

Do yellow-bellied marmots respond to predator vocalisations?

Louise Cooley

Ohio Wesleyan University, Delaware, Ohio

The Rocky Mountain Biological Laboratory, Gothic, Colorado

Research Experience for Undergraduates Program 2004

Mentor: Dr. Daniel T. Blumstein

*Correspondence: L. Cooley, Department of Zoology, Ohio Wesleyan University,
Delaware, OH 43015, U.S.A. (email: lbcooley@owu.edu).*

We designed an experiment to determine whether yellow-bellied marmots, *Marmota flaviventris*, discriminate among predator vocalisations, and if so, whether the recognition mechanism is learned or innate. We broadcast to marmots the social sounds of coyotes, *Canis latrans*, wolves, *Canis lupus*, and golden eagles, *Aquila chrysaetos*, as well as marmot alarm calls. Coyotes and eagles are extant predators at our study site, while wolves have been absent since the mid-1930s. In a follow-up experiment, we reversed the eagle call and presented marmots with forward and reverse calls to control for response to structural characteristics of the call. Marmots suppressed foraging and increased looking most after presentation of the alarm call and least after that of the coyote, with moderate responses to wolf and eagle calls. Marmots foraged significantly less and looked significantly more after hearing the forward eagle call as compared to the reverse call. Our results show that marmots do differentiate between predators based on acoustic stimuli. The response to currently novel wolf calls suggests that they have an innate ability to identify predators acoustically. Marmots' response to predator vocalisations is not unexpected because 25 of 30 species in which this has been studied have a demonstrated ability to respond to acoustic cues from their predators.

Individual animals use sensory cues in a variety of modalities (e.g. olfactory, visual, and acoustic) to assess predation risk and make subsequent behavioural decisions (Lima & Dill 1990). In some cases, individuals respond appropriately to these cues the first time they encounter them (i.e., they are innate); 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 innate, because it is a reliable predictor of predator presence, and because the evolution of predator form is convergent (Blumstein et al. 2000b). Olfactory cues can be misleading in that they remain once an animal is no longer in the area (Bouskila & 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 & Magurran 2003; Kristensen & Closs 2004). Although acoustic cues reliably predict the presence of a predator, acoustic recognition may depend on relatively specific cues, because predator vocalisations are structurally divergent (Blumstein et al. 2000b). Thus, it seems likely that the mechanism involved is learned rather than innate (Berger et al. 2001; Gil-da-Costa et al. 2003). Although predators are usually quiet while hunting, 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 results). 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 is theoretically interesting (Lima & Dill 1990), 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. 2000b), while others lose their responsiveness. If responding to non-predators as though they are predators when no predators are present is costly, then recognition abilities may be lost under relaxed selection. Once recognition abilities are lost, prey will be vulnerable to former predators upon re-contact (Coss 1999). If the mechanism 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.

We conducted a playback experiment designed to determine the degree to which yellow-bellied marmots discriminate among and respond to the vocalisations 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 U.S. 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, Colorado in early June, 2004; a dispersal of nearly 500 miles, if she moved on her own (Elliott 2004). The effect of wolf reintroduction 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 while coyotes are extant. A response to wolves as well as to coyotes and eagles might suggest that acoustic predator recognition is innate in marmots. Response to coyotes and eagles, but not to wolves, could be interpreted as either loss of an innate mechanism or existence of a learned mechanism.

METHODS

Literature Review

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 & Bell (1997) and Wilson & Reeder (1993), and then created a partial phylogeny with MacClade 4.03 (Maddison & Maddison 2001) of the 30 species for which acoustic predator recognition had been studied. We then reconstructed, using parsimony, the evolution of acoustic predator recognition.

Predator Playback Experiment

We conducted all experiments with free-living marmots in the East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL), in Gunnison County,

Colorado, USA during the summer of 2004 (May – July). 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 vocalisations, as well as to playback of marmot 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 & Armitage 1997). Blumstein & Armitage (1997) found that marmots do not respond to familiar non-predator avian contact calls. Thus, in order to minimize the number of playbacks heard by subjects, we did not include a familiar, non-predator control stimulus in this experiment. The structure of contact and social calls are often systematically different from those of alarm and mobbing vocalizations (Marler 1955; Johnson et al. 2003). Thus, to minimize the number of experimental presentations, and thus reduce the risk of overall habituation to our experiment, we did not include a novel, non-predator control stimulus. 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) to sample natural variation in acoustic structure (Fig. 1). Calls were obtained from commercial sound archives and were not recorded locally. We recorded

alarm calls 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) 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, Massachusetts), to a Macintosh PowerBook G4 (Apple Computer, Cupertino, California), 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 for playback through an iPod (Apple Computer, Cupertino, California). We used eight different alarm call exemplars, with all marmots hearing alarm calls from unfamiliar animals from different social groups.

