



# Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles

DANIEL T. BLUMSTEIN & JANICE C. DANIEL

Department of Ecology and Evolutionary Biology, University of California, Los Angeles

(Received 27 April 2003; initial acceptance 6 August 2003;  
final acceptance 16 December 2003; published online 29 September 2004; MS. number: A9597)

Unlike individually distinctive territorial calls, contact calls, or calls that aid in the recognition of young by their parents, the function or functions of individually distinctive alarm calls (vocalizations produced in response to predators) is not immediately apparent. Yellow-bellied marmots, *Marmota flaviventris*, ground-dwelling sciurid rodents, produce individually distinctive alarm calls. Using an habituation–recovery playback protocol, we show that marmots can perceive differences between the calls of different adult females. We further show that marmots are able to discriminate between at least one broad age–sex category. In contrast to what has been reported in other species, playback of calls from juveniles elicited a greater response (i.e. marmots increased vigilance and suppressed foraging) than did playback of calls from adult females. No other age–sex category led to responses significantly different from adult females. Future studies will seek to understand why individual discriminative abilities exist, but we have shown that individuals are able to identify when young, and presumably vulnerable, marmots are calling, and to respond by engaging in vigilance.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The structure of predator-elicited alarm calls varies along a number of domains. Some species produce functionally referential signals that both covary with predator type and communicate the type of predator present to conspecifics (reviewed in Evans 1997). The structure of other species' alarm vocalizations vary according to the degree of risk a caller experiences when it utters a call, and playback experiments have shown that variation in risk is communicated to perceivers (e.g. Blumstein & Arnold 1995; Blumstein 1999; Warkentin et al. 2001). The alarm calls of some species have been reported to be individually specific (e.g. Owings & Leger 1980; Leger et al. 1984; Cheney & Seyfarth 1990; Nikol'skii & Suchanova 1994; Blumstein & Armitage 1997a; Hare 1998), but there have been few studies that have conducted the required playback experiments (Beecher et al. 1994) to understand whether conspecifics are able to differentiate calls from different individuals (but see Cheney & Seyfarth 1988; Hare 1998; Hare & Atkins 2001).

Unlike individually distinctive group or territorial calls (Conner 1985; Tyack 2000; Hopp et al. 2001), contact calls (Rendall et al. 1996), copulation calls (Semple 2001) or calls that aid in the recognition of young by their parents (Leonard et al. 1997; Jouventin et al. 1999; Insley 2000), the function (or functions) of individually distinctive alarm calls is not immediately apparent. Alarm calls could be individually distinctive to allow individuals to assess the reliability or kinship of callers (Cheney & Seyfarth 1990; Hare 1998; Hare & Atkins 2001). In either of these scenarios, information about caller identity might help a receiver respond appropriately. For instance, if a certain individual frequently calls when no predators are nearby, its calls do not reliably predict the presence of a predator (Haftorn 2000; Hare & Atkins 2001). If responding to alarm calls is costly, animals hearing that caller would not benefit from responding (in a costly way) to an unreliable caller. Additionally, individuals might value the calls from kin more than the calls from nonkin who may not share the same home range. Alternatively, classes of individuals may have structurally distinctive calls when selection has favoured the discrimination between certain classes of callers. For instance, young individuals may call in response to more stimuli, many of which are not threatening to

Correspondence: D. T. Blumstein, Department of Ecology and Evolutionary Biology, 621 Young Drive South, University of California, Los Angeles, CA 90095-1606, U.S.A. (email: [marmots@ucla.edu](mailto:marmots@ucla.edu)).

adults (Cheney & Seyfarth 1990; Hanson & Coss 1997), and it might be advantageous to 'discount' the calls from young.

The yellow-bellied marmot, *Marmota flaviventris*, is a 2–4-kg, moderately social ground-dwelling sciurid rodent (Frase & Hoffmann 1980; Blumstein & Armitage 1999). Individuals live in matrilineal groups with one or more breeding adult female(s) and their juvenile young, as well as with yearling and nonbreeding adult female offspring from previous years (Armitage 1991). Like all marmots (Blumstein & Armitage 1997b), yellow-bellied marmots produce alarm calls, and use these alarm calls to communicate degree of risk by varying the number of calls and the rate at which they are produced (Blumstein & Armitage 1997a).

Yellow-bellied marmot alarm calls are individually distinctive. Previous work has shown that microstructural differences in the calls permit statistical discrimination between individuals at a level greater than expected by chance (Blumstein & Armitage 1997a). Call duration, minimum and maximum frequency, peak frequency and the starting and ending frequencies all were found to covary with individual caller. These and other acoustic variables (that were known to covary with degree of risk a caller experienced when calling) were entered into a stepwise discriminant function model. Duration and maximum frequency together classified 25.8% of calls correctly to caller (compared with an expected 8.3%). More recent analyses with a larger sample size and more variables measured strengthened this conclusion: although there is variation in call structure within individuals, there is more variation between individuals (D. T. Blumstein, unpublished data).

The evolution of individual recognition systems may result from selection on the signaller to have unique calls, and/or on the receiver to differentiate between signallers (e.g. Beecher 1989; Beecher et al. 1989; Beecher & Stoddard 1990). In the first case, we would expect substantial selection on individuals to produce individually distinctive calls, such as seen in the parent–offspring recognition systems of swallows, penguins and seals (Leonard et al. 1997; Jouventin et al. 1999; Insley 2000). In the second case, we would expect selection to act on the discrimination abilities of receivers. Thus, after finding statistical evidence of an association between signaller and call structure, it is reasonable to ask whether marmots are able to discriminate between individual callers and if so, to explore some consequences of this variation.

