

## **AVIAN COMMUNICATION IN URBAN NOISE: CAUSES AND CONSEQUENCES OF VOCAL ADJUSTMENT**

Author(s): Gail L. Patricelli and Jessica L. Blickley

Source: The Auk, 123(3):639-649. 2006.

Published By: The American Ornithologists' Union

DOI: [http://dx.doi.org/10.1642/0004-8038\(2006\)123\[639:ACIUNC\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2006)123[639:ACIUNC]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.1642/0004-8038%282006%29123%5B639%3AACIUNC%5D2.0.CO%3B2>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.



## OVERVIEW

# AVIAN COMMUNICATION IN URBAN NOISE: CAUSES AND CONSEQUENCES OF VOCAL ADJUSTMENT

GAIL L. PATRICELLI<sup>1</sup> AND JESSICA L. BLICKLEY

*Section of Evolution and Ecology, One Shields Avenue, University of California, Davis, California 95616, USA*

SUCCESSFUL ACOUSTIC COMMUNICATION requires that sounds propagate through the environment between the sender and receiver; vocalizations that transmit effectively in the habitat in which they are used are favored by natural selection. This “acoustic adaptation” hypothesis (Morton 1975, Wiley and Richards 1978, Richards and Wiley 1980, Ryan and Brenowitz 1985) laid the groundwork for the “sensory drive” concept (Endler 1992), which describes how environment affects the evolution of sensory systems and signals in all modalities. By allowing us to examine animal signals as adaptations shaped by selection, this framework has led to a greater understanding of the bewildering diversity of animal signals.

One of the environmental factors that exerts selection pressure on acoustic signals is ambient noise (Ryan and Brenowitz 1985). To elicit a response from a receiver, signals must be detectable in background noise; the detectability of a signal is determined by the signal-to-noise ratio (SNR) and the masked auditory detection threshold of the receiver (Marten and Marler 1977, Brenowitz 1982, Dooling 2004). Within a given frequency band, signals with an SNR below the detection threshold of the receiver are “masked.” Background noise thus plays a fundamental role in determining which “receivers” can hear a vocalization and the fidelity of the signal received. Noise varies among locations, and there is evidence that many species have evolved signals that maximize the habitat-specific SNR (reviewed in Brumm and Slabbekoorn 2005). For birds in and around urban areas and roads, the background noise is largely anthropogenic. Urban development

thus provides a unique opportunity for a “natural” experiment studying how signals change in response to rapid change in the acoustic environment. This natural experiment can inform us about how sensory drive can change signals and about the mechanism by which these changes occur. Understanding this process also has important conservation implications, allowing us to predict how birds will adjust to urban development and potentially to mitigate the effects of this development on communicating birds.

In this issue of *The Auk*, Wood and Yezerinac (2006) present evidence that Song Sparrows (*Melospiza melodia*) adjust their vocalizations to reduce masking by urban noise, and they propose and discuss several mechanisms by which these changes may arise. In a study of urban Song Sparrows in Portland, Oregon, Wood and Yezerinac found a positive relationship between the minimum frequency of male song and the amplitude of anthropogenic noise. They also found that males shifted more energy into the higher frequencies (4–9 kHz) of their songs in noisy areas. Urban noise is loudest between 1–2 kHz, so both of these responses should serve to decrease masking by shifting the spectral energy of the vocalization away from the spectral energy of the noise (Lohr et al. 2003). These results suggest that Song Sparrows, like several other birds (Slabbekoorn and Peet 2003, Brumm 2004b, Fernández-Juricic et al. 2005), respond to changes in the acoustic environment by altering their songs; we refer to this process as “vocal adjustment.” All known examples of avian vocal adjustment in response to urban noise have involved song, but other types of vocalizations—such as begging calls, alarm calls, and food calls—may also be adjusted (Warren et al. 2006).

In this overview, we ask three questions: (1) what features of a bird's vocalization can

<sup>1</sup>E-mail: gpatricelli@ucdavis.edu

be adjusted to reduce masking, (2) how do these adjustments come about, and (3) what are the consequences of these changes for individual fitness and population persistence? The answers to these questions depend on the morphological, developmental, and behavioral underpinnings of the vocalization, and the context in which the vocalization is used. This is an area where knowledge of physiology, developmental neurobiology, animal behavior, and behavioral ecology all contribute to understanding how animals adjust (or fail to adjust) to anthropogenic change.

#### OPPORTUNITIES FOR VOCAL ADJUSTMENT

Four of the most salient features of animal sounds are the frequency structure, amplitude (i.e., loudness), temporal structure (timing of modulations, notes, and syllables within vocalizations), and timing of vocal delivery (repetition rate of vocalizations, diel patterns). Animals use variation in these features to detect and discriminate relevant sounds from background noise. How can a signaling bird increase its chances of being perceived in a noisy environment? Here, we discuss changes in the frequency, amplitude, and timing of vocalizations that might reduce masking and some of the physical and morphological constraints that might limit an individual's ability to make these changes.

