

Effects of Noise Pollution on Birds: A Brief Review of Our Knowledge

Author: Ortega, Catherine P., Ecosphere Environmental Services, 776 E.

Second Avenue, Durango, Colorado 81301, USA

Source: Ornithological Monographs No. 74

Published By: American Ornithological Society

URL: https://doi.org/10.1525/om.2012.74.1.6

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete 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.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



CHAPTER 2

EFFECTS OF NOISE POLLUTION ON BIRDS: A BRIEF REVIEW OF OUR KNOWLEDGE

CATHERINE P. ORTEGA

Ecosphere Environmental Services, 776 E. Second Avenue, Durango, Colorado 81301, USA

ABSTRACT.—Many avian species have long been exposed to loud natural sounds such as streams, waterfalls, and wind. However, anthropogenic noise pollution is a relatively recent phenomenon that birds now have to cope with throughout much of the world. Early investigations on bird responses to noise tended to focus on physical damage to ears, stress responses, flight or flushing responses, changes in foraging, and other behavioral reactions. These studies were often conducted under laboratory conditions because determining effects of noise on freeranging birds is particularly difficult, in that we rarely have the opportunity to isolate noise as a single testable variable. By coupling introduced noise on the landscape (e.g., from gas well compressors) with ecologically similar controls, investigators have recently found additional responses, including avoidance of noisy areas, changes in reproductive success, and changes in vocal communication. Numerous investigators have compared urban birds with their rural counterparts in quieter surroundings and found that at least some birds can compensate for the masking effect of noise through shifts in vocal amplitude, song and call frequency, and song component redundancies, as well as temporal shifts to avoid noisy rush-hour traffic. Sounds have presumably always been part of the environment, but noise pollution has escalated over the past century, especially the past few decades, disturbing the integrity of natural ecosystems. This review provides general background information, updates on the most current literature, and suggestions for future research that will enhance our comprehensive knowledge and ability to mitigate negative effects of noise.

Key words: birds, communication, hearing, noise pollution, soundscape.

Efectos de la Polución Sonora en Aves: una Breve Revisión de Nuestro Conocimiento

RESUMEN.—Muchas especies de aves han sido expuestas prolongadamente a sonidos naturales fuertes, como arroyos, cascadas y viento. Sin embargo, la polución sonora antropogénica es un fenómeno relativamente reciente con el que las aves tienen que lidiar ahora en casi todo el mundo. Las primeras investigaciones sobre la respuesta de las aves al ruido tendían a enfocarse en el daño físico a los oídos, las repuestas de estrés, las respuestas de vuelo o huída, los cambios en el forrajeo y otras reacciones de comportamiento. Estos estudios fueron frecuentemente conducidos bajo condiciones de laboratorio porque determinar los efectos del ruido sobre aves libres es particularmente difícil, ya que rara vez se tiene la oportunidad de aislar el ruido como única variable que se pone a prueba. Al acoplar el ruido introducido en el paisaje, como el de los compresores de pozos de gas, con controles ecológicamente similares, los investigadores recientemente han encontrado respuestas adicionales, incluyendo la evasión de áreas ruidosas, cambios en el éxito reproductivo y cambios en la comunicación vocal. Numerosos investigadores han comparado

E-mail: ortega_cp@yahoo.com

Ornithological Monographs, Number 74, pages 6–22. ISBN: 978-0-943610-93-1. © 2012 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintlnfo.asp. DOI: 10.1525/om.2012.74.1.6.

aves urbanas con sus contrapartes rurales que ocupan áreas más silenciosas, y encontraron que al menos algunas aves pueden compensar el efecto de enmascaramiento del ruido por medio de cambios en la amplitud vocal, la frecuencia del canto y los llamados, y las redundancias en los componentes del canto. Las aves también exhiben cambios temporales para evitar el ruido de las horas pico del tráfico. Presumiblemente, los sonidos siempre han sido parte del ambiente, pero la polución sonora ha crecido a lo largo del siglo pasado y especialmente durante las últimas décadas, perturbando la integridad de los ecosistemas naturales. Esta revisión provee información general de base, información de la literatura más reciente y sugerencias para investigación futura que va a mejorar nuestro conocimiento y la habilidad para mitigar los efectos negativos del ruido.

