

Do yellow-bellied marmots respond to predator vocalizations?

Daniel T. Blumstein · Louise Cooley ·
Jamie Winternitz · Janice C. Daniel

Received: 26 September 2006 / Revised: 9 July 2007 / Accepted: 17 August 2007 / Published online: 19 September 2007
© Springer-Verlag 2007

Abstract We conducted four experiments to determine whether yellow-bellied marmots, *Marmota flaviventris*, discriminate among predator vocalizations, and if so, whether the recognition mechanism is learned or experience-independent. First, we broadcast to marmots the social sounds of coyotes, *Canis latrans*, wolves, *Canis lupus*, and golden eagles, *Aquila chrysaetos*, as well as conspecific alarm calls. Coyotes and eagles are extant predators at our study site, while wolves have been absent since the mid-1930s. In three follow-up experiments, we reversed the eagle call and presented marmots with forward and reverse calls to control for response to general properties of call structure rather than those specifically associated with eagles, we tested for novelty by comparing responses to familiar and unfamiliar birds, and we tested for the duration of predator sounds by comparing a wolf howl (that was much longer than the coyote in the first experiment) with a long coyote howl of equal duration to the original wolf. Marmots suppressed foraging and increased looking most after presentation of the conspecific alarm call and least after that of the coyote in the first experiment, with moderate responses to wolf and eagle calls. Marmots responded more to the forward eagle call than the reverse call, a finding

consistent with a recognition template. Marmots did not differentiate vocalizations from the novel and familiar birds, suggesting that novelty itself did not explain our results. Furthermore, marmots did not differentiate between a wolf howl and a coyote howl of equal duration, suggesting that the duration of the vocalizations played a role in the marmots' response. Our results show that marmots may respond to predators based solely on acoustic stimuli. The response to currently novel wolf calls suggests that they have an experience-independent ability to identify certain predators acoustically. Marmots' response to predator vocalizations is not unexpected because 25 of 30 species in which acoustic predator discrimination has been studied have a demonstrated ability to respond selectively to cues from their predators.

Keywords Acoustic predator recognition · Predation risk assessment · Yellow-bellied marmots

Introduction

Individual animals use sensory cues in a variety of modalities (e.g., olfactory, visual, and acoustic) to assess predation risk and make subsequent behavioral decisions (Lima and Dill 1990). In some cases, individuals respond appropriately to these cues the first time they encounter them; in other cases, animals must learn to respond to stimuli (Berger et al. 2001; Griffin et al. 2001; Gil-da-Costa et al. 2003). Different modalities may employ different mechanisms. Visual predator recognition is likely to be relatively experience independent because visual cues are reliable predictors of predator presence and because the evolution of predator form is convergent (Blumstein et al. 2000a). Olfactory cues can be misleading in that they

Communicated by P. Bednekoff

D. T. Blumstein (✉) · J. Winternitz · J. C. Daniel
Department of Ecology and Evolutionary Biology,
University of California,
621 Young Drive South,
Los Angeles, CA 90095-1606, USA
e-mail: marmots@ucla.edu

L. Cooley
The Rocky Mountain Biological Laboratory,
Crested Butte, CO, USA

remain once an animal is no longer in the area (Bouskila and Blumstein 1992). Evidence from a variety of fish suggests that olfactory recognition typically involves learning, whereas visual predator recognition skills are largely based on unlearned predispositions (Kelley and Magurran 2003; Kristensen and Closs 2004). Although acoustic cues reliably predict the presence of a predator, acoustic recognition may depend on relatively specific cues because predator vocalizations are structurally divergent (Blumstein et al. 2000a). Thus, it seems likely that the recognition mechanism should involve learning (Berger et al. 2001; Gil-da-Costa et al. 2003). Although predators are usually quiet while hunting, individual prey have chances to detect predators when they are not hunting because predators often live and socialize in their vicinity. A systematic literature review suggests that many species of birds and mammals do respond to the sounds of their predators or to predator-related sounds (see below). Given the general ability of a variety of species to recognize predators acoustically, we aimed to determine whether yellow-bellied marmots, *Marmota flaviventris*, are capable of acoustic predator recognition, and if so, to identify the mechanisms involved.

This topic is theoretically interesting (Lima and Dill 1990; Caro 2005), as well as having applied value in conservation (Berger 1998; Jones et al. 2004). With the widespread contraction of large carnivore ranges over the last century (Pyare et al. 2004), many former prey species have fewer significant predators (Berger et al. 2001). Predator recognition capacities may be lost or not, depending on the mechanism used. Some species retain effective responses to predators after long periods of isolation (Blumstein et al. 2000a; Blumstein 2006), while others lose their responsiveness. If responding to non-predators as though they are a threat when no predators are present is costly, then recognition abilities may be selected against. Once recognition abilities are lost, prey will be vulnerable to former predators upon re-contact (Coss 1999). If the predator recognition is learned, however, prey should be able to adapt quickly to the presence of reintroduced predators (Griffin et al. 2000). Berger et al. (2001) found that acoustic predator recognition in moose, *Alces alces*, is learned; naïve moose are capable of processing information about novel predators within a single generation. Rapidly learning to avoid newly reintroduced predators may be a key component to the survival of many endangered prey species over the next several centuries, and such learning may be founded upon unlearned predispositions.

Our study had several parts. We first conducted a literature review to determine the taxonomic distribution of acoustic predator recognition. We did so because many people's first response to this topic is "predators are silent while hunting". Our results demonstrate that prey's ability

to respond to predators is a widespread phenomenon and that marmots should respond to the sounds of their predators. We then conducted a series of playback experiments designed to determine the degree to which yellow-bellied marmots discriminate among and respond to the vocalizations of coyotes, *Canis latrans*, wolves, *Canis lupus*, and golden eagles, *Aquila chrysaetos*. The ability of marmots to respond to wolf calls is topical because wolves have been reintroduced into Wyoming, Idaho, Montana, New Mexico, and Arizona by the US Fish and Wildlife Service over the past decade and may disperse into Colorado within the next few years (Colorado Division of Wildlife 2004). A young wolf from Yellowstone was found dead near Denver, CO in early June, 2004, a dispersal of nearly 500 miles, if she moved on her own (Elliott 2004). The effect of wolf recolonization on marmot populations depends to some extent on the marmots' ability to respond to wolves as threatening. While wolf and coyote calls are somewhat similar in structure, wolves are currently extinct in our area, while coyotes are extant. A response to wolves as well as to playbacks of coyotes and eagles might suggest that acoustic predator recognition requires no prior experience in marmots. Response to coyotes and eagles, but not to wolves, could be interpreted as either loss of an experience-independent mechanism, or the existence of a learned mechanism.

Literature review

Methods

We conducted a literature review to document the phylogenetic distribution of species that respond to the sounds of their predators and to reconstruct the evolution of acoustic predator recognition. We used the 1969–2004 Biosis database to search the key phrases "acoustic predator recognition," "predator vocalizations," "predator vocalisations", "response to predators," and "playback experiments and predation." We then used the Web of Science to find additional papers that cited the initial set of articles. We determined relationships between species using McKenna and Bell (1997) and Wilson and Reeder (1993) and created a partial phylogeny with MacClade 4.03 (Maddison and Maddison 2001) of the 30 species for which acoustic predator recognition had been studied. Using parsimony, we reconstructed the evolution of acoustic predator recognition.