We conducted a series of experiments designed to determine whether marmots perceive differences between the calls from individuals, and whether the calls from different age and sex classes are differentially evaluated. We used an habituation–recovery protocol to test individual discrimination (Evans 1997). We hypothesized that calls from juveniles (young-of-the-year) might be less meaningful than calls from other age and sex classes, because juvenile marmots, like young vervet monkeys, *Cercopithecus aethiops* (Cheney & Seyfarth 1990) and California ground squirrels, *Spermophilus beecheyi* (Hanson & Coss 1997) appear to alarm-call in response to more stimuli, a subset of which probably represents true threats to adults. We first tested responsiveness to alarm calls from juveniles by comparing them to the responses elicited

from the alarm calls of adult females. Following this, we tested whether calls from nonjuveniles (yearling females and males, adult females and males) elicited different degrees of response.

## METHODS

All studies were conducted with free-living marmots in the East River Valley in and around the Rocky Mountain Biological Laboratory in Gunnison County, Colorado, U.S.A. Marmots at this site have been continuously studied for the past 41 years (Armitage 1991; Schwartz et al. 1998; Armitage & Schwartz 2000). 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 marmots captured in live traps using Audix OM-3xb microphones (frequency response = 40 Hz–20 kHz), 20–40 cm from calling subjects, onto digital audio tape decks (Sony PCM-M1 or Tascam DA-P1) at a sampling rate of 44.1 kHz with 16-bit resolution. Our use of calls recorded on DAT equipment from trapped marmots ensured the highest quality of recorded calls. Moreover, because yellow-bellied marmots communicate risk, not predator type (Blumstein & Armitage 1997a), we also controlled the context (and presumably the degree of risk) that calling marmots experienced. 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 (Charif et al. 1995). Stimuli were then edited and normalized to match peak amplitudes in SoundEdit 16 (Macromedia 1995), and transferred using s/pdif digital transfer protocols back to a Tascam DA-P1 for playback through Advent AV570 Powered Partners (Recoton Home Audio, Benicia, California; frequency response = 40 Hz–20 kHz). To our ears, the playbacks sounded natural and, like in previous experiments (e.g. Blumstein & Armitage 1997a), marmots obviously responded to broadcast alarm calls.

For playback, we focused on the whistle, the most commonly produced yellow-bellied marmot alarm call (Blumstein & Armitage 1997a). Subjects were baited with a handful of Omolene 300 horse feed (Ralston Purina Inc., St Louis, Missouri, U.S.A.) to a location 1–2 m from their burrow. By baiting animals to a set location, and spreading out our playbacks throughout the morning active period, we attempted to target solitary marmots. We observed marmots from distances that did not obviously affect their behaviour (30–100 m depending upon the social group). Alarm calls were broadcast from a speaker hidden 10–14 m from a burrow. Foraging marmots were videotaped using mini-DV digital video equipment (a Cannon GL-1 or a Sony DSR-20) for 1 min before beginning playback and during the playback itself. Because responses to playback may either be ephemeral or may be more appropriately measured over longer time frames, we examined responses on a variety of timescales.

The design and analyses of experiments 1, 3 and 4 (described in detail below) were identical and were within-subject designs where the response of different categories was compared. For these experiments, calls were broadcast over 1 min. We analysed the responses for the initial 10 s and the entire 60 s of playback to examine both the initial response and a sustained response. Experiment 2 employed an habituation–recovery protocol (described in detail below).

Videotapes were scored using JWatcher (Blumstein et al. 2000) where we noted the onset of each bout of foraging, standing quadrupedally and looking, rearing and looking while slouching bipedally on the hind legs, rearing up and looking while standing erect bipedally on the hind legs or toes, self-grooming, walking, running, and time spent in burrow. Focal records were analysed using JWatcher where we calculated the proportion of time allocated to foraging, heightened vigilance (rearing and rearing up and looking), normal vigilance (standing and looking), locomotion (walking and running) and time spent in the burrow. Because not all individuals engaged in all types of vigilance, we combined measures of heightened vigilance and normal vigilance into a total vigilance category. Ultimately, while we visually explored all the data, most formal analyses focused on the time allocated to foraging because all subjects foraged before playback and marmots mainly traded off foraging with vigilance (i.e. locomotion and disappearing into burrows was rare). Our experiments were designed to identify moderate to large effects. We calculated  $d$ , a measure of the effect size of pairwise comparisons, using the pooled standard deviation (Cohen 1988). For ANOVAs, we calculated the partial  $\eta^2$  as a measure of effect size using SPSS. By tradition, small effects have  $d$  values around 0.2, medium effects are around 0.5, and large effects are around 0.8 (Cohen 1988). One way to visualize effect size is to think about the percentage of overlap in two normally distributed distributions with homogeneous variance. An effect size of 0.2 would have only 14.7% of the distributions not overlapping, an effect size of 0.5 implies that 33% of the distributions are not overlapping, and an effect size of 0.8 implies that 47.4% of the distributions are not overlapping (Cohen 1988). Partial  $\eta^2$  is interpreted as the amount of independent variation explained by a variable, after controlling for variation explained by all other variables and is interpreted as one would interpret a squared coefficient of determination.

### Experiment 1: Do Marmots Respond Differently to Calls from Familiar and Unfamiliar Individuals?

To properly design the planned playbacks, we needed to know whether familiarity with an individual caller influenced responsiveness. We selected 10 calls from adult females and used these to create ‘familiar’ and ‘unfamiliar’ playback stimuli. Familiar calls were those from group members and unfamiliar calls were those from marmots in acoustically isolated groups. Both playback stimuli included a 60-s baseline period, followed by four quickly paced

alarm calls (four calls in the first 2 s), followed by a call 8 s later to enable us to measure the initial response, and then four more calls, one every 10 s, for the remainder of the minute to enable us to measure a sustained response. The playback was thus designed to permit us to compare the immediate response to different categories of calls, as well as to look for differential habituation over time.

