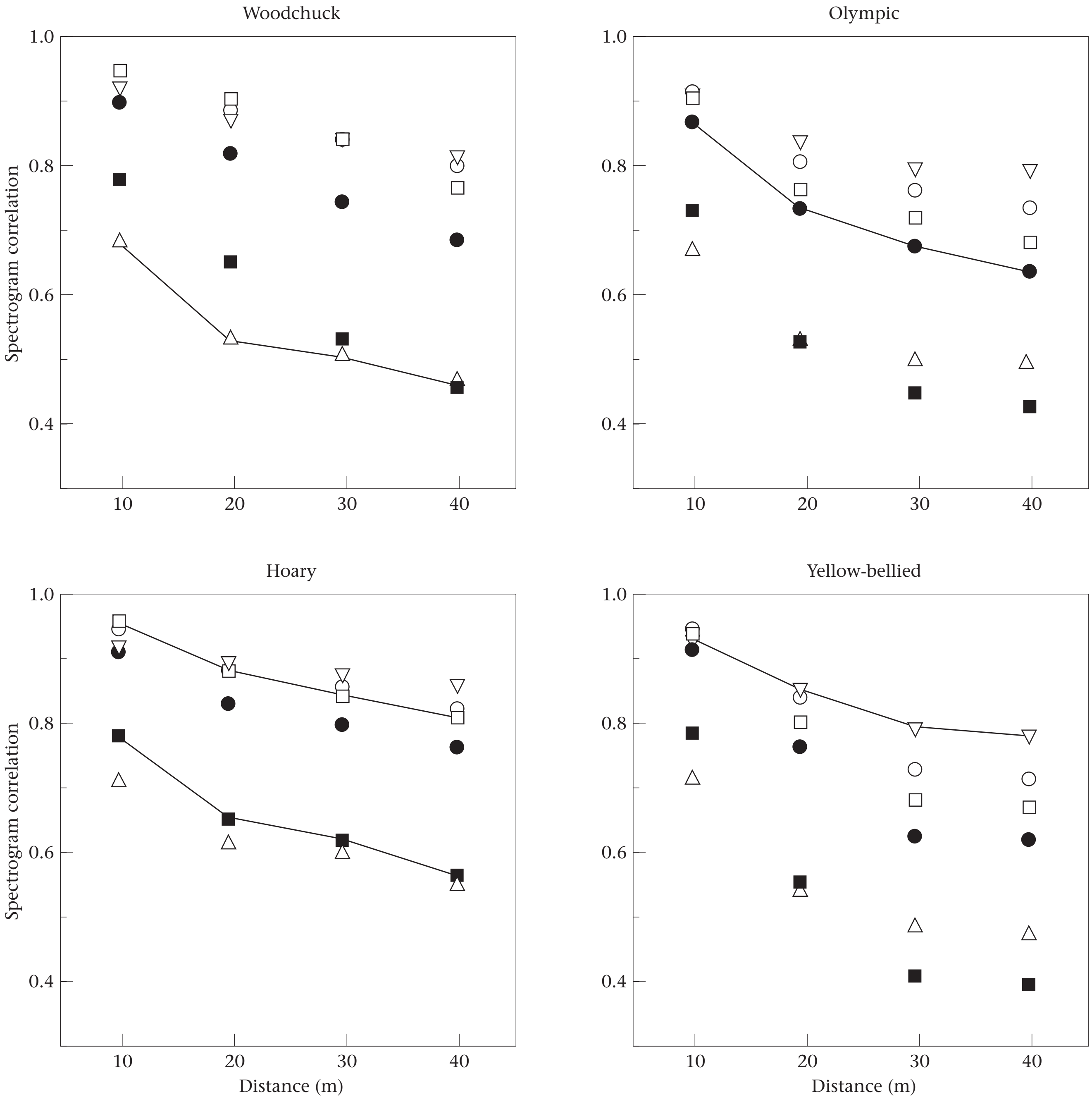

Figure 4. Average normalized spectrogram correlations of the six call types (symbol designation as in Fig. 3) as a function of distance in each of the four habitats. Call types broadcast through native habitats are connected with lines. Call types did not necessarily transmit with less overall degradation in their native habitats compared with foreign call types. See Results for post hoc comparisons significant at the 5% experimentwise level.