Results

Twenty-five of 30 species of birds and mammals, for which playback experiments have been conducted to study

acoustic predator recognition, responded to vocalizations from their predators (Fig. 1, Table 1). A reconstruction using parsimony suggests that this is an ancestral trait in birds and mammals. Moreover, because the clade including yellow-bellied marmots (i.e., the rodents *Spermophilus*, *Jaculus*, and *Eliomys*) all had the ability to respond to predator vocalizations, we predicted that yellow-bellied marmots would be able to respond to the vocalizations of at least some of their predators.

Experiment 1—predator playback

Methods

We conducted this and the following playback experiments with free-living marmots in the East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL), in Gunnison County, CO, USA. The first two

experiments were conducted during the summer of 2004 (May–July); the third experiment was conducted in 2005, and the fourth experiment was conducted in 2006. Marmots were live-trapped and individually marked with ear tags (for permanent identification) and non-toxic fur dye (for identification from a distance, Armitage 1982) as part of a long-term study of the East River Valley marmot population.

We observed the reaction of foraging marmots to playback of golden eagle, wolf, and coyote social vocalizations, as well as to playback of conspecific alarm calls. The populations under observation are currently exposed to coyote and golden eagle predation (Van Vuren 2001). Wolves were mostly eradicated in Colorado by the mid-1930s, with five individuals reported for all Colorado National Forests in 1941 (Warren 1942). Marmots are known to respond to conspecific alarm calls, which are associated with potentially threatening stimuli; marmot alarm calls communicate risk, but not predator type (Blumstein and Armitage 1997). Blumstein and Armitage (1997) found that marmots do not respond to familiar non-predator avian contact calls. Thus, to minimize the number of playbacks heard by subjects and to reduce the overall risk of habituation to our experiment, we did not include a familiar, non-predator control stimulus in this first experiment. We interpreted any change from baseline time allocation as a response to the acoustic stimulus.

We used two exemplars of each type of predator call (sample rate 44.1 kHz, 16-bit amplitude encoding; Fig. 2), and tested for exemplar-specific effects on responsiveness (there were none). Calls (coyote and wolf howls and eagle territorial calls) were obtained from commercial sound archives and were not recorded locally. We recorded conspecific alarm calls using Audix OM-3xb microphones (frequency response=40 Hz–20 kHz) placed 20–40 cm from subjects, onto digital audio tape decks (Sony PCM-M1 or Tascam DA-P1) sampling at 44.1 kHz with 16-bit resolution from marmots contained in live traps. Alarm calls were acquired or transferred through a MOTU 828 Firewire external digital board (Mark of the Unicorn, Cambridge, MA, USA) to a Macintosh PowerBook G4 (Apple Computer, Cupertino, CA, USA) using Canary 1.2 (Charif et al. 1995). All stimuli were then edited and normalized to match peak amplitudes in SoundEdit 16 (Macromedia 1995) and transferred as uncompressed AIF files for playback using an iPod (Apple Computer) and through a powered speaker (Advent AV 570, Recoton Home Audio, Benici, CA, USA). We used eight different four-note conspecific alarm call exemplars (a relatively high-risk alarm) to ensure that marmots heard alarm calls from unfamiliar animals from different social groups.

Marmots were baited with a handful of Omolene 300 horse feed (Ralston Purina, St. Louis, MO, USA) to a

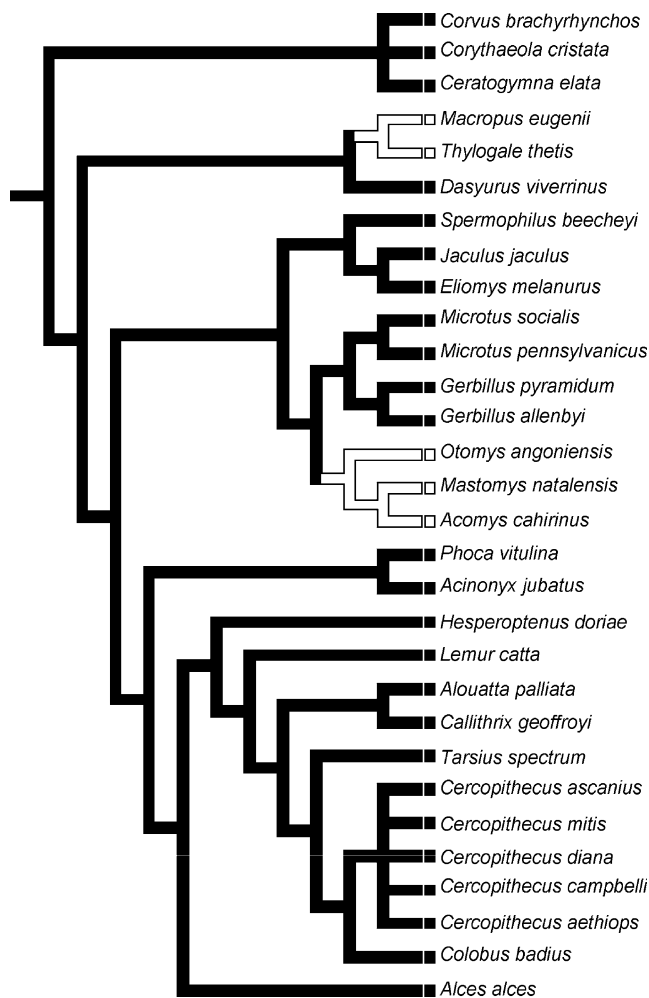


Fig. 1 Parsimonious reconstruction of acoustic predator recognition abilities (black=demonstrated ability to identify predators, white=failed to identify predators). Data come from playback studies designed to test acoustic predator discrimination

Table 1 Species for which playback studies have been performed to test for acoustic predator discrimination