Wood and Yezerinac's (2006) findings add to a small but growing body of evidence that oscine birds adjust the frequency structure of their vocalizations to reduce masking by anthropogenic noise; similar shifts have been observed in Great Tits (*Parus major*; Slabbekoorn and Peet 2003) and House Finches (*Carpodacus mexicanus*; Fernández-Juricic et al. 2005). These changes mirror those observed in the vocalizations of birds living in areas with high levels of natural noise (e.g., from waterfalls or other animals; Dubois and Martens 1984, Slabbekoorn and Smith 2002b). The three described cases of frequency adjustment in response to low-frequency urban noise involve reduction in the frequency range of songs (i.e., increased minimum frequency but no change in maximum frequency; Slabbekoorn and Peet 2003, Fernández-Juricic et al. 2005, Wood and Yezerinac 2006). A second means by which birds could adjust the frequency structure of their vocalizations to reduce masking is by shifting the entire vocalization

to a higher frequency. We are not aware of any examples of this kind of adjustment in response to urban noise; use of this adjustment will be limited by several morphological and kinematic factors that constrain the maximum frequencies that a bird can produce, including head angle, beak gape, and beak shape (Westneat et al. 1993, Palacios and Tubaro 2000, Podos et al. 2004, Nelson et al. 2005). A third means by which birds could adjust the frequency structure of their vocalizations is by changing the relative amplitude of different frequency components. Rabin et al. (2003) found that California ground squirrels (*Spermophilus beecheyi*) in areas with low-frequency noise from wind turbines shifted the peak energy of their calls from lower to higher harmonics. Wood and Yezerinac (2006) found that Song Sparrows shifted more energy into higher frequencies in noisier areas, but this pattern appears to reflect the use of fewer low-frequency notes rather than a change in the relative amplitude of notes.

Laboratory psychoacoustic studies have shown that sounds with a greater bandwidth and higher rate of frequency modulation are more difficult to detect from noise (Lohr et al. 2003). Animals in habitats with high levels of natural noise converge on songs with primarily pure tones (e.g., Dubois and Martens 1984). No examples of these changes have yet been found in response to anthropogenic noise; the studies reporting changes in frequency content of songs measured the minimum and maximum frequency of songs, rather than notes within songs (Slabbekoorn and Peet 2003, Fernández-Juricic et al. 2005, Wood and Yezerinac 2006). This remains an interesting possibility for future study.

Birds living in noisy habitats may also increase the signal-to-noise ratio during communication by boosting the amplitude of their vocalizations, a response called the "Lombard effect" (Rabin and Greene 2002, Warren et al. 2006). The Lombard effect appears to be taxonomically widespread among birds and mammals (Brumm and Slabbekoorn 2005) and may be the most common mechanism for increasing SNR in urban noise. Whether birds can increase their amplitude sufficiently to rise above background noise is likely constrained by body size (Brackenbury 1979, Brumm 2004b) as well as by the energetic costs of producing louder sounds (Oberweger and Goller 2001).

The temporal structure of a vocalization may also affect the ability of receivers to detect the sound in masking noise, and thus may also be adjusted in urban environments. Laboratory psychoacoustic studies have shown that increased repetition and duration increase the detectability of sounds in white noise; vocalizations of some avian species living in areas with high natural noise have these features (see recent reviews by Brumm and Slabbekoorn [2005], Warren et al. [2006]). Increased duration of vocalizations has been observed in other taxa; Foote et al. (2004) found that killer whales (*Orcinus orca*) increase the duration of their vocalizations in the presence of boat noise. Interestingly, Fernández-Juricic et al. (2005) found a significant reduction in the number of notes in House Finch songs in noisy areas, which is the opposite of psychoacoustic predictions. Similarly, Wood and Yezerinac (2006) found a weak trend toward fewer notes. Fernández-Juricic et al. (2005) suggested that decreased song length may reflect a trade-off between energetic costs associated with increasing the amplitude of songs and the length of songs; this possibility requires further examination.

In addition to adjusting the temporal structure of their vocalizations, birds may adjust the timing of vocalizations (Brumm and Slabbekoorn 2005, Warren et al. 2006). Many species of birds vary the time at which they vocalize to avoid interference from neighboring birds and other sources of noise (Ficken et al. 1974), so this capacity may be well developed. Some sources of urban noise are variable over time, and birds may be able to time their songs to take advantage of small gaps in noise (Popp 1989, Lohr et al. 2003) or diel fluctuations in noise levels (Warren et al. 2006). Avoidance of acoustic interference is one hypothesis for the evolution of the dawn chorus, predicting that its timing may shift with the timing of rush-hour traffic (Bergen and Abs 1997, Warren et al. 2006). Complex responses at the community level may result from temporal shifts of song; for example, suppression of call rates in one species in response to urban noise may stimulate increased song rates in another species, as was recently found in frogs (*Microhyla bulteri*, *Rana nigrovittata*, *R. taipehensis*, and *Kaloula pulchra*) exposed to anthropogenic noise (Sun and Narins 2005).

Another means by which animals may increase the efficacy of communication amid noise is by shifting emphasis to another

modality (Brumm and Slabbekoorn 2005). The “backup” or “redundant signaling” hypothesis proposes that animals have multiple sexually selected signals so that if one modality fails to transmit to the receiver (e.g., because of masking), other signals will do the job (Møller and Pomiankowski 1993, Hebets and Papaj 2005). It would be interesting to examine whether males in species with multiple sexual signals emphasize visual displays over acoustic displays in noisy urban environments and whether females and competing males correspondingly shift their attention while assessing these displays.

There are many features of a signal that can be changed to decrease masking; what determines which of these changes will be made? We have discussed mechanistic constraints that may limit vocal adjustment. In the following two sections, we will discuss how the bird’s developmental program may facilitate or limit vocal adjustment, and the consequences of these adjustments on fitness. Because the variation within a species’ existing repertoire will also be shaped by mechanisms of production, developmental processes, and fitness consequences, it is reasonable to predict that vocal adjustment is most likely to occur along an axis (amplitude, frequency, or time) on which a species already exhibits variation in its song.

