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Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls

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Individuals produce distinctive vocalizations that may contain considerable potential information about a signaller. Simply finding significant covariation between call structure and some individual attribute does not itself mean that there has been selection on callers to produce individually distinctive calls, nor on receivers to discriminate between them. Moreover, acoustic variation may degrade while being transmitted through the environment, making it potentially difficult for receivers to extract potential information. We focused on the individually distinctive calls of yellow-bellied marmots, *Marmota flaviventris*, to describe attributes of individuals encoded in calls. Using discriminant function analysis, we found significant potential information about identity, age and sex encoded in calls. When calls were broadcast and re-recorded over 10 m and 40 m, identity, age and sex remained statistically discriminatable. Key variables that enabled discrimination were repeatable (they had high intraclass correlation coefficients), whereas those that did not enable discrimination were less repeatable. Finally, statistics developed to describe, in a standardized and comparative way, the information about individual signallers contained in vocalizations, revealed that marmot alarm calls contained at least 3.37 bits of information about identity. When compared to other species for which the information content of signals has been calculated, marmots may have not undergone strong selection for individually distinctive vocalizations. The fact that receivers discriminate between individuals suggests that receivers benefit by doing so.

Vocalizations can potentially contain considerable information about the signaller. For instance, caller size (Davies & Halliday 1978; Clutton-Brock & Albon 1979), arousal (Bercovitch et al. 1995; Hammerschmidt & Fischer 1998), identity (Leger et al. 1984; Cheney & Seyfarth 1990; Hare 1998), age (Cheney & Seyfarth 1990; Nesterova 1996; Blumstein & Daniel 2004) and sex (Tomaszycki et al. 2001) may all be encoded in vocalizations. Such information-laden signals may change the behaviour of individuals hearing these vocalizations. Vervet monkeys, *Cercopithicus aethiops* (Cheney & Seyfarth 1990), bonnet macaques, *Macaca radiata* (Ramakrishnan & Coss 2000), California ground squirrels, *Spermophilus beecheyi* (Hanson & Coss 2001), and steppe marmots, *Marmota bobak* (Nesterova 1996) all respond less to alarm calls from juveniles than adults. However, simply because there is measurable variation in a signal does not mean that receivers will respond differently to that variation (Blumstein 1995). Regardless of whether listeners respond differently, the environment through which calls are broadcast has a strong influence on the structure of sounds (Wiley & Richards 1978; Dabelsteen et al. 1993; McComb et al. 2003). All signals attenuate and degrade while travelling through the environment (Bradbury & Vehrencamp 1998) and it is not obvious that minute differences between calls will actually reach a receiver in a sufficiently undegraded state to allow receivers to perceive and respond to acoustic variation. For instance, a recent study of individually specific long-distance elephant calls demonstrated that infrasonic components became embedded in low-frequency background noise and were of limited use by distant elephants aiming to identify the vocalizing individual (McComb et al. 2003).

Social signalling systems, such as those in elephants (McComb et al. 2003), penguins (Jouventin et al. 1999), seals (Insley 2000) and swallows (Beecher 1989b), might generally be expected to have undergone selection to maximize differences between individual's vocalizations, as well as selection on receivers to differentiate signals (Beecher et al. 1989). Yet alarm calls (calls produced by

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a signaller when exposed to some threat) may also be individually distinct (Cheney & Seyfarth 1990; Blumstein & Armitage 1997). In this case, potential information contained in a call might not have been strongly selected for, per se, but rather may result from individual or systematic variation in vocal track morphology (e.g. Fitch & Hauser 1995, 2003). Even without strong selection on signallers to produce individually unique calls, there could be selection for receivers to discriminate among calls from certain individuals, or certain demographic classes.

Here we focus on the alarm calls of yellow-bellied marmots to understand the relation between what potential information about the signaller is encoded in calls and what is potentially useful by a distant receiver. Previous research (Blumstein & Armitage 1997) demonstrated that marmot alarm calls encode the relative risk a caller experiences when it calls (marmots call more and faster as threat increases). Additionally, there is some degree of individuality in marmot alarm whistles (Blumstein & Armitage 1997). More recent playback experiments show that marmots are able to discriminate among individuals based on their calls alone (Blumstein & Daniel 2004), and that assessing perceived caller reliability is likely to be the key factor that has been selected for the evolution of discrimination abilities (Blumstein et al. 2004).