Latin name	Common name	References
<i>Corvus</i>	American crow	Hauser and Caffrey 1994
<i>brachyrhynchos</i>		
<i>Corythaeola cristata</i>	Great blue turaco	Hauser and Wrangham 1990
<i>Ceratogymna elata</i>	Yellow-casqued hornbill	Rainey et al. 2004
<i>Macropus eugenii</i>	Tammar wallaby	Blumstein et al. 2000a
<i>Thylogale thetis</i>	Red-necked pademelon	Blumstein et al. 2002
<i>Dasyurus viverrinus</i>	Tasmanian eastern quoll	Jones et al. 2004
<i>Spermophilus</i>	California ground squirrel	Swaisgood et al. 1999
<i>beecheyi</i>		
<i>Jaculus jaculus</i>	Lesser Egyptian jerboa	Hendrie et al. 1998
<i>Eliomys melanurus</i>	Asian garden dormouse	Hendrie et al. 1998
<i>Microtus socialis</i>	Social vole	Eilam et al. 1999; Hendrie et al. 1998
<i>Microtus</i>	Meadow vole	Pusenius and Ostfeld 2000
<i>pennsylvanicus</i>		
<i>Gerbillus pyramidum</i>	Greater Egyptian gerbil	Abramsky et al. 1996
<i>Gerbillus allenbyi</i>	Allenby's gerbil	Abramsky et al. 1996
<i>Otomys angoniensis</i>	Angoni Vlei rat	Crafford et al. 1999
<i>Mastomys natalensis</i>	Natal multimammate mouse	Crafford et al. 1999
<i>Acomys cahirinus</i>	Cairo spiny mouse	Eilam et al. 1999; Hendrie et al. 1998
<i>Phoca vitulina</i>	Harbour seal	Deecke et al. 2002
<i>Acinonyx jubatus</i>	Cheetah	Durant 2000
<i>Hesperoptenus doriae</i>	False serotine bat	Petrzelkova and Zukal 2001
<i>Lemur catta</i>	Ring-tailed lemur	Karpany and Grella 2001; Macedonia and Yount 1991
<i>Alouatta palliata</i>	Mantled howler monkey	Gil-da-Costa et al. 2003
<i>Callithrix geoffroyi</i>	Geoffroy's marmoset	Searcy and Caine 2003
<i>Tarsius spectrum</i>	Spectral tarsier	Gursky 2002, 2003
<i>Cercopithecus ascanius</i>	Red-tailed monkey	Hauser and Wrangham 1990; Treves 1999
<i>Cercopithecus mitis</i>	Blue monkey	Hauser and Wrangham 1990
<i>Cercopithecus diana</i>	Diana monkey	Zuberbühler et al. 1999; Zuberbühler 2000
<i>Cercopithecus campbelli</i>	Campbell's monkey	Zuberbühler 2001
<i>Cercopithecus aethiops</i>	Vervet monkey	Cheney and Seyfarth 1990
<i>Colobus badius</i>	Red colobus monkey	Bshary and Noe 1997; Gebo et al. 1994; Hauser and Wrangham 1990; Noë and Bshary 1997; Treves 1999
<i>Alces alces</i>	Moose	Berger et al. 2001

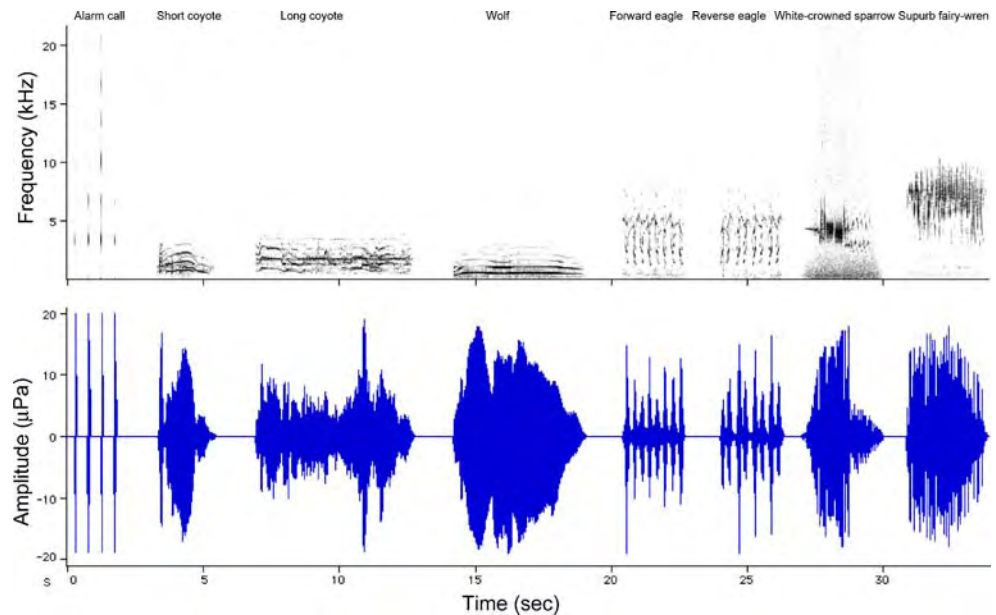
Bold indicates that a species has been demonstrated to respond acoustically to predators

location 1–2 m from their burrow. For all experiments, we broadcast calls to non-pups (i.e., yearlings and adults). We have no evidence to suggest that systematic differences exist in how these different age–sex categories respond to playbacks. Calls were broadcast to 28 subjects (six adult females, three adult males, nine yearling females, ten yearling males) in six groups (River South Mound, River Spruce Mound, Marmot Meadow Main Talus, Marmot Meadow Aspen Burrow, Bench, and Gothic Townsite). Each subject was exposed to four different stimuli, typically

no more than one per day. For this and other experiments, the order of stimulus presentation was counterbalanced to control for order effects.

Once animals were foraging at the bait, the 2-min sound track was started. Normalized calls were played back at 95 dB SPL (measured at 1 m) from a speaker placed 10–12 m from the bait. Each sound track started with 1 min of silence to obtain baseline time allocation for an individual. This was followed by an additional minute, with the playback commencing at the beginning of this period and

Fig. 2 Exemplars of acoustic stimuli used to study predator discrimination illustrated by spectrograms and waveforms. Sampling rate 44.1 kHz, 1024 point FFT (frequency resolution 175 Hz), gray scale represents -40 dB from peak amplitude



lasting between 2–7 s. We observed and video-recorded foraging marmots with a Cannon GL-1 mini-DV digital video recorder at distances that did not obviously affect their behavior (40–80 m, depending upon the individuals and the terrain).

While we aimed to have subjects hear only their “own” playback stimuli, there were times when more than a single individual was at the bait or was within earshot of the speaker. On average, an individual heard 3.3 other playbacks ($SD=3.0$ median=3) before each of their predator playbacks, including the other playbacks directed to the individual. Of these, an individual heard an average of 1.8 playbacks ($SD=2.4$, median=1) directed to an individual other than itself. There were 92 cases where a subject heard a playback not directed to itself (32 alarm calls, 23 coyote howls, 20 eagle calls, and 20 wolf howls). The average interval between playbacks for an individual was 51.1 h ($SD=81.5$ h, median=23 h).

For this and the other three experiments, videotapes were scored using the event recorder JWatcher (Blumstein et al. 2000b). We noted the onset of bouts of foraging, standing quadrupedally and looking, rearing up and looking bipedally, walking, running, self grooming, social interactions, time spent in burrow, and time spent out-of-sight. For each playback, we subtracted time allocation after stimulus presentation from the 1-min baseline period to control for differences in the amount of time allocated to foraging by each individual at the start of an experiment. We calculated the difference from baseline in the proportion of time allocated to foraging, heightened vigilance (rearing and looking), total vigilance (stand looking and rear looking), locomotion (walking and running), and time spent in the burrow. While we visually explored all the data, the difference from baseline in time allocated by individuals

to foraging was our primary assay because all subjects foraged before playback and responded to the playback by decreasing foraging. After playback, marmots primarily traded off foraging with vigilance, but they also spent some time in locomotion or inside their burrow. We analyzed time allocation in the first 15 s of playback because responses to acoustic stimuli were brief and subjects resumed their initial behavior within a minute.

We calculated 95% confidence intervals of the difference from baseline and interpreted those significantly different from zero as indicating a response to the stimulus. We then fitted repeated-measures general linear models to explain variation in the difference from baseline in the proportion of time spent foraging and the difference from baseline in the proportion of time spent engaged in high vigilance combined with the proportion of time spent in the burrow (hereafter high vigilance plus burrow) during the first 15 s of playback. We used Mauchly’s test to test for sphericity (Keppel 1991); in all cases, we did not reject the hypothesis of sphericity. We thus report p values that assume sphericity. We used a Bonferroni adjustment to control for multiple comparisons after setting our experiment-wise significance level at 5%.