#### DEVELOPMENT OF ADJUSTED VOCALIZATIONS

The labile nature of song in many bird species offers the possibility of vocal adjustment in a changing acoustic environment, but how do these adjustments arise? Wood and Yezerinac (2006) propose several non-mutually exclusive alternative hypotheses for the mechanism of vocal adjustment in Song Sparrows. Adjustments may develop as short-term responses to increased ambient noise levels (“short-term adjustment” hypothesis). Long-term ontogenetic adjustments may occur through mechanisms such as active modification during periods of vocal plasticity (“developmental modification” hypothesis), selective attrition of masked songs (“selective attrition” hypothesis), and passive acquisition of vocalizations or portions of vocalizations that transmit well (“passive acquisition” hypothesis). Finally, these adjustments may result from genetic changes in urban bird populations (“evolution” hypothesis). We will discuss each of these hypotheses, evaluating the potential for these mechanisms to operate in birds

with different programs for vocal development. Before testing these hypotheses, it is necessary to rule out alternative explanations for an observed relationship between ambient noise levels and bird vocalizations in an area: that birds preferentially settle onto territories in which their vocalizations propagate effectively, or that the observed relationship is an artifact of the noise level of the recording location (i.e., if lower frequencies are masked by noise, or if high-amplitude background noise inflates the measured amplitude of the vocalization; Slabbekoorn and Peet 2003, Wood and Yezerinac 2006).

#### SHORT-TERM ADJUSTMENT

Short-term adjustment of vocalizations may be achieved through selective use of unmasked songs from a repertoire, or through the temporary adjustment of signal characteristics such as frequency, amplitude, temporal structure, and timing of song (Brumm and Slabbekoorn 2005, Warren et al. 2006, Wood and Yezerinac 2006). Short-term responses do not require learning, though use of this mechanism of adjustment will be constrained by an individual's ability to detect masking and make subsequent changes to their vocalizations. Auditory feedback is important for maintaining song structure in birds with a wide variety of vocal-development programs (Nordeen and Nordeen 1992, Okanoya and Yamaguchi 1997) and is a likely way for birds to detect masking. The ubiquity of the Lombard effect, as discussed above, suggests that at least some forms of short-term adjustment may commonly be used to mitigate the effects of masking. Studies that track vocalizing individuals in environments with and without urban noise are needed to separate short-term adjustments from long-term ontogenetic adjustments (discussed below).

#### LONG-TERM ONTOGENETIC ADJUSTMENTS

Vocal adjustments may result from active modification of signal design during periods of vocal plasticity (Rabin and Greene 2002, Wood and Yezerinac 2006), which we refer to as the developmental modification hypothesis. A naïve individual's ability to change the structure of its vocalization to reduce masking will be determined both by its ability to perceive masking and the onset and duration of vocal plasticity.

Perception of masking is most likely to occur through auditory feedback, which plays a critical role in matching vocal output to song template during song development (Margoliash 2002). Timing of vocal plasticity is highly variable among species; open-ended species may continue to acquire and modify songs throughout their adult lives (Chaiken et al. 1994), which increases the potential for active modification in a changing environment. In closed-ended species of songbird, the plastic period of vocal development, during which birds practice and modify their songs before they are crystallized, occurs early in life (Hultsch and Todt 2004). This may limit an individual's ability to make subsequent adjustments to the song. However, Wood and Yezerinac (2006) note that seasonal variation in the neural song-control circuitry has been linked to vocal plasticity, and has been observed in both closed-ended and open-ended species (Smith et al. 1997, Brenowitz 2004). These seasonal changes in vocal plasticity offer potential flexibility for vocal adjustment into adulthood.

Birds may also avoid masking by selecting only unmasked songs for their repertoire (selective attrition hypothesis; Wood and Yezerinac 2006). Selective attrition is characterized by overproduction of song templates during vocal development and crystallization of only a portion of the repertoire, which is retained into adulthood (Marler and Peters 1982). The extent to which birds can use selective attrition to reduce masking depends on the processes guiding song selection as well as the timing of selective attrition. Song Sparrows, among other species, use selective attrition postdispersal, which potentially allows them to tailor song selection to the acoustic environment of their breeding territory (Nordby et al. 2001). Individuals typically select songs that match those of their nearest neighbors (Nordby et al. 1999, 2000), which suggests that repertoire selection involves feedback from the environment (Marler and Peters 1982). However, the role of background noise in informing the song selection process is currently unknown. This option is not available to all birds, because only some species undergo selective attrition during song development (e.g., Marler and Peters 1982, Nelson 1992, Gil and Slater 2000); in species that do, it has the potential to be an important mechanism for reducing masking.



Birds may also acquire modified songs passively (passive acquisition hypothesis); song-learning birds form a template for songs by listening to other birds during a sensitive period of song development (Hultsch and Todt 2004), and these birds may hear and acquire only songs or the portions of songs that are not masked (Rabin and Greene 2002, Wood and Yezerinac 2006). The timing of the sensitive period influences not only what birds the novice bird learns from, but also the environment in which it learns. Thus, passive acquisition may only be an effective means of matching songs to background noise if birds develop song templates in areas with noise levels similar to those in their breeding territories (i.e., dispersal within noisy areas, or song learning after dispersal). Laboratory and field studies have found that the sensitive period occurs within the first year of life for many songbirds (Hultsch and Todt 2004), but that many species, like the Song Sparrow, will continue to learn new songs up to their first breeding season (Nordby et al. 2001), which allows passive adjustment to the acoustic environment beyond their natal territories.

