Anthropogenic Noise and its Effect on Animal Communication: An Interface Between Comparative Psychology and Conservation Biology

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Conservation biology and comparative psychology rarely intersect, in part because conservation biology typically emphasizes populations whereas comparative psychology concentrates on individual organisms. However, both fields could benefit from their integration. Conservation biology can profit from an enhanced understanding of individual-level impacts of habitat alteration and the resulting implications for conservation mitigation strategies. Comparative psychology can gain from increased attention to the mechanisms of adjustment used by organisms to "in vivo experiments" created by anthropogenic change. In this paper, we describe a conceptual framework useful for applying our understanding of animal communication to conservation biology. We then review studies of animal communication with conservation implications, and report our own preliminary work that demonstrates our framework in action.

Studies that attempt to synthesize the fields of animal behavior and conservation biology have historically been underrepresented in the journals of both fields (Sutherland, 1998), in part because these fields emphasize different levels of biological organization. Whereas animal behavior typically focuses on understanding the behavior of individuals, conservation biology more often attempts to account for processes at levels above the individual such as population viability, demographics and life history. Likewise, conservation research has emphasized how loss of genetic diversity through genetic drift, inbreeding and hybridization will affect rare and threatened populations. Because the field of conservation biology most often attempts to protect and manage natural *populations* of wildlife, there has been relatively less interest in attempting to understand how *individual-level* phenomena (including social behavior, mate choice, mechanisms of dispersal, and communication) can contribute to the science of conservation. While the potential contributions of animal behavior to the field of conservation biology have not been widely recognized in the past, some are beginning to formalize this synthesis. For example, three edited volumes have recently surveyed the interface between behavioral studies and the field of conservation biology (Caro, 1998; Clemmons & Buchholz, 1997; Gosling & Sutherland, 2000). Likewise, Sutherland's (1998) review has emphasized the benefits that the field of conservation biology can gain through the application of behavioral ecology to conservation issues. Still, there is much room for growth in this synthesis.

Though the applications are not always immediately obvious, knowledge of the proximate processes of individual behavior can be important considerations in developing conservation management strategies. While it is often the case that

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conservation biologists are ultimately interested in maintaining population viability, it is also true that a population's viability depends in part on the health of the individuals in that population. Thus, understanding the behavior of individuals may allow managers to work at the level of the individual to insure positive population growth and limit the probability of local extinction.

Work with sea turtle visual systems illustrates how a knowledge of individual-level behavioral mechanisms can help solve population-level conservation problems. Sea turtle hatchlings, after emerging from their natal nests on sandy beaches, must locomote to the ocean where they will spend the majority of their lives. However, hatchlings appear to be attracted away from the water by artificial light sources inland, a problem that results in hundreds of thousands of hatchling deaths each year (Witherington, 1997). This is an important conservation problem because six of the seven sea turtle species are listed as threatened or endangered. Research conducted on the sensory biology of sea turtles has addressed this problem by demonstrating that individuals are less attracted to light in the yellow and red wavelengths than they are to light with shorter wavelengths (Lohmann et al., 1997). Witherington (1997) subsequently proposed that broad-spectrum light sources near nesting beaches should be replaced by longer wavelength light sources, such as low-pressure-sodium-vapor lights or yellow "bug" lights, in order to reduce the impact of artificial light on hatchling locomotory behavior. Thus, research on the sensory biology of sea turtles has allowed us to explore effective conservation strategies in order to manage individuals of these threatened species. Clearly, an understanding of the mechanisms underlying individual behavior can shed light on effective population management strategies for the purpose of conservation.

Application of the data and approaches of comparative psychology to the conservation of wildlife remains especially underdeveloped in our efforts to synthesize animal behavior and conservation science. However in our view, the synthesis of conservation biology and comparative psychology is potentially worthwhile because of the following distinctive set of emphases that comparative psychology brings to the study of behavior and can similarly bring to conservation biology:

(1) A focus on proximate processes. This includes intensive study of the immediate dynamics of the functioning of behavioral systems (Beecher, 1991; Berridge, 1996; Owings & Hennessy, 1984; Timberlake & Lucas, 1989), detailed exploration of the ontogeny of behavioral systems in "natural" or modified environmental contexts (Alberts, 1987; Beecher et al., 1997; Gottlieb, 1991; Lehrman, 1970; Lickliter, 2000; Mason, 1979b; Schneirla, 1965), and an explicit concern for the role of plasticity in generating a fit between an organism's characteristics and the environmental demands it faces (Beecher et al., 1997; Coss & Globus, 1979; Gottlieb, 1992; Kuo, 1967; West, King, & Freeberg, 1994).

(2) A view of organism-environment relations as fundamentally transactional. Organisms are in two-way commerce with their environments, both operating on their environments and adjusting their behavior in response to environmental inputs (Gibson, 1979/1986; Mason, 1979a; Owings, Rowe, & Rundus, 2002; West & King, 1990). Some of these transactions involve short time frames, as when a California ground squirrel (*Spermophilus beecheyi*) aggressively evokes rattling by a rattlesnake, and assesses the danger posed by the snake on the basis of

the rattling sound (Rowe & Owings, 1978; Swaisgood, Rowe, & Owings, 1999). Other transactions involve more extended time frames and actual environmental modification by animals. This appears to be the case when black-tailed prairie dogs clip down tall vegetation, apparently as a means of increasing the visibility of approaching predators (Hoogland, 1995).

(3) Recognition that behavioral processes are patterned at multiple levels, each with emergent properties. For example, ground squirrel vocal behavior is patterned at multiple structural levels, including the form of individual calls, the temporal organization of call series, and the combination of calling with visual signals (Owings et al., 1986; Smith, 1986). Similarly, all communication systems are organized at a minimum of three functional levels–signal production, signal deployment, and response to the signals of others (Mason, 1985; Seyfarth & Cheney, 1997). This multiple-level approach explicitly acknowledges the potential of higher-level processes to compensate for problems or deficiencies at a lower level (Anderson & Mason, 1974; West, King, & Freeberg, 1997). For instance, rhesus monkeys that cannot attain high social status on their own may be able to do so through skillful deployment of signals in order to recruit the assistance of allies (Anderson & Mason, 1978; Mason, 1985). Similarly, animals in an altered environment may be able to compensate for an inability to adjust communicative behavior at one level with adjustment at another level or levels.

A behavioral framework characterized by these three features highlights the mutual benefits available to comparative psychology and conservation biology from a synthesis of these two fields. To the field of conservation biology, comparative psychology can contribute a focus on the proximate dynamics of behavior, including the impact of these dynamics on the potential for evolutionary change. Nevertheless, it is also clear that studies of the effects of human disturbance on natural populations provide excellent "in vivo" research opportunities for comparative psychologists. Human disturbances are imposed on animals that are otherwise living in the context of the rich environmental resources historically available in their developmental systems (Oyama, Griffiths, & Gray, 2001). The study of behavior in such altered but still rich environments has the potential to lead to the discovery of some very interesting developmental processes and outcomes, including behavioral neophenotypes (Kuo, 1967).

The primary focus of this paper is to describe how animal communication studies undertaken within this comparative psychological framework can provide insight into issues relevant to conservation biologists and to those who manage wildlife in their natural habitats. Though we will emphasize what the study of communication can contribute to conservation biology, we also believe that conservation-oriented behavioral work has much to contribute to comparative psychology.

Synthesis of Animal Communication and Conservation Biology

Communication among organisms is an important component of many daily activities. Effective use of communication contributes immediately to an individual's completion of its daily tasks and ultimately to its survival and reproductive success. Animals participate in communication as a means of finding food (Elowson, Tannenbaum, & Snowdon, 1991; Marler, Dufty, & Pickert, 1986; Stokes, 1971), acquiring mates (Patricelli et al., 2002; Ryan, 1985; Stokes, 1971),

assessing others (Owings et al., 2002; Parker, 1974; Sullivan, 1984), evading predation (Greig-Smith, 1980; Marler, 1955; Vieth, Curio, & Ernst, 1980), and defending resources (Alatalo, Glynn, & Lundberg, 1990; Falls, 1963; Zuberbuehler, Noe, & Seyfarth, 1997). It follows logically that human environmental alterations that impair communication might have significant effects on animals living in modified habitat.