Calls were broadcast to 10 subjects (eight adult females, two adult males) in five groups (River South Mound, River Spruce Mound, Marmot Meadow Main Talus, Stonefield South Mound and Stonefield Main Mound). Normalized alarm calls were played back at a sound pressure level, SPL, of 100 dB (measured at 1 m from the speaker using a SPER Scientific 840029 digital sound level meter, accuracy of  $\pm 0.7$  dB SPL, weighting level A, peak response). Each subject received, in a random order, both a familiar and unfamiliar playback series in a repeated measures design.

We aimed to have subjects hear only their ‘own’ playback series, but sometimes an individual emerged during another subject’s playback. In these cases, a subject’s second playback series included calls that he/she had already heard. On average, an individual heard a mean  $\pm$  SD of  $1.15 \pm 1.09$  playback series (median = 1.0) before each of their own playbacks. The average  $\pm$  SD interval between their own two playbacks was  $19.4 \pm 9.28$  h (median = 23.6 h).

### Experiment 2: Do Marmots Respond Differently to Calls from Different Individuals?

We used the calls from six adult females to make our playback stimuli for this experiment, and we chose 10 alarm call exemplars from each individual. The 10 whistles from each of the six females were sourced from two bouts of alarm calling and were selected based on their quality. Based on the results from the familiarity experiment, we used the calls from unfamiliar marmots (individuals in other acoustically isolated social groups).

Calls were played back to 19 nonjuvenile subjects (five female yearlings, two male yearlings, eight adult females, four adult males) in the River South Mound, River Spruce Mound, Bench, RMBL town site, Marmot Meadow Aspen Burrow, Marmot Meadow Main Talus, Stonefield South Mound and Stonefield Main Mound social groups. We used an habituation–recovery protocol (Evans 1997) where the goal was to expose each subject to a fixed-length series of different calls from the same individual and then either to ‘probe’ it with either a different set of calls from the same individual, the control calls, or a set of novel calls from a different individual, the test calls. We used a repeated measures design where each subject received both a control series, where the habituation series was followed by the novel calls from the same individual, and a test series, where the same habituation series was followed by the novel calls from the novel individual. These were presented in a random order.

For this experiment, calls were played back (at 98 dB SPL) for 2 min at a constant rate of one call/10 s. This rate was chosen because it is the average long-term rate of alarm calls elicited from dogs, a high-risk stimulus

(D. T. Blumstein, unpublished data). This habituation series consisted of calls from a single individual arranged in a random order. Following the 2-min habituation series, each subject heard, in a random order, the test or control stimuli series (five more calls played back at the same rate of one call/10 s). The test stimuli consisted of five different calls from a different individual, and the control stimuli consisted of five calls from the same individual that were different from those used during the habituation series. The use of multiple calls from multiple individuals, which were assigned randomly to test and control series, allowed us to make general inferences about individual discrimination (McGregor et al. 1992).

The key comparison is how individuals respond to the novel calls. If marmots respond more to the novel calls from a novel individual, we would infer individual discrimination. This is possible because the calls were normalized and thus matched for amplitude. Thus, the only differences between calls were individually specific frequency and time differences, which have been shown previously to permit the statistical discrimination between individuals (Blumstein & Armitage 1997a). Thus, if subjects respond differently to them, we would infer that marmots can discriminate between individuals based solely on the acoustic structure of their alarm calls. Because we provided supplemental food and focused on foraging animals, we specifically predicted that marmots would suppress foraging in response to the test series, but not the control series, if they perceived a difference between calls.

We repeated a series (i.e. rebroadcast it on a separate occasion) if the subject: stopped foraging after playback of the calls and never resumed foraging; moved out of sight into its burrow for the entire duration of the playback; left the experimental area during playback; or if a 'real' predator or other alarming stimulus was present during the playback series (predators sometimes walked by or flew overhead once a playback series was underway).

On average, an individual heard a mean  $\pm$  SD of  $2.00 \pm 2.05$  playback series (median = 1.0) before each of their own playbacks. The average  $\pm$  SD interval between their own two playbacks was  $28.0 \pm 16.01$  h (median = 24.3 h).

Using Wilcoxon matched-pairs signed-ranks tests, we compared the response of subjects to the test and control stimuli in the 10 s, 20 s and 60 s following the playback of the first alarm call in the probe series. We chose these intervals to represent an immediate, intermediate and longer-term measure of responsiveness.

### Experiment 3: Are Marmots Less Responsive to the Calls from Juveniles?

For the third experiment we created two 1-min playback series similar in design to experiment 1. Whistles from four juveniles and four adult females were used for this experiment. From each recorded individual, we selected five high-quality whistle exemplars. Playback stimuli were broadcast to 13 nonjuvenile subjects (eight adult females, three yearling females, two adult males): eight received different exemplars from an unfamiliar adult female on one occasion and different exemplars from an unfamiliar

juvenile on another occasion; five received calls from both familiar juveniles and adults. There was no effect of familiarity (see Results), so we combined the responses to familiar and unfamiliar callers for analysis. These experiments were conducted only in areas where subjects could hear calls from juveniles naturally (River South Mound, River Spruce Mound, Marmot Meadow Aspen Burrow, Marmot Meadow Main Talus, Stonefield South Mound and Stonefield Main Mound).

Calls were broadcast at 98 dB SPL. Videos were scored and analysed as in experiment 1. All subjects responded to the first alarm calls by increasing vigilance and suppressing foraging. Analyses focused on the total time allocated to foraging during the first 10 s and the entire 60 s of playback and were carried out using a Wilcoxon matched-pairs signed-ranks test.

On average, an individual heard a mean  $\pm$  SD of  $1.23 \pm 1.39$  playback series (median = 1.0) before each of their own playbacks. The average  $\pm$  SD interval between their own two playbacks was  $25.6 \pm 14.98$  h (median = 24.0 h).