Alternatively, marmot alarm calls could be structured to avoid detection and localization by predators (Marler 1955, 1957). For either case, certain call structures might be better suited for the perceptual capacities of one predator type rather than another (Marler 1955, 1957). If differences exist between species with respect to these predator interactions, then divergence between call types could result. In general, these questions have not yet been rigorously examined. However, these four species of marmots are probably exposed to similar predator types (D. T. Blumstein, unpublished data), which suggests (but does not preclude) that species-specific predator interactions are an unlikely explanation for alarm call divergence in marmots.

Marmot alarm calls could be structured to transmit over biologically relevant distances that reflect the spatial distribution of populations (Tubaro & Segura 1994; Fotheringham et al. 1997). Marmots live in social groups that vary in home range size. Of these four species, the hoary marmot has the largest home range size (Holmes

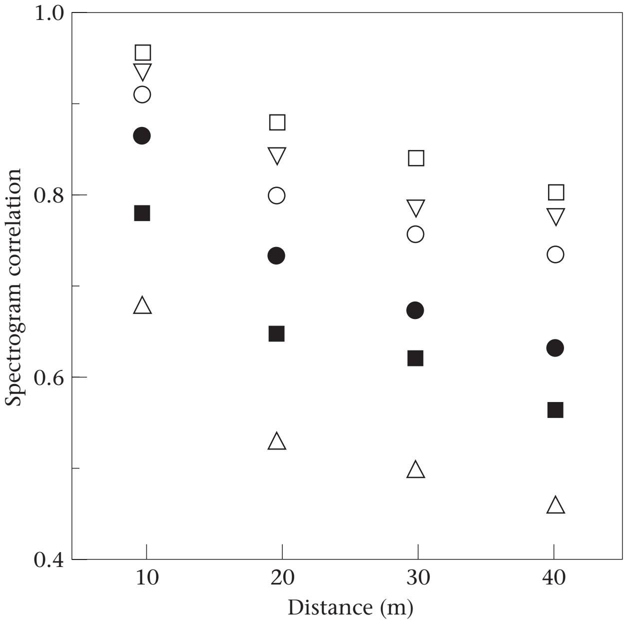

Figure 5. Average normalized spectrogram correlations of the six call types (symbol designation as in Fig. 3) broadcast through native habitat as a function of distance. Post hoc tests found that the woodchuck call transmitted with significantly greater degradation over distance than all other calls. Transmission fidelity of the hoary flat call, the yellow-bellied whistle and the Olympic flat call were statistically indistinguishable.

1979), followed by the Olympic marmot (Barash 1973), the yellow-bellied marmot (Armitage 1975, 1988), and the woodchuck (Ferron & Ouellet 1989). Species with relatively large home ranges may structure their calls to communicate over larger distances than the calls of species with smaller home ranges. Our data do not support this hypothesis. The transmission fidelity of the hoary flat call, the yellow-bellied whistle, and the Olympic flat call broadcast through native habitat were not statistically distinguishable from each other (Fig. 5). A rank correlation between each species' home range size and the relative degradation of each species' most frequently used alarm call broadcast in its native habitat showed a nonsignificant relationship (r_S=0.8, N=4, one-tailed P=0.083; see Fig. 5 for ranking of alarm calls). Thus, the structure of species' specific alarm calls does not seem to be significantly explained by the distance over which each species may need to communicate.

It is possible that insufficient evolutionary time has elapsed to allow calls to become adapted to their specific environments. Relatively recent environmental changes may result in vocalizations not being acoustically adapted to the contemporary environment. For example, the songs of grassland-dwelling rufous-collared sparrows, *Zonotrichia capensis*, often use fast trills, whereas forest-dwelling sparrows tend to use slow trills (Handford 1988). This association is greater, however, with the original vegetation structure that existed before human modification (within the last 200 years) than with contemporary vegetation structure (see also Tubaro et al. 1993). Woodchuck habitat structure may have been influenced by agriculture, and other human development, within the recent past. However, the habitat structures of the other three species probably have not been drastically altered during this same period.

Environmental instability at a larger time scale may also constrain acoustic adaptation to the local environment. The genus *Marmota* is currently believed to have originated between 9 and 11.5 million years ago (Black 1963, 1972; Thomas & Martin 1993). For our four species, an eastern woodchuck ancestor is hypothesized to have split from its western counterpart during the early Pleistocene (70 000 to 1.8 million years ago), followed by a more recent divergence during the late Pleistocene (10 000–130 000 years ago) of the other three species (Hoffmann & Nadler 1968; Black 1972). Multiple glaciations and interglacial periods during the Quaternary changed both plant community distribution and composition throughout the current ranges of the four marmot species (Barnosky et al. 1987). Fossil evidence for Eurasian marmots suggests that the geographical distribution of *marmots* also changed during the Pleistocene (Bibikow 1996). The extent to which the vegetation structures in the habitats of the four marmot species we studied has been altered over this period is not known.