We tested for order effects by fitting a repeated-measures general linear model focusing on the first 15 s of playback where the playback order, rather than the playback stimulus, was the factor. Finally, we regressed the number of previous playbacks heard and the number of other individuals above ground and within 50 m of the focal subject (i.e., within hearing range of the speaker) during the playback against our dependent variables: the difference from baseline in the proportion of time spent foraging and the difference from baseline in the proportion of time spent in high vigilance plus burrow.

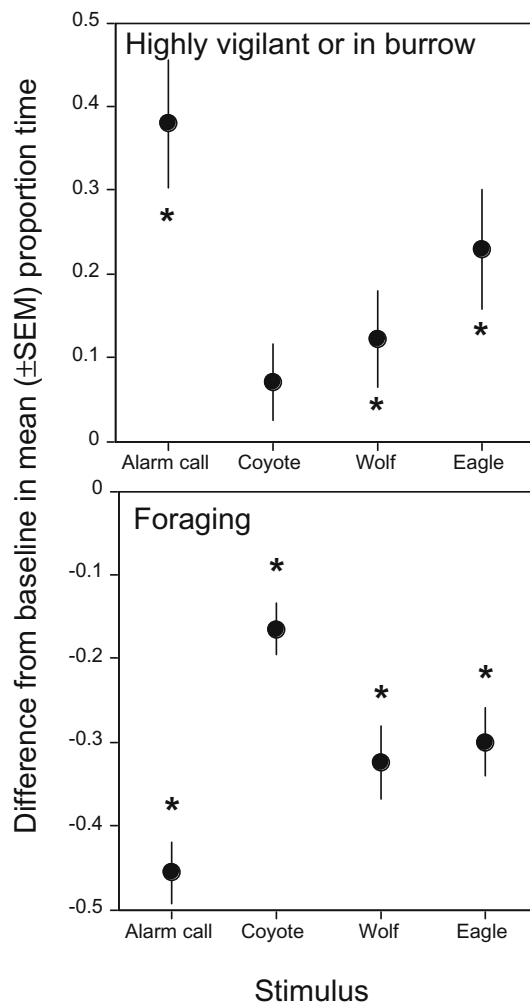


Fig. 3 Difference from baseline in mean ($\pm$ SEM) proportion of time engaged in high vigilance plus burrow, and foraging in the 15 s including and immediately after playback of conspecific alarm calls as well as the vocalizations from coyotes, wolves, and golden eagles. Asterisks (*) indicate 95% confidence intervals that were significantly less than zero for foraging and significantly greater than zero for high vigilance plus burrow. $N=28$ subjects

For all experiments, we calculated partial η^2 as a measure of effect size for general linear models and Cohen's d as a measure of effect size for pairwise comparisons using the pooled standard deviation (Cohen 1988). By tradition, small effects are inferred when $d=0.2$, medium effects when $d=0.5$, and large effects when $d=0.8$ (Cohen 1988). For multiple comparisons, we calculated the Bonferroni p critical value by dividing the alpha level of 0.05 by the number of comparisons. We calculated all statistics in SPSS 11.0 for the Macintosh (SPSS Inc. 2002).

Results

Marmots foraged significantly less in response to all playbacks compared to baseline and engaged in significantly more high vigilance plus time spent within the burrow compared to baseline in response to all but the coyote howl (Fig. 3).

Playback stimulus influenced both time allocated to foraging ($F_{3,81}=11.118$, $p<0.001$, partial $\eta^2=0.292$, Fig. 3) and high vigilance plus burrow ($F_{3,81}=5.106$, $p=0.003$, partial $\eta^2=0.159$, Fig. 3). Marmots suppressed foraging significantly more, and significantly increased high vigilance plus burrow, after hearing alarm calls than after hearing coyote calls. In addition, marmots significantly suppressed foraging after hearing alarm calls than eagle calls. They also suppressed foraging significantly more after hearing wolf calls than after hearing coyote calls (Table 2).

There was no significant difference over the 1-min baseline period in the proportion of time allocated to foraging ($F_{3,81}=2.030$, $p=0.116$, partial $\eta^2=0.070$) or high vigilance plus burrow ($F_{3,81}=0.429$, $p=0.733$, partial $\eta^2=0.016$) across playback types.

There were no confounding effects of playback order ($F_{3,81}=2.491$, $p=0.066$, partial $\eta^2=0.084$), the number of

Table 2 Pairwise comparisons of predator playbacks and marmot alarm call for Experiment 1

Response	Stimulus 1	Stimulus 2	<i>p</i> value	Cohen's <i>d</i>
Forage	Alarm call	Coyote short	<0.001	1.611
	Alarm call	Eagle	0.001	0.754
	Alarm call	Wolf	0.031	0.616
	Coyote short	Eagle	0.020	0.107
	Coyote short	Wolf	0.001	0.790
	Eagle	Wolf	0.675	0.698
	Alarm call	Coyote short	0.005	0.940
Highly vigilant or in burrow	Alarm call	Eagle	0.065	0.384
	Alarm call	Wolf	0.020	0.735
	Coyote short	Eagle	0.061	0.503
	Coyote short	Wolf	0.447	0.184
	Eagle	Wolf	0.164	0.321

Alpha level is set at 0.05. The Bonferroni p critical value is 0.008 (0.05 divided by six comparisons equals 0.008). Significant comparisons after the Bonferroni adjustment are shown in bold.

previous playbacks heard ($p=0.167$, $R=0.131$), or the number of other individuals within hearing range of the speaker ($p=0.628$, $R=-0.046$) for the difference from baseline in time spent foraging. Nor were there confounding effects for the difference from baseline in time spent in high vigilance plus burrow of playback order ($F_{3,81}=1.760$, $p=0.161$, partial $\eta^2=0.061$), the number of previous playbacks heard ($p=0.125$, $R=0.146$), or the number of other individuals within hearing range of the speaker during the playback ($p=0.346$, $R=0.090$).

Experiment 2—forward/reverse eagle playback

Methods

Preliminary observations suggested that marmots responded more to eagle calls than to other predator vocalizations. We thought that marmots might attend to the acoustic features of the eagle call rather than respond to the species per se; the call's pulse-like structure is reminiscent of marmot alarm calls (Fig. 2), and a previous study demonstrated that marmots can respond to alarm calls from novel species (Blumstein and Armitage 1997). Therefore, we conducted an experiment where we reversed the eagle call and contrasted the response to the reversed call with the response to an unmanipulated eagle call. Because the eagle calls are not tonal and because reversed calls sounded very different, a differential response to the forward and reverse calls would suggest that marmots attend to the underlying meaning of the call rather than simply react to an alarming pulse-like sound.