In the previous study of individually specific variation in marmot alarm calls (Blumstein & Armitage 1997), measurements focused on quantifying characteristics of the fundamental frequency component of these complex harmonic calls. However, marmot whistles have up to six harmonics below 20 kHz (Fig. 1) and we wished to make additional measurements on these overtones because they

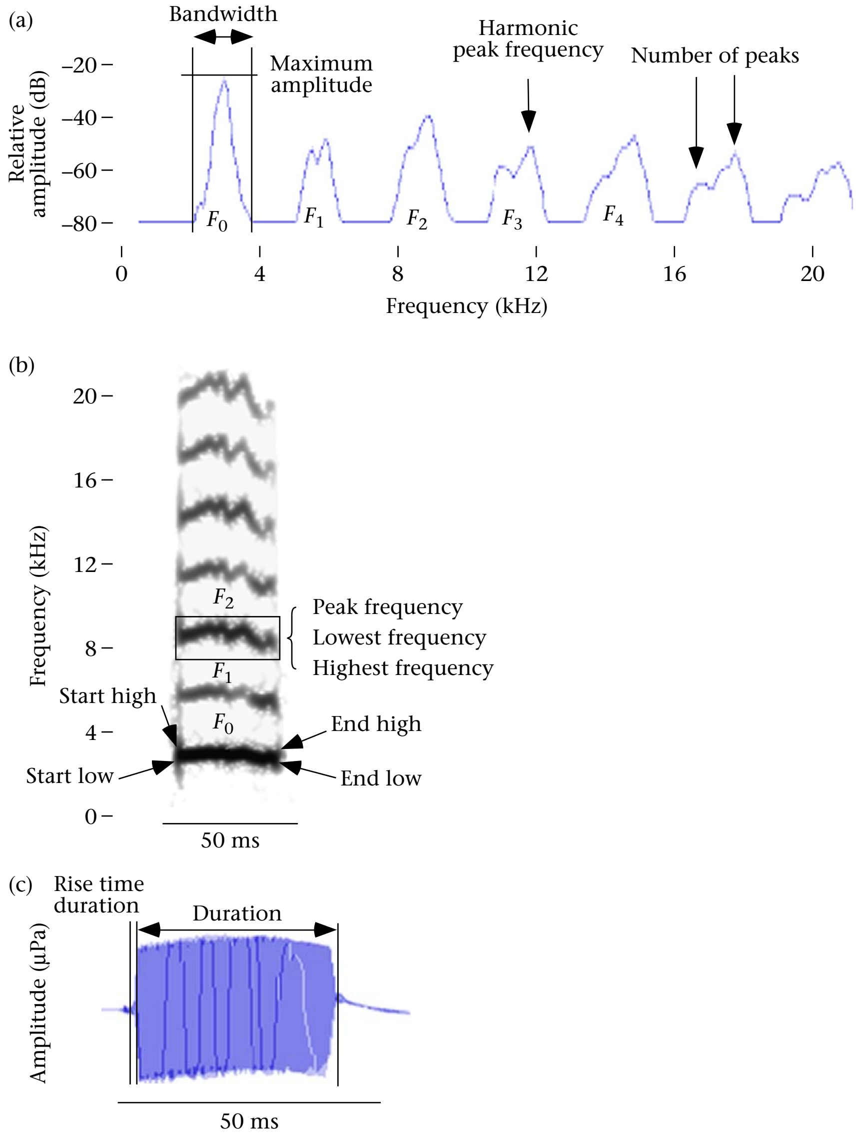

Figure 1. Illustration of the 43 acoustic measurements made on the: (a) spectrum (bandwidth, maximum amplitude, peak frequency and number of peaks were measured on the fundamental and the next four harmonics); (b) spectrogram (starting low frequency, starting high frequency, ending low frequency, ending high frequency, lowest frequency, highest frequency and peak frequency were measured on the fundamental and the next two harmonics); and (c) waveform (rise time and duration) of yellow-bellied marmot alarm whistles used to study potential information contained in calls about caller age, sex and identity.

too could contain important information (e.g. Slobodchikoff et al. 1991). In addition to searching for the potential of calls to encode individuality, we aimed to understand what additional information about sex and age was contained in calls. For instance, in other species of marmots (e.g. steppe marmots), calls from juveniles have significantly higher dominant frequencies than calls from older individuals (Nesterova 1996). However, because any potential information contained in calls is only valuable if it can be transmitted faithfully through the environment, we broadcast calls from adults, yearlings and juveniles of both sexes through marmot habitat to determine whether calls re-recorded at a distance still contained discriminative information.