THE WORD NOISE dates back to the 13th century, and its etymology reveals the disdain that humans have long felt for noise. It originates from the Latin word nausea and is defined as unwanted sound or sound that interferes with hearing other sounds. Sound is typically defined as vibrations that move through the environment (e.g., air, water, or another medium) and provide an auditory sensation. Noise is a subjective perception with intra- and interspecific variation. One person may perceive a symphonic piece as glorious music while another perceives the same piece as disturbing noise. Similarly, important communication for one species may be perceived as noise by another species. For example, a loud chorus of frogs may interfere with the ability of owls to hear their prey, and cicadas (Slabbekoorn and Smith 2002) or colonies of seabirds (Feare et al. 2003) create a "deafening" experience to any other listener. The sounds of nature can be unwanted at times and can interfere with hearing or interpreting other sounds (Coates 2005), but the term "noise pollution" generally refers to unwanted sounds resulting from human activities.

Anthropogenic noise is related to human population density; therefore, we can assume that it has and will continue to increase as human populations increase. Cities have always been noisy (Rosen 1974), but noise pollution has dramatically increased since the industrial revolution. More recent technologies, especially recreational vehicles and modern conveniences, have exacerbated the problem. Although urban and suburban areas are noisier than less developed areas, natural areas are becoming increasingly noisy. No place on Earth is free from noise pollution because aircraft noise penetrates even the most remote locations. Noisy off-highway vehicles have also become common, even in formerly secluded areas (Barton and Holmes 2007).

Although noise has escalated over many decades, published studies on the effects of noise on birds have surged only in the past decade, possibly as a result of new instruments, song analysis

programs, and opportunities to control noise. Most of this recent work has occurred in the field of vocal communication, often within the context of evolution of communication. Many papers have reviewed the effects of noise pollution on birds and other wildlife (Larkin et al. 1996, Warren et al. 2006, Dooling and Popper 2007, Slabbekoorn and Bouton 2008, Slabbekoorn and Ripmeester 2008, Brumm and Naguib 2009, Barber et al. 2010), but no recent review has covered the wide range of established and possible effects on birds. Therefore, the purpose of the present review is to (1) provide a general background for those unfamiliar with noise literature, (2) provide an update on the most current literature, and (3) suggest areas in need of future research that will enhance our comprehensive knowledge and ability to mitigate negative effects of noise.

How Sound Moves and Is Measured

Sound travels through air or other media in compression and expansion waves. The intensity of these waves produces a sound pressure level, which can be measured with a sound pressure meter. Sound pressure levels are typically measured over a period of time and expressed as a mean, which is most useful for studies of relatively continuous noise. For studies of intermittent noise, maximum sound levels may provide more meaningful measurements, as might other noise metrics that are reviewed in detail by Pater et al. (2009). The commonly used unit of measurement of sound pressure is the decibel (dB), a logarithmic measurement that can accommodate a wide range of frequencies. To put the dB scale in perspective, in the absence of environmental interference, an increase of 6 dB represents a doubling of loudness.

Not all sound pressures are perceived as equally loud because the ear (human or nonhuman) does not respond to all frequencies equally. For our convenience, we use a filter on sound level meters that respond to frequencies similarly to the human ear

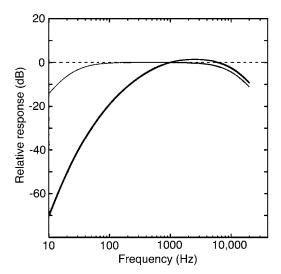


FIG. 1. A (thick line), C (thin line), and flat (black dashed line) decibel weighting systems.