We reversed the call using SoundEdit 16 (Macromedia 1995; Fig. 2). Each foraging marmot was exposed to a standard eagle call and the same call in reverse on a different day. We used the same experimental technique as with the previous experiment; the order of the calls was counterbalanced as before. Calls were broadcast to 16 subjects (six adult females, one adult male, three yearling females, and six yearling males) in six groups (River South Mound, River Spruce Mound, Marmot Meadow Main Talus, Marmot Meadow Aspen Burrow, Bench, and Gothic Townsite); all individuals had been previously exposed to the predator playback sequence. On average, an individual heard 0.67 other eagle playbacks ($SD=0.66$, median=1) before each of their eagle playbacks, including the other playbacks directed to the individual in this experiment. Of these, an individual heard an average of 0.2 playbacks ($SD=0.4$, median=0) directed to another subject. There were three cases where a subject heard a playback not directed to itself (one forward eagle, two reverse eagle playbacks). We aimed to conduct playbacks on subsequent days; however, subjects did not always accommodate us;

the average interval between playbacks was 100.0 h ($SD=109.9$ h, median=23.9 h).

We calculated 95% confidence intervals of the difference from baseline and interpreted those significantly different from zero as indicating a response to the stimulus. We then used paired t tests to test for the effect of stimulus direction as well as playback order. We regressed the number of previous playbacks heard and the number of other individuals above ground and within 50 m (i.e., within hearing range of the speaker) of the focal subject during the playback against difference from baseline in the proportion of time spent foraging and difference from baseline in the proportion of time spent in high vigilance.

Results

Marmots responded to both normal and reversed eagle calls by decreasing foraging compared to baseline, although their response to normal calls was stronger than to reversed calls (Fig. 4). Marmots increased time allocated to high vigilance significantly compared to baseline after hearing the forward eagle but not the reversed eagle calls (Fig. 4).

Marmots suppressed foraging more after hearing the forward than the reverse eagle call ($t=-2.495$, $df=15$, $p=0.025$, $d=0.793$, Fig. 4). No subjects retreated to their burrows after playbacks. There was no difference in high vigilance after the forward playback compared to the reversed call ($t=1.003$, $df=15$, $p=0.332$, $d=0.398$).

There was no significant difference in the baseline period in the time allocated to foraging ($t=0.206$, $df=15$, $p=0.839$, $d=0.044$) or in the time allocated to high vigilance ($t=-1.000$, $df=15$, $p=0.333$, $d=0.314$) between forward and reverse playbacks.

There was no effect of playback order ($t=-0.806$, $df=15$, $p=0.433$, $d=0.277$), the number of previous playbacks heard ($p=0.353$, $R=0.176$) or the number of other individuals within hearing range of the speaker during the playback ($p=0.278$, $R=-0.198$) on the difference from baseline in the proportion of time spent foraging. There was also no effect of playback order ($t=0.906$, $df=15$, $p=0.379$, $d=0.341$), the number of previous playbacks heard ($p=0.063$, $R=-0.343$), or the number of other individuals within hearing range of the speaker during the playback ($p=0.089$, $R=0.306$) on the difference from baseline in the proportion of time engaged in high vigilance.

Experiment 3—novelty

Methods

To more directly test whether marmots responded simply to novelty, we observed the reaction of foraging marmots to

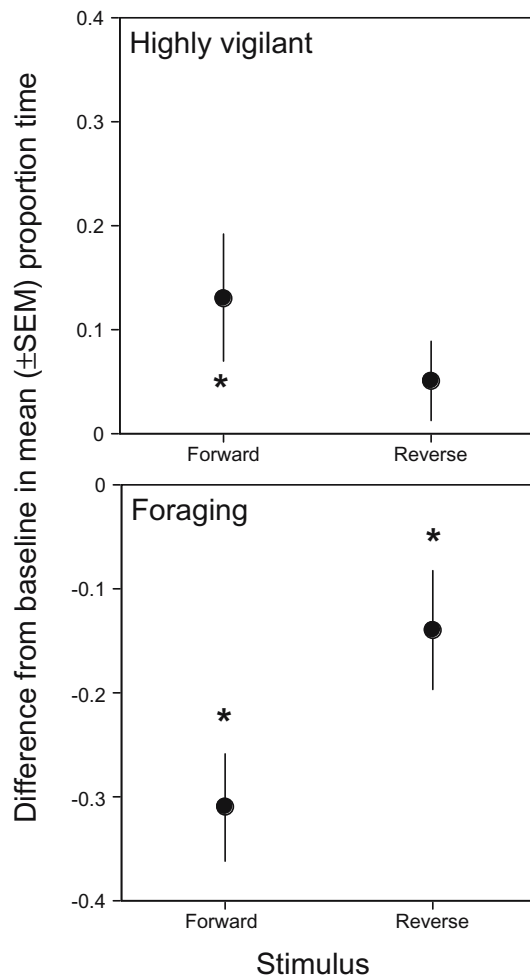


Fig. 4 Difference from baseline in mean ($\pm$ SEM) proportion of time spent highly vigilant and foraging in the 15 s including and immediately after the playback of forward and reverse golden eagle vocalizations. No subjects retreated to their burrows following playback. Asterisks (*) indicate 95% confidence intervals that were significantly less than zero for foraging and significantly greater than zero for high vigilance. $N=16$ subjects

playback of songs of mountain white-crowned sparrows, a common resident, superb fairy-wrens, an Australian bird with a song that was novel to the marmots, and conspecific alarm calls (Fig. 2). Sparrow song and conspecific alarm calls were recorded locally; superb fairy-wren song was obtained from Stewart (2000). We used three exemplars of each type of avian song to sample natural variation in acoustic structure. We used eight different individuals' alarm calls, with all marmots hearing alarm calls from unfamiliar animals. Playback methods were identical to the above protocols.

Vocalizations were broadcast to 16 subjects (seven adult females, five yearling females, four adult males) in six social groups (River South Mound, River Spruce Mound, Marmot Meadow Middle, Marmot Meadow Main Talus, Marmot Meadow Aspen Burrow, and Gothic Townsite)

during June and July 2005. On average, an individual heard 1.23 other playbacks ($SD=1.10$, median=1) before each of their playbacks, including the other playbacks directed to the individual. Of these, an individual heard an average of 0.2 playbacks ($SD=0.5$, median=0) directed to another subject. There were eight cases where a subject heard a playback not directed to itself (three alarm calls, two sparrow songs, and three wren playbacks). The average interval between playbacks was 41.29 h ($SD=53.37$ h, median=24.03 h).

Statistics were calculated as per Experiment 1, except we report Huynh–Feldt corrected p values in cases where we rejected sphericity for repeated repeated-measures general linear models. And, in this experiment, there were only two cases where other individuals were present along with the subject during the playback presentation; we therefore did not regress the number of other individuals above ground and within 50 m of the focal subject against our dependent variables.