#### ROLE OF SONG LEARNING IN VOCAL ADJUSTMENT

Song learning may increase the ability of a species to adjust its vocalizations in response to an altered acoustic environment. Indeed, the four cases described to date of vocal adjustment in response to urban noise are in oscine passerines (Slabbekoorn and Peet 2003, Brumm 2004b, Fernández-Juricic et al. 2005, Wood and Yezerinac 2006). But even among song-learning species, the broad variation of vocal plasticity is likely to result in a wide range of responses to urban noise, making generalizations and predictions about the phylogenetic distribution of vocal adjustment difficult.

With a few exceptions, vocal development in suboscine and nonpasserine birds is a largely innate process and does not require exposure to a tutor (Kroodsma 2004). Further, suboscine birds do not appear to use auditory feedback in the development of their vocalizations (Kroodsma and Konishi 1991). The relative rigidity of vocal development in nonoscines reduces the opportunity for long-term ontogenetic modification of vocalizations. However, short-term changes may still be possible. The Lombard effect has been found in laboratory studies of non-song-learning

birds (Brumm and Slabbekoorn 2005), and many non-song-learners adjust the timing of their vocalizations in response to conspecifics (e.g., Ficken et al. 1974, Gibson and Bradbury 1985) and may do the same in response to urban noise. Evidence from other taxa that do not learn song—such as Bornean tree-hole frogs (*Metaphrynella sundana*), which rapidly adjust the frequency of their calls to maximize propagation from tree holes (Lardner and bin Lakim 2002)—suggests that sophisticated responses may not be restricted to song-learners or species with complex vocalizations.

#### EVOLUTIONARY CHANGE

Given the recent introduction of urban noise and the well-described plasticity of song learning in birds, the vocal adjustments observed to date are unlikely to have arisen through evolution, though this possibility cannot be excluded (Warren et al. 2006, Wood and Yezerinac 2006). As anthropogenic noise becomes a more prominent feature of local landscapes, selection may favor individuals with unmasked vocalizations or the flexibility to adjust their vocalizations. Selection may also favor receivers with ears that are tuned for detecting signals in urban noise. For some species, however, the small fragmented populations found in urban areas may lack the genetic variation in vocal structures and behaviors that is necessary for selection to shape such adaptations.

#### CONSEQUENCES OF VOCAL ADJUSTMENT

Wood and Yezerinac (2006) note that male Song Sparrows have many reasons to overcome masking of their songs by urban noise, because songs are crucial for intrasexual competition and female choice. But are there also costs to vocal adjustment in terms of individual fitness and population stability? What, if any, are the management implications? The ability to adjust vocalizations in response to masking noise may itself be an adaptation to varying levels of noise in the natural world (Brumm and Slabbekoorn 2005), but urbanization and its attendant noise is a recent phenomenon, and we cannot assume that observed responses are adaptive in urban settings. No studies have measured the fitness consequences of vocal adjustment to individuals or populations, so for now we are left with

informed guesswork. We will discuss some potential costs of vocal adjustment during courtship and competition over mates, and in other interactions with conspecifics. We will then discuss the potential implications of these costs and benefits to conservation of bird populations.

#### FITNESS COSTS

Acoustic communication plays a central role in sexual selection and social integration in an enormous variety of birds (Catchpole and Slater 1995). If animals must change their vocalizations in noisy environments, this may have effects that reverberate throughout many facets of their lives.

Some of the potential costs of vocal adjustment will be incurred regardless of the type of vocalization and the context in which it is given. For example, vocalizing more loudly in noisy environments may have energetic costs that decrease the net benefits of vocal adjustment and alter the bird's energy budget (Brumm 2004a, b; Warren et al. 2006; Wood and Yezerinac 2006). Shifting their songs to higher frequencies may also impose energetic costs (Lambrechts 1996). The net benefits of frequency adjustment may be further reduced by excess attenuation, given that higher frequencies do not propagate as effectively as low frequencies, especially through complex urban environments (Warren et al. 2006). We cannot assume, therefore, that an increase in frequency leads to a net increase in the area over which the vocalization can be detected (Brumm and Slabbekoorn 2005, Leader et al. 2005). The auditory sensitivity of a species is often tightly tuned to the frequencies used in communication (e.g., Okanoya and Dooling 1988); thus, there may also be a trade-off between maximizing the efficacy of transmission in noise and the efficacy of perception by receivers (Wood and Yezerinac 2006).

Other costs of vocal adjustment will vary depending on the context in which the signal is used. For example, changing the frequency and temporal content of vocalizations may affect individual and species recognition by conspecifics, as well as the effectiveness of the signal in eliciting a beneficial response from the receiver. The following paragraphs discuss the potential effects of vocal adjustment on female choice, male-male competition, and other types of communication.