(Fig. 1). This filter provides measurements on the "A scale," weighted for the range of human hearing. It is the most commonly used scale because much of our concern about noise is anthropocentric. In studies of potential effects of noise on nonhuman animals, especially those able to hear low frequencies, the C scale can be useful. For example, compared with humans, doves have ~40 dB more sensitivity at 1-10 Hz (Yodlowski et al. 1977, Kreithen and Quine 1979, Warchol and Dallos 1989, Schermuly and Klinke 1990); therefore, sounds in this range must be louder for us to hear them. The C scale used in conjunction with the A scale is useful to identify low-frequency sound because if the sound pressure levels consistently measure higher on the C scale than on the A scale, the difference might be explained by low-frequency noise. Alternatively, the distribution of acoustic energy can be assessed via analysis of recordings of the sound.

Degradation of sound structure differs with habitat as a result of differences in atmospheric spread, air turbulence, reflections, and scatter through materials such as vegetation (Brumm and Naguib 2009). This occurs through three main mechanisms: attenuation, reverberations, and irregular fluctuations in amplitude (Slabbekoorn et al. 2007). Attenuation is frequency dependent, with lower frequencies (sounds with longer wavelengths) being less affected by small objects (even molecules in the air) than higher frequencies; therefore, higher-frequency sounds usually attenuate faster, and lower frequencies

travel farther. Reverberations, or echoes, reflect off surfaces in the environment numerous times and almost always arrive at the receiver later than the original signal, producing a variety of effects (Warren et al. 2006). Irregular fluctuations in amplitude are caused by air turbulence and accumulation of reverberations.

Under conditions without disruption of sound waves, sound levels decrease by 6 dB(A) with every doubling of distance from the sound source (Larkin et al. 1996). Therefore, if the study aims to identify effects of noise on birds, distance of a bird to the sound source must be considered. For a nest study, this involves measuring sound pressure level at the nest. For bird surveys, it requires taking Universal Transverse Mercator coordinates, compass bearing, and distance from the survey location to each bird detected; these values can be used with trigonometric functions to determine distance from each bird to the noise source. However, this method does not consider topography, vegetation, and other conditions that could alter noise attenuation. If it is practical, the investigator can also measure the sound level at the location of a bird after survey completion.

Effects of Noise on Birds

Many studies have focused on effects of landscape-scale conversions of visually differentiated habitat, but noise has received far less attention. Larkin et al. (1996:8) noted that

Like other related fields such as effects of vehicles or recreation on wildlife..., effects of noise on wildlife often appear in the "gray literature" of conference proceedings and unpublished reports and manuscripts, rather than in the refereed scientific literature.

We have come some distance since 1996, but relatively few investigators currently work on this challenging new field of study.

Noise pollution affects birds in myriad ways, including (1) physical damage to ears; (2) stress responses; (3) fright–flight responses; (4) avoidance responses; (5) changes in other behavioral responses, such as foraging; (6) changes in reproductive success; (7) changes in vocal communication; (8) interference with the ability to hear predators and other important sounds; and (9) potential changes in populations. Reactions to noise depend on the type of noise produced, including frequency, loudness, consistency, and

duration. Some species react more negatively to noise than others. Colonial birds are highly susceptible to noise because when one bird reacts, many or all birds in a colony will react similarly (Burger 1998), whether the group responds directly to the noise or to the first bird(s) that responded.

Physical damage to ears.—Exposure to loud sounds damages sensory hair cells. In mammals, this results in permanent hearing loss. However, birds regenerate these hairs to some extent (Niemiec et al. 1994); therefore, damage is more temporary but with species-specific variation in recovery times (Ryals et al. 1999). Niemiec et al. (1994) reported increased recovery time with repeated exposure, which may have important implications for birds exposed to chronic or repeated noise. Physical damage to birds' ears occurs either with short-duration but very loud sounds (>140 dB[A] for single blasts or 125 dB[A] for multiple blasts; e.g., construction noise) or continuous (>72 h) exposure to noise >110 dB(A) (Dooling and Popper 2007). Some Federal agencies set noise standards within buffer zones for nests of high-priority species such as eagles, hawks, and owls; however, little else protects wild animals from noise.