Though this line of inquiry remains underdeveloped, Endler (1997) has explored the potential impact that environmental modifications might have on successful visual communication. Visually-communicative species like lekking birds have evolved color patterns that are adapted for conspicuous communication in the specific light environments where they reside (e.g., forest shade, small light gaps). In fact, some lekking species, such as the Guianian cock-of-the-rock (*Rupicola rupicola*), often display *only* under appropriate lighting conditions. These birds inhabit tropical forests of northeastern South America, in the Guianas. Male plumage is mostly orange-red with yellowish-orange fringe feathers on the wings. *R. rupicola* males only display when light from small forest gaps (rich in yellow-orange wavelengths) passes over their heads. They cease to display when local light conditions change (Endler & Thery, 1996). Clearly, the Guianian cock-of-the-rock display is highly sensitive to specific ambient lighting conditions. Endler (1997) points out that anthropogenic changes to their visual signaling environment, like clearcutting, selective logging, or conversion of forest to agricultural plots, could dramatically affect a male's ability to display to mates by reducing the number of small light gaps in *R. rupicola* habitat.

Evaluating the actual extent of disruption created by such disturbances will be greatly facilitated if we are sensitive to the possibility of behavioral plasticity. Conservation studies in the past have emphasized population changes in evolutionary time frames, but plasticity can also allow for individual developmental adjustments to environmental modifications (Rabin & Greene, 2002). Plasticity might play an especially important role when heritable variation is not sufficient for evolutionary changes mediated by selection. However, a more typical scenario might involve the interplay between evolutionary and developmental processes. For example, developmentally-plastic adjustments can have evolutionary effects, including "bridging the gap" until heritable variation does become available or even increasing the phenotypic expression of latent genetic variation (Bateson, 1988; Cairns, Gariepy, & Hood, 1990).

Assessing the impact of human disturbance can also be enhanced by sensitivity to the multiple levels at which communicative behavior is organized. For example, it is unlikely that *R. rupicola* could make rapid adjustments in the color of its plumage to compensate for disturbances to lighting conditions. If we were to consider only the level of signal structure, we might expect serious threats to the well-being of this species as a result of changes in lighting. These consequences might well be found, but we would be remiss if we did not also investigate the possibility of modifications in *how* they deploy their displays in modified habitats. Such birds might actively pursue small forest gaps over much more widely spaced gaps in order to find suitable signaling space in altered environments.

Similarly, mammals have in general exhibited very limited plasticity at the level of the structure of individual vocalizations (for exceptions see Boughman, 1998; Elowson & Snowdon, 1994; McCowan & Reiss, 1995; McCowan, Reiss, &

Gubbins, 1998; Snowdon & Elowson, 1999). In contrast, mammalian vocal plasticity has been described at the level of signal use, including the contexts of vocalizing and the means of responding to the vocalizations of others (Mason, 1985; Seyfarth & Cheney, 1997). Consequently, many mammals subjected to intermittent anthropogenic noise may have limited developmental capacity to change the frequency distribution of their calls to avoid the noisy part of the frequency spectrum. However, these mammals may be able to compensate with other behavioral modifications, such as confining their vocal behavior to times of low noise.

Studies of change in communicative behavior at multiple organizational levels will be important for identifying avenues of vulnerability and adaptability to anthropogenic environmental modifications. Research along these lines will have real-world applications since an understanding of anthropogenic impacts on communicative systems will allow decision makers to construct management protocol that could minimize these impacts in the future. Once a protocol had been put into practice, additional investigation would allow both comparative psychologists and decision makers to track behavioral responses to mitigation strategies in order to evaluate their effectiveness.

As the field of animal communication advances technologically (McCowan, 1995; Owings & Morton, 1998, Chapter 1), so too does our understanding of acoustic communication and the processes involved in effective signal production, deployment, transmission, perception, and response given the challenges of different signaling environments (Bradbury & Vehrencamp, 1998; Owings & Morton, 1998). Because of our rapidly accumulating knowledge in the study of animal communication, comparative psychology is now provided with a valuable opportunity to ask questions with applied components, including questions regarding the conservation of rare or otherwise ecologically important species in altered environments. For example, our understanding of antipredator communication in California ground squirrels has facilitated our research on the impact of highway noise on California ground squirrel communication. This line of inquiry specifically addresses how wildlife and their communicative systems can be affected by one type of anthropogenic habitat alteration. A body of research on the impact of habitat characteristics on sound transmission, and vocal adjustments to these conditions, indicates that animals have the potential to adapt to changes in their acoustic environments. But this work has left unanswered questions about the mechanisms and rapidity of these adjustments.

Effective Transmission of Acoustic Signals Through a Modified Signaling Medium

In any acoustic signaling environment, differences in humidity, temperature gradients, foliage, and topography will generate certain distorting properties that must be overcome to maintain signal effectiveness. Wiley and Richards (1978; 1982) and Morton (1975) have investigated these properties across a variety of habitats and have identified two categories of problems they create, attenuation and degradation, which must be surmounted to maintain signal efficacy. Attenuation is the process by which all signal components decline equally in intensity due primarily to spherical spread, the dispersion of signal energy over an expanding sphere during transmission. Excess attenuation, beyond that produced by spherical spread, can result from additional factors such as atmospheric absorption, scattering, and

boundary interference. Degradation is the destruction of acoustic signal structure, as a result of reverberation, amplitude fluctuations and differential attenuation at different frequencies. Because attenuation and degradation are important properties of acoustic signal transmission, many species have evolved signals that are spectrally designed to resist these effects and allow for effective signaling in their given habitat (Marten & Marler, 1977; Marten, Quine, & Marler, 1977; Morton, 1975; Waser & Brown, 1986; Wiley & Richards, 1978; Wiley & Richards, 1982). Animals can also alter their daily patterns and locations of calling to minimize the effects of both attenuation and degradation of their signals (Bradbury & Vehrencamp, 1998; Wiley & Richards, 1978; Wiley & Richards, 1982).

Rapid anthropogenic modifications to foliage, topography, temperature gradients, humidity gradients, etc. have the potential to alter the ways in which acoustic signals are transmitted by increasing excess attenuation or degradation of acoustic signals. These alterations can influence the conservation of rare or ecologically important species by reducing the effectiveness of their communicative signals. Though excess attenuation and degradation of signals due to anthropogenic habitat alterations should be of interest to those studying both animal communication and conservation biology (for a review, see Rabin & Greene, 2002), we have chosen to focus on an additional problem, the masking of acoustic signals by anthropogenic noise. Masking increases both with the proximity of signal and noise in the frequency spectrum, and with the amplitude of the noise relative to the signal (Patterson & Green, 1978). As masking increases, signals become increasingly difficult to detect.

In any habitat, masking by the historical noise regime has generally resulted from noise sources such as wind, water, and the signals of conspecifics and heterospecifics (Wiley & Richards, 1978). In response to these historical noise regimes, populations have evolved strategies that minimize acoustic interference between signal and noise (Drewry & Rand, 1983; Ficken, Ficken, & Hailman, 1974; Grafe, 1996; Lang, 1996). Yet, modern human societies have generated entirely new patterns of noise that are likely to modify both selection pressures and developmental influences on these communicative systems (Bowles, 1995; Richardson, 1998). Although we do not know the extent to which recent anthropogenic noise regimes will impact wildlife, it is often the case that the amplitude of anthropogenic noise exceeds that of historical noise (see Table 1). Similarly, the spectral characteristics of anthropogenic noise may be unique when compared with historic noise. The presence of these novel noise sources could challenge the potential for proximate and ultimate adjustments to communicative systems of animals and thus, threaten rare or ecologically important animal populations.

Previous Reports on the Effects of Anthropogenic Noise on Wildlife

Human-generated noise is known to affect animals in a range of ways, from annoyance, to chronic stress, to hearing loss (Bowles, 1995; Workman & Bunch, 1991). Noise may directly affect reproductive physiology or energetic consumption as individuals incur energetic costs or lose mating or foraging opportunities by repeatedly reacting to or avoiding noise (Anderson, Rongstad, & Mytton, 1990; Delaney et al., 1999; Edge & Marcum, 1985; Harrington & Veitch, 1992; Krausman, Leopold, & Scarbrough, 1986). Animals may also be forced to

Table 1
Representative Sound Pressure Levels (SPL) Under Either "Natural" Noise Regimes or Under Anthropogenic Noise Regimes.