Marmots were baited with a handful of Omolene 300 horse feed (Ralston Purina Inc., St. Louis, Missouri) to a 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 animal was exposed to four calls, typically no more than one per day. The order of call presentation was counterbalanced, to control for order effects.

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

at the beginning of the second minute. 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 behaviour (40 – 80 m, depending upon the individuals and the terrain).

We aimed to have subjects hear only their ‘own’ playback stimuli, but sometimes, more than a single individual was at the bait. On average, an individual heard 2.9 other playbacks (SD = 2.6, median = 2) before each of their predator playbacks, including the other playbacks directed to an individual. The average interval between playbacks was 51.1 h (SD = 81.5 h, median = 23 h).

Forward/Reverse Eagle Playback Experiment

Preliminary observations suggested that marmots responded more to eagle calls compared to other predator vocalisations. We thought that marmots might be attending to the acoustic features of the eagle call, rather than responding to the species *per se*; the call’s pulse-like structure is reminiscent of marmot alarm calls (Fig. 1) and a previous study demonstrated that marmots can respond to alarm calls from novel species (Blumstein & Armitage 1997). Therefore, we conducted an additional playback experiment where we reversed the eagle call and contrasted the response to the reversed call with the response to an un-manipulated eagle call. No difference in response between the two calls would suggest that marmots did not attend to the underlying meaning of the call; rather, they reacted to an alarming pulse-like sound.

We reversed the call using SoundEdit 16 (Macromedia 1995, Fig. 1). Each foraging marmot was exposed to a standard eagle call, and the same call in reverse on a

subsequent 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 an individual in this experiment. The average interval between playbacks was 100.0 h ($SD = 109.9$ h, median = 23.9).

Data Analysis

A single observer (L.B.C.) scored the videotapes for both experiments using JWatcher (Blumstein et al. 2000a). 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 following 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. Following playback, marmots primarily traded-off foraging with vigilance, but they also spent some time in locomotion or inside their burrow. We analysed time allocation in the first 15 s of playback because responses to acoustic stimuli were brief and subjects resumed their initial behaviour.

For the first experiment, we 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 time spent in the burrow (hereafter high vigilance plus burrow) during the first post-stimulus 15 s time bin of the playback. We used Mauchly's test to test for sphericity; in all cases we were unable to 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 also fitted repeated-measures general linear models examining the response of marmots over the entire minute including and following the playback to look for any significant interaction between stimulus and time. Specifically, we fitted a model that included stimulus, time in the four 15 s time bins, and the interaction between stimulus and time. We tested for order effects by fitting a repeated-measures general linear model focusing on the first 15 s 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 in the vicinity of the focal subject (within earshot of the speaker) during the playback against the difference from baseline in the proportion of time spent foraging and difference in time spent in high vigilance plus burrow. We

calculated 95% confidence intervals of the difference from baseline and interpreted those significantly different from zero as indicating a response to the stimulus.

For the second experiment, we 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 in the vicinity (within earshot 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. We also calculated 95% confidence intervals of the difference from baseline and interpreted those significantly different from zero as indicating a response to the stimulus.

We calculated partial η^2 as a measure of effect size for general linear models, and Cohen' *d* as a measure of effect size for pair-wise comparisons, using the pooled standard deviation (Cohen 1988). For multiple comparisons we calculated the Bonferroni correction by multiplying the observed *P*-value by the number of comparisons (six), and interpreted $P < 0.05$ as significant. We report the Bonferroni-corrected *P*-value. We calculated all statistics in SPSS 10.0 for the Macintosh (SPSS Inc. 2000).

RESULTS

Literature Review

Twenty-five of 30 species of birds and mammals for which playback experiments have been conducted to study acoustic predator recognition responded to vocalisations from their predators (Fig. 2, 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 vocalisations, we predicted that yellow-bellied marmots would be able to respond to the vocalisations of at least some of their predators.