Stress and fright–flight responses.—Chronic stress causes numerous physiological responses, including elevated heart rate, changes in hormone levels, and weight loss. Chronic stress also impairs the ability of birds to resist diseases and reduces their reproductive success (Blickley and Patricelli 2010). Some studies on noise and domesticated and laboratory animals have demonstrated frightflight, avoidance, and agitation responses to noise (Environmental Protection Agency [EPA] 1980, Bowles 1995), yet these laboratory approaches to studying the effects of noise provide very little insight regarding how natural populations respond to noise. Much of the work conducted on stress and fright-flight responses under natural conditions focused on moving vehicles, such as aircraft (Brown 1990, Conomy et al. 1998, Trimper et al. 1998, Ward et al. 1999, Goudie 2006) and watercraft (Burger 1998, Rodgers and Schwikert 2002), which introduces confounding variables, especially visual disturbance.

Avoidance responses.—Avoidance appears to be the most common response to human disturbance, but some species are surprisingly tolerant and even seek out association with humans and disturbed habitats, including noisy habitats (e.g., House Finch [Carpodacus mexicanus] and Black-chinned Hummingbird [Archilochus alexandri]; Francis et al. 2009).

Anthropogenic noise is almost always associated with other confounding disturbance variables (e.g., visual disturbances, vegetation, food resources, pollutants, concrete or asphalt effects on temperature, and perceived risks), which are difficult, if not impossible, to control.

Even though studies of road traffic noise are severely confounded by other variables, the effects of road-associated variables, including noise, measured by occupancy and densities, are consistently negative for most birds. Brotons and Herrando (2001), Forman and Deblinger (2000), and Fernandez-Juricic (2001) found lower occupancy of birds near roads and attributed the lower numbers, in part, to traffic noise. In the Netherlands, Reijnen et al. (1995) controlled for visual aspects of the highway and found that noise was an important variable explaining lower occupancy near major roads. Although roads negatively affect a variety of taxa (Haskell 2000, Brotons and Herrando 2001, Reijnen and Foppen 2006), the overall effect of traffic noise on nesting birds, measured through lack of habitat occupancy, may extend >300 m on both sides of roadways (Forman and Deblinger 2000). From these and similar findings in the Netherlands (Reijnen et al. 1995), Forman (2000) and Forman and Alexander (1998) estimated that one-fifth of the United States is directly affected by traffic noise. Clearly, these studies have demonstrated that fragmentation and its associated variables, including noise, produce environmental and ecological impacts well beyond the edge of the physically altered habitat.

A few studies that controlled for noise as a single testable variable found species-specific avoidance of noisy areas. In New Mexico, Mourning Doves (Zenaida macroura) avoided gas-well-compressor noise, and several species nested significantly farther from well pads with noisy compressors than from gas well pads without compressors, including the Gray Flycatcher (Empidonax wrightii), Gray Vireo (Vireo vicinior), Black-throated Gray Warbler (Setophaga nigrescens), and Spotted Towhee (Pipilo maculatus) (Francis et al. 2009). During surveys, Western Scrub-Jays (Aphelocoma californica) and several other species were detected significantly more often on sites without compressors (Francis et al. 2009, Ortega and Francis 2012). In Canada, Bayne et al. (2008) found avoidance of noisy areas by Red-eyed Vireos (V. olivaceus), Yellow-rumped Warblers (S. coronata), and White-throated Sparrows (Zonotrichia albicollis); furthermore, they found 1.5× greater density of breeding birds near

noiseless energy facilities than near sites with noisy compressors.

Changes in foraging responses.—Results of a few studies have suggested negative effects of noise on foraging behavior. In Florida, Burger and Gochfeld (1998) observed significantly reduced foraging in five species with the presence of people compared with the absence of people, and the percentage of time spent foraging decreased with increased noise made by people. Similarly, but under laboratory conditions, Quinn et al. (2006) observed that Common Chaffinches (Fringilla coelebs) experienced reduced foraging with added white noise up to 68 dB(A). Canaday and Rivadeneyra (2001) found that machinery noise from petroleum exploration affected foraging guilds in Ecuador.