GENERAL METHODS

Recording, Editing and Measuring the Alarm Calls

All studies were conducted with free-living marmots in the East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, U.S.A. Marmots at this site have been studied continuously for the past 42 years (Armitage 1991; Schwartz et al. 1998; Armitage & Schwartz 2000; Schwartz & Armitage 2003). Social groups and social group membership are known. Detailed methods of marmot trapping and marking can be found in Armitage (1982).

For this study, we recorded alarm calls of 124 marmots (Table 1) captured in live traps using Audix OM-3xb microphones (frequency response: 40 Hz–20 kHz) 20–40 cm from calling subjects, on digital audio tape decks (Sony PCM-M1 or Tascam DA-P1) sampling at 44.1 kHz with 16-bit resolution. Our use of calls recorded on DAT equipment and from trapped marmots ensured the highest quality of recorded calls. Moreover, because yellow-bellied marmots communicate risk, not predator type (Blumstein & Armitage 1997), we also controlled the context (and presumably the degree of risk) that calling marmots experienced, which allowed us to focus on other information potentially contained in calls. Alarm calls were acquired or transferred through a MOTU 828 Firewire external digital board (Mark of the Unicorn, Cambridge, Massachusetts, U.S.A.) to a Macintosh PowerBook G4 (Apple computer, Cupertino, California, U.S.A.), using Canary 1.2.4 (Charif et al. 1995).

After having recorded and transferred the bouts of alarm calls, the best five calls per recording were edited into 100-ms single-alarm-call files and saved in aif format. Each call was then normalized to peak amplitude using SoundEdit 16 (Macromedia 1995). With these normalized calls, we calculated spectrograms and the average spectrum using Canary (spectrogram: fast Fourier transformation, FFT, size = 1024, overlap = 99.61%, filter bandwidth = 1066.32 Hz, frequency grid resolution = 3.07 Hz, clipping level = −80 dB; average spectrum: FFT size = 512, overlap = 99.8%, filter bandwidth = 533.16 Hz, frequency grid resolution = 86.13 Hz, clipping level = −80 dB). We then measured a number of features from the waveform, the fundamental frequency (F_0) and the next two harmonics (F_1 and F_2) from the spectrogram, and the fundamental (F_0) and next four harmonics (F_1, F_2, F_3 and F_4) from the spectrum. In total, each call was described by 43 quantitative measurements (Fig. 1).

SPECIFIC QUESTIONS

Do Marmot Alarm Calls Contain Information about Identity, Age and Sex?

Methods

We conducted a number of discriminant function analyses (DFA) to classify calls according to individual caller, sex and age. We recognize that some of our 43 variables (e.g. harmonics) were correlated. However, we focused our analyses on these raw variables to help us identify those features that specifically allow discrimination to facilitate designing follow-up playback experiments. In some cases, particularly when dealing with higher-frequency overtones, which were somewhat attenuated, our matrix of acoustic measurements contained missing values (Table 2). Because discriminant analysis requires a full data matrix, we replaced missing values with each variable's average value to preserve the full

Table 1. Number of individuals and bouts of recordings per individual used for discrimination analyses

Categories	N	$N \geq 2$ recordings	$\overline{X} \pm \mathrm{SD}$	Range
Juveniles				
Male	34	14	2.15±1.84	1–7
Female	33	13	1.61±0.82	1–3
Total	67	27	1.88±1.33	
Yearlings				
Male	9	2	1.33±0.5	1–2
Female	19	14	2.84±1.95	1–7
Total	28	16	2.36±1.22	
Adults				
Male	10	4	2.70±2.73	1–9
Female	19	12	3.37±3.53	1–12
Total	29	16	3.14±3.13	
Total	124	59	2.28±1.9	

Table 2. Percentage of missing values in the databases used for discriminant function analyses

	Spectrogram			Spectrum				
Database	F_0	F_1	F_2	F_0	F_1	F_2	F_3	F_4
Full database*		0.10	3.30		0.10	1.20	10.60	18.50
Original†						7.00	7.00	18.00
Distance‡								
10 m							0.30	8.30
40 m		12.00	3.30		0.30		53.70	84.00

*$N = 1415$ calls.

†Average value for each acoustic variable for all sites and distances used for the degradation analyses.