Predator Playback Experiment

Marmots reduced foraging compared to baseline levels of foraging in response to all playbacks. Confidence intervals for the difference from baseline in the proportion of time spent foraging were significantly less than zero for all four stimuli: alarm call (95% C.I. = -0.532 – -0.380), coyote (-0.229 – -0.101), eagle (-0.300 – -0.041) and wolf (-0.414 – -0.234). Marmots increased high vigilance plus burrow use in response to all but the coyote playback. Confidence intervals for the difference from baseline in the proportion of time engaged in high vigilance plus burrow were significantly greater than zero for three of the four stimuli: alarm call (95% C.I. = 0.222 – 0.535), eagle (0.083 – 0.375) and wolf (0.004 – 0.239). There was no change from baseline behaviour in high vigilance plus burrow in response to the coyote playback (-0.024 – 0.165).

There was a significant effect of playback stimulus on the proportion of 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) in the 15 s time bin that included the playback. Marmots suppressed foraging significantly more after hearing alarm calls than after hearing coyote ($P < 0.001$, $d = 1.611$) or eagle calls ($P = 0.004$, $d = 0.754$). They also suppressed foraging significantly more after hearing wolf calls than after hearing coyote calls ($P = 0.009$, $d = 0.790$). There were no significant pair-wise differences in the proportion of time spent foraging following playbacks of

alarm calls and wolf calls ($P = 0.186$, $d = 0.616$), wolf and eagle calls ($P = 0.121$, $d = 0.698$) and eagle and coyote calls ($P = 1.000$, $d = 0.107$). Marmots spent a greater proportion of time engaged in high vigilance plus burrow after hearing alarm calls than after hearing coyote calls ($P = 0.029$, $d = 0.940$). There were no significant pair-wise differences in the proportion of time spent engaged in high vigilance plus burrow following playbacks of alarm calls and eagle calls ($P = 0.391$, $d = 0.384$), wolf and coyote calls ($P = 1.000$, $d = 0.184$), alarm calls and wolf calls ($P = 0.120$, $d = 0.735$), wolf and eagle calls ($P = 0.984$, $d = 0.321$) and eagle and coyote calls ($P = 0.368$, $d = 0.503$).

There was no significant difference over the 1 min baseline period in the proportion of time allocated to foraging ($P = 0.116$, observed power = 0.503) or high vigilance plus burrow ($P = 0.733$, observed power = 0.132) across playback types.

While there were main effects of both stimulus ($F_{3,75} = 11.271$, $P < 0.001$, partial $\eta^2 = 0.311$) and time ($F_{3,75} = 24.051$, $P < 0.001$, partial $\eta^2 = 0.490$) for foraging over the 1 min period including and following playback, there was no significant stimulus x time interaction ($F_{9,225} = 0.683$, $P = 0.692$, partial $\eta^2 = 0.027$). There were also main effects of stimulus ($F_{3,75} = 4.444$, $P = 0.011$, partial $\eta^2 = 0.151$) and time ($F_{3,75} = 4.048$, $P = 0.029$, partial $\eta^2 = 0.139$) for high vigilance plus burrow, but there was no significant stimulus x time interaction ($F_{9,225} = 1.104$, $P = 0.362$, partial $\eta^2 = 0.042$).

There were no confounding effects of playback order ($F_{3,81} = 2.491$, $P = 0.066$, partial $\eta^2 = 0.084$), the number of previous playbacks heard ($P = 0.167$, $R = 0.131$) or the number of other individuals out within earshot 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 out during the playback ($P = 0.346$, $R = 0.090$).

Forward/Reverse Eagle Playback Experiment

Marmots reduced foraging compared to baseline levels in response to both the forward and reversed eagle playback. Confidence intervals for the difference from baseline in the proportion of time spent foraging were significantly less than zero, although the reversed eagle's interval approached zero: forward eagle (95% C.I. = -0.412 – -0.211), reversed eagle (-0.251 – -0.029). Marmots increased high vigilance in response to hearing a forward eagle call (95% C.I. = 0.012 – 0.248), but they did not substantially increase high vigilance in response to the reversed eagle call (95% C.I. = -0.025 – 0.123).