*Female choice.*—Female birds in many species use vocalizations to determine whether a male is an appropriate potential mate (i.e., species recognition), so if males in urban areas adjust the frequency or temporal features of their vocalizations to avoid masking by noise, they may no longer be recognized by conspecific females (Slabbekoorn and Peet 2003, Wood and Yezerinac 2006). Though birds can discriminate fine changes in frequency in the laboratory (Dooling 2004), field studies suggest that frequency changes within 2–3 standard deviations (SD) of the population mean do not significantly affect response (Nelson 1988, 1989; Klump 1996). Males may therefore have some flexibility in adjusting their vocalizations without paying the cost of reduced recognition by females. This further suggests that in species where there is more natural variation in the frequency of male vocalizations (i.e., higher SD), recognition is less likely to be reduced by vocal adjustment (note that even if songs are recognized as conspecific, they may be viewed as less attractive if females assess deviation from the population mean as an indicator of song learning; Nowicki et al. 2002).

Wood and Yezerinac (2006) note that breakdown in mate recognition might eventually lead to reproductive isolation and speciation between urban and nonurban populations of Song Sparrows (see also Slabbekoorn and Peet 2003, Warren et al. 2006). Song has been shown to play an important role in maintaining reproductive isolation between two subspecies of Song Sparrows (Patten et al. 2004), and females in the northeastern United States were found to discriminate against dialects from >34 km away, with discrimination increasing with distance (Searcy et al. 2002). If adjusted songs are functionally equivalent to dialects, symmetrical premating isolation may emerge between urban and nonurban populations. The role of dialect formation in speciation is controversial, but it is clear that dialect formation does not necessarily lead to genetic differentiation (Price 1998, Slabbekoorn and Smith 2002a). Slabbekoorn and Smith (2002a) suggested that genetic divergence is more likely to accompany dialect divergence when habitats are sufficiently different to favor local adaptation (Patten et al. 2004). That is likely to be true in regard to urban versus nonurban environments. Fragmentation may also lead to less gene flow between urban

and nonurban populations than we might predict on the basis of distance alone, which would facilitate speciation. If variation in urban noise persists, speciation remains a long-term possibility, but not a certainty.

In addition to using vocalizations to recognize conspecific males, females use vocalizations to choose their mates from among these competing males; males that adjust their vocalizations in response to urban noise may therefore face trade-offs between transmission and attractiveness. One obvious trade-off is between song amplitude and song rate; the energetic costs of increasing the amplitude of vocalizations may preclude singing at the high rate preferred by females (Oberweger and Goller 2001, Brumm 2004b, Fernández-Juricic et al. 2005, Warren et al. 2006). Trade-offs may also be present when males adjust the frequency of their vocalizations. For example, in species in which females prefer males with low-frequency vocalizations (e.g., Beani and Dessì-Fulgheri 1995), males that increase their frequency to avoid masking may increase the number of females who detect their vocalizations but decrease their attractiveness to those females. Wood and Yezerinac (2006) found that male Song Sparrows increased the minimum frequency of the "buzz" note, but not the maximum frequency, leading to a lower-frequency bandwidth. This adjustment may reduce the attractiveness of the male song in species in which females assess frequency bandwidth as an aspect of vocal performance (Podos 2001, Ballentine et al. 2004). Males may also reduce their attractiveness by dropping lower-frequency songs from their repertoire to avoid masking, if females assess repertoire size during mate choice (e.g., Reid et al. 2005). If females choose their mates using a comparative tactic (Luttbegg 1996, Bateson and Healy 2005), and if all males adjust their vocalizations, male vocal adjustment may not lead to a decrease in relative attractiveness, though the usefulness of the male signal as an indicator of male quality may be diminished.

*Male-male competition.*—Many of the potential trade-offs faced by males during communication with females (described above) may also be faced during communication with competing males, because vocal adjustment may affect both recognition of conspecifics and assessment of the information content of the signal (i.e., the signaler's condition and motivation to fight). In

Song Sparrows, males are less discriminating than females in response to foreign dialects, and will respond with similar aggressiveness toward dialects from up to 540 km away (Searcy et al. 2002). This suggests that vocal adjustment is more likely to be costly in reducing recognition by females than by males; the same pattern may be true in many other species (e.g., Searcy 1990; but see Nelson and Soha 2004). Even if vocalizations are recognized by conspecific males, vocal adjustment may incur costs if it decreases the likelihood of eliciting a beneficial response from receivers. For example, low-frequency, broad-band vocalizations are often used in threat displays (Morton 1977). Males that shift to higher frequencies or purer tones to avoid noise may be interpreted as less threatening unless there is a corresponding shift in the interpretation of the signal. Song matching is important in territory defense in Song Sparrows and many other species (Krebs et al. 1981; Beecher et al. 2000a, b). Males who adjust their songs or drop low-frequency songs from their repertoire may not have the song types required for these interactions, unless neighboring males adjust their songs similarly.

*Other types of communication.*—Thus far, we only have evidence that male birds adjust their songs in response to urban noise, but other kinds of vocalizations are crucial to survival and reproduction and may also be adjusted (Katti and Warren 2004, Warren et al. 2006). These include alarm calls, begging calls, contact calls, flight calls, and food calls and can be given between pair-bonded mates, between parents and offspring, among offspring, and between flock-mates (Marler 2004). With all of these calls, senders may face trade-offs between increased SNR and decreased recognition or incorrect interpretation by receivers. If calls are adapted to minimize eavesdropping by predators (Marler 1955, Klump and Shalter 1984), vocal adjustment may also affect the risk of predation.