‡Average value for each acoustic variable at 10 m and 40 m across all sites ($N = 300$ calls).

matrix. This adjustment was conservative because discrimination was more difficult (i.e. replaced values showed less variation). The forward stepwise procedure in SPSS 10 (SPSS 2000) was used to compute discriminant functions. Variables were added based on the change in Wilk's lambda with the *F* value to enter equal to 3.84 and the *F* value to remove equal to 2.71. For the DFA for classifying calls to individual, we included only those individuals that were recorded on two or more occasions. Individuals were represented by at least 10 different calls, recorded over two bouts of calling (Table 1). For the DFAs for sex and age, we included one randomly selected set of five recordings from each subject.

We used a two-step classification process. First, we used stepwise DFA to identify the most discriminating variables. Then, we split the data to separate demographic categories and re-ran a stepwise DFA on the different demographic groups. For individual discriminations, we re-ran analyses with these 'key variables' on males and females alone, and on adults, yearlings and juveniles. For age, we analysed the sexes separately. For sex, we analysed the ages (juveniles, yearlings, adults) separately. Key variables were defined as those that emerged from the stepwise individual discrimination procedure. Comparisons of the percentage correct classification across these categorizations are not exactly comparable for two reasons. First, the expected classifications differ based on the number of categories that needed to be discriminated. Second, DFAs perform better with fewer classes and a large number of exemplars per class, and the different categories had different ratios of these.

Results

Any way examined, caller identity could be distinguished with measured variables at levels substantially greater than chance (Fig. 2). Stepwise DFA classified 62.8% of the calls correctly to individual, compared with a 0.6% random expected classification (which calculated prior probabilities that were proportional to the number of calls included in each different group). The percentage of calls correctly classified to individual increased when split by sex (69.2% correct classification of females and 79.2% correct classification of males), and when split by age (79.5% correct classification of adults, 89.4% correct classification of yearlings and 74.9% correct classification of juveniles). Thus, some acoustic features that enable discrimination of individuals (Table 3) are also shared with sex and age (Table 4).

Caller sex could be distinguished with measured variables at levels substantially greater than chance (Fig. 2). Stepwise DFA classified 70.2% of the observations correctly, compared with 50% random classification. When split by age, classification of sex increased (adults: 71.4%; yearlings: 75%; juveniles: 74.4%).

Caller age could be distinguished with measured variables at levels substantially greater than chance (Fig. 2). Stepwise DFA classified 72.4% of the observations correctly, compared with a 33% random classification. With a split by sex, classification increased for males (80.4%), but was about the same for females (71.8%). Again, we defined 'key variables' as those that were most useful for the individual discrimination.

Is Information about Identity, Age, or Sex Transmitted Faithfully through the Environment?

Methods

Call selection, playback and re-recording. We selected two bouts of five calls from each of five individuals (these came

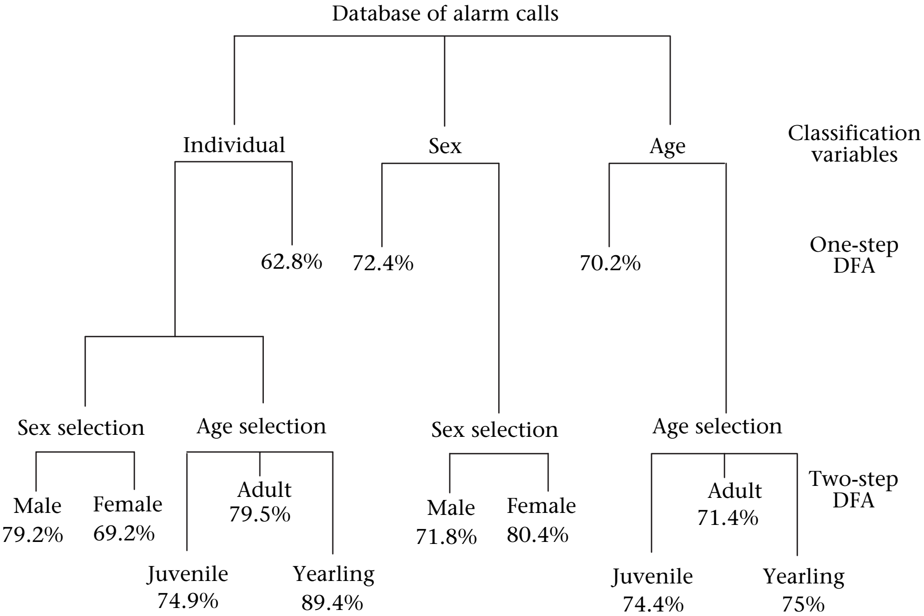

Figure 2. Percentage correct classification of marmot calls based on discriminant function analyses as a function of individual, sex and age. Sample sizes from Table 1.