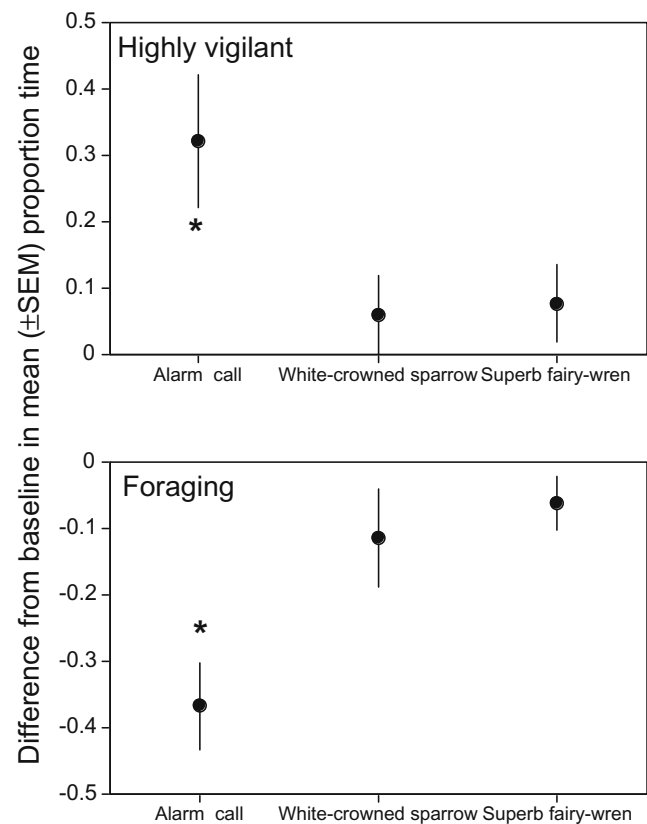


Fig. 5 Difference from baseline in mean ($\pm$ SEM) proportion of time spent highly vigilant and foraging in the first 15 s including and immediately after playback of marmot alarm calls, the songs of white-crowned sparrows (familiar stimulus) or the songs of superb fairy wrens (novel stimulus). No subjects retreated to their burrows after playback. Asterisks (*) indicate 95% confidence intervals that were significantly less than zero for foraging and significantly greater than zero for high vigilance. $N=16$ subjects

Results

Marmots foraged less and engaged in more high vigilance compared to baseline after hearing the conspecific alarm calls, but not the bird songs (Fig. 5). Marmots did not flee to their burrows in this experiment.

Playback stimuli influenced marmots' time allocated to foraging ($F_{2,30}=8.73$, $p<0.001$, partial $\eta^2=0.368$, Fig. 5) and high vigilance ($F_{1,12,16,81}=6.37$, $p=0.019$, partial $\eta^2=0.298$, Fig. 5). Marmots suppressed foraging significantly more after hearing alarm calls than after hearing sparrow songs or wren songs (Table 3). Marmots spent a greater proportion of time engaged in high vigilance after hearing alarm calls than after hearing sparrow songs (Table 3).

There was no significant difference over the 1-min baseline period in the proportion of time allocated to foraging ($F_{2,30}=0.939$, $p=0.402$, partial $\eta^2=0.059$) or high vigilance (no subjects ever reared and looked during baseline periods) across playback types.

There were no confounding effects of playback order ($F_{2,30}=1.139$, $p=0.334$, partial $\eta^2=0.071$) or the number of previous playbacks heard ($p=0.956$, $R=0.008$) for the difference from baseline in time spent foraging. Similarly, there were no confounding effects of playback order ($F_{2,30}=0.346$, $p=0.710$, partial $\eta^2=0.023$) or the number of previous playbacks heard ($p=0.638$, $R=0.070$) for the difference from baseline in time spent highly vigilant.

Experiment 4—duration of predator vocalizations

Methods

Because the wolf howls were longer than the coyote howls in the first experiment (wolves, 5–8 s; short coyote, 2–3 s) and marmots had a greater response to wolves than to coyotes, we wondered whether the greater response to the wolf was due to the length alone of that vocalization. We therefore observed the reaction of foraging marmots to the playback of similar length wolf howls (5–6 s) and longer coyote howls (about 6 s each; Fig. 2). We used two

exemplars of each type of predator howl to sample natural variation in acoustic structure. Playback methods were identical to the above protocols; the order of the calls was counterbalanced as before.

Vocalizations were broadcast to 17 subjects (12 adult females, 5 adult males) in six social groups (River South Mound, River Spruce Mound, Marmot Meadow Main Talus, Marmot Meadow Aspen Burrow, Bench, and Horse Mound) during June and July 2006. On average, an individual heard 0.71 other playbacks (SD=0.80, median=1) before each of their playbacks, including the other playbacks directed to the individual. Of these, an individual heard an average of 0.2 playbacks (SD=0.5, median=0) directed to another subject. There were six cases where a subject heard a playback not directed to itself (three coyote long howls, three wolf howls). The average interval between playbacks was 49.04 h (SD=31.74 h, median=24.03 h).

Statistics were calculated as per Experiment 2, except in this experiment, there was never more than one other individual above ground and within 50 m (i.e., within hearing range of the speaker) of the focal subject during the playback; we therefore used a t test to compare the difference from baseline in the proportion of time spent foraging and difference from baseline in the proportion of time spent in high vigilance when another individual was present vs absent.

Results

Marmots suppressed foraging significantly compared to baseline in response to both wolves and long coyote howls (Fig. 6). They increased time allocated to high vigilance significantly compared to baseline after the long coyote howls, but not the wolf howls (Fig. 6).

There was no significant difference in foraging between the wolf or long coyote howls ($t=-0.522$, $df=16$, $p=0.602$, $d=0.179$, Fig. 6). No subjects retreated to their burrows after playbacks. There was no significant difference in high vigilance after the long coyote or wolf playback ($t=1.047$, $df=16$, $p=0.311$, $d=0.393$).

Table 3 Pairwise comparisons of sparrow (familiar bird song), wren (novel bird song), and marmot alarm call playbacks for Experiment 3

Response	Stimulus 1	Stimulus 2	p value	Cohen's d
Forage	Alarm call	Sparrow	0.011	0.910
	Alarm call	Wren	<0.001	1.401
	Sparrow	Wren	0.523	0.216
Highly vigilant	Alarm call	Sparrow	0.015	0.793
	Alarm call	Wren	0.030	0.747
	Sparrow	Wren	0.497	0.078

Alpha level is set at 0.05. The Bonferroni p critical value is 0.017 (0.05 divided by three comparisons equals 0.017). Significant comparisons after the Bonferroni adjustment are shown in bold.

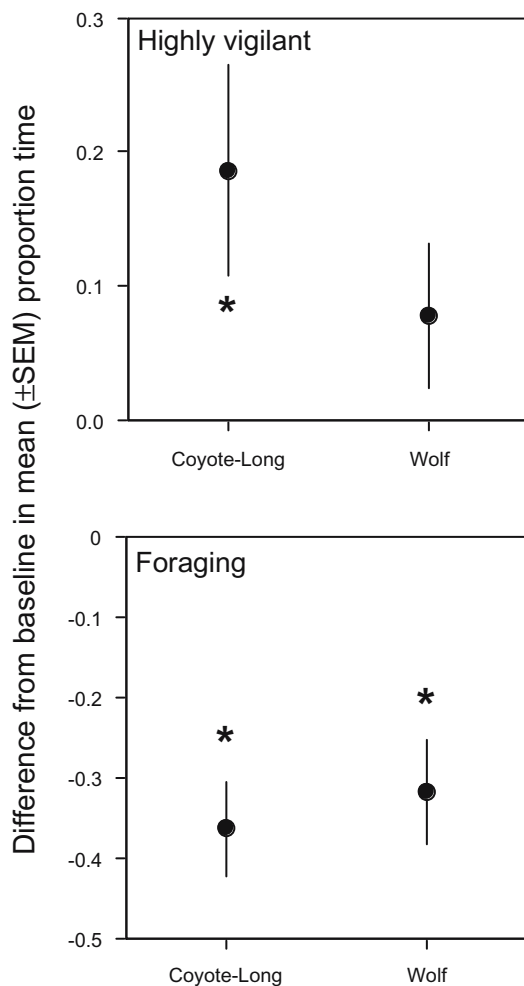


Fig. 6 Difference from baseline in mean ($\pm$ SEM) proportion of time spent highly vigilant and foraging in the first 15 s including and immediately after playback of a long coyote howl and a wolf howl. No subjects retreated to their burrows following playback. Asterisks (*) indicate 95% confidence intervals that were significantly less than zero for foraging and significantly greater than zero for high vigilance. $N=17$ subjects

There was no significant difference in the baseline period in the time allocated to foraging ($t=-0.647$, $df=16$, $p=0.527$, $d=0.180$) or in the time allocated to high vigilance (all values were zero) between wolf and long coyote playbacks.