Changes in reproductive success.—Noise may affect egg production, incubation, brooding, predators, brood parasites, and abandonment, as well as the ability to find or attract a mate and the ability of parents to hear and respond to begging calls. Any species that regularly experience fright–flight responses (Southern and Southern 1979, Burger 1998) or an inability to attract mates and defend territories (Slabbekoorn and Ripmeester 2008) because of noise likely suffer reproductive loss. For some species, this may result in population declines.

Results of studies designed to determine effects of noise on reproductive success suggest species-specific variation. In Francis et al.'s (2009) study in northwest New Mexico, we found higher nest success near noisy gas well compressors than in quiet control sites because predators and cowbirds avoided noisy sites. However, as previously mentioned, many species avoided noisy areas and did not benefit from the lower level of predators and parasites. Black-chinned Hummingbirds preferred noisy sites, and House Finches often used gas-well-compressor equipment for nest sites where the sound pressure levels reached 85 dB(A) at the nest.

Noise may interfere with the ability to attract mates and maintain pair bonds. For example, in Alberta, Canada, male Ovenbirds (*Seiurus aurocapilla*) near gas well compressors experienced a 15% decrease in mate attraction (Habib et al. 2007). Additionally, Habib et al. (2007) found 18% more inexperienced (first-year) Ovenbirds at noisy compressor sites than at quieter control sites, which suggests that noise reduces the quality of habitat for these birds. Reproductive failure or reduced reproductive success can

result in pair-bond degradation. In a laboratory experiment, Swaddle and Page (2007) reported that female Zebra Finches' (*Taeniopygia guttata*) preferences for their pair-bonded males decreased significantly with background noise. They suggested that in areas of high-amplitude environmental noise, birds may develop extrapair behaviors because of weakened pair bonds.

Barton and Holmes (2007) reported reduced nest success close (<100 m) to trails with noisy offhighway vehicles compared with more distant locations in California. As in Francis et al.'s (2009) study, predators appeared to avoid the noisier sites. Barton and Holmes (2007) found 4× more nest abandonment near trails, whereas abandonment did not differ between noisy treatment sites and control sites in Francis et al.'s (2009) study (C. P. Ortega and C. D. Francis unpubl. data); the difference might be explained by chronic (24 h per day, 7 days per week) noise in the latter study compared with intermittent loud noise in the former. If birds select nest sites with chronic noise, to some degree they accept the conditions and may not abandon their nests in response to the noise. In areas with off-road vehicles, birds may select nest sites during the week when the immediate environment seems quiet compared with weekends, or they may select nest sites before the onset of the recreation season. In these cases, birds may not accept noisy conditions as part of the nest selection process, and this may result in nest abandonment.

Changes in vocal communication.—Across taxa, social relationships rely on communication, and vocal communication dominates much of the first-order contact in birds. Even though background noise can critically impair vocal communication, historically investigators did not focus on noise in studies of animal communication (Brumm and Slabbekoorn 2005). Over the past decade, many ornithological studies have focused on the effect of noise on communication.

Although we have a good understanding of a few species-specific responses—for example, in the Domestic Fowl (*Gallus gallus domesticus*; Brumm et al. 2009), Little Greenbul (*Andropadus virens*; Slabbekoorn and Smith 2002), Gray Flycatcher (*E. wrightii*) and Ash-throated Flycatcher (*Myiarchus cinerascens*; Francis et al. 2011), Great Tit (*Parus major*; Slabbekoorn and Peet 2003, Slabbekoorn and den Boer-Visser 2006, Pohl et al. 2009), Gray Shrike-thrush (*Colluricincla harmonica*; Parris and Schneider 2009), Gray Fantail (*Rhipidura*

fuliginosa; Parris and Schneider 2009), Common Nightingale (Luscinia megarhynchos; Brumm and Todt 2002; Brumm 2004, 2006), Eurasian Blackbird (Turdus merula; Nemeth and Brumm 2009, Ripmeester et al. 2010), Common Chaffinch (Brumm and Slater 2006), Song Sparrow (Melospiza melodia; Wood and Yezerinac 2006), Dark-eyed Junco (Junco hyemalis; Slabbekoorn et al. 2007), and House Finch (Badyaev et al. 2008)—we still have a great deal to learn about the responses of most species. However, many investigators have laid the groundwork for additional studies of noise.