#### IMPLICATIONS FOR CONSERVATION

There is evidence that urbanization and road development have negative effects on population densities of at least some avian species (van der Zande et al. 1980, Reijnen et al. 1996, Forman et al. 2002, Rheindt 2003, Ingelfinger and Anderson 2004, Peris and Pescador 2004);



however, we know very little about the degree to which noise contributes to these declines (Reijnen et al. 1995) and can only speculate about the role that vocal adjustment plays in increasing or mitigating the effects of noise (Katti and Warren 2004, Warren et al. 2006). If vocal adjustment decreases masking of a vocalization, should we therefore view it as an example of animals acclimating and thus thriving in an urban environment? Or are we seeing symptoms of communication breakdown that should be of management concern? We cannot answer these questions until we have measurements of the net benefits of vocal adjustment to individuals and of the effect of vocal adjustment on populations. This is an area ripe for future research.

There is enormous variation in how species respond to urbanization; some species clearly thrive near human development, and others disappear. If vocal adjustment yields a net benefit to individuals, then species that have this capacity may adapt more readily to human development (Rabin and Greene 2002, Rabin et al. 2003, Slabbekoorn and Peet 2003, Warren et al. 2006). Are species that adjust their songs thus less affected by urbanization than species that do not adjust? This question necessitates a comparative approach, which requires that we learn more about the phylogenetic distribution of vocal adjustment. Vocal adjustment is likely only one factor among many that affect how animals respond to urbanization, but understanding its effect may improve our ability to predict the effects of proposed developments on bird populations. Future research on acoustic communication in urban environments will make an important contribution to conservation efforts and, at the same time, improve our understanding of vocal development, the plasticity of vocal behavior, and how the process of sensory drive shapes the diversity of animal signals.

#### ACKNOWLEDGMENTS

We thank T. Hahn, A. Krakauer, N. Losin, L. Rabin, K. Sewall, and E. West for constructive comments on this manuscript. Some of the ideas in this paper emerged from discussions facilitated by the Road Ecology Center at the University of California, Davis, and from research funded by the Bureau of Land Management and National Science Foundation (grant no. IOB-0528563).

#### LITERATURE CITED

- BALLENTINE, B., J. HYMAN, AND S. NOWICKI. 2004. Vocal performance influences female response to male bird song: An experimental test. *Behavioral Ecology* 15:163–168.
- BATESON, M., AND S. D. HEALY. 2005. Comparative evaluation and its implications for mate choice. *Trends in Ecology and Evolution* 20: 659–664.
- BEANI, L., AND F. DESSÌ-FULGHERI. 1995. Mate choice in the Grey Partridge, *Perdix perdix*: Role of physical and behavioural male traits. *Animal Behaviour* 49:347–356.
- BEECHER, M. D., S. E. CAMPBELL, J. M. BURT, C. E. HILL, AND J. C. NORDBY. 2000a. Song-type matching between neighbouring Song Sparrows. *Animal Behaviour* 59:21–27.
- BEECHER, M. D., S. E. CAMPBELL, AND J. C. NORDBY. 2000b. Territory tenure in Song Sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour* 59: 29–37.
- BERGEN, F., AND M. ABS. 1997. Etho-ecological study of the singing activity of the Blue Tit (*Parus caeruleus*), Great Tit (*Parus major*) and Chaffinch (*Fringilla coelebs*). *Journal für Ornithologie* 138:451–467.
- BRACKENBURY, J. H. 1979. Power capabilities of the avian sound producing system. *Journal of Experimental Biology* 78:163–166.
- BRENEWITZ, E. A. 1982. The active space of Red-winged Blackbird song. *Journal of Comparative Physiology* 147:511–522.
- BRENEWITZ, E. A. 2004. Plasticity of the adult avian song control system. Pages 560–585 in *Behavioral Neurobiology of Birdsong* (H. P. Zeigler and P. Marler, Eds.). *Annals of the New York Academy of Sciences*, vol. 1016.
- BRUMM, H. 2004a. Causes and consequences of song amplitude adjustment in a territorial bird: A case study in Nightingales. *Anais da Academia Brasileira de Ciências* 76:289–295.
- BRUMM, H. 2004b. The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology* 73:434–440.
- BRUMM, H., AND H. SLABBEKOORN. 2005. Acoustic communication in noise. *Advances in the Study of Behavior* 35:151–209.
- CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. *Bird Song: Themes and Variations*. Cambridge University Press, Cambridge, United Kingdom.