Finally, it may be that drift processes, where calls slowly diverge over time in the absence of selection, may have played an important role in the divergence of species-specific marmot alarm calls. Hoary and Olympic marmots, which are hypothesized to be sibling species (Hoffmann et al. 1979), show great similarity in call structure. In addition, Eurasian species which are hypothesized to be closely related, such as *M. bobac*, *M. baibacina* and *M. sibirica*, are qualitatively more similar to each other in call structure than to other less closely related Eurasian species, such as *M. caudata* and *M. menzbieri* (Bibikow 1996; Nikol'skii 1996).

Our study is not the first one to fail to support the acoustic adaptation hypothesis. Studies examining differences in signal structure between broad categories of habitat, such as open versus forested habitat, for either many species or many geographical variants of one species, have often supported the hypothesis (Chappuis 1971; Morton 1975; Nottebohm 1975; Ryan & Brenowitz 1985; Sorjonen 1986b; Handford 1988; Wiley 1991). In contrast, studies using a variety of methods to examine either fewer species, fewer geographical variants within a species, or finer differences between habitats, have typically not supported the acoustic adaptation hypothesis (Lemon et al. 1981; Rothstein & Fleischer 1987; Smith & Yu 1992; Date & Lemon 1993; Williams & Slater 1993; Fotheringham et al. 1997).

Studies that failed to support the acoustic adaptation hypothesis suggest a relatively small 'effect size' (Cohen 1988) of the acoustic environment in shaping signal structure. Perhaps, it is too hopeful to expect the environment to select for fine differences in signal structure. Many other factors, such as exposure to predators (Marler 1955, 1957), social complexity (Blumstein & Armitage 1997b), and the relative distribution of signal recipients (Sorjonen 1986a; Tubaro & Segura 1994; Fotheringham et al. 1997), may be relatively more important than the habitat in shaping signal structure. Future studies seeking to explain microstructural signal variation should simultaneously consider other causal hypotheses.

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References

Abacus Concepts 1993. *StatView 4.01*. Berkeley, California: Abacus Concepts.

Armitage, K. B. 1975. Social behavior and population dynamics of marmots. *Oikos*, **26,** 341–354.

Armitage, K. B. 1988. Resources and social organization of ground-dwelling squirrels. In: *The Ecology of Social Behavior* (Ed. by C. N. Slobodchikoff), pp. 131–155. San Diego, California: Academic Press.

Barash, D. P. 1973. The social biology of the Olympic marmot. *Animal Behaviour Monographs*, **6,** 173–245.

Barash, D. P. 1989. *Marmots: Social Behavior and Ecology*. Stanford, California: Stanford University Press.

Barnosky, C. W., Anderson, P. M. & Bartlein, P. J. 1987. The northwestern U.S. during deglaciation; vegetational history and paleoclimatic implications. In: *North America and Adjacent Oceans During the Last Deglaciation* (Ed. by W. F. Ruddiman & H. E. Wright, Jr), pp. 289–321. Boulder, Colorado: Geological Society of America.

Bibikow, D. I. 1996. *Die Murmeltiere der Welt*. Heidelberg: Spektrum Akademischer Verlag.

Black, C. C. 1963. A review of the North American tertiary Sciuridae. *Harvard University, Bulletin of the Museum of Comparative Zoology*, **130,** 109–248.

Black, C. C. 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). *Evolutionary Biology*, **6,** 305–322.

Blumstein, D. T. 1998. Quantifying predation risk for refuging animals: a case study with golden marmots. *Ethology*, **104**, 501–516.

Blumstein, D. T. & Armitage, K. B. 1997a. Alarm calling in yellow-bellied marmots: I. The meaning of situationally specific calls. *Animal Behaviour*, **53,** 143–171.

Blumstein, D. T. & Armitage, K. B. 1997b. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist*, **150,** 179–200.

Blumstein, D. T. & Daniel, J. C. 1997. Inter- and intraspecific variation in the acoustic habitats of three marmot species. *Ethology*, **103,** 325–338.