There was no effect of playback order ($t=-1.337$, $df=16$, $p=0.200$, $d=0.439$) or the number of previous playbacks heard ($p=0.892$, $R=0.024$) on the difference from baseline in the proportion of time spent foraging. We did not analyze the potential effect of the presence of other marmots because only 4 out of 34 playbacks had a second individual present. There was also no effect of playback order ($t=-0.699$, $df=16$, $p=0.494$, $d=0.264$) or the number of previous playbacks heard ($p=0.860$, $R=0.031$) on the difference from baseline in the proportion of time engaged in high vigilance.

Discussion

In the first experiment, marmots responded most to conspecific alarm calls and least to short coyote howls, with moderate responses to eagle calls and wolf howls. Coyotes and eagles are familiar predators, whereas wolves are currently novel predators. The response to currently novel wolf howls is consistent with the hypothesis that yellow-bellied marmots have an experience-independent mechanism that allows them to respond to the sounds of some of their predators. In the second experiment, the greater response to normal forward eagle calls compared to reverse eagle calls suggests that marmots possess some sort of discrimination/recognition template that enables them to discriminate predators from non-predators. The comparative analysis suggested that the ability of prey to respond to vocalizations of their predators is an ancestral trait found in most of the species of birds and mammals in which it has been studied. Given that our reconstruction predicted that yellow-bellied marmots would respond to some predator vocalizations, the fact that they did is not surprising.

Conspecific alarm calls were more evocative than predator calls, suggesting that they denoted a higher risk than the social vocalizations of predators. Perhaps this is because predator vocalizations are not typically associated with hunting predators, whereas alarm calls indicate that a potentially threatening predator has been detected.

It is possible that marmots responded to wolf howls simply due to their novelty. While golden eagles live around the RMBL, we have never heard a golden eagle vocalize here during the marmot active season, and thus, the response to the eagle could be considered a novel vocalization. However, novelty, per se, is not alarming; in the third experiment, marmots did not respond to a genuinely novel bird song. Additionally, the greater response to the forward than to the reverse eagle calls suggests that marmots did associate the forward playbacks with predators rather than just responding to the rapidly paced and broadband eagle call. Specifically, the fact that the entirely novel reversed call elicited no heightened vigilance response, and only reduced foraging slightly below baseline levels, implies that novelty alone was not the only factor influencing the response. The results in the second experiment are consistent with Macedonia and Yount's (1991) finding of greater anti-predator response in ring-tailed lemurs, *Lemur catta*, to normally played-back hawk vocalizations than to reverse hawk vocalizations.

It is possible that stimulus duration influenced the relative magnitude of the responses in the first experiment and that this might explain the greater response to wolf howls compared to the relatively shorter coyote howls. The fourth experiment supports this hypothesis: coyote howls of similar duration to the original wolf howls produced

equivalent responses. Thus, the relative duration of at least certain stimuli does influence response magnitude. We are therefore unable to conclude whether marmots truly discriminate among the calls of coyotes and wolves, but they certainly may respond to them.

Unlike Diana monkeys, *Cercopithecus diana*, and Campbell's monkeys, *C. campbelli*, which utter referentially specific alarm calls in response to playback of a specific predator call (Zuberbühler et al. 1999; Zuberbühler 2001), yellow-bellied marmots do not have functionally referential alarm calls (Blumstein and Armitage 1997; Blumstein 1999). If marmots emitted referential alarm calls in response to specific predator vocalizations, we would have had a powerful assay of recognition. Thus, even if we were to demonstrate discrimination with differential responses among predators, we would not be able to demonstrate true recognition.

Perhaps marmots respond to currently novel wolf howls because of their similarity to coyote calls. Wolf howls typically differ from coyote howls in at least two dimensions: they are often longer and they contain lower frequencies (because wolves are larger). However, the many common features of the calls may allow marmots to easily generalize from coyote calls to wolves. Thus, although it has been argued that the recognition mechanism for predator vocalizations should involve learning because predator vocalizations are more likely to be structurally divergent than visual cues derived from predator form (Berger et al. 2001; Blumstein et al. 2000a; Gil-da-Costa et al. 2003), it may not be surprising that we find experience-independent mechanisms in cases where the structure of predator vocalizations are also convergent.

With respect to conservation implications, because naive marmots respond to wolf howls, we would predict that marmots will be able to respond to real wolf howls the first time that they naturally encounter them, and thus, marmots should not go extinct after wolf recolonization.

Acknowledgments Louise Cooley was an NSF-REU fellow during this research. We thank Dan Jones for fast Ethernet, and for help trapping marmots, Esa Crumb, Louise Lochhead, Mark Luterra, Lucas Moyer-Horner, Amanda Nicodemus, Lucretia Olsen, Arpat Ozgul, David Pelletier, Weiwei Shen, Brian Smith, Tricia Stark, Ryan Trojan, Tyler Van Fleet, Thea Wang, Tina Wey, and Veronica Yovovich. Research protocols were approved by both the Rocky Mountain Biological Laboratory (RMBL) and by the University of California Los Angeles (UCLA) Animal Research Committee (No. 2001-191-03 approved on 3/8/04). Marmots were trapped under permits issued by the Colorado Division of Wildlife. Partial support for this research came from NSF-DBI-0242960 (to RMBL), the UCLA Faculty Senate Faculty Research Grants, a UCLA Assistant Professor's Initiative grant, and the UCLA Division of Life Sciences Dean's recruitment and retention funds (to DTB). We are extremely grateful to Peter Bednekoff and two anonymous reviewers whose comments helped us shorten the paper and improve its clarity.