### Experiment 4: Do Marmots Differentiate Calls from Other Age-Sex Classes?

For the final experiment we created four 1-min playback series that were presented to subjects in a random order. Whistles from four adult females, four yearling females, four adult males, and four yearling males were used for this experiment. From each recorded individual, we selected five high-quality whistle exemplars and broadcast them as in experiment 1. Unfamiliar playback stimuli were broadcast to 16 nonjuvenile subjects (10 adult females, two yearling females, two yearling males, two adult males), each receiving the different exemplars in a counterbalanced design. We conducted these experiments in the following colonies: River South Mound, River Spruce Mound, Bench, Marmot Meadow Aspen Burrow, Marmot Meadow Main Talus and Stonefield Main Mound.

Calls were broadcast at 98 dB SPL. Videos were scored and analysed as in experiment 1. All subjects responded to the first alarm calls by increasing vigilance and suppressing foraging. Analyses focused on the total time allocated to foraging during the first 10 s and the entire 60 s of playback and were carried out using Friedman nonparametric ANOVA.

On average, an individual heard 2.33 a mean  $\pm$  SD of  $\pm 1.89$  playback series (median = 2.0) before each of their own four playbacks. The average  $\pm$  SD interval between their own four playbacks was  $26.0 \pm 23.50$  h (median = 23.7 h).

## RESULTS

### Experiment 1: Do Marmots Respond Differently to Calls from Familiar and Unfamiliar Individuals?

There was no effect of caller familiarity on the proportion of time allocated to foraging within 10 s of



hearing the first alarm call ( $\bar{X}_{\text{familiar}} \pm \text{SE} = 0.19 \pm 0.074$ ;  $\bar{X}_{\text{unfamiliar}} \pm \text{SE} = 0.23 \pm 0.076$ ; Wilcoxon matched-pairs signed-ranks tests:  $Z = -0.30$ ,  $N = 10$ ,  $P = 0.767$ ,  $d = 0.162$ ) or during the entire minute of playback ( $\bar{X}_{\text{familiar}} \pm \text{SE} = 0.40 \pm 0.087$ ;  $\bar{X}_{\text{unfamiliar}} \pm \text{SE} = 0.43 \pm 0.084$ ;  $Z = -0.53$ ,  $N = 10$ ,  $P = 0.594$ ,  $d = 0.094$ ).

We tested for, and found no effect of, playback order on the proportion of time allocated to foraging in the first 10 s following playback ( $Z = -1.01$ ,  $N = 10$ ,  $P = 0.314$ ,  $d = 0.414$ ), or in the entire minute of playback ( $Z = -0.53$ ,  $N = 10$ ,  $P = 0.594$ ,  $d = 0.118$ ).

## Experiment 2: Do Marmots Respond Differently to Calls from Different Individuals?

Marmots suppressed foraging significantly more in the 10 s ( $Z = -2.42$ ,  $N = 19$ ,  $P = 0.016$ ,  $d = 0.979$ ) and 20 s ( $Z = -2.01$ ,  $N = 19$ ,  $P = 0.044$ ,  $d = 0.653$ ) but not the 60 s ( $Z = -1.37$ ,  $N = 19$ ,  $P = 0.171$ ,  $d = 0.331$ ) following playback of test calls (i.e. calls from a novel individual) compared with the control calls (i.e. novel call exemplars from the same individual from whom they had just heard 11 different alarm calls; Fig. 1). Thus, subjects showed an ability to distinguish between individuals based on their calls alone.

We found no significant effect of treatment order on time allocated to foraging in the 10 s, 20 s, or 60 s during the probe phase ( $Z_{10\text{ s}} = -0.72$ ,  $N = 19$ ,  $P = 0.469$ ,  $d = 0.225$ ;  $Z_{20\text{ s}} = -1.77$ ,  $N = 19$ ,  $P = 0.077$ ,  $d = 0.455$ ;  $Z_{60\text{ s}} = -1.01$ ,  $N = 19$ ,  $P = 0.314$ ,  $d = 0.230$ ).

Additional results strengthen the interpretation of the results of our manipulation. We report the results for the 10-s and 20-s analyses for which there were significant differences (see above). Marmots initially responded and then habituated to the habituation series; they foraged significantly less compared with baseline in the 10 s after hearing the first call and in the 20 s after hearing the first two calls of the habituation series (10 s:  $Z_{\text{control}} = -2.62$ ,  $P = 0.009$ ,  $d = 0.958$ ;  $Z_{\text{test}} = -3.82$ ,  $P < 0.001$ ,  $d = 1.970$ ; 20 s:  $Z_{\text{control}} = -2.25$ ,  $P = 0.024$ ,  $d = 0.701$ ;