Blumstein, D. T., Steinmetz, J., Armitage, K. B. & Daniel, J. C. 1997. Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. *Animal Behaviour*, **53,** 173–184.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.

Brown, C. H., Gomez, R. & Waser, P. M. 1995. Old world monkey vocalizations: adaptation to the local habitat? *Animal Behaviour*, **50,** 945–961.

Brown, T. J. & Handford, P. 1996. Acoustic signal amplitude patterns: a computer simulation investigation of the acoustic adaptation hypothesis. *Condor*, **98,** 608–623.

Chappuis, C. 1971. Un exemple de l'influence du milieu sur les emissions vocales des oiseaux: l'evolution des chants en forets equatoriale. *Terre et Vie*, **25,** 183–202.

Charif, R. A., Mitchell, S. & Clark, C. W. 1995. *Canary 1.2 User's Manual*. Ithaca, New York: Cornell Laboratory of Ornithology.

Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*, 2nd edn. Hillsdale, New Jersey: L. Erlbaum.

Daniel, J. C. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. M.A. thesis, University of Kansas, Lawrence.

Date, E. M. & Lemon, R. E. 1993. Sound transmission: a basis for dialects in birdsong? *Behaviour*, **124,** 3–4.

Dusenbery, D. B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information*. New York: W. H. Freeman.

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist Supplement*, **139,** 125–153.

Ferron, J. & Ouellet, J. P. 1989. Temporal and intersexual variation in the use of space with regard to social organization in the woodchuck (*Marmota monax*). *Canadian Journal of Zoology*, **67,** 1642–1649.

Forrest, T. G. 1994. From sender to receiver: propagation and environmental effects on acoustic signals. *American Zoologist*, **34,** 644–654.

Fotheringham, J. R., Martin, P. R. & Ratcliffe, L. 1997. Song transmission and auditory perception of distance in wood warblers (Parulinae). *Animal Behaviour*, **53,** 1271–1285.

Frase, B. A. & Hoffmann, R. S. 1980. *Marmota flaviventris*. *Mammalian Species*, **135,** 1–8.

Gish, S. L. & Morton, E. S. 1981. Structural adaptations to local habitat acoustics in Carolina wren songs. *Zeitschrift für Tierpsychologie*, **56,** 74–84.

Handford, P. 1988. Trill rate in the rufous-collared sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Canadian Journal of Zoology*, **66,** 2658–2670.

Hansen, P. 1979. Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behaviour*, **27,** 1270–1271.

Hoffmann, R. S. & Nadler, C. F. 1968. Chromosomes and systematics of some North American species of the genus *Marmota* (Rodentia: Sciuridae). *Experientia*, **24,** 740–742.

Hoffmann, R. S., Koeppl, J. W. & Nadler, C. F. 1979. The relationships of the Amphiberingian marmots (Mammalia: Sciuridae). *The University of Kansas, Occasional Papers of the Museum of Natural History*, **83,** 1–56.

Holmes, W. G. 1979. Social behavior and foraging strategies of hoary marmots (*Marmota caligata*) in Alaska. Ph.D. thesis, University of Washington, Seattle.

Hunter, M. L. & Krebs, J. R. 1979. Geographical variation in the song of the great tit (*Parus major*) in relation to ecological factors. *Journal of Animal Ecology*, **48,** 759–785.

Keller, E. 1992. *Signalyze*. Version 2. Lausanne, Switzerland: InfoSignal.

Khanna, H., Gaunt, S. L. L. & McCallum, D. A. 1997. Digital spectrographic cross-correlation: tests of sensitivity. *Bioacoustics*, **7**, 209–234.

Klump, G. M. & Shalter, M. D. 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. *Zeitschrift für Tierpsychologie*, **66**, 189–226.

Lemon, R. E., Struger, J., Lechowicz, M. J. & Norman, R. F. 1981. Song features and singing heights of American warblers: maximization or optimization of distance? *Journal of the Acoustical Society of America*, **69**, 1169–1176.

Lloyd, J. E. 1972. Vocalization in *Marmota monax*. *Journal of Mammalogy*, **53**, 214–216.

McGregor, P. K. 1994. Sound cues to distance: the perception of range. In: *Perception and Motor Control in Birds* (Ed. by M. N. O. Davies & P. R. Green), pp. 74–94. Berlin: Springer-Verlag.

McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhardt, H. C., Gilbert, F., Horn, A. G., Klump, G. M., Kroodsma, D. E., Lambrechts, M. M., McComb, K. E., Nelson, D. A., Pepperberg, I. M., Ratcliffe, L., Searcy, W. A. & Weary, D. M. 1992. Design of playback experiments: The Thornbridge Hall NATO ARW consensus. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 1–9. New York: Plenum.

MacroMind-Paracomp, Inc. 1990. *MacRecorder Soundsystem Pro*. San Francisco, California: MacroMind-Paracomp.

Marler, P. 1955. Characteristics of some animal calls. *Nature*, **176**, 6–8.

Marler, P. 1957. Specific distinctiveness in the communication signals of birds. *Behaviour*, **11**, 13–39.

Marten, K. & Marler, P. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. *Behavioral Ecology and Sociobiology*, **2**, 271–290.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17–34.

Morton, E. S. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. *Behaviour*, **99**, 65–86.

Nikol'skii, A. A. 1984. *Sound Signals of the Mammals in the Evolutionary Process*. Moscow: Nauka.

Nikol'skii, A. A. 1994. Geographical variability of the alarm call rhythmical structure in *Marmota baibacina*. In: *Actual Problems of Marmot Investigations* (Ed. by V. Y. Rumiantsev), pp. 111–126. Moscow: ABF.

Nikol'skii, A. A. 1996. Species specificity and interspecies parallelisms of alarm call in Eurasian marmots. In: *Biodiversity in Marmots* (Ed. by M. Le Berre, R. Ramousse & L. Le Guelte), pp. 187–192. Moscow-Lyon: International Network on Marmots.

Nottebohm, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *American Naturalist*, **109**, 605–624.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Richards, D. G. & Wiley, R. H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *American Naturalist*, **115**, 381–399.

Rothstein, S. I. & Fleischer, R. C. 1987. Vocal dialects and their possible relation to honest status signalling in the brown-headed cowbird. *Condor*, **89**, 1–23.

Ryan, M. J. & Brenowitz, E. A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist*, **126**, 87–100.

Ryan, M. J., Cocroft, R. B. & Wilczynski, W. 1990. The role of environmental selection in intraspecific divergence of mate recognition of signals in the cricket frog, *Acris crepitans*. *Evolution*, **44**, 1869–1872.

SAS Institute 1990. *SAS/STAT User's Guide*. Version 6. Cary, North Carolina: SAS Institute.

Smith, J. I. & Yu, H. T. 1992. The association between vocal characteristics and habitat type in Taiwanese passerines. *Zoological Science*, **9**, 659–664.

Sorjonen, J. 1986a. Song structure and singing strategies in the genus *Luscinia* in different habitats and geographical areas. *Behaviour*, **98**, 274–285.

Sorjonen, J. 1986b. Factors affecting the structure of song and singing behaviour of some Northern European passerine birds. *Behaviour*, **98**, 286–304.

Tabachnick, B. G. & Fidell, L. S. 1996. *Using Multivariate Statistics*. New York: Harper Collins College Publishers.

Taulman, J. F. 1977. Vocalizations of the hoary marmot, *Marmota caligata*. *Journal of Mammalogy*, **58**, 681–683.

Thomas, W. K. & Martin, S. L. 1993. A recent origin of marmots. *Molecular Phylogenetics and Evolution*, **2**, 330–336.

Tubaro, P. L. & Segura, E. T. 1994. Dialect differences in the song of *Zonotrichia capensis* in the southern Pampas: a test of the acoustic adaptation hypothesis. *Condor*, **96**, 1084–1088.

Tubaro, P. L., Segura, E. S. & Handford, P. 1993. Geographic variation in the song of the rufous-collared sparrow in eastern Argentina. *Condor*, **95**, 588–595.

Waring, G. H. 1966. Sounds and communications of the yellow-bellied marmot (*Marmota flaviventris*). *Animal Behaviour*, **14**, 177–183.

Waser, P. M. & Brown, C. H. 1986. Habitat acoustics and primate communication. *American Journal of Primatology*, **10**, 135–154.

Wiley, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist*, **138**, 973–993.

Wiley, R. H. & Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, **3**, 69–94.

Wiley, R. H. & Richards, D. G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds* (Ed. by D. E. Kroodsma, E. H. Miller & H. Ouellet), pp. 131–181. New York: Academic Press.

Williams, J. M. & Slater, P. J. B. 1993. Does chaffinch *Fringilla coelebs* song vary with the habitat in which it is sung? *Ibis*, **135**, 202–208.