Numerous studies have shown that environmental conditions constrain sound transmission. Vegetation affects the way that sound moves through different habitats (Ryan 1986, Slabbekoorn and Smith 2002, Hansen et al. 2005, Boncoraglio and Saino 2007, Simons et al. 2007, Pacifici et al. 2008) and different topographic environments (Brumm 2004, Warren et al. 2006, Slabbekoorn et al. 2007). Natural sounds (e.g., insect and other animal vocalizations, rain, wind, streams, and thunder) and anthropogenic noise can interfere with the detection and discrimination of vocal signals (often referred to as "masking"). Therefore, both natural sounds and anthropogenic noise play an essential role in determining the efficacy of vocal communication and also exert a selective pressure on the evolution of communication, often resulting in song frequencies that transmit most efficiently through a given environment (Morton 1975, Ryan and Brenowitz 1985).

Sound transmission differs with habitat (Slabbekoorn and Smith 2002, Slabbekoorn et al. 2007), but at least some birds compensate for these differences. For example, Slabbekoorn and Smith (2002) reported that song frequency of the Little Greenbul varies across habitat gradient in African rainforests. On an evolutionary scale, urban habitat is relatively novel, but some investigators pointed out that some urban settings are acoustically similar to cliffs, canyons, and other natural environments (Brumm 2004, Warren et al. 2006, Slabbekoorn et al. 2007). However, canyons and cliffs do not exist throughout all landscapes; therefore, many species are not adapted for the acoustics of canyons and cliffs. Furthermore, canyons and cliffs have not been well studied as selection pressures for communication in birds. Because urban areas are expanding on a global basis (Slabbekoorn et al. 2007), anthropogenic noise exerts an evolutionarily novel pressure on many birds worldwide.

In addition to environmental conditions, other selective pressures and constraints, such as body size (Morton 1975), vocal apparatus size (e.g., syrinx and bill characteristics; Ryan and Brenowitz 1985, Badyaev et al. 2008), and phylogeny (Ryan and Brenowitz 1985), influence evolution of bird song, with a trend of lower frequencies produced by larger birds (Ryan and Brenowitz 1985). When environmental conditions change, including background noise levels, natural selection will favor vocalizations that move effectively through the local habitat. Thus, changes in noise will affect both vocalizations and sensory drives (Ryan and Brenowitz 1985, Endler 1992). Other constraints, however, may preclude changes in vocalizations. For example, Badyaev et al. (2008) suggested that urban background noise should favor higherfrequency songs, but bill morphology, which is influenced by available food resources, may limit changes in song characteristics. In Arizona, they found that urban House Finches feed on larger, harder foods than their counterparts in the less disturbed Sonoran desert (e.g., sunflower seeds vs. cacti and grass seeds, respectively); they suggested that directional selection has favored larger bills in the urban population, resulting in a tradeoff between bill size and song characteristics important in courtship, particularly trills.

Noise can mask communication.—Masking occurs when sounds hide or interfere with the detection of a biologically relevant sound, such as vocal communication or sounds made by predators. Anthropogenic noise that masks vocal communication among birds can have serious consequences because birds use vocal communication to attract mates and defend territories (Slabbekoorn and Smith 2002, Wood and Yezerinac 2006, Barber et al. 2010); furthermore, noise can mask begging and alarm calls (Warren et al. 2006). Contact calls contribute to maintaining group cohesion, and if noise masks these calls, it can potentially result in lost individuals or breakdown of group cohesion. Exacerbating this problem, the "dawn chorus" temporally overlaps with one of the heaviest commuter-traffic rush hours. Therefore, noise may determine both habitat quality and reproductive success.