Study	Noise source	SPL range	Location of measurement
"Natural" Noise Studies			
Waser and Brown (1986)	Ambient rain forest	27-32 dB	Kibale and Kakamega Forests, Uganda and Kenya
Waser and Brown (1986)	Ambient savanna	20-36 dB	Mchelelo Forest, Kenya
Waser and Brown (1986)	Ambient riverine forest	28-40 dB	Mchelelo Forest, Kenya
Romer et al. (1989)	Bushcricket chorusing	40-60 dB	Cutler Road/King's Park, Near Perth, Australia
Waser and Waser (1977)	Cicada chorusing	70-80 dB	Coastal forest, Near Edea, Cameroun
Schwartz and Wells (1983)	Tree frog chorusing	75-80 dB	Gamboa, Panama
Anthropogenic Noise Studies			
Delaney et al. (1999)	Chain saw noise	51-56 dB	Under spotted owl roosts, Lincoln Nat. Forest, New Mexico
Current Study	Highway noise	82-86 dB	High-noise sites near highways (this study)
Delaney et al. (1999)	Helicopter noise	89-96 dB	Under spotted owl roosts, Lincoln Nat. Forest, New Mexico
Burger (1981)	Subsonic jet noise	88-101dB	Herring gull colonies, near Kennedy Airport, New York
Rabin, unpublished data	Wind turbine noise	59-103 dB	Ground squirrel burrows, Altamont Pass, California
Burger (1981)	Supersonic jet noise	101-116 dB	Herring gull colonies, near Kennedy Airport, New York

Note. Though each study reported on noise sources and their respective decibel levels, acoustic weighting was not consistent between studies. Similarly, distances between the noise source and the SPL meter were not standardized across all studies. Nevertheless, these values provide a representative sample of noise associated with different noise sources.

retreat from favorable habitat in order to avoid aversive anthropogenic noise levels (VanDyke et al., 1986; Watkins & Schevill, 1975).

Though the direct effects of noise on wildlife may be the most obvious, noise may also have indirect effects on population dynamics through changes in habitat use (Anderson et al., 1990), courtship and mating, reproduction and parental care (Algers & Jensen, 1985; Harrington & Veitch, 1992), and possibly migration patterns (VanDyke et al., 1986; Watkins & Schevill, 1975). Excessive noise may also affect mortality rates of adults by causing hearing loss, a serious hazard in predator-prey interactions (Kastak & Schusterman, 1996; Webster & Webster, 1992).

Other effects of noise on wildlife are likely to be subtler, such as those affecting heart rate (Weisenberger et al., 1996) or communication (Algers & Jensen, 1985). In species that rely on acoustic communication, anthropogenic noise may adversely affect individual behavior by making signal detection difficult and thus altering the dynamic interaction between the producers and perceivers of communicative signals (Algers & Jensen, 1985; Bowles et al., 1994; Terhune, Stewart, & Ronald, 1979). For example, anthropogenic noise appears to interfere with communication and interaction among individuals of marine mammal species (Richardson, 1998), an effect that could disrupt such fundamental processes as the coordination of activity within social groups. This new line of investigation into animal communication will have applications for the field of conservation biology and ecosystem management.

Case Study: The Effect of Highway Noise on California Ground Squirrel Vocalizations

Study Species

The California ground squirrel (*Spermophilus beecheyi*) is a vocal and abundant species that lives under widely varying degrees of anthropogenic noise. These characteristics make this species useful as a model for examining the effects of noise on vocal communication in more threatened and endangered species. California ground squirrels are grassland-dwelling, social animals that live in large and sometimes dense colonies. *S. beecheyi* responds to predators with several categories of calls, including chatters, whistles, and single-note repetitive calls. All of these are harmonically structured vocalizations, but chatters differ from whistles and repetitive calls in often containing high levels of frequency modulation. Given the body size of this species, all calls have a relatively low fundamental frequency between 2.8 and 5.1 kHz (Leger, Owings, & Gelfand, 1980; Owings et al., 1986; Owings & Virginia, 1978). Chatters and repetitive calls are the most common vocalizations produced in response to mammalian predators, but whistles, which are typically elicited by raptors, are also emitted in response to mammalian predators under conditions of high urgency (Leger & Owings, 1978; Leger et al., 1980; Owings et al., 1986; Owings & Virginia, 1978). California ground squirrels exhibit potentially meaningful variation in the structure of chatter calls, producing statistically different chatters to snakes, badgers, other mammalian predators, raptors, and conspecific adversaries (Owings & Leger, 1980; Owings & Virginia, 1978). Such findings suggest that these vocalizations are variable enough to allow for structural adjustments in response to environmental noise.

Location and Study Site

A preliminary study was conducted to seek a relationship between highway traffic noise and the acoustic structure of predominantly single-note repetitive calls, an alarm call produced by *S. beecheyi*. Two high noise sites were located in fallow agricultural fields adjacent to Highway 99 near Tulare and Tipton, California. These high-noise sites were exposed to traffic noise with amplitudes ranging from 82-86 dB ("C" weighting) and a maximum frequency of approximately 4 kHz (see Figure 1). Two low noise sites were situated in fallow agricultural fields near Lindsay and Porterville, California. The low noise sites contained a narrower spectral band of ambient noise resulting predominantly from wind. Noise at low-noise sites had amplitudes ranging from 66-70 dB ("C" weighting) and a maximum frequency of approximately 1.5 kHz (see Figure 1). No differences in topographic features were noticeable between the control and experimental sites. All sites lacked residual crop material and sloped less than 1%.
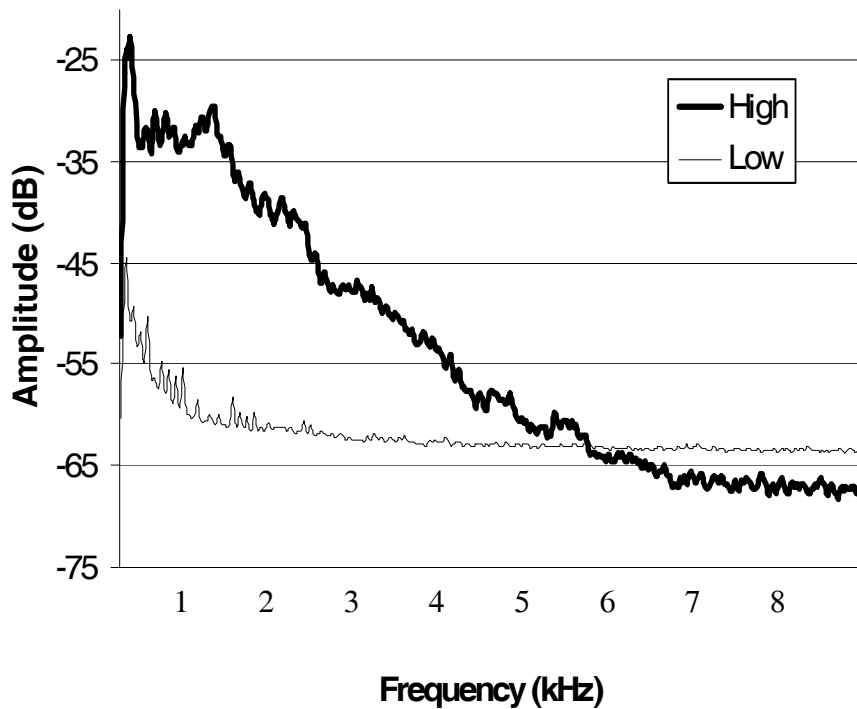

Figure 1. Averaged power spectra of ambient noise at high-noise highway locations (thick line) and low-noise locations (thin line). Each power spectrum was generated by averaging five independent 5s recordings of ambient noise. Gain was identical for all recordings.

Method

S. beecheyi alarm calling bouts were recorded in response to either a human or to a human-led domesticated dog that was approximately 10-20 m from the focal squirrel. Two bouts of vocalizations were recorded during single recording sessions for each of two identified squirrels at each of the four colonies (two high-noise and two low-noise). During calling, each squirrel was recorded facing toward a microphone at a distance of approximately 20 m. Vocalizations were recorded using a Tas-

cam DAT recorder (44 kHz sampling rate) and an Audio-Technica AT4071 directional microphone (22 kHz in frequency range).

During each recording bout, the observer indicated the identity of the vocalizer, whether the "predator" type was a human or a human+dog, the study site where the call was recorded, and the distance between the microphone and the focal squirrel. Each calling bout from each individual at each site was processed for the repetitive calls. Vocalizations from both low and high noise sites were filtered for background noise using identical procedures, which included standard parametric filtering (1.5-16 kHz Butterworth bandpass filter) and the noise reduction feature available in Cool Edit Pro software (Syntrillium). The noise reduction feature in Cool Edit Pro removes background noise by generating a filter from a chosen segment of noise, in this case a segment of traffic noise. Background noise using this feature was removed from all recorded vocalizations with a loss of only 1-3 dB in signal (see Figure 3). To ensure that this filtering procedure did not adversely alter signal structure or relative amplitude, we used a computer to generate tones with a 3500 Hz fundamental and two additional harmonics of known amplitudes in Cool Edit Pro. We then filtered and noise reduced these tones using the same protocol as described above. Filtering and noise reduction had no significant effect on frequency, time, and amplitude measurements of the tones. Differences of only 1-10 Hz in frequency, 5-10 ms in duration and 1-3 dB in amplitude were found between filtered and non-filtered tones.