- CHAIKEN, M., J. BOHNER, AND P. MARLER. 1994. Repertoire turnover and the timing of song acquisition in European Starlings. *Behaviour* 128:25–39.
- DOOLING, R. F. 2004. Audition: Can birds hear everything they sing? Pages 178–205 in *Nature's Music* (P. Marler and H. Slabbekoorn, Eds.). Elsevier Academic, London.
- DUBOIS, A., AND J. MARTENS. 1984. A case of possible vocal convergence between frogs and a bird in Himalayan torrents. *Journal für Ornithologie* 125:455–463.
- ENDLER, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139 (Supplement):S125–S153.
- FERNÁNDEZ-JURICIC, E., R. POSTON, K. DE COLLIBUS, T. MORGAN, B. BASTAIN, C. MARTIN, K. JONES, AND R. TREMINIO. 2005. Microhabitat selection and singing behavior patterns of male House Finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. *Urban Habitats* 3:49–69.
- FICKEN, R. W., M. S. FICKEN, AND J. P. HAILMAN. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* 183:762–763.
- FOOTE, A. D., R. W. OSBORNE, AND A. R. HOELZEL. 2004. Whale-call response to masking boat noise. *Nature* 428:910.
- FORMAN, R. T. T., B. REINEKING, AND A. M. HERSPERGER. 2002. Road traffic and nearby grassland bird patterns in a suburbanizing landscape. *Environmental Management* 29:782–800.
- GIBSON, R. M., AND J. W. BRADBURY. 1985. Sexual selection in lekking grouse: Phenotypic correlates of male mating success. *Behavioral Ecology and Sociobiology* 18:117–123.
- GIL, D., AND P. J. B. SLATER. 2000. Multiple song repertoire characteristics in the Willow Warbler (*Phylloscopus trochilus*): Correlations with female choice and offspring viability. *Behavioral Ecology and Sociobiology* 47:319–326.
- HEBETS, E. A., AND D. R. PAPA. 2005. Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57:197–214.
- HULTSCH, H., AND D. TODT. 2004. Learning to sing. Pages 80–106 in *Nature's Music* (P. Marler and H. Slabbekoorn, Eds.). Elsevier Academic, London.
- INGELFINGER, F., AND S. ANDERSON. 2004. Passerine response to roads associated with natural gas extraction in a sagebrush steppe habitat. *Western North American Naturalist* 64:385–395.
- KATTI, M., AND P. S. WARREN. 2004. Tits, noise and urban bioacoustics. *Trends in Ecology and Evolution* 19:109–110.
- KLUMP, G. M. 1996. Bird communication in the noisy world. Pages 321–338 in *Ecology and Evolution of Acoustic Communication in Birds* (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.
- KLUMP, G. M., AND M. D. SHALTER. 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance of alarm signals and their evolution. *Zeitschrift für Tierpsychologie* 66:189–226.
- KREBS, J. R., R. ASHCROFT, AND K. VAN ORSDOL. 1981. Song matching in the Great Tit *Parus major* L. *Animal Behaviour* 29:918–923.
- KROODSMA, D. E. 2004. The diversity and plasticity of bird song. Pages 108–130 in *Nature's Music* (P. Marler and H. Slabbekoorn, Eds.). Elsevier Academic, London.
- KROODSMA, D. E., AND M. KONISHI. 1991. A suboscine bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Animal Behaviour* 42:477–488.
- LAMBRECHTS, M. M. 1996. Organization of birdsong and constraints on performance. Pages 305–320 in *Ecology and Evolution of Acoustic Communication in Birds* (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.
- LARDNER, B., AND M. BIN LAKIM. 2002. Tree-hole frogs exploit resonance effects. *Nature* 420:475.
- LEADER, N., J. WRIGHT, AND Y. YOM-TOV. 2005. Acoustic properties of two urban song dialects in the Orange-tufted Sunbird (*Nectarinia osea*). *Auk* 122:231–245.
- LOHR, B., T. F. WRIGHT, AND R. J. DOOLING. 2003. Detection and discrimination of natural calls in masking noise by birds: Estimating the active space of a signal. *Animal Behaviour* 65:763–777.
- LUTTBEG, B. 1996. A comparative Bayes tactic for mate assessment and choice. *Behavioral Ecology* 7:451–460.
- MARGOLIASH, D. 2002. Evaluating theories of bird song learning: Implications for

- future directions. *Journal of Comparative Physiology A* 188:851–866.
- MARLER, P. 1955. Characteristics of some animal calls. *Nature* 176:6–8.
- MARLER, P. 2004. Bird calls: A cornucopia for communication. Pages 132–176 in *Nature's Music* (P. Marler and H. Slabbekoorn, Eds.). Elsevier Academic Press, London.
- MARLER, P., AND S. PETERS. 1982. Developmental overproduction and selective attrition: New processes in the epigenesis of birdsong. *Developmental Psychobiology* 15:369–378.
- MARTEN, K., AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. *Behavioral Ecology and Sociobiology* 2:271–290.
- MØLLER, A. P., AND A. N. POMIANKOWSKI. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology* 32:167–176.
- 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.
- NELSON, B. S., G. J. L. BECKERS, AND R. A. SUTHERS. 2005. Vocal tract filtering and sound radiation in a songbird. *Journal of Experimental Biology* 208:297–308.
- NELSON, D. A. 1988. Feature weighting in species song recognition by the Field Sparrow (*Spizella pusilla*). *Behaviour* 106:158–182.
- NELSON, D. A. 1989. Song frequency as a cue for recognition of species and individuals in the Field Sparrow (*Spizella pusilla*). *Journal of Comparative Psychology* 103:171–176.
- NELSON, D. A. 1992. Song overproduction and selective attrition lead to song sharing in the Field Sparrow (*Spizella pusilla*). *Behavioral Ecology and Sociobiology* 30:415–424.
- NELSON, D. A., AND J. A. SOHA. 2004. Male and female White-crowned Sparrows respond differently to geographic variation in song. *Behaviour* 141:53–69.
- NORDBY, J. C., S. E. CAMPBELL, AND M. D. BEECHER. 1999. Ecological correlates of song learning in Song Sparrows. *Behavioral Ecology* 10:287–297.
- NORDBY, J. C., S. E. CAMPBELL, AND M. D. BEECHER. 2001. Late song learning in Song Sparrows. *Animal Behaviour* 61:835–846.
- NORDBY, J. C., S. E. CAMPBELL, J. M. BURT, AND M. D. BEECHER. 2000. Social influences during song development in the Song Sparrow: A laboratory experiment simulating field conditions. *Animal Behaviour* 59:1187–1197.
- NORDEEN, K. W., AND E. J. NORDEEN. 1992. Auditory-feedback is necessary for the maintenance of stereotyped song in adult Zebra Finches. *Behavioral and Neural Biology* 57:58–66.
- NOWICKI, S., W. A. SEARCY, AND S. PETERS. 2002. Quality of song learning affects female response to male bird song. *Proceedings of the Royal Society of London, Series B* 269:1949–1954.
- OBERWEGER, K., AND F. GOLLER. 2001. The metabolic cost of birdsong production. *Journal of Experimental Biology* 204:3379–3388.
- OKANOYA, K., AND R. F. DOOLING. 1988. Hearing in the Swamp Sparrow, *Melospiza georgiana*, and the Song Sparrow, *Melospiza melodia*. *Animal Behaviour* 36:726–732.
- OKANOYA, K., AND A. YAMAGUCHI. 1997. Adult Bengalese Finches (*Lonchura striata* var. *domestica*) require real-time auditory feedback to produce normal song syntax. *Journal of Neurobiology* 33:343–356.
- PALACIOS, M. G., AND P. L. TUBARO. 2000. Does beak size affect acoustic frequencies in woodcreepers? *Condor* 102:553–560.
- PATTEN, M. A., J. T. ROTENBERRY, AND M. ZUK. 2004. Habitat selection, acoustic adaptation, and the evolution of reproductive isolation. *Evolution* 58:2144–2155.
- PERIS, S. J., AND M. PESCADOR. 2004. Effects of traffic noise on passerine populations in Mediterranean wooded pastures. *Applied Acoustics* 65:357–366.
- PODOS, J. 2001. Correlated evolution of morphology and vocal signature in Darwin's finches. *Nature* 409:185–188.
- PODOS, J., J. A. SOUTHALL, AND M. R. ROSSI-SANTOS. 2004. Vocal mechanics in Darwin's finches: Correlation of beak gape and song frequency. *Journal of Experimental Biology* 207:607–619.
- POPP, J. W. 1989. Temporal aspects of singing interactions among territorial Ovenbirds (*Seiurus aurocapillus*). *Ethology* 82:127–133.
- PRICE, T. 1998. Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society of London, Series B* 353:251–260.