For effective communication, sounds transmitted by the sender must be detected by the receiver in forms with unaltered meaning. On the basis of data from 49 avian species tested both physiologically and behaviorally, Dooling and

Popper (2007) reported that birds hear, on average, best at frequencies between 1 and 5 kHz and hear well at the most sensitive frequencies of 2–4 kHz (Dooling 1982). In comparison, humans hear better over a broader frequency (20 Hz to 20 kHz, with most sensitivity 0.5-4.0 KHz; Dooling and Popper 2007); in other words, in general, birds must hear sounds at higher amplitudes than humans. Owls represent an exception and can hear much softer sounds than passerines and many nonpasserines (Dooling and Popper 2007), and some birds can hear in the ultrasonic range (Boncoraglio and Saino 2007). Dooling and Popper (2007) reported a general trend in which passerines and smaller birds also hear better at high frequencies whereas larger birds hear better at low frequencies. Long-distance communication ranges from 0.5 to ~6.0 kHz for typical birds; therefore, studies of masking communication should focus on this range (Dooling and Popper 2007). It may also be useful to provide a signal-tonoise ratio because detection and discrimination depend on both the signal and the background noise (Brumm and Todt 2002; Brumm 2004, 2006).

In Australia, Haff and Magrath (2010) investigated responses of nestling White-browed Scrubwrens (Sericornis frontalis) to various sounds; even though they responded (by ceasing begging calls) more strongly to natural predators than to white noise, they responded to broadband (both smooth and erratic) sounds more than to tonal sounds. Earlier, Maurer et al. (2003) had reported that nestling White-browed Scrubwrens begged to parental alarm calls, but they obtained their results under laboratory food-deprivation conditions. Magrath et al. (2007) also reported that adults emit a "food call" when they arrive with food, presumably to reduce the risk of erroneous begging. In Canada, Leonard and Horn (2008) found that nestling Tree Swallows (Tachycineta bicolor) responded to experimentally added white noise by emitting begging calls at higher minimum frequency and narrower frequency range, but added noise did not affect nestling growth. However, they used nest boxes, whereas Tree Swallows in natural conditions use cavities. Nestling-parent communication is likely muffled by wood, which differs between boxes and natural cavities. Little work has been done on responses of nestlings to various anthropogenic noise sources (but see Swaddle et al. 2012); however, the studies cited above suggest that noise pollution may affect communication between parents and nestlings.

Very little work has been conducted on birds' responses to what I would call "vocal communication interference levels." This has been extensively studied in humans and is referred to as "speech interference level" (Kryter 1994). It differs from the complete masking phenomenon that covers up or hides sounds; with speech interference, the sound (speech, song, call, etc.) can be heard (it may even be very loud), but the sounds are unintelligible. For example, one can hear people talking very loudly in a room next door yet not understand one word of the conversation. Habib et al. (2007) proposed "song distortion" as an alternative hypothesis to complete masking of vocalization to explain why 15% fewer Ovenbirds experienced successful pairing near noisy compressors compared with quieter control sites. The effects of, or responses to, these garbled sounds may or may not be similar to the effects of complete masking (sounds that cannot even be heard). Pohl et al. (2009) tested this with Great Tits under laboratory conditions and found that noise interfered with signal detection; interestingly, detections were worse during simulations of the dawn chorus compared with both urban and woodland noises.

Birds can change their vocalizations to compensate for the masking effect through (1) changes in song or call frequency, (2) changes in amplitude, (3) changes in song component redundancies, and (4) temporal shifts to avoid morning rush hour or other noise. Birds might also respond to masking by changing their position within the vegetation layer to maximize vocal transmission, but this has not, to my knowledge, been investigated. However, Patricelli et al. (2007, 2008) found that male Red-winged Blackbirds (*Agelaius phoeniceus*) orient themselves to maximize the intent or message of their vocalizations.