Marmots suppressed foraging more after hearing the forward than the backward eagle call ($t = -2.495$, $P = 0.025$, $d = 0.793$, Fig. 4). No subjects retreated to their burrows following playbacks. They did not engage in significantly higher vigilance following the forward playback ($t = 1.003$, $P = 0.332$, $d = 0.398$). There was no significant difference in the baseline period in the time allocated to foraging ($t = 0.206$, $P = 0.839$, $d = 0.044$) or in the time allocated to high vigilance ($t = -1.000$, $P = 0.333$, $d = 0.314$) between forward and reverse playbacks. There was no effect of playback order ($t = -0.806$, $P = 0.433$, $d = 0.277$), the number of previous playbacks heard ($P = 0.353$, $R = 0.176$) or the number of other individuals out 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 ($P = 0.379$, $d = 0.341$, $t = 0.906$), the number of previous playbacks heard ($P = 0.063$, $R = -0.343$), or the number of other individuals out during the playback ($P = 0.089$, $R = 0.306$) on the difference from baseline in the proportion of time engaged in high vigilance.

DISCUSSION

Marmots responded most to conspecific alarm calls and least to coyote calls, with moderate responses to eagle and wolf calls. Taken together, these results suggest that yellow-bellied marmots respond to at least some predator vocalizations, and that they discriminate among them. The ability of prey to respond to vocalisations of their predators is an ancestral trait found in most of the species of birds and mammals in which it has been studied. Our reconstruction predicted that yellow-bellied marmots would respond to some predator vocalisations, and that is what we found. Alarm calls were more evocative than predator calls, suggesting that they denoted a higher risk than the social vocalisations of predators. Perhaps this is because predator vocalisations are not typically associated with hunting predators, whereas alarm calls indicate that a potentially threatening predator has been detected.

While golden eagles live around the RMBL, we have never heard a golden eagle vocalise here during the marmot active season. It is possible that for the marmots this was a novel vocalisation. However, the greater response to the forward than to the reversed eagle calls suggests that marmots did associate the forward playbacks with predators, rather than just responding to the rapidly paced and broad-band eagle call.

Specifically, the fact that the entirely novel reversed call elicited no heightened vigilance response, and did not substantially reduce foraging below baseline levels, implies that novel sounds, *per se*, are not necessarily alarming. This is consistent with Macedonia & Yount's (1991) finding of greater antipredator response in ringtailed lemurs, *Lemur catta*, upon hearing normally played-back hawk vocalisations compared to reversed hawk vocalisations.

The greater response to wolf than to coyote playback may be because it lasted more than twice as long as the second longest stimulus (Fig. 1), and thus elicited sustained reactions. Alternatively, marmots may have responded more to wolf than coyote calls because wolves are currently novel predators. Our experiment did not specifically include a non-predator novel control because we aimed to limit the number of stimuli any given subject was exposed to so as to reduce the likelihood of habituation to the entire experimental protocol. Future experiments might examine the issue of novelty directly; the greater response to wolf and eagle calls than to coyote calls may be because both are novel sounds. However, the greater response to the forward than to the reversed eagle call suggests that novelty, *per se*, is not necessarily alarming; thus, the elevated response to wolf calls could also be interpreted as evidence of predator discrimination. If so, this ability must be viewed as innate. Regardless of the mechanism, however, marmots do suppress foraging after hearing wolf calls, and we would predict that they would adjust to wolf re-colonization.

Marmots respond to the sight of coyotes and coyotes are their major predator. Thus, the limited response to coyote calls is paradoxical. The lack of response may be due to habituation, because it is not uncommon to hear coyotes howling during the day, while

marmots are in earshot. We have seen marmots respond similarly to bouts of natural coyote howls (i.e. no response). It is also possible that marmots associate calling coyotes with a non-threatening situation.

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 (Zuberbuhler et al. 1999; Zuberbuhler 2001), yellow-bellied marmots do not have functionally referential alarm calls (Blumstein & 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, while a greater response to eagle and wolf than to coyote calls suggests that marmots may discriminate among the calls of some predators, we have not demonstrated true recognition.

Acknowledgements

Thank you to Dan Blumstein for his guidance and energy in constructing, carrying out, and completing this project; to Janice Daniel for help with data analysis and for comments on a previous version of this paper; to Dan Jones for fast Ethernet; and to billy barr for his supply of chocolate. For help trapping marmots I thank Louise Lochhead, Amanda Nicodemus, Lucretia Olsen, Arpat Ozgul, David Pelletier, Tricia Stark and Tyler Van Fleet. Research protocols were approved by both the Rocky Mountain Biological Laboratory 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).