Repetitive calls recorded from each individual were then measured separately using the methods described by McCowan (1995), McCowan and Reiss (2001) and McCowan and Hooper (2002). Over the length of each call, sixty measurements were digitally extracted from the spectrogram (sampling rate of 44 kHz; 1024-point FFT spectrum with a Hamming filter; time resolution of 12 ms; frequency resolution of 50 Hz). For each of these sixty measurements across time, the frequency with the highest amplitude was recorded using Cool Edit Pro software and automated custom macros developed by the second author. Several acoustic variables defining various call spectral, temporal, and amplitude parameters were calculated from these call measurements. Due to the small sample size for each subject, a small subset of variables was chosen for statistical analysis: mean frequency, frequency at peak amplitude, and maximum frequency. Mean frequency is a calculated average for each call, of the 60 frequency measurements taken. Frequency at peak amplitude is the frequency with the highest amplitude of the 60 frequency measurements taken for each vocalization.

Maximum frequency is the highest frequency of the 60 frequencies measured within a single vocalization. We chose these specific variables because we predicted that the calls of individuals from colonies of the high-noise condition would show a frequency shift of the fundamental of these calls beyond the range of traffic noise.

Results

For high noise colonies, we analyzed the 26-57 calls emitted from each of 4 focal squirrels (two squirrels at each colony); 85 of these vocalizations were human-elicited, and 72 were human+dog-elicited. For low noise colonies, we analyzed the 23-46 calls emitted from each of 4 focal squirrels (two squirrels at each colony); 47 were human-elicited, and 83 were human+dog-elicited. Vocalizations were recorded during alarm calling bouts that lasted between 1.1-7.1 min in high noise colonies and between 1.2-8.3 min in low noise colonies.

Though we predicted that the fundamental frequency of calls emitted in high-noise conditions would show a frequency shift, we found an even more interesting difference. The frequency of the first harmonic remained unchanged but acoustic power was often shifted to the second and even the third harmonic of alarm calls under high-noise conditions. For Maximum Frequency, the range for individuals at low-noise sites was 3860.8-4510.9 Hz, whereas for high noise sites, these values were 5043.5-7248.6 Hz. Comparable low versus high noise values were 3357.7-3949.8 Hz versus 3793.7-4621.9 Hz for Mean Frequency, and 3332.7-3889.4 Hz versus 3733.7-4847.9 Hz for Frequency at Peak Amplitude (see also Figures 2 and 3). An emphasis of higher harmonics placed the peak energy of

these "high-noise site" alarm calls out of the range of interference by highway traffic noise (see Figure 1).
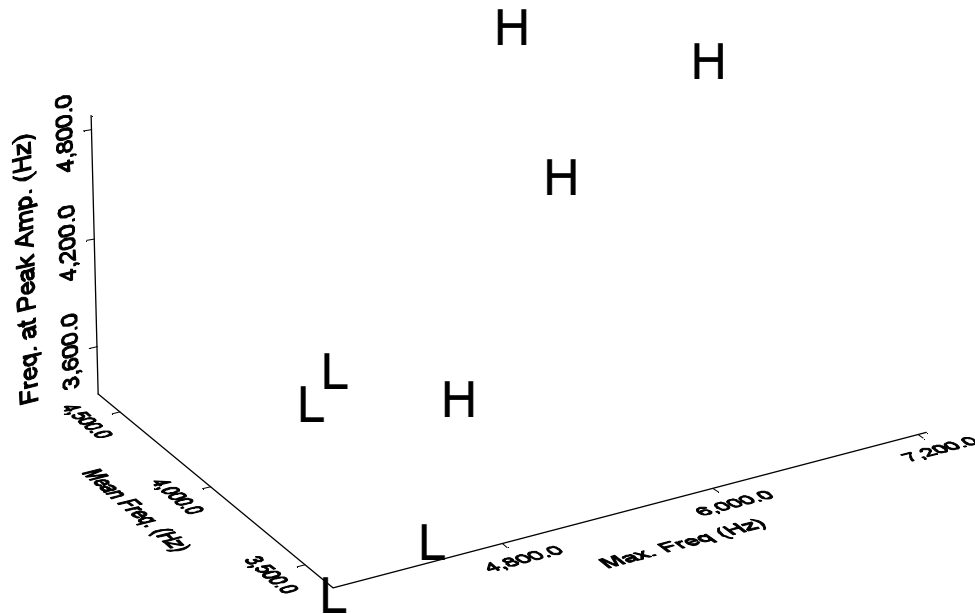

Figure 2. Three-dimensional plot of the average of each of the three variables (X-axis: maximum frequency, Y-axis: mean frequency and Z-axis: frequency at peak amplitude shown in Hz) distinguishing low (L) and high (H) noise colonies by individual ($N_{ID} = 8$; $N_{Voc} = 287$).

This shift in acoustic emphasis by subjects from high-noise locations (see Figure 3e-h) was confirmed by statistical differences. In a mixed effects linear regression (Pinheiro & Bates, 2000), the values for all three variables were significantly higher for high noise locations than for low noise locations (mean frequency: $F_{(1,6)} = 42.7$, $p = 0.0006$; frequency at peak amplitude: $F_{(1,6)} = 16.4$, $p = 0.007$; maximum frequency: $F_{(1,6)} = 62.3$, $p = 0.0002$). These differences are not due to subject idiosyncrasies or predator type, since we controlled for the effects of these variables by including them in the regression as a grouped-variable random effect or repeated measure (subjects within colonies), and a random effect (predator type: dog vs. human+dog).

Cross-validation discriminant analysis on the three variables also support this result. The degree to which call structure differed between high and low noise conditions can be assessed by using a classification procedure, in which calls are assigned to the most probable group (either high-noise or low-noise colony) based on their discriminant function scores alone. In such a procedure, low-noise colony calls were correctly classified (i.e., to their actual group of origin), 86% of the time and high-noise colony calls were correctly classified 67% of the time (average correct classification = 77%). These values are each significantly above the percentage expected to be classified correctly based on chance alone (50%). Classification by chance was calculated by conducting a series of discriminant analyses on the data after randomly assigning the calls to low and high noise sites based upon the original sample sizes at each location. The analysis of 20 independent tests revealed that, for randomly assigned calls, between 40-58% of calls were classified