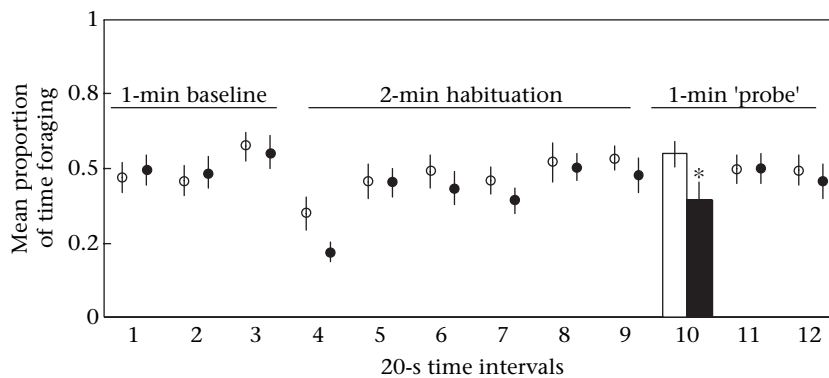
$Z_{\text{test}} = -3.74$ ,  $P < 0.001$ ,  $d = 1.700$ ) but, by the end of the habituation series, had returned to baseline levels of foraging (10 s:  $Z_{\text{control}} = -1.09$ ,  $P = 0.277$ ,  $d = 0.273$ ;  $Z_{\text{test}} = -0.24$ ,  $P = 0.809$ ,  $d = 0.021$ ; 20 s:  $Z_{\text{control}} = -0.89$ ,  $P = 0.376$ ,  $d = 0.181$ ;  $Z_{\text{test}} = -0.60$ ,  $P = 0.546$ ,  $d = 0.151$ ). When probed with novel alarm call exemplars in the control series, in the 10-s analysis, we found that time allocated to foraging increased from baseline ( $Z_{\text{control}} = -2.25$ ,  $P = 0.024$ ,  $d = 0.690$ ), but in the 20-s analysis, time allocated to foraging was not significantly different from baseline ( $Z_{\text{control}} = -1.09$ ,  $P = 0.277$ ,  $d = 0.254$ ). However, time allocated to foraging during the test series decreased significantly from baseline levels in both analyses (10 s:  $Z_{\text{test}} = -1.97$ ,  $P = 0.049$ ,  $d = 0.483$ ; 20 s:  $Z_{\text{test}} = -2.50$ ,  $P = 0.013$ ,  $d = 0.632$ ).

## Experiment 3: Are Marmots Less Responsive to the Calls from Juveniles?

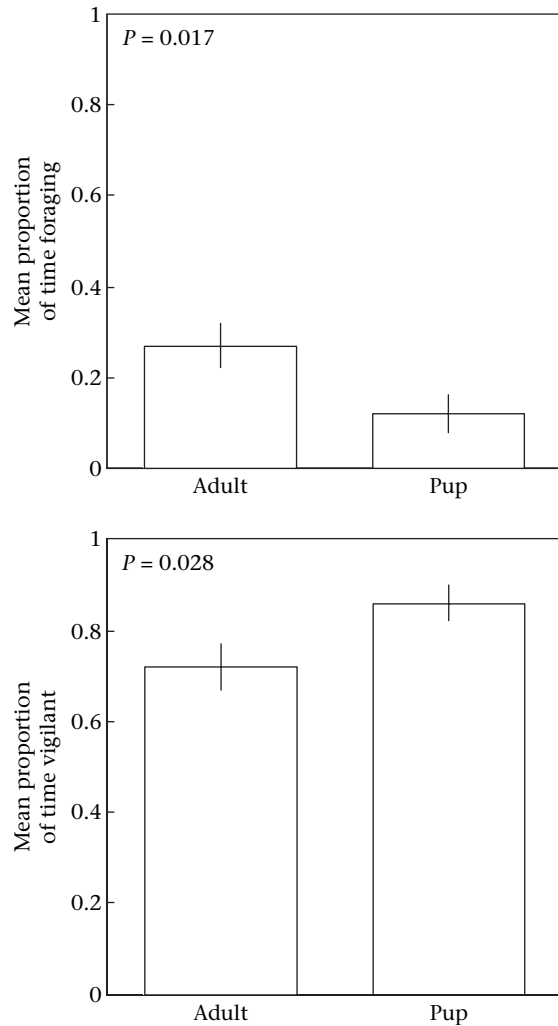
In the 10 s following playback, all subjects immediately suppressed foraging but there was no difference in the response to a call from a juvenile compared to the call from an adult ( $Z = -1.35$ ,  $N = 13$ ,  $P = 0.176$ ,  $d = 0.616$ ). However, during the entire 60 s of playback, subjects suppressed foraging more while hearing calls from juveniles than while hearing calls from adults ( $Z = -2.51$ ,  $N = 13$ ,  $P = 0.012$ ,  $d = 0.765$ ; Fig. 2). This result implies that there was differential response over time; after hearing a juvenile call, animals suppressed foraging for a longer period. During the 60-s playback period, marmots increased total vigilance while hearing calls from juveniles compared with adults ( $Z = -2.35$ ,  $N = 12$  because one subject disappeared into its burrow following playback and was excluded,  $P = 0.019$ ,  $d = 0.342$ ).

We found no effect of playback order on time allocated to foraging in the first 10 s following playback ( $Z = -1.01$ ,  $N = 13$ ,  $P = 0.314$ ,  $d = 0.002$ ) or in the entire minute of playback ( $Z = -0.53$ ,  $N = 13$ ,  $P = 0.594$ ,  $d = 0.114$ ).

Consistent with the results of experiment 1, there was no effect of familiarity on time allocated to foraging during the



**Figure 1.** Mean  $\pm$  SE proportion of time yellow-bellied marmots allocated to foraging in 20-s time bins during a 1-min baseline period, 2-min habituation period and 1-min 'probe' period for control series (○) and test series (●). During the 1-min probe interval, individuals heard novel calls from either the same individual (□) or a novel individual (■). The key comparison was the difference in response to the control and test calls during the probe period. The histogram shows the results from the first 20 s of the probe period (\* $P = 0.016$ , Wilcoxon matched-pairs signed-ranks test; see text for details). Similar results were obtained when analysed with 10-s time bins (see text for details).