References

- Abramsky, Z., Strauss, E., Subach, A., Kotler, B. P. & 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, K. B. 1982. Yellow-bellied marmot. In: *CRC handbook of census methods for terrestrial vertebrates* (Ed. by Davis, D. E.), pp. 148-149. Boca Raton, Florida: CRC Press, Inc.
- Berger, J. 1998. Future prey: some consequences of the loss and restoration of large carnivores. In: *Behavioral ecology and conservation biology* (Ed. by Caro, T. M.), pp. 80-100. New York: Oxford Univ. Press.
- Berger, J., Swenson, J. E. & Persson, I.-L. 2001. Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science*, **291**, 1036-1039.
- Blumstein, D. T. 1999. The evolution of functionally referential alarm communication: multiple adaptations; multiple constraints. *Evolution of Communication*, **3**, 135-147.
- Blumstein, D. T. & Armitage, K. B. 1997. Alarm calling in yellow-bellied marmots: I. The meaning of situationally-specific calls. *Animal Behaviour*, **53**, 143-171.
- Blumstein, D. T., Evans, C. S. & Daniel, J. C. 2000a. JWatcher 0.9. An introductory user's guide. <http://www.jwatcher.ucla.edu>.
- Blumstein, D. T., Daniel, J. C., Griffin, A. S. & Evans, C. S. 2000b. Insular tammar

- wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behavioral Ecology*, **11**, 528-535.
- Blumstein, D. T., Daniel, J. C., Schnell, M. R., Ardron, J. G. & Evans, C. S. 2002. Antipredator behaviour of red-necked pademelons: a factor contributing to species survival? *Animal Conservation*, **5**, 325-331.
- Bouskila, A. & Blumstein, D. T. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. *American Naturalist*, **139**, 161-176.
- Bshary, R. & Noe, R. 1997. Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behavioral Ecology and Sociobiology* **41**, 321-333.
- Charif, R. A., Mitchell, S. & Clark, C. W. 1995. *Canary 1.2 user's manual*. Ithaca, NY: Cornell Laboratory of Ornithology.
- 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: Lawrence Erlbaum Assoc.
- Colorado Division of Wildlife. 2004. Species conservation: gray wolf management. [www.wildlife.state.co.us/species_cons/graywolf/index.asp]
- Coss, R. G. 1999. Effects of relaxed natural selection on the evolution of behavior. *Geographic variation in behavior: perspectives on evolutionary mechanisms*. Foster, S. A. & Endler, J. A. Oxford: Oxford University Press: 180-208.
- Crafford, D., Ferguson, J. & Kemp, A. 1999. Why do grass owls (*Tyto capensis*) produce clicking calls? *Journal of Raptor Research*, **33**, 134-142.
- Deecke, V. B., Slater, P. J. B. & Ford, J. K. B. 2002. Selective habituation shapes

- acoustic predator recognition in harbour seals. *Nature*, **420**, 171-173.
- Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624.
- Eilam, D., Dayan, T., Ben-Eliyahu, S., Schulman, I., Shefer, G. & Hendrie, C. A. 1999. Differential behavioural and hormonal responses of voles and spiny mice to owl calls. *Animal Behaviour*, **58**, 1085-1093.
- Elliott, D. 2004. Yellowstone wolf found dead near Denver. *Casper Star Tribune*. Casper, WY. [www.casparstartribune.net/articles/2004/06/08/news/wyoming]
- Gebo, D. L., Chapman, C. A., Chapman, L. J. & Lambert, J. 1994. Locomotor response to predator threat in red-colobus monkeys. *Primates*, **35**, 219-223.
- Gil-da-Costa, R., Palleroni, A., Hauser, M. D., Touchton, J. & Kelley, J. P. 2003. Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. *Proceedings of the Royal Society of London, Series B*, **270**, 605-610.
- Griffin, A. S., Blumstein, D. T., & Evans, C. S. 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, **14**, 1317-1326.
- Griffin, A. S., Evans, C. S., & Blumstein, D. T. 2001. Learning specificity in acquired predator recognition. *Animal Behaviour*, **62**, 577-589.
- Gursky, S. 2002. Determinants of gregariousness in the spectral tarsier (Prosimian: *Tarsius spectrum*). *Journal of Zoology, London*, **256**, 401-410.
- Gursky, S. 2003. Predation experiments on infant spectral tarsiers (*Tarsius spectrum*). *Folia Primatologica*, **74**, 272-284.
- Hauser, M. D. & Caffrey, C. 1994. Anti-predator response to raptor calls in wild crows, *Corvus brachyrhynchos hesperis*. *Animal Behaviour*, **48**, 1469-1471.