Table 3. Key and nonkey variables that allowed discrimination of individual yellow-bellied marmot alarm calls

Key variables*	Nonkey variables
Discrimination analysis	
Waveform	
Duration (ms)	Rise time duration (ms)
Spectrogram	
Harmonic 1: start lowest frequency (kHz)	Fundamental: end highest frequency (kHz)
Harmonic 2: highest frequency (kHz)	Harmonic 1: lowest frequency (kHz)
	Harmonic 2: end lowest frequency (kHz)
Spectrum	
Fundamental: bandwidth (Hz)	Harmonic 1: peak frequency (kHz)
Fundamental: maximum relative amplitude (−dB)	Harmonic 2: maximum relative amplitude (−dB)
Harmonic 3: maximum relative amplitude (−dB)	Harmonic 3: number of peaks
Harmonic 4: maximum relative amplitude (−dB)	
Degradation analysis	
Waveform	
Duration (ms)	
Rise time duration (ms)	
Spectrogram	
Fundamental: start lowest frequency (kHz)	Harmonic 1: lowest frequency (kHz)
Fundamental: start highest frequency (kHz)	Harmonic 2: end lowest frequency (kHz)
Fundamental: end lowest frequency (kHz)	
Spectrum	
	Fundamental: peak frequency (kHz)
	Harmonic 1: bandwidth (kHz)
	Harmonic 3: number of peaks

*Variables that enabled discrimination of individuals in a stepwise discriminant function analysis.

from recordings made on two different occasions) from each of the six age/sex categories (adult females, adult males, yearling females, yearling males, juvenile females, juvenile males). All selected calls were processed as before, and then normalized calls were digitally transferred to a Tascam DA-P1 for subsequent playback through marmot habitats. Calls were broadcast through three different marmot groups that included a variety of microhabitats found in and around RMBL. All playbacks were conducted on two consecutive days (14 and 15 June 2003) when there was limited wind to minimize background noise during propagation (e.g. Bradbury & Vehrencamp 1998). Alarm calls were broadcast through an Advent AV 570 Powered Partner speaker (Recoton Home Audio Benici, California; frequency response: 40 Hz–20 kHz) elevated 0.4 m off the ground to simulate a rearing and calling marmot, and re-recorded successively to digital tape at two different distances (10 m and 40 m) with an Audix OM-3xb microphone mounted on a tripod 0.2 m above the ground to simulate the height of a standing marmot's ears. These distances are biologically salient. Although home ranges average 3.65 ha (Blumstein et al. 2001), group members who are above ground are often within 10–40 m of each other. Calls were sampled and measured as described above.

Discriminant function analyses. For each distance, 10 m and 40 m, and across all three sites, we averaged each call's values for each measured acoustic variable to create three databases with the original calls, those recorded at 10 m, and those recorded at 40 m. We then conducted a series of stepwise DFAs on the broadcast subset of original calls, those recorded at 10 m, and those recorded at 40 m to classify calls according to caller identity, age and sex. Features that enabled discrimination at 40 m proved to be somewhat different from those that enabled discrimination of other calls. We assumed that features useful for discrimination at 40 m were those that transmitted well through the environment and thus might be more generally useful for discrimination. Therefore, we re-ran DFAs for the undegraded calls and the calls recorded at 10 m, specifying only those variables that allowed individual discrimination at 40 m.

Results

The ability of the DFA to classify calls according to caller, age or sex was not substantially affected by 40-m transmission through marmot habitat. Using stepwise DFA, calls could be correctly classified to caller, age and

Table 4. Descriptive statistics ($\overline{X}\pm$SD) of the key variables for different demographic groups that allow individual discrimination

	Total	Males	Females	Juveniles	Yearlings	Adults
	$\overline{X}\pm$SD	$\overline{X}\pm$SD	$\overline{X}\pm$SD	$\overline{X}\pm$SD	$\overline{X}\pm$SD	$\overline{X}\pm$SD
Duration (ms)	29.7±8.6	32.6±8.3	27.8±8.3	35.3±7.6	24.6±5.9	25.5±6.8
Harmonics 1: start low (kHz)	6.3±0.7	6.1±0.6	6.5±0.7	6.4±0.7	6.6±0.6	6.0±0.6
Harmonics 2: highest (kHz)	10.9±1.2	10.6±1.1	11.2±1.2	11.2±1.2	11.2±0.8	10.3±1.0
Fundamental 1: bandwidth (Hz)	1307.8±305.9	1275.1±271.9	1328.6±324.2	1396.2±340.4	1303.1±226.2	1186.5±260.6
Fundamental 1: maximum relative amplitude (−dB)	27.4±2.7	27.6±3.2	27.3±2.3	28.1±3.1	27.1±2.3	26.8±2.0
Harmonics 3: maximum relative amplitude (−dB)	55.7±7.9	55.6±7.7	55.9±8.1	55.6±7.1	56.0±7.7	55.7±9.2
Harmonics 4: maximum relative amplitude (−dB)	56.2±7.8	55.6±8.0	56.6±7.7	56.8±7.5	56.1±6.9	55.4±8.7