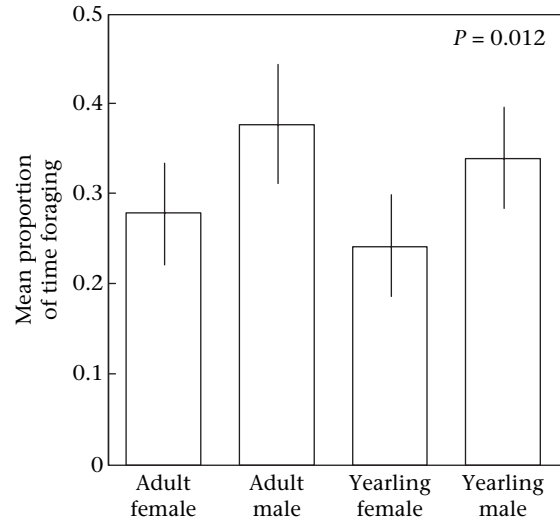


**Figure 2.** Mean  $\pm$  SE proportion of time yellow-bellied marmots allocated to foraging and vigilance during the 60 s while hearing calls from juveniles or adults. Significance determined by a Wilcoxon matched-pairs signed-ranks test.

first 10 s of playback (repeated measures ANOVA, one between- and one within-subjects factors:  $F_{1,11} = 0.322$ ,  $P = 0.582$ , partial  $\eta^2 = 0.028$ ), or during the 60 s of playback ( $F_{1,11} = 1.21$ ,  $P = 0.296$ , partial  $\eta^2 = 0.099$ ). Nor was there an interaction between stimulus and familiarity (10 s:  $F_{1,11} = 0.127$ ,  $P = 0.728$ , partial  $\eta^2 = 0.011$ ; 60 s:  $F_{1,11} = 0.181$ ,  $P = 0.679$ , partial  $\eta^2 = 0.016$ ).

#### Experiment 4: Do Marmots Differentiate Calls from Other Age–Sex Classes?

In the 10 s following playback, all subjects immediately suppressed foraging but there was no difference in the response to the four age–sex classes (Friedman ANOVA:  $\chi^2_3 = 4.72$ ,  $N = 16$ ,  $P = 0.194$ , partial  $\eta^2 = 0.192$ ). Overall, there was a small effect of age–sex class on time allocated to foraging during the 1 min of playback ( $\chi^2_3 = 10.92$ ,  $N = 16$ ,  $P = 0.012$ , partial  $\eta^2 = 0.127$ ). However, after using a Bonferroni correction for multiple



**Figure 3.** Mean  $\pm$  SE proportion of time yellow-bellied marmots allocated to foraging during the entire 60 s while hearing calls from different age–sex classes. Significance determined by Friedman nonparametric ANOVA. Similar results were obtained for the initial 10-s interval (see text for details).

comparisons, there were no significant differences between pairs of age–sex classes ( $P$  critical = 0.0083; uncorrected  $P$  values ranged from  $P = 0.047$ ,  $d = 0.436$ , for the comparison between yearling males and females, to  $P = 0.408$ ,  $d = 0.151$ , for the comparison between yearling males and adult males; Fig. 3). There was a moderate, but not significant, effect of sex when yearling and adults of each sex were combined and compared (Wilcoxon matched-pairs signed-ranks tests:  $Z = -1.71$ ,  $N = 16$ ,  $P = 0.088$ ,  $d = 0.471$ ).

There was no effect of playback order on our measures of responsiveness (Friedman ANOVA on duration of time spent foraging: the first 10 s of the playback period:  $\chi^2_3 = 5.53$ ,  $P = 0.137$ , partial  $\eta^2 = 0.124$ ,  $N = 16$ ; entire 1-min playback period:  $\chi^2_3 = 4.94$ ,  $P = 0.176$ , partial  $\eta^2 = 0.158$ ,  $N = 16$ ).

## DISCUSSION

Taken together our results suggest that yellow-bellied marmots are able to distinguish between the calls of individuals and are most responsive to calls from juveniles. The results of the first experiment suggest that marmots do not differentiate between the calls of familiar and unfamiliar individuals. Thus, to eliminate potential problems using calls from familiar individuals (such as a past history of unreliable calls from certain individuals), in all but one experiment, we used calls only from unfamiliar individuals. The results of the second experiment provide the first evidence that an adult sciurid rodent is able to differentiate individuals solely on the basis of their alarm calls. This is a strong statement made possible by the rigorous experimental design. Individual discrimination of alarm calls has only been found in two other species, vervet monkeys (Cheney & Seyfarth 1988)

and juvenile Richardson's ground squirrels, *Spermophilus richardsonii* (Hare 1998). This finding is a prerequisite for subsequent studies of other types of distinctions marmots can make, as well as for studies of the function of such individually distinctive calls.

Individual recognition is required for reciprocal altruism to function so that defectors can be identified and punished (Trivers 1971; Wilkinson 2002). The results from experiment 2 show that individuals can be quickly classified as 'unreliable'; marmots quickly habituated to our broadcast calls that were not associated with an actual predator. A study of Richardson's ground squirrels suggests that this type of categorization may persist over multiple days (Hare & Atkins 2001). However, whether marmots use this categorization or, more generally, use this discrimination ability in a reciprocal calling system remains unknown. While not formally examined, we are aware of no evidence that any rodents 'take turns' calling, or that when surrounded by unreliable callers, stop calling (Blumstein, in press). Reciprocity is thus unlikely to explain the evolution of individual discrimination abilities in marmots, and perhaps more generally in alarm-calling systems.

It is possible that individual discrimination abilities help a receiver determine whether there are multiple callers. Marmots utter alarm calls in situations when we cannot identify the stimulus, and some individuals call in response to nonthreatening stimuli (e.g. deer). From a receiver's perspective, the likelihood of a predator being present is much greater when two or more individuals give alarm calls. Discriminating between callers should not be based solely on amplitude differences because amplitude communicates relative risk (Blumstein & Armitage 1997a; Blumstein, in press). Thus, discriminating between individuals based on microstructural variation in the frequency and time domains might be important.

It is possible that discrimination evolved to differentiate calls from conspecifics and heterospecifics. Although sympatric species may respond to each other's alarm calls (Blumstein & Armitage 1997a; Shriner 1998), the reliability, and thus the value, of heterospecific callers probably varies (Shriner 1998). Specifically, if a small species has more predators than a larger species, the smaller species will be more likely to alarm-call in situations that are not threatening to the larger species. Thus, from the larger species' perspective, calls from the smaller species are less reliable. This question requires testing. Because marmot alarm calls are not used in territorial defence (but see suggestions about the congeneric alpine marmot, *M. marmota*, by Bopp 1955) or mate assessment, but rather in situations that are threatening to the caller, alternative functions are more likely.