correctly (the average percentage of calls correctly classified across jackknife tests = 50%).
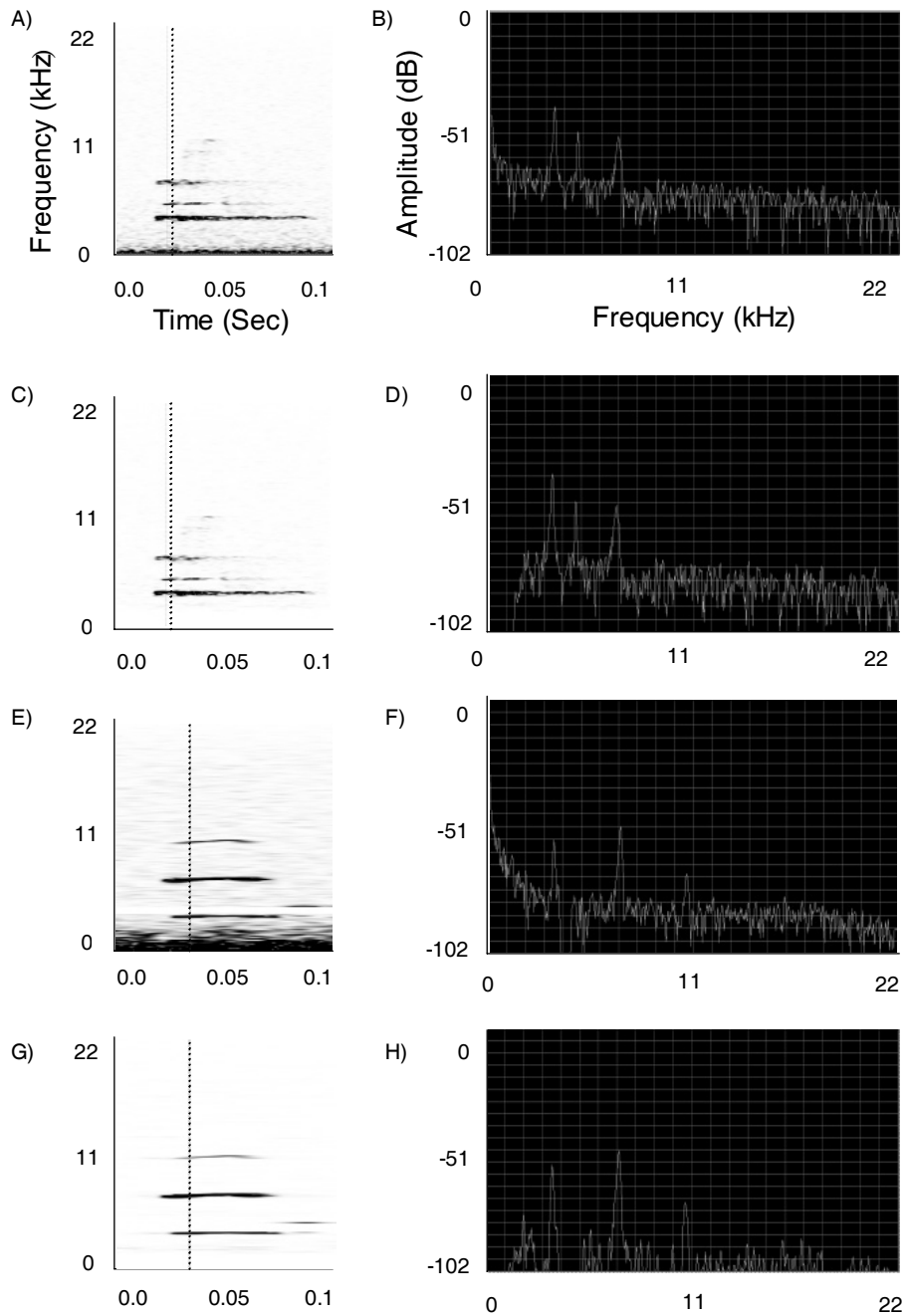

Figure 3. Comparison of single-note repetitive calls at high-noise sites vs. low-noise sites: (A) Spectrogram representative of a repetitive call from a low noise site. (B) Power spectrum of call "A" at the time indicated by the dashed line. (C) Spectrogram "A" after noise reduction. (D) Power spectrum at the time indicated by the dashed line in "C". (E) Spectrogram representative of a repetitive call from a high noise site. (F) Power spectrum of call "E" at the time indicated by the dashed line. (G) Spectrogram "E" after noise reduction. (H) Power spectrum at the time indicated by the dashed line in "G". Note the emphasis of the second harmonic at the high-noise site compared to the emphasis of the fundamental frequency at the low-noise site.

It is unlikely that differential habitat filtering, due to small differences in topographical features between sites, drove the between-site (high noise vs. low noise) variability. At one low noise and one high noise site, computer-generated tones with a 3500 Hz fundamental and two additional harmonics were broadcast 15 times each at 90 dB with an Advent Wireless Amplified Speaker and rerecorded at a distance of 20 m using the equipment described above. Discriminant analysis on these rerecorded harmonic tones was performed using the same variables as in the analysis of ground squirrel calls to determine if rerecorded tones differed between low and high noise sites. Percent correct classification of tones to site type (noisy vs. quiet) was 40% for tones broadcast at both the low and high noise sites. These results demonstrate that the rerecorded tones could not be discriminated by site and that the variables analyzed were not likely affected by differential habitat filtering. ANOVA tests produced a similar result. None of the quantified variables of the harmonic tones significantly differed between sites. Consequently, between-site variability in recordings of ground squirrel vocalizations represents differences in actual signal production.

Discussion

Response of California Ground Squirrels to Highway Noise. In our case study on the effects of highway noise on California ground squirrel communication, we have described one prevalent anthropogenic environmental alteration and one means by which California ground squirrels are able to respond to this habitat alteration. Our preliminary investigation suggests that ground squirrels are able to modify their vocalizations in response to highway noise by shifting acoustic energy in their calls to harmonics that do not overlap with highway noise (see Figures 2 and 3). How these squirrels are accomplishing these vocal changes is currently unknown. One possibility is that they reflect the Lombard effect, a reflexive increase in vocal amplitude to high noise exhibited by humans and other animals. This phenomenon can also involve modifications in vocal structure (Cynx et al., 1998; Junqua, 1996; Manabe, Sadr, & Dooling, 1998). Consistent with our interpretation of our results, Lombard-Effect related changes are typically viewed as functioning to maintain communicative efficacy under noise. Variation in the effects of the Lombard reflex support the idea that it functions to maintain the social impact of vocalizations; the specific adjustments produced by the Lombard reflex vary with the level and form of the noise.

Additional work on ground squirrel adjustments to noise has yielded data also indicating that the form of vocal adjustment depends on noise structure. Preliminary analyses of the calls of squirrels exposed to anthropogenic noise with different spectral signatures indicates that squirrels can exhibit a different type of spectral change, lowering the fundamental frequency of their calls out of the range of acoustic interference with those noise sources (L. Rabin, unpublished data). We do not yet know whether such structural changes make a difference to perceivers of these vocalizations. Nevertheless, playback studies with this species have demonstrated that comparably subtle differences in vocal structure do evoke different behavioral responses (Leger & Owings, 1978).

If replication verifies these effects of highway noise, we will attempt to determine whether these vocal modifications are accomplished through evolutionary processes, immediate "online" modifications to call structure, developmental

plasticity, or a combination of these three factors. Our results do hint at a role for plasticity and/or online adjustments to noise. Individual variation in the spectral distribution of calls was observed; individual squirrels in high-noise colonies usually, but not invariably, emphasized the second harmonic (see Figure 3) or third harmonic of their vocalizations. In the future, experimental trials that concurrently record both alarm calls and noise levels will allow us to look for correlations between the spectral distribution of calls and the level and spectral distribution of simultaneous noise. Data showing that vocalizations consistently change as noise conditions change, would provide evidence for immediate, "online," vocal adjustments to anthropogenic noise. On the other hand, evidence of developmental vocal plasticity might initially be revealed by comparisons of adult and pup vocal structure. If adults at high-noise sites emphasize harmonics out of the spectral band of masking but pups do not, this might mean that experience is required to optimize vocal structure under local noise regimes.

There is yet another explanation for our results. One might argue that a systematic difference in body size between high and low noise sites could be causing the differences in vocalizations in our study. In fact, there is evidence that the spectral distribution of calls varies within species as a function of body size. A negative relationship between body size and call frequency has been described, based on variation either in fundamental frequency (Morton, 1977), or formant frequencies (Fitch, 1997). We cannot directly judge this hypothesis because we did not weigh the animals in our preliminary study. Nevertheless, we tentatively reject this hypothesis for the following reason: Covariation between body size and vocalization frequency has its roots in size differences in the vocal apparatus. If the animals at our high-noise sites had smaller vocal structures, they should have invariably emphasized higher frequencies. But our subjects from high-noise locations varied in their vocal emphasis, usually stressing the second or third harmonic, but sometimes emphasizing the first. Consequently, the differences in call structure between sites are not likely to be the result of either body-size differences or differences in the size of the vocal apparatus.

Utility of Studying a Common Species to Gain Insight Into Conservation-Related Issues. Because California ground squirrels are an abundant species, readers may wonder why we have chosen *S. beecheyi* for our conservation-motivated research. We admit that using California ground squirrels to gain insight into conservation related issues is unusual. Species of conservation priority are typically rare, threatened, and in immediate danger of becoming extinct. However, where rare species rely on abundant ones for food, shelter, or other daily essentials, it will be important to prevent environmental perturbations from causing a decline in the abundant species. A decline of the abundant species could have community level effects that would jeopardize the viability of the rare population. For California ground squirrels, this is likely the case.

In oak-savanna communities where California ground squirrels typically reside, species of special concern depend on *S. beecheyi* as a source of food and shelter. For example, California ground squirrels have been reported to make up more than 25% of the diet of golden eagles (Carnie, 1954). Similarly, burrowing owls and California red-legged frogs use *S. beecheyi* burrows for shelter (Bente, 1938; Jennings & Hayes, 1994; Rowe, Coss, & Owings, 1986). Both golden eagles and burrowing owls are species of special concern and California red-legged frogs

are federally listed. Any impacts on California ground squirrels due to habitat alteration and anthropogenic noise, thus have the potential to affect species that are a conservation priority in *S. beecheyi* habitat.