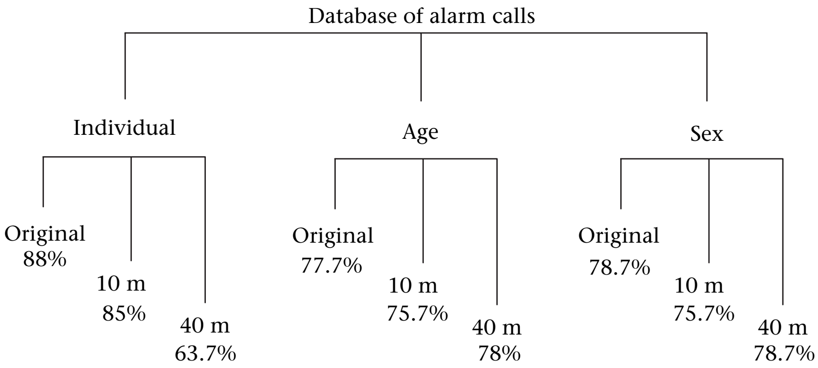

Figure 3. Percentage correct classification of marmot calls based on stepwise discriminant function analyses of degraded calls as a function of individual, age and sex. Sample sizes from Table 1.

sex at levels much greater than chance at 10 m and at 40 m (Fig. 3). When we used only those variables extracted from the individual discrimination stepwise DFA at 40 m to classify undegraded calls and calls recorded at 10 m, we again found that caller, age and sex were classified at levels much greater than chance.

How Consistent Are These ‘Key Variables’ for Individual Discrimination?

The intraclass correlation coefficient (r_{IC}, Sokal & Rohlf 1981) is a measure of consistency. To measure the consistency of ‘key variables’ (as defined by the stepwise DFA), we compared the r_{IC} of these seven ‘key variables’ to those of the same number of randomly selected variables that did not enter into the stepwise DFA (Table 3). We also examined the consistency of both ‘40-m key variables’ and a set of randomly selected variables in the subset of calls that were broadcast and re-recorded at 10 m and 40 m.

Methods

We selected all individuals from the discrimination database that were recorded on more than one occasion. These individuals thus had 10 or more calls from two or more bouts of calling ($\overline{X} \pm \mathrm{SD} = 3.7 \pm 2.19$ bouts). We then calculated the r_{IC} for the seven key variables from the entire analysis, and compared this value, using a Mann–Whitney U test, to the r_{IC} calculated from seven nonkey variables.

We conducted two DFAs: one with the key variables and one with the randomly selected set of nonkey variables. We used the structure matrix from each discriminant function analysis along with each function’s eigenvalue to compute, for each variable, a weighted index of that variable’s relative importance in the discriminant analysis. Specifically, we multiplied the squared structure score (i.e. the squared correlation between the DFA function and variables, x_{ij}^2) by the function’s eigenvalue (y_j). A given variable’s ‘index of importance’ (I_i) is the proportion that a given variable contributes to the total product of structure scores and eigenvalues, summed across all variables and all functions.

$$I_i = \frac{\sum_j \left(x_{ij}^2 y_j\right)}{\sum_i \sum_j \left(x_{ij}^2 y_j\right)} \times 100 \qquad (1)$$

We then calculated the Spearman rank order correlation coefficient between our index of importance and the intraclass correlation coefficient for ‘key variables’ and for a randomly selected set of nonkey variables.

To identify the consistency of ‘40-m key variables’ when broadcast and re-recorded through marmot habitat, we focused on the calls used in the degradation experiments (the degradation database). We identified ‘40-m key variables’ as those that enabled individual discrimination at 40 m. We then calculated r_{IC} with the ‘40-m key variables’ on the undegraded calls, calls recorded at 10 m and calls recorded at 40 m. We compared the r_{IC} for these five key variables to five randomly selected variables using a Mann–Whitney U test.