Discrimination abilities may also have evolved to allow marmots to differentiate between classes of callers, such as juveniles or adults, or perhaps males and females. Selection for such discriminative abilities (Beecher et al. 1989) might be expected if the reliability of classes of callers varies (e.g. Gouzoules et al. 1996) or if there are differential benefits from responding to the calls of certain classes of individuals.

The results of the third experiment show that marmots treat calls from juveniles as more salient than calls from

adults. Upon hearing a series of alarm calls from juveniles, marmots suppressed foraging significantly more than after hearing a series of calls from adults. This was an unexpected result. We predicted that calls from adults would be more salient than calls from juveniles because adult California ground squirrels (Hanson & Coss 2001), steppe marmots, *Marmota bobac* (Nesterova 1996), vervet monkeys (Seyfarth & Cheney 1980, 1986), and bonnet macaques, *Macaca radiata* (Ramakrishnan & Coss 2000) 'devalue' calls from juveniles. Instead, we found the opposite. Because all social groups in our experiments only had weaned juveniles, any novelty of hearing calls from juveniles cannot explain this result. Because calls were played back at a constant amplitude, microstructural differences between adult and juvenile calls can be the only explanation for the different responses. Thus, we conclude that marmots can indeed distinguish and differentially evaluate the risk associated with at least the calls of juveniles from those of adult females. To our ears, calls from juveniles are distinguished from adult calls by their relatively high pitch. Future studies will focus specifically on identifying the microstructural differences between adult and juvenile calls and their salience.

Functionally, marmots may be more alarmed by calls from juveniles because calls from juveniles are likely to be produced by offspring or other young relatives in a matriline. A previous study suggested that yellow-bellied marmots produce alarm calls to warn their vulnerable young (Blumstein et al. 1997). Our current results suggest that they may have evolved an ability to respond specifically to any vulnerable young by engaging in vigilance.

The results from the fourth experiment suggest that marmots do not evaluate a specific level of risk to calls from different age-sex classes (juveniles notwithstanding). This suggests that individual discrimination abilities, if used by marmots, are not simply used to devalue calls from unreliable yearling males (who, when being evicted from their natal groups, are likely to call in 'social' situations; Blumstein et al. 1997) and may therefore be less reliable in predicting predator presence than others, but rather are possibly used to discriminate between individuals. Hare & Atkins (2001) found that juvenile Richardson's ground squirrels habituate selectively to unreliable callers. We know from the second experiment that marmots can habituate quickly to calls that are not associated with a visible threat. Future experiments will be required to determine whether and how marmots specifically devalue reliable and unreliable callers.

### Acknowledgments

We dedicate this paper to Ken Armitage on the occasion of his 79th birthday. Ken has generously shared equipment, laboratory space and data on marmot kinship and matriline structure, and also provided considerable advice about working with yellow-bellied marmots at RMBL. For help trapping and marking animals we thank: Judy Daniels, Amanda Nicodemus, Arpat Ozgul, Findley Ransler, Mona Seymour and Brett Woods. Chris Evans provided extremely helpful advice on the proper design

and analysis of discrimination experiments. Research protocols were approved by both the Rocky Mountain Biological Laboratory and by the University of California Los Angeles (UCLA) Animal Research Committee (No. 2000-148-01 approved on 14 February 2001 and No. 2001-191-01 approved on 25 April 2002). Marmots were trapped under permits issued by the Colorado Division of Wildlife. Partial support for this project came from the UCLA Academic Senate Council on Research; additional support came from the UCLA Division of Life Sciences.