References

- Abramsky Z, Strauss E, Subach A, Kotler BP, Riechman A (1996) The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia* 105:313–319
- Armitage KB (1982) Yellow-bellied marmot. In: Davis DE (ed) CRC handbook of census methods for terrestrial vertebrates. CRC, Boca Raton, Florida, pp 148–149
- Berger J (1998) Future prey: some consequences of the loss and restoration of large carnivores. In: Caro TM (ed) Behavioral ecology and conservation biology. Oxford University Press, New York, pp 80–100
- Berger J, Swenson JE, Persson I-L (2001) Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039
- Blumstein DT (1999) The evolution of functionally referential alarm communication: multiple adaptations; multiple constraints. *Evol Commun* 3:135–147
- Blumstein DT (2006) The 'multi-predator' hypothesis and the evolutionary persistence of antipredator behaviour. *Ethology* 112:209–217
- Blumstein DT, Armitage KB (1997) Alarm calling in yellow-bellied marmots: I. The meaning of situationally-specific calls. *Anim Behav* 53:143–171
- Blumstein DT, Daniel JC, Griffin AS, Evans CS (2000a) Insular tamar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behav Ecol* 11:528–535
- Blumstein DT, Evans CS, Daniel JC (2000b) JWatcher 0.9. An introductory user's guide. <http://www.jwatcher.ucla.edu>
- Blumstein DT, Daniel JC, Schnell MR, Ardrone JG, Evans CS (2002) Antipredator behaviour of red-necked pademelons: a factor contributing to species survival? *Anim Conserv* 5:325–331
- Bouskila A, Blumstein DT (1992) Rules of thumb for predation hazard assessment: predictions from a dynamic model. *Am Nat* 139:161–176
- Bshary R, Noe R (1997) Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behav Ecol Sociobiol* 41:321–333
- Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago
- Charif RA, Mitchell S, Clark CW (1995) Canary 1.2 user's manual. Cornell Laboratory of Ornithology, Ithaca, NY
- Cheney DL, Seyfarth RM (1990) How monkeys see the world. University of Chicago Press, Chicago
- Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Lawrence Erlbaum Assoc., Hillsdale, NJ
- Colorado Division of Wildlife (2004) Species conservation: gray wolf management. http://www.wildlife.state.co.us/species_cons/gray_wolf/index.asp
- Coss RG (1999) Effects of relaxed natural selection on the evolution of behavior. In: Foster SA, Endler JA (eds) Geographic variation in behavior: perspectives on evolutionary mechanisms. Oxford University Press, Oxford, pp 180–208
- Crafford D, Ferguson J, Kemp A (1999) Why do grass owls (*Tyto capensis*) produce clicking calls? *Raptor Res* 33:134–142
- Deecke VB, Slater PJB, Ford JKB (2002) Selective habituation shapes acoustic predator recognition in harbour seals. *Nature* 420:171–173
- Durant SM (2000) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behav Ecol* 11:624
- Eilam D, Dayan T, Ben-Eliyahu S, Schulman I, Shefer G, Hendrie CA (1999) Differential behavioural and hormonal responses of voles and spiny mice to owl calls. *Anim Behav* 58:1085–1093
- Elliott D (2004) Yellowstone wolf found dead near Denver. *Casper Star Tribune*, Casper, WY

- Gebo DL, Chapman CA, Chapman LJ, Lambert J (1994) Locomotor response to predator threat in red-colobus monkeys. *Primates* 35:219–223
- Gil-da-costa R, Palleroni A, Hauser MD, Touchton J, Kelley JP (2003) Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. *Proc R Soc Lond B* 270:605–610
- Griffin AS, Blumstein DT, Evans CS (2000) Training captive-bred or translocated animals to avoid predators. *Conserv Biol* 14:1317–1326
- Griffin AS, Evans CS, Blumstein DT (2001) Learning specificity in acquired predator recognition. *Anim Behav* 62:577–589
- Gursky S (2002) Determinants of gregariousness in the spectral tarsier (Prosimian: *Tarsius spectrum*). *J Zool Lond* 256:401–410
- Gursky S (2003) Predation experiments on infant spectral tarsiers (*Tarsius spectrum*). *Folia Primatol* 74:272–284
- Hauser MD, Caffrey C (1994) Anti-predator response to raptor calls in wild crows, *Corvus brachyrhynchos hesperis*. *Anim Behav* 48:1469–1471
- Hauser MD, Wrangham RW (1990) Recognition of predator and competitor calls in non-human primates and birds: a preliminary report. *Ethology* 86:116–130
- Hendrie CA, Weiss SM, Eilam D (1998) Behavioural response of wild rodents to the calls of an owl: a comparative study. *J Zool Lond* 245:439–446
- Jones ME, Smith GC, Jones SM (2004) Is anti-predator behaviour in Tasmanian eastern quolls (*Dasyurus viverrinus*) effective against introduced predators? *Anim Conserv* 7:155–160
- Karpanty SM, Grella R (2001) Lemur responses to diurnal raptor calls in Ranomafana National Park, Madagascar. *Folia Primatol* 72:100–103
- Kelley JL, Magurran AE (2003) Learned predator recognition and antipredator responses in fishes. *Fish Fish* 5:216–226
- Keppel GL (1991) Design and analysis: a researcher's handbook, 3rd edn. Prentice Hall, Englewood Cliffs, NJ
- Kristensen EA, Closs GP (2004) Anti-predator response of naive and experienced common bully to chemical alarm cues. *J Fish Biol* 64:643–652
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Macedonia JM, Yount PL (1991) Auditory assessment of avian predator threat in semi-captive ringtailed lemurs (*Lemur catta*). *Primates* 32:169–182
- Macromedia (1995) SoundEdit 16. Macromedia, Inc., San Francisco
- Maddison WP, Maddison DR (2001) MacClade: analysis of phylogeny and character evolution. Version 4.03. Sinauer Associates, Sunderland, MA
- McKenna MC, Bell SK (1997) Classification of mammals above the species level. Columbia University Press, New York
- Noë R, Bshary R (1997) The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proc R Soc Lond B* 264:253–259
- Petrzelkova K, Zukal J (2001) Emergence behaviour of the serotine bat (*Eptesicus serotinus*) under predation risk. *Neth J Zool* 51:395–414
- Pusenius J, Ostfeld RS (2000) Effects of stoat's presence and auditory cues indicating its presence on tree seedling predation by meadow voles. *Oikos* 91:123–130
- Pyare S, Cain S, Moody D, Schwartz C, Berger J (2004) Carnivore re-colonisation: reality, possibility and a non-equilibrium century for grizzly bears in the southern Yellowstone ecosystem. *Anim Conserv* 7:71–77
- Rainey HJ, Zuberbühler K, Slater PJB (2004) Hornbills can distinguish between primate alarm calls. *Proc R Soc Lond B* 271:755–759
- Searcy YM, Caine NG (2003) Hawk calls elicit alarm and defensive reactions in captive Geoffroy's Marmosets (*Callithrix geoffroyi*). *Folia Primatologica* 74:115–125
- Stewart D (2000) Australian bird calls favourites. Nature Sound, Mullumbimby, NSW
- SPSS, Inc. (2002) SPSS-11 for the Macintosh. SPSS Inc., Chicago, IL
- Swaigood RR, Rowe MP, Owings DH (1999) Assessment of rattlesnake dangerousness by California ground squirrels: exploitation of cues from rattling sounds. *Anim Behav* 57:1301–1310
- Treves A (1999) Has predation shaped the social systems of arboreal primates? *Int J Primatol* 20:35–67
- Van Vuren D (2001) Predation on yellow-bellied marmots (*Marmota flaviventris*). *Am Midl Nat* 145:94–100
- Warren ER (1942) The mammals of Colorado: their habits and distribution, 2 edn. University of Oklahoma Press, Norman
- Wilson DE, Reeder DM (1993) Mammal species of the world: a taxonomic and geographic reference, 2nd edn. Smithsonian Institution Press, Washington, DC
- Zuberbühler K (2000) Causal knowledge of predators' behaviour in wild Diana monkeys. *Anim Behav* 59:209–220
- Zuberbühler K (2001) Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behav Ecol Sociobiol* 50:414–422
- Zuberbühler K, Cheney DL, Seyfarth RM (1999) Conceptual semantics in a nonhuman primate. *J Comp Psychol* 113:33–42