Our use of ground squirrels in our conservation-related case study also stems from our belief that new analytical tools and general experimental methodologies, like those described here, can later be utilized to study a diversity of species including those that are threatened or endangered. Developing these methodologies will allow us to better understand the impacts that humans are having on natural habitats and their resident animals that communicate acoustically.

Whether or not squirrels have adapted, responded developmentally, or made "online" vocal adjustments in response to highway noise, our results currently suggest that California ground squirrels may be able to cope with noise from highways. This is not entirely surprising since California ground squirrels have proven to be highly flexible in their ability to live in different environments under different degrees of human influence (Grinnell & Dixon, 1918). In fact, *S. beecheyi* is often considered a "weedy" species due to its abundance in a variety of habitats that vary in their degree of human influence. However, as our research continues, potential impacts of highway noise on California ground squirrel communication may be uncovered. For example, future playback studies might determine that signal reception is in some way impeded near noisy highways thus compromising the ability of ground squirrels to warn conspecifics about the presence of predators nearby.

If additional studies show that squirrels are unable to adequately cope with the potential adverse effects of highway noise, our results could affect the planning of highways in areas where species of special concern rely on ground squirrels. While it is unlikely that our results would influence the siting of highways, our data might provide an incentive to develop inexpensive mitigation strategies (e.g., building walls along highway barriers that block sound) to reduce the impacts of highway noise on wildlife. We thus believe that these investigations into communicative behavior, have the potential to contribute to the science of wildlife management and conservation.

Encouraging Discussion Between Comparative Psychologists and Conservation Biologists. As the human "footprint" on the natural world becomes larger, we are presented with the opportunity to better understand how human behavior and our associated technologies can affect patterns of animal movement, dispersal, social relations, and communication. This understanding will allow us to gauge the impact that humans have on animal behavior so that these impacts can be considered in conservation biology and plans for species preservation.

A synthesis between comparative psychology and conservation biology will be worthwhile in allowing both disciplines to undertake a greater number of scientific investigations that are integrative and include consideration of multiple levels of analysis. As stated previously, the field of conservation biology has traditionally focused on population level phenomena and on understanding how evolutionary constraint may prevent populations from tracking habitat change. Comparative psychology on the other hand, has emphasized studies at the level of the individual by exploring the proximate dynamics of behavior throughout ontogeny. Both fields might benefit by considering behavioral issues at levels of analysis that have not traditionally been represented in their disciplines. For conservation biolo-

gists, this means considering such factors as sensory biology, development, and behavior when planning conservation strategy. For comparative psychologists, this suggests a greater consideration for evolutionary processes and population level phenomena that have occurred in response to habitat alteration.

Though we have largely described a means by which communicative studies and comparative psychology can contribute to conservation biology, it is also true that exploring individual responses to habitat alterations can allow for a better understanding of the dynamics of real-time and developmental changes in communication. For example, results described from our case study have predictive implications for understanding the mechanisms that promote and constrain vocal plasticity. On those uncommon occasions when plasticity has been found in mammalian vocal structure, it has typically been with the rich environmental support of normal social contexts. In fact, vocal plasticity can also be enhanced in song-birds by normal social contexts (see Snowdon & Hausberger, 1997 for a collection of relevant chapters). Such contextual support for vocal plasticity was also available in our work. Nevertheless, vocal structure is only one level at which communicative behavior might exhibit plasticity. Future research will also allow us to test for plasticity in the temporal patterning of calling, the pairing of calling with visual signaling, and the response to the calls of others. Elucidating these mechanisms has the potential to advance the field of animal communication and communication theory. Species forced to reside in an acoustically-noisy habitat may switch entirely to another modality when signaling (e.g., visual or tactile communication) or increase their usage of alternate modalities during signaling in the presence of noise. All of these responses require a certain amount of communicative plasticity. As a result, the study of both communicative and non-communicative behavioral plasticity in the wild may uncover previously unexpected flexibility in behavioral systems (as in Gottlieb, 1993; Lickliter, 1991).

Concluding Remarks

The practice of conserving rare and endangered species, by necessity, benefits from research that investigates natural patterns and processes from both a theoretical and applied perspective. Though some have commented on the divide between conservation theory and practice (e.g., Caughley, 1994), it is becoming increasingly clear that those interested in management and those interested in more theoretical issues are making efforts to work together in order to effectively manage natural ecosystems (Hedrick et al., 1996).

In the case of sea turtle hatchling disorientation in the presence of artificial light sources, knowledge gained from sensory studies on their visual systems has been directly incorporated into United States sea turtle recovery plans. For the loggerhead, leatherback, hawksbill, and east Pacific green turtles; short-wavelength and broad-wavelength artificial lighting have been listed as general threats to their survival. At the same time, sea turtle recovery plans have made recommendations to evaluate, implement, and enforce artificial lighting regulations along beaches (NMFS & USFWS, 1993; NMFS & USFWS, 1998; USFWS & NMFS, 1992; USFWS & NMFS, 1993). In the hawksbill and loggerhead recovery plans, additional recommendations have involved the development of informational brochures and public service announcements to educate the public about problems associated with beachfront lighting (NMFS & USFWS, 1993; USFWS & NMFS, 1993). This

integration between sensory studies and conservation decision making appears to have been successful since there has been a drastic reduction in hatchling disorientation where lighting regulations have been put into place (NMFS & USFWS, 1993; USFWS & NMFS, 1992; USFWS & NMFS, 1993).

We hope that in the future, a greater number of comparative psychologists will attempt to seek ways in which theoretical questions from their own research can contribute to conservation management and the preservation of natural ecosystems and their resident populations of organisms. Such an endeavor can only help us in our effort to maintain a diversity of ecosystems and organisms while minimizing human-generated rarity and extinction.

References

Alatalo, R. V., Glynn, C., & Lundberg, A. (1990). Singing rate and female attraction in the pied flycatcher: An experiment. *Animal Behaviour,* **39**, 601-603.

Alberts, J. R. (1987). Early learning and ontogenetic adaptation. In N. Krasnegor, E. Blass, M. Hofer & W. Smotherman (Eds.), *Perinatal development: A psychological perspective* (pp. 11-37). Orlando, FL: Academic Press.

Algers, B., & Jensen, P. (1985). Communication during suckling in the domestic pig: Effects of continuous noise. *Applied Animal Behavior Science,* **14**, 49-61.

Anderson, C. O., & Mason, W. A. (1974). Early experience and complexity of social organization in groups of young rhesus monkeys (*Macaca mulatta*). *Journal of Comparative and Physiological Psychology,* **87**, 681-690.

Anderson, C. O., & Mason, W. A. (1978). Competitive social strategies in groups of deprived and experienced rhesus monkeys. *Developmental Psychobiology,* **11**, 289-299.

Anderson, D. E., Rongstad, O. J., & Mytton, W. R. (1990). Home range changes in raptors exposed to increased human activity levels in southeastern Colorado. *Wildlife Society Bulletin,* **18**, 134-142.

Bateson, P. (1988). The active role of behaviour in evolution. In M. W. Ho, & S. W. Fox (Eds.), *Evolutionary processes and metaphors* (pp. 191-207). New York: Wiley and Sons.

Beecher, M. D. (1991). Successes and failures of parent-offspring recognition in animals. In P. G. Hepper (Ed.), *Kin recognition* (pp. 94-124). Cambridge, UK: Cambridge University Press.

Beecher, M. D., Campbell, S. E., Nordby, J. C., Burt, J. M., & Hill, C. E. (1997). What is the function of song learning in songbirds? In D. H. Owings, M. D. Beecher, & N. S. Thompson (Eds.), *Perspectives in ethology, Vol. 12: Communication* (pp. 77-97). New York: Plenum Press.

Bente, A. C. (1938). Life histories of North American birds of prey. Part 2. *U.S. National Museum Bulletin*, 170.

Berridge, K. C. (1996). Food reward: Brain substrates of wanting and liking. *Neuroscience and Biobehavioral Reviews,* **20**, 1-25.

Boughman, J. W. (1998). Vocal learning by greater spear-nosed bats. *Proceedings of the Royal Society of London Series B Biological Sciences,* **265**, 227-233.

Bowles, A. E. (1995). Responses of wildlife to noise. In R. Knight & K. Gutzwiller (Eds.), *Wildlife and recreationists: Coexistence through management and research* (pp. 109-156).

Bowles, A. E., Smultea, M., Wursig, B., Demaster, D. P., & Palka, D. (1994). Relative abundance and behavior of marine mammals exposed to transmissions from Heard Island feasibility test. *Journal of the Acoustical Society of America,* **96**, 2469-2484.

Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer Associates.

Burger, J. (1981). Behavioral responses of herring gulls *Larus argentatus* to aircraft noise. *Environmental Pollution (Series A) Ecological & Biological,* **24**, 177-184.

Cairns, R. B., Gariepy, J. L., & Hood, K. E. (1990). Development, microevolution, and social behavior. *Psychological Review,* **97**, 49-65.

Carnie, S. K. (1954). Food habits of nesting golden eagles in the coast ranges of California. *Condor,* **56**, 3-12.

Caro, T. M. (1998). *Behavioral ecology and conservation biology*. New York: Oxford University Press.

Clemmons, J. R., & Buchholz, R. (1997). *Behavioral approaches to conservation in the wild*. Cambridge, UK: Cambridge University Press.

Coss, R. G., & Globus, A. (1979). Social experience affects the development of dendritic spines and branches on tectal interneurons in the jewel fish. *Developmental Psychobiology,* **12**, 347-358.

Cynx, J., Lewis, R., Tavel, B., & Hanson, T. (1998). Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata. Animal Behaviour,* **56**, 107-113.

Delaney, D., Grubb, T., Beier, P., Pater, L., & Reiser, M. H. (1999). Effects of helicopter noise on Mexican spotted owls. *Journal of Wildlife Management,* **63**, 60-76.

Drewry, G. E., & Rand, A. S. (1983). Characteristics of an acoustic community: Puerto-Rican frogs of the genus *Eleutherodactylus. Copeia,* **4**, 941-953.

Edge, W. D., & Marcum, C. L. (1985). Movements of elk in relation to logging disturbances. *Journal of Wildlife Management,* **49**, 741-744.

Elowson, A. M., & Snowdon, C. T. (1994). Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Animal Behaviour,* **47**, 1267-1277.

Elowson, A. M., Tannenbaum, P. L., & Snowdon, C. T. (1991). Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour,* **42**, 931-937.

Endler, J. A. (1997). Light, behavior, and conservation of forest dwelling organisms. In J. Clemmons & R. Buchholz (Eds.), *Behavioral approaches to conservation in the wild* (pp. 329-355). Cambridge, UK: Cambridge University Press.

Endler, J. A., & Thery, M. (1996). Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *American Naturalist,* **148**, 421-452.

Falls, J. B. (1963). Properties of song eliciting responses from territorial males. *Proceedings of the 13th International Ornithological Congress,* **1**, 259-271.

Ficken, R. W., Ficken, M. S., & Hailman, J. P. (1974). Temporal pattern shifts to avoid acoustic interference in singing birds. *Science,* **183**, 762-763.

Fitch, W. T. (1997). Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America,* **102**, 1213-1222.

Gibson, J. J. (1979/1986). *The ecological approach to visual perception*. Hillsdale, NJ: Erlbaum.

Gosling, L. M., & Sutherland, W. J. (2000). *Behaviour and conservation*. New York: Cambridge University Press.

Gottlieb, G. (1991). Social induction of malleability in ducklings. *Animal Behaviour,* **41**, 953-962.

Gottlieb, G. (1992). *Individual development and evolution: The genesis of novel behavior*. New York: Oxford University Press.

Gottlieb, G. (1993). Social induction of malleability in ducklings: Sensory basis and psychological mechanism. *Animal Behaviour,* **45**, 707-719.

Grafe, T. U. (1996). The function of call alternation in the African reed frog (*Hyperolius marmoratus*): Precise call timing prevents auditory masking. *Behavioral Ecology and Sociobiology,* **38**, 149-158.

Greig-Smith, P. W. (1980). Parental investment in nest defence by stonechats (*Saxicola torquata*). *Animal Behaviour,* **28**, 604-619.

Grinnell, J., & Dixon, J. (1918). California ground squirrels. *The Monthly Bulletin: California State Commission of Horticulture,* **7**, 599-708.

Harrington, F. H., & Veitch, A. M. (1992). Calving success of woodland caribou exposed to low-level jet fighter overflights. *Arctic,* **45**, 213-218.

Hedrick, P. W., Lacy, R. C., Allendorf, F. W., & Soule, M. E. (1996). Directions in conservation biology: Comments on Caughley. *Conservation Biology,* **10**, 1312-1320.

Hoogland, J. L. (1995). *The black-tailed prairie dog: Social life of a burrowing mammal*. Chicago, IL: University of Chicago Press.

Jennings, M. R., & Hayes, M. P. (1994). California red-legged frog *Rana aurora draytonii. Amphibian and Reptile Species of Special Concern in California* (pp. 62-66). Rancho Cordova, CA: California Department of Fish and Game, Inland Fisheries Division.

Junqua, J. C. (1996). The influence of acoustics on speech production: A noise-induced stress phenomenon known as the Lombard reflex. *Speech Communication,* **20**, 13-22.

Kastak, D., & Schusterman, R. (1996). Temporary threshold shift in a harbor seal (*Phoca vitulina*). *Journal of the Acoustical Society of America,* **100**, 1905-1908.

Krausman, P. R., Leopold, B. D., & Scarbrough, D. L. (1986). Desert mule deer response to aircraft. *Wildlife Society Bulletin,* **14**, 68-70.

Kuo, Z. Y. (1967). *The dynamics of behavioral development: An epigenetic view.* New York: Random House.

Lang, F. (1996). Noise filtering in the auditory system of *Locusta migratoria. Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology,* **179**, 575-585.

Leger, D. W., & Owings, D. H. (1978). Responses to alarm calls by California ground squirrels: Effects of call structure and maternal status. *Behavioral Ecology and Sociobiology,* **3**, 177-186.

Leger, D. W., Owings, D. H., & Gelfand, D. L. (1980). Single-note vocalizations of California ground squirrels: Graded signals and situation specificity of predator and socially-evoked calls. *Zeitschrift fur Tierpsychologie,* **52**, 227-246.

Lehrman, D. S. (1970). Semantic and conceptual issues in the nature-nurture problem. In L. Aronson, E. Tobach, D. Lehrman & J. Rosenblatt (Eds.), *Development and evolution of behavior* (pp. 17-52). San Francisco, CA: W H Freeman & Co.

Lickliter, R. (1991). Context and animal behavior II: The role of conspecifics in species-typical perceptual development. *Ecological Psychology,* **3**, 11-23.

Lickliter, R. (2000). An ecological approach to behavioral development: Insights from comparative psychology. *Ecological Psychology,* **12**, 319-334.

Lohmann, K. J., Witherington, B. E., Lohmann, C. M. F., & Salmon, M. (1997). Orientation, navigation, and natal beach homing in sea turtles. In P. L. Lutz & J. A. Musick (Eds.), *The biology of sea turtles* (p. 107-135). Boca Raton, FL: CRC Press.

Manabe, K., Sadr, E. I., & Dooling, R. J. (1998). Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): Differential reinforcement of vocal intensity and the Lombard effect. *Journal of the Acoustical Society of America,* **103**, 1190-1198.

Marler, P. (1955). Characteristics of some animal calls. *Nature,* **176**, 6-8.

Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver? *Animal Behaviour,* **34**, 188-193.

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

Marten, K., Quine, D., & Marler, P. (1977). Sound transmission and its significance for animal vocalization II: Tropical forest habitats. *Behavioral Ecology and Sociobiology,* **2**, 291-302.

Mason, W. A. (1979a). Ontogeny of social behavior. In P. Marler & J. G. Vandenbergh (Eds.), *Handbook of behavioral neurobiology: Vol. 3* (pp. 1-28). New York: Plenum Press.

Mason, W. A. (1979b). Wanting and knowing: A biological perspective on maternal deprivation. In E. Thoman (Ed.), *Origins of the infant's social responsiveness* (pp. 225-249). Hillsdale, NJ: Erlbaum.

Mason, W. A. (1985). Experiential influences on the development of expressive behaviors in rhesus monkeys. In G. Zivin (Ed.), *The development of expressive behavior: Biology-environment interactions* (pp. 117-152). Orlando, FL: Academic Press.

McCowan, B. (1995). A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (Delphinidae, *Tursiops truncatus*). *Ethology,* **100**, 177-193.

McCowan, B., & Hooper, S. L. (2002). Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. *Journal of the Acoustical Society of America,* **111**, 1157-1160.

McCowan, B., & Reiss, D. (1995). Whistle contour development in captive-born infant bottlenose dolphins. *Journal of Comparative Psychology,* **109**, 242-260.