- Hauser, M. D. & Wrangham, R. W. 1990. Recognition of predator and competitor calls in non-human primates and birds: a preliminary report. *Ethology*, **86**, 116-130.
- Hendrie, C. A., Weiss, S. M. & Eilam, D. 1998. Behavioural response of wild rodents to the calls of an owl: a comparative study. *Journal of Zoology, London*, **245**, 439-446.
- Johnson, F.R., McNaughton, E. J., Shelley, C. & Blumstein, D. T. 2003. Mechanisms of heterospecific recognition in avian mobbing calls. *Australian Journal of Zoology*, **51**, 577-585.
- Jones, M. E., Smith, G. C. & Jones, S. M. 2004. Is anti-predator behaviour in Tasmanian eastern quolls (*Dasyurus viverrinus*) effective against introduced predators? *Animal Conservation*, **7**, 155-160.
- Karpanty, S. M. & Grelle, R. 2001. Lemur responses to diurnal raptor calls in Ranomafana National Park, Madagascar. *Folia Primatologica*, **72**, 100-103.
- Kelley, J. L. & Magurran, A. E. 2003. Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, **4**, 216-226.
- Kristensen, E. A. & Closs, G. P. 2004. Anti-predator response of naïve and experienced common bully to chemical alarm cues. *Journal of Fish Biology*, **64**, 643-652.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.
- Macedonia, J. M. & Yount, P. L. 1991. Auditory assessment of avian predator threat in semi-captive ringtailed lemurs (*Lemur catta*). *Primates*, **32**, 169-182.
- Macromedia. 1995. *SoundEdit 16*. San Francisco: Macromedia, Inc.
- Maddison, W. P. & Maddison, D. R. 2001. *MacClade: analysis of phylogeny and character evolution. Version 4.03*. Sunderland, Mass.: Sinauer Associates.

- Marler, P. 1955. Characteristics of some animal calls. *Nature*, **176**, 6-8.
- McKenna, M. C. & Bell, S. K. 1997. *Classification of mammals above the species level*.
New York: Columbia University Press.
- Noe, R. & Bshary, R. 1997. The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proceedings of the Royal Society of London, Series B*, **264**, 253-259.
- Petrzelkova, K. & Zukal, J. 2001. Emergence behaviour of the serotine bat (*Eptesicus serotinus*) under predation risk. *Netherlands Journal of Zoology*, **51**, 395-414.
- Pusenius, J. & Ostfeld, R. S. 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. *Animal Conservation*, **7**, 71-77.
- Rainey, H. J., Zuberbühler, K. & Slater, P. J. B. 2004. Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society of London, Series B*, **271**, 755-759.
- Searcy, Y. M. & Caine, N. G. 2003. Hawk calls elicit alarm and defensive reactions in captive Geoffroy's Marmosets (*Callithrix geoffroyi*). *Folia Primatologica*, **74**, 115-125.
- SPSS, Inc. 2000. SPSS-10 for the Macintosh. SPSS Inc., Chicago, IL.
- Swaigood, R. R., Rowe, M. P. & Owings, D. H. 1999. Assessment of rattlesnake dangerousness by California ground squirrels: exploitation of cues from rattling

- sounds. *Animal Behaviour*, **57**, 1301-1310.
- Treves, A. 1999. Has predation shaped the social systems of arboreal primates? *International Journal of Primatology*, **20**, 35-67.
- Van Vuren, D. H. 2001. Predation on yellow-bellied marmots (*Marmota flaviventris*). *American Midland Naturalist*, **145**, 94-100.
- Warren, E. R. 1942. *The mammals of Colorado: their habits and distribution*. Norman: University of Oklahoma Press.
- Wilson, D. E. & Reeder, D. M. 1993. *Mammal species of the world: a taxonomic and geographic reference*. Washington: Smithsonian Institution Press.
- Zuberbühler, K. 2000. Causal knowledge of predators' behaviour in wild Diana monkeys. *Animal Behaviour*, **59**, 209-220.
- Zuberbühler, K. 2001. Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behavioral Ecology Sociobiology*, **50**, 414-422.
- Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. 1999. Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, **113**, 33-42.