- RABIN, L. A., AND C. M. GREENE. 2002. Changes to acoustic communication systems in human-altered environments. *Journal of Comparative Psychology* 116:137–141.
- RABIN, L. A., B. MCCOWAN, S. L. HOOPER, AND D. H. OWINGS. 2003. Anthropogenic noise and its effects on animal communication: An interface between comparative psychology and conservation biology. *International Journal of Comparative Psychology* 16: 172–192.
- REID, J. M., P. ARCESE, A. L. E. V. CASSIDY, S. M. HIEBERT, J. N. M. SMITH, P. K. STODDARD, A. B. MARR, AND L. F. KELLER. 2005. Fitness correlates of song repertoire size in free-living Song Sparrows (*Melospiza melodia*). *American Naturalist* 165:299–310.
- REIJNEN, R., R. FOPPEN, C. TER BRAAK, AND J. THISSEN. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology* 32:187–202.
- REIJNEN, R., R. FOPPEN, AND H. MEEUWSEN. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation* 75:255–260.
- RHEINDT, F. E. 2003. The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? *Journal für Ornithologie* 144:295–306.
- RICHARDS, D. G., AND R. H. WILEY. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *American Naturalist* 115:381–399.
- RYAN, M. J., AND E. A. BRENOWITZ. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist* 126:87–100.
- SEARCY, W. A. 1990. Species recognition of song by female Red-Winged Blackbirds. *Animal Behaviour* 40:1119–1127.
- SEARCY, W. A., S. NOWICKI, M. HUGHES, AND S. PETERS. 2002. Geographic song discrimination in relation to dispersal distances in Song Sparrows. *American Naturalist* 159:221–230.
- SLABBEKOORN, H., AND M. PEET. 2003. Birds sing at a higher pitch in urban noise. *Nature* 424: 267.
- SLABBEKOORN, H., AND T. B. SMITH. 2002a. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London, Series B* 357:493–503.
- SLABBEKOORN, H., AND T. B. SMITH. 2002b. Habitat-dependent song divergence in the Little Greenbul: An analysis of environmental selection pressures on acoustic signals. *Evolution* 56:1849–1858.
- SMITH, G. T., E. A. BRENOWITZ, M. D. BEECHER, AND J. C. WINGFIELD. 1997. Seasonal changes in testosterone, neural attributes of song control nuclei, and song structure in wild songbirds. *Journal of Neuroscience* 17: 6001–6010.
- SUN, J. W. C., AND P. M. NARINS. 2005. Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation* 121:419–427.
- VAN DER ZANDE, A. N., W. J. TER KEURS, AND W. J. VAN DER WEIJDEN. 1980. The impact of roads on the densities of four bird species in an open field habitat—Evidence of a long-distance effect. *Biological Conservation* 18: 299–321.
- WARREN, P. S., M. KATTI, M. ERMAN, AND A. BRAZEL. 2006. Urban bioacoustics: It's not just noise. *Animal Behaviour* 71:491–502.
- WESTNEAT, M. W., J. H. LONG, JR., W. HOESE, AND S. NOWICKI. 1993. Kinematics of birdsong: Functional correlation of cranial movements and acoustic features in sparrows. *Journal of Experimental Biology* 182:147–171.
- WILEY, R. H., AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3:69–94.
- WOOD, W. E., AND S. M. YEZERINAC. 2006. Song Sparrow (*Melospiza melodia*) song varies with urban noise. *Auk* 123:650–659.