McCowan, B., & Reiss, D. (2001). The fallacy of 'signature whistles' in bottlenose dolphins: A comparative perspective of 'signature information' in animal vocalizations. *Animal Behaviour,* **62**, 1151-1162.

McCowan, B., Reiss, D., & Gubbins, C. (1998). Social familiarity influences whistle acoustic structure in adult female bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals,* **24**, 27-40.

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

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist,* **111**, 855-869.

NMFS, & USFWS. (1993). *Recovery plan for U.S. population of loggerhead turtle (Caretta caretta).* Bethesda, MD: United States Fish and Wildlife Service and National Marine Fisheries Service.

NMFS, & USFWS. (1998). *Recovery plan for U.S. Pacific populations of the east Pacific green turtle (Chelonia mydas).* Silver Spring, MD: National Marine Fisheries Service.

Owings, D. H., & Hennessy, D. F. (1984). The importance of variation in Sciurid visual and vocal communication. In J. O. Murie & G. R. Michener (Eds.), *The biology of ground-dwelling squirrels* (pp. 169-200). Lincoln, NE: University of Nebraska Press.

Owings, D. H., Hennessy, D. F., Leger, D. W., & Gladney, A. B. (1986). Different functions of "alarm" calling for different time scales: A preliminary report. *Behaviour, 99,* 101-116.

Owings, D. H., & Leger, D. W. (1980). Chatter vocalizations of California ground squirrels: Predator- and social-role specificity. *Zeitschrift fur Tierpsychologie, 54,* 163-184.

Owings, D. H., & Morton, E. S. (1998). *Animal vocal communication: A new approach.* New York: Cambridge University Press.

Owings, D. H., Rowe, M. P., & Rundus, A. S. (2002). The rattling sound of rattlesnakes (*Crotalus viridis*) as a communicative resource for ground squirrels (*Spermophilus beecheyi*) and burrowing owls (*Athene cunicularia*). *Journal of Comparative Psychology, 116,* 197-205.

Owings, D. H., & Virginia, R. A. (1978). Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Zeitschrift fur Tierpsychologie, 46,* 58-70.

Oyama, S., Griffiths, P. E., & Gray, R. D. (2001). *Cycles of contingency: Developmental systems and evolution.* Cambridge, MA: MIT Press.

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology, 47,* 223-243.

Patricelli, G. L., Uy, J. A. C., Walsh, G., & Borgia, G. (2002). Male displays adjusted to female's response - Macho courtship by the satin bowerbird is tempered to avoid frightening the female. *Nature, 415,* 279-280.

Patterson, R. D., & Green, D. M. (1978). Auditory masking. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of perception IV: Hearing* (pp. 337-361). New York: Academic Press.

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effects models in S and S-Plus.* New York: Springer Verlag.

Rabin, L. A., & Greene, C. M. (2002). Changes to acoustic communication systems in human-altered environments. *Journal of Comparative Psychology, 116,* 137-141.

Richardson, J. W. (1998). *Marine mammals and noise.* New York: Academic Press.

Romer, H., Bailey, W., & Dadour, I. (1989). Insect hearing in the field: III. Masking by noise. *Journal of Comparative Physiology A, 164,* 609-620.

Rowe, M. P., Coss, R. G., & Owings, D. H. (1986). Rattlesnake rattles and burrowing owl hisses: A case of acoustic Batesian mimicry. *Ethology, 72,* 53-71.

Rowe, M. P., & Owings, D. H. (1978). The meaning of the sound of rattling by rattlesnakes to California ground squirrels. *Behaviour, 66,* 252-267.

Ryan, M. J. (1985). *The Túngara frog: A study in sexual selection and communication.* Chicago, IL: University of Chicago Press.

Schneirla, T. C. (1965). Aspects of stimulation and organization in approach/withdrawal processes underlying vertebrate behavioral development. In D. S. Lehrman, R. A. Hinde & E. Shaw (Eds.), *Advances in the study of behavior* (pp. 1-74). New York: Academic Press.

Schwartz, J. J., & Wells, K. D. (1983). An experimental study of acoustic interference between two species of neotropical treefrogs. *Animal Behaviour, 31,* 189-190.

Seyfarth, R., & Cheney, D. (1997). Some general features of vocal development in nonhuman primates. In C. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 249-273). Cambridge, UK: Cambridge University Press.

Smith, W. J. (1986). Signaling behavior: Contributions of different repertoires. In R. J. Schusterman, J. A. Thomas & F. G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 315-330). Hillsdale, NJ: Erlbaum.

Snowdon, C. T., & Elowson, A. M. (1999). Pygmy marmosets modify call structure when paired. *Ethology, 105,* 893-908.

Snowdon, C. T., & Hausberger, M. (1997). *Social influences on vocal development.* Cambridge, UK: Cambridge University Press.

Stokes, A. W. (1971). Parental and courtship feeding in red jungle fowl. *Auk, 88,* 21-29.

Sullivan, K. A. (1984). Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour, 91,* 294-311.

Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Animal Behaviour, 56*, 801-809.

Swaisgood, 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.

Terhune, J. M., Stewart, R. E. A., & Ronald, K. (1979). Influence of vessel noises on underwater vocal activity of harp seals. *Canadian Journal of Zoology, 57*, 1337-1338.

Timberlake, W., & Lucas, G. A. (1989). Behavior systems and learning: From misbehavior to general principles. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning* (pp. 237-275). Hillsdale, NJ: Erlbaum.

USFWS, & NMFS. (1992). *Recovery plan for leatherback turtles, (Dermochelys coriacea), in the U.S. Caribbean, Atlantic, and Gulf of Mexico*. Washington DC: National Marine Fisheries Service.

USFWS, & NMFS. (1993). *Recovery plan for the hawksbill turtle, (Eretmochelys imbricata), in the U.S. Carribean, Atlantic and Gulf of Mexico*. Washington DC: National Marine Fisheries Service and United States Fish and Wildlife Service.

VanDyke, F. G., Brocke, R. H., Shaw, H. G., Ackerman, B. B., Hemker, T. P., & Lindzey, F. G. (1986). Reactions of mountain lions to logging and human activity. *Journal of Wildlife Management, 50*, 95-102.

Vieth, W., Curio, E., & Ernst, U. (1980). The adaptive significance of avian mobbing: III. Cultural transmission of enemy recognition in blackbirds: Cross-species tutoring and properties of learning. *Animal Behaviour, 28*, 1217-1229.

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

Waser, P. M., & Waser, M. S. (1977). Experimental studies of primate vocalization: Specializations for long-distance propagation. *Zeitschrift fur Tierpsychologie, 43*, 239-263.

Watkins, W. A., & Schevill, W. E. (1975). Sperm whales (*Physeter catadon*) react to pingers. *Deep-sea Research and Oceanographic Abstracts, 22*, 123-129.

Webster, D. B., & Webster, M. (1992). Kangaroo rat auditory thresholds before and after middle-ear reduction. *Brain, Behavior, and Evolution, 5*, 41-53.

Weisenberger, M. E., Krausman, P. R., Wallace, M. C., DeYoung, D. D., & Maughan, O. E. (1996). The effects of simulated low-level aircraft noise on heart rate and behavior of desert ungulates. *Journal of Wildlife Management, 60*, 52-61.

West, M. J., & King, A. P. (1990). Mozart's starling. *American Scientist, 78*, 106-114.

West, M. J., King, A. P., & Freeberg, T. M. (1994). The nature and nurture of neophenotypes: A case history. In L. A. Real (Ed.), *Behavioral mechanisms in evolutionary ecology* (pp. 238-257). Chicago, IL: University of Chicago Press.

West, M. J., King, A. P., & Freeberg, T. M. (1997). Building a social agenda for the study of bird song. In C. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 41-56). Cambridge, UK: Cambridge University Press.

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

Wiley, R. H., & Richards, D. G. (1982). Adaptations for acoustic communication in birds: Sound transmission and signal detection. In D. Kroodsma & E. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 131-181). New York: Academic Press.

Witherington, B. E. (1997). The problem of photopollution for sea turtles and other nocturnal animals. In J. Clemmons & R. Buchholz (Eds.), *Behavioral approaches to conservation in the wild* (pp. 303-328). Cambridge, UK: Cambridge University Press.

Workman, G. W., & Bunch, T. D. (1991). *Sonic boom/animal stress project report on elk (Cervus canadensis).* (p. 87). Logan, UT: Utah State University for U.S. Air Force.

Zuberbuehler, K., Noe, R., & Seyfarth, R. M. (1997). Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behaviour, 53*, 589-604.