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

Latin name	Common name	References
<i>Corvus</i>		
<i>brachyrhynchos</i>	American crow	Hauser & Caffrey 1994
<i>Corythaeola</i>		
<i>cristata</i>	great blue turaco	Hauser & Wrangham 1990
<i>Ceratogymna</i>		
	yellow-casqued	
<i>elata</i>	hornbill	Rainey et al. 2004
<i>Macropus</i>		
<i>eugenii</i>	tammar wallaby	Blumstein et al. 2000b
	red-necked	
<i>Thylogale thetis</i>	pademelon	Blumstein et al. 2002
<i>Dasyurus</i>		
	Tasmanian	
<i>viverrinus</i>	eastern quoll	Jones et al. 2004
<i>Spermophilus</i>		
	California ground	
<i>beecheyi</i>	squirrel	Swaigood et al. 1999
	lesser Egyptian	
<i>Jaculus jaculus</i>	jerboa	Hendrie et al. 1998
<i>Eliomys</i>		
	Asian garden	
<i>melanurus</i>	dormouse	Hendrie et al. 1998
<i>Microtus</i>	social vole	Eilam et al. 1999; Hendrie et al. 1998

socialis

Microtus

pennsylvanicus meadow vole Pusenius & Ostfeld 2000

Gerbillus greater Egyptian

pyramidum gerbil Abramsky et al. 1996

Gerbillus

allenbyi Allenby's gerbil Abramsky et al. 1996

Otomys

angoniensis Angoni Vlei rat Crafford et al. 1999

natal

Mastomys multimammate

natalensis mouse Crafford et al. 1999

Acomys Cairo spiny

cahirinus mouse Eilam et al. 1999; Hendrie et al. 1998

Phoca vitulina harbor seal Deecke et al. 2002

Acinonyx

jubatus Cheetah Durant 2000

Hesperoptenus

doriae false serotine bat Petrzalkova & Zukal 2001

Lemur catta ringtailed lemur Karpanty & Grella 2001; Macedonia & Yount 1991

Alouatta mantled howler

palliata monkey Gil-da-Costa 2003

<i>Callithrix</i>	Geoffroy's	
<i>geoffroyi</i>	marmoset	Searcy & Caine 2003
<i>Tarsius</i>		
<i>spectrum</i>	spectral tarsier	Gursky 2002; Gursky 2003
<i>Cercopithecus</i>	red-tailed	
<i>ascanius</i>	monkey	Hauser & Wrangham 1990; Treves 1999
<i>Cercopithecus</i>		
<i>mitis</i>	blue monkey	Hauser & Wrangham 1990
<i>Cercopithecus</i>		
<i>diana</i>	Diana monkey	Zuberbühler et al. 1999; Zuberbühler 2000
<i>Cercopithecus</i>	Campbell's	
<i>campbelli</i>	monkey	Zuberbühler 2001
<i>Cercopithecus</i>		
<i>aethiops</i>	vervet monkey	Cheney & Seyfarth 1990
	red colobus	Bshary & Noe 1997; Gebo et al. 1994; Hauser &
<i>Colobus badius</i>	monkey	Wrangham 1990; Noe & Bshary 1997; Treves 1999
<i>Alces alces</i>	moose	Berger et al. 2001

Figure Legends

Fig. 1. Spectrograms and waveforms of the acoustic stimuli used to study predator discrimination. Sampling rate 44.1 kHz, 1024 point FFT (frequency resolution 174 Hz), grey scale represents -40 dB from peak amplitude.

Fig. 2. Reconstruction using parsimony 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.

Fig. 3. Difference from baseline in average ($\pm$ SEM) proportion of time engaged in high vigilance plus burrow, and foraging, in the 15 s following playback of conspecific alarm calls, as well as the vocalisations from coyotes, wolves, and golden eagles.

Fig. 4. Difference from baseline in average ($\pm$ SEM) proportion of time spent highly vigilant, and foraging, for forward and reverse golden eagle playbacks. No subjects retreated to their burrows following playback.