Results

Although intraclass correlation coefficients were generally greater for key variables than nonkey variables, in the full data set we detected significant differences only for the discrimination of identity (Table 5). Our index of importance was perfectly associated with the intraclass

Table 5. Comparisons of the intraclass correlation coefficients for key and nonkey variables

	Discrimination analyses			Degradation experiment		
	Identity (>1 call)	Age	Sex	Original	10 m	40 m
Key variables						
$\overline{X}$	0.594	0.105	0.021	0.687	0.691	0.644
SD	0.243	0.115	0.026	0.178	0.231	0.129
Nonkey variables						
$\overline{X}$	0.134	0.033	0.024	0.589	0.565	0.269
SD	0.180	0.042	0.053	0.162	0.310	0.264
P	0.004	0.161	0.911	0.388	0.487	0.021

The discrimination analyses assigned identity, age and sex of caller. The degradation analyses focused only on caller identity.

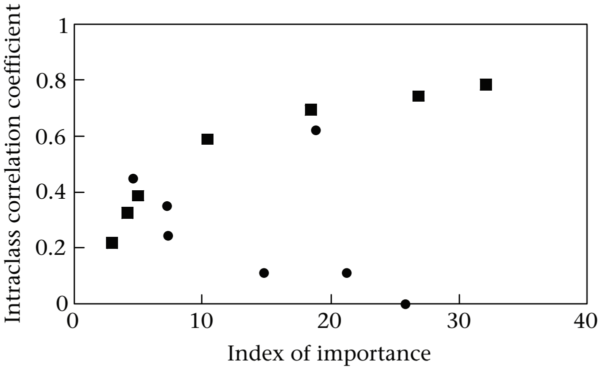

Figure 4. Correlation between the 'importance' of a variable (see equation 1) and the variable's intraclass correlation coefficient for key variables (■) and a set of randomly selected nonkey variables (●).

correlation coefficient for key variables ($r_S = 1.0$, $N = 7$, $P < 0.0001$), but not for randomly selected nonkey variables ($r_S = -0.085$, $N = 7$, $P = 0.873$; Fig. 4). In the analysis of degraded calls, key variables had consistently higher intraclass correlation coefficients than nonkey variables, however, this difference was only statistically significant at 40 m (Table 5).

Is There Evidence of Selection on Callers to Transmit Individually Specific Information?

Methods

Beecher (1989a) used information theory to estimate the potential individually specific information encoded in acoustic signals. The approach assumes that acoustic measurements adequately describe individuality. In contrast to the results from the stepwise analyses described above, DFA models that used all measured variables were able to correctly classify calls to individual 94.3% of the time. Thus, our set of measured variables allowed us to determine the types of individual information encoded in calls and to compare these values with previously published values from other similarly well-described species (e.g. Jorgensen & French 1998; Frommolt et al. 2003). With this key assumption satisfied, we made two calculations.

Beecher's (1989a) method generates an overall measure of individuality that can be compared between species. To calculate this value, we first standardized the dependent variables as described in Beecher (1989a). Then, we ran a principal components analysis that reduced our set of 43 measurements to six uncorrelated factors. The between-subject variance for each of these six factors was then estimated using a random-effects ANOVA. We used the following formula from Beecher (1989a, page 253):

$$H(s) = \log_2 \sqrt{\frac{F+n-1}{n}} \qquad (2)$$

where $H(s)$ is a standardized measure of the information about identity contained in an acoustic variable; F is the F value from a random-effects ANOVA in which the independent variable is marmot identity and the dependent variable is the acoustic variable; and n is the sample size (124 individuals). In this way, we calculated the total information about individuals contained in marmot alarm calls. We also calculated the information contained in each of the key variables and selected nonkey variables. These numbers were correlated with our index of importance (described above).

Results

Overall, marmot alarm calls contained at least 3.37 bits of information about individual identity. This value would allow discrimination of about 10 individuals (i.e. $2^{3.37} = 10.3$). By contrast, Beecher (1991) found that calls of two colonial swallows (cliff, *Hirundo pyrrhonata*; bank, *Riparia riparia*) had 8.74 and 10.2 bits, respectively, whereas those of two noncolonial swallows (barn, *Hirundo rustica*; rough-winged, *Stelgidopteryx serripennis*) had 4.57 and 3.83 bits, respectively. Additionally, $H(s)$ for each key marmot variable was highly correlated with our index of importance ($r_S = 1.0$, $P < 0.0001$), but $H(s)$ for nonkey variables was uncorrelated with our index of importance ($r_S = -0.143$; $P = 0.760$).