## References

- Armitage, K. B.** 1982. Yellow-bellied marmot. In: *CRC Handbook of Census Methods for Terrestrial Vertebrates* (Ed. by D. E. Davis), pp. 148–149. Boca Raton, Florida: CRC Press.
- Armitage, K. B.** 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics*, **22**, 379–407.
- Armitage, K. B. & Schwartz, O. A.** 2000. Social enhancement of fitness in yellow-bellied marmots. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 12149–12152.
- Beecher, M. D.** 1989. Signalling systems for individual recognition: an information theory approach. *Animal Behaviour*, **38**, 248–261.
- Beecher, M. D. & Stoddard, P. K.** 1990. The role of bird song and calls in individual recognition: contrasting field and laboratory perspectives. In: *Comparative Perception. Vol. II: Complex Sounds* (Ed. by M. Berkley & W. C. Stebbins), pp. 375–408. New York: J. Wiley.
- Beecher, M. D., Loesche, P., Stoddard, P. K. & Medvin, M. B.** 1989. Individual recognition by voice in swallows: signal or perceptual adaptation? In: *The Comparative Psychology of Audition: Perceiving Complex Sounds* (Ed. by R. J. Dooling & S. H. Hulse), pp. 277–292. Hillsdale, New Jersey: L. Erlbaum.
- Beecher, M. D., Campbell, S. E. & Burt, J. M.** 1994. Song perception in the song sparrow: birds classify by song type but not by singer. *Animal Behaviour*, **47**, 1343–1351.
- Blumstein, D. T.** 1999. Alarm calling in three species of marmots. *Behaviour*, **136**, 731–757.
- Blumstein, D. T.** In press. The evolution of alarm communication: structure, function, and the puzzle of apparently altruistic calling in rodents. In: *Rodent Societies* (Ed. by J. O. Wolff & P. W. Sherman). Chicago: University of Chicago Press.
- 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. & Armitage, K. B.** 1999. Cooperative breeding in marmots. *Oikos*, **84**, 369–382.
- Blumstein, D. T. & Arnold, W.** 1995. Situational-specificity in alpine-marmot alarm communication. *Ethology*, **100**, 1–13.
- Blumstein, D. T., Steinmetz, J., Armitage, K. B. & Daniel, J. C.** 1997. Alarm calling in yellow-bellied marmots: II. Kin selection or parental care? *Animal Behaviour*, **53**, 173–184.
- Blumstein, D. T., Evans, C. S. & Daniel, J. C.** 2000. *JWatcher 0.9. An Introductory User's Guide*. <http://www.marmotburrow.ucla.edu>.
- Bopp, P.** 1955. Der schrei des murmelieres als akustische territoriumsmarkierung. *Säugetierkundliche Mitteilungen*, **3**, 28.
- Charif, R. A., Mitchell, S. & Clark, C. W.** 1995. *Canary 1.2 User's Manual*. Ithaca, New York: Cornell Laboratory of Ornithology.
- Cheney, D. L. & Seyfarth, R. M.** 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, **36**, 477–486.
- Cheney, D. L. & Seyfarth, R. M.** 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.
- Cohen, J.** 1988. *Statistical Power Analysis for the Behavioral Sciences*. 2nd edn. Hillsdale, New Jersey: L. Erlbaum.
- Conner, D. A.** 1985. The function of the pika short call in individual recognition. *Zeitschrift für Tierpsychologie*, **67**, 131–143.
- Evans, C. S.** 1997. Referential communication. *Perspectives in Ethology*, **12**, 99–143.
- Frase, B. A. & Hoffmann, R. S.** 1980. *Marmota flaviventris*. *Mammalian Species*, **135**, 1–8.
- Gouzoules, H., Gouzoules, S. & Miller, K.** 1996. Skeptical responding in rhesus monkeys (*Macaca mulatta*). *International Journal of Primatology*, **17**, 549–568.
- Haftorn, S.** 2000. Contexts and possible functions of alarm calling in the willow tit, *Parus montanus*; the principle of 'better safe than sorry'. *Behaviour*, **137**, 437–449.
- Hanson, M. T. & Coss, R. G.** 1997. Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to avian and mammalian predators. *Journal of Comparative Psychology*, **111**, 174–184.
- Hanson, M. T. & Coss, R. G.** 2001. Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. *Ethology*, **107**, 259–275.
- Hare, J. F.** 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. *Animal Behaviour*, **55**, 451–460.
- Hare, J. F. & Atkins, B. A.** 2001. The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral Ecology and Sociobiology*, **51**, 108–112.
- Hopp, S. L., Jablonski, P. G. & Brown, J. R.** 2001. Recognition of group membership by voice in Mexican jays, *Aphelocoma ultramarina*. *Animal Behaviour*, **62**, 297–303.
- Insley, S. J.** 2000. Long-term vocal recognition the northern fur seal. *Nature*, **406**, 404–405.
- Jouventin, P., Aubin, T. & Lengagne, T.** 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Animal Behaviour*, **57**, 1175–1183.
- Leger, D. W., Berney-Key, S. D. & Sherman, P. W.** 1984. Vocalizations of Belding's ground squirrels (*Spermophilus beldingi*). *Animal Behaviour*, **32**, 753–764.
- Leonard, M. L., Horn, A. G., Brown, C. R. & Fernandez, N. J.** 1997. Parent-offspring recognition in tree swallows, *Tachycineta bicolor*. *Animal Behaviour*, **54**, 1107–1116.
- 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 Studies of Animal Communication: Problems and Prospects* (Ed. by P. K. McGregor), pp. 1–9. New York: Plenum.
- Macromedia** 1995. *SoundEdit 16*. San Francisco: Macromedia.
- Nesterova, N. L.** 1996. Age-dependent alarm behaviour and response to alarm call in bobac marmots (*Marmota bobac* Müll.). In: *Biodiversity in Marmots* (Ed. by M. Le Berre, R. Ramousse & L. Le Guelte), pp. 181–186. Moscow-Lyon: International Network on Marmots.
- Nikol'skii, A. A. & Suchanova, M. V.** 1994. Individual variability of alarm call in steppe marmot (*Marmota bobac* Müll., 1776). In: *Actual Problems of Marmots Investigation* (Ed. by V. Y. Rumiantsev), pp. 169–181. Moscow: ABF.



- Owings, D. H. & Leger, D. W. 1980. Chatter vocalizations of California ground squirrels: predator- and social-role specificity. *Zeitschrift für Tierpsychologie*, **54**, 163–184.
- Ramakrishnan, U. & Coss, R. G. 2000. Age differences in the responses to adult and juvenile alarm calls by bonnet macaques (*Macaca radiata*). *Ethology*, **106**, 131–144.
- Rendall, D., Rodman, P. S. & Emond, R. E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.
- Schwartz, O. A., Armitage, K. B. & Van Vuren, D. H. 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology*, **246**, 337–346.
- Seyfarth, R. M. & Cheney, D. L. 1980. The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift für Tierpsychologie*, **56**, 25–32.
- Seyfarth, R. M. & Cheney, D. L. 1986. Vocal development in vervet monkeys. *Animal Behaviour*, **34**, 1640–1658.
- Semple, S. 2001. Individuality and male discrimination of female copulation calls in the yellow baboon. *Animal Behaviour*, **61**, 1023–1028.
- Shriner, W. M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. *Animal Behaviour*, **55**, 529–536.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35–57.
- Tyack, P. L. 2000. Dolphins whistle a signature tune. *Science*, **289**, 1310–1311.
- Warkentin, K. J., Keeley, A. T. H. & Hare, J. F. 2001. Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. *Canadian Journal of Zoology*, **79**, 569–573.
- Wilkinson, G. S. 2002. Reciprocal altruism. In: *Encyclopedia of Evolution* (Ed. by M. Pagel), pp. 985–990. New York: Oxford University Press.