DISCUSSION

Yellow-bellied marmot alarm calls contain potential information about the caller. Discriminant function analysis permits the assignment of calls to individual, sex and age at frequencies substantially greater than would be expected by chance. This variation persisted after calls were degraded by broadcasting them through the environment. Discrimination, however, relied on a subset of key acoustic features that were substantially less variable than nonkey features. Blumstein & Armitage (1997) suggested that calling rate encodes risk-based information (yellow-bellied marmot alarm calls communicate the degree of risk that a caller faces), whereas duration and frequency components encode information about identity. Our current findings, which measured many more acoustic components, are consistent with the hypothesis that frequency-based characteristics may encode information about caller identity. As discussed before (Blumstein & Armitage 1997), such variable features probably differ from invariant features that permit species identification (Marler 1960), as well as features that are likely to encode situational variation (Ivins & Smith 1983; Leger et al. 1984; Conner 1985; Nikolskii et al. 1990).

A fundamental question in animal communication is the relative importance of selection on signallers to produce variable signals, versus that of selection on receivers to extract information from signals (Blumstein, in press). In cooperative systems, we expect both the signaller and receiver to receive fitness benefits (Beecher & Stoddard 1990). However, all systems need not be cooperative (Dawkins & Krebs 1978) and there should generally be strong selection on receivers to extract meaningful information from signallers.

While alarm calls directed towards conspecifics, particularly relatives (Blumstein & Armitage 1997), are cooperative in that both the caller and the recipient presumably gain fitness, there is no a priori reason to expect that communicating individuality, per se, is mutually beneficial. The alarm calls of yellow-bellied marmots are such a system where receivers would presumably benefit by extracting information about caller identity. Marmot calls contain significant information about individuality, but relatively less than that expected in more complex social situations where both signallers and receivers would benefit from having individually distinctive calls (e.g. Beecher 1989b; Beecher & Stoddard 1990). In systems where parents leave their young in colonies, we expect selection to act on the young to produce individually distinctive vocalizations and on parents to discriminate based on vocalizations.

Although marmot calls contain only a modest amount of information about identity (3.4 bits), receivers indeed extract it. Playback experiments demonstrated that receivers discriminate between calls from different individuals and are more aroused after hearing the calls from juveniles compared with other age/sex categories (Blumstein & Daniel 2004). Recent work comprehensively demonstrated that receivers extract information about caller reliability (Blumstein et al. 2004), and from our current and previous results, we provisionally conclude that, in this marmot system, selection has focused on the receiver. Future comparative work focusing on both more social sciurid rodents and less social sciurid rodents will be required to properly evaluate this hypothesis. By contrast, parent–offspring systems are likely to have selection acting on both the signaller and the receiver.

An alternative way of viewing these results is that the number of potential interactants is somewhat limited, and calls have sufficient information to permit individuals to make needed discriminations. Beecher (1989a) pointed out that information encoded in calls should parallel the need to encode information. Yellow-bellied marmots are matrilineal. While the typical matriline contains one adult female, fitness is maximized when there are three adult females (Armitage & Schwartz 2000). Breeding females may recruit their daughters, and thus, groups may have as many as eight resident yearlings (Armitage 1991). Thus, 3.37 bits of information should allow discrimination of approximately 10 callers, a value greater than the number of a group's permanent residents.

Groups, however, contain other individuals. At our RMBL study site, adult females breed most years and wean an average of 4.1 young (Schwartz & Armitage 2003). Playback results suggest that older marmots respond significantly more to calls from pups than other individuals (Blumstein & Daniel 2004). Alarm calls from yearlings do not elicit significantly different responses than calls from adult females, but the key experiments to determine whether marmots can distinguish individual yearlings solely based on their alarm calls remain to be done. Our results suggest that calls contain sufficient information about individuality to permit discrimination of individual yearlings in a colony.

More generally, the results of this and other playback studies (Blumstein & Daniel 2004; Blumstein et al. 2004) demonstrate that even when there is not strong selection on signallers to be individually distinctive, receivers may benefit from making such discriminations nevertheless. In the marmot alarm calling system, it seems that the need of receivers to assess caller reliability is essential (Blumstein et al. 2004). Certain acoustic features are faithfully transmitted through the environment and we hypothesize that these are the key variables responsible for discrimination. Playback studies will be required to determine whether discrimination is more likely to be abolished by manipulating key features (Table 4) than nonkey features.

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