Changes in song frequency.—Patricelli and Blickley (2006) suggested two ways in which birds adjust frequency in response to low-frequency noise: (1) by increasing the lowest frequency with no change in the highest frequency, or (2) by shifting the entire vocalization to higher frequency. Slabbekoorn and Peet (2003), Slabbekoorn and den Boer-Visser (2006), and Mockford and Marshall (2009) discovered that Great Tits sing at a higher minimum frequency in noisy locations than in quieter locations. Great Tits apparently have plasticity in their vocal repertoires that enables them to breed successfully in locations with varying noise levels. Halfwerk and Slabbekoorn (2009)

also demonstrated that Great Tits responded to experimentally added low-frequency noise with songs consisting of higher minimum frequency, and they responded to experimentally added high-frequency noise with songs consisting of lower maximum frequency. At least some birds respond to noise with vocal repertoires consisting of songs that differ in frequency (Arcese et al. 2002) and by singing the songs least masked by background noise or by changing the frequency of particular songs in their repertoire (Wood and Yezerinac 2006, Halfwerk and Slabbekoorn 2009). Individuals may learn, during their own sensitive periods, particular songs least masked by noises around them (Wood and Yezerinac 2006).

Many species have shown the same pattern in different parts of the world. Wood and Yezerinac (2006) reported that Song Sparrows in urban areas in and near Portland, Oregon, sing higherfrequency low notes compared with their counterparts living in rural areas. Slabbekoorn et al. (2007) found that Dark-eyed Juncos in urban California sing at higher minimum frequency than populations living in forests. In Vienna, Austria, Nemeth and Brumm (2009) found higher song frequencies and shorter, albeit not statistically significant, intervals between singing bouts among urban Eurasian Blackbirds. Ripmeester et al. (2010) reported that city-dwelling Eurasian Blackbirds in the Netherlands sang at a higher peak frequency than their counterparts in forests. In Australia, Gray Shrikethrushes increased the frequency of their songs in response to traffic noise (Parris and Schneider 2009). Individual Black-capped Chickadees (Poecile atricapillus) also shift the frequency of their song, but this has been reported in social contexts rather than in the context of background noise (Ratcliffe and Weisman 1985, Hill and Lein 1987). Nemeth and Brumm (2009) suggested, as an alternative to masking, that motivational states of higher arousal from higher urban bird densities may also explain the faster-paced, higher-frequency songs. Nemeth and Brumm (2010) further suggested that among urban Great Tits and Eurasian Blackbirds, vocal amplitude had a much larger effect on transmission distance than vocal pitch, and that song frequency shifts might be a side effect of singing at higher amplitudes.

Changes in amplitude.—Amplitude shifts, also referred to as the "Lombard effect" and first described as a human response (Brumm and Todt 2002, Warren et al. 2006; name derived from Lombard 1911), may allow birds to be heard in

noisy areas. For example, Common Nightingales increase the volume of their singing with traffic noise (Brumm 2004) and white noise (Brumm and Todt 2002). This response has also been reported in Blue-throated Hummingbirds (Lampornis clemenciae), Zebra Finches and Budgerigars (Melopsittacus undulatus; reviewed in Warren et al. 2006), and Domestic Fowl (Brumm et al. 2009). Some birds may already produce songs or portions of songs at maximum levels; for example, although Brumm and Todt (2002) found that Common Nightingales sing at higher amplitudes in noisy environments, some elements or portions of their song did not increase in response to increased noise because, presumably, those elements were already at the highest possible amplitude.

Changes in song components and redundancies.—Brumm and Slater (2006) found that in naturally noisy areas, male Common Chaffinches sing some song components for longer bouts than their counterparts in quieter areas. However, they delivered fast trills in shorter bouts, which perhaps suggests a tradeoff between attracting females (attracted to trills) and reducing neuromuscular fatigue. Beyond this study, to my knowledge, very little work has been conducted in this area.

Temporal changes in singing.—We do not know much about species-specific reactions to noise that involve temporal shifts in singing. However, Brumm (2006) found that Common Nightingales can adjust the timing of their peak singing to avoid acoustic interference (in this case, playbacks of other species' songs), and Ficken et al. (1974) reported that Least Flycatchers (Empidonax minimus) and Red-eyed Vireos shifted their timing to avoid heterospecific overlap. Fuller et al. (2007) reported shifts from diurnal to nocturnal singing among European Robins (Erithacus rubecula). Similar temporal shifts have also been reported in frogs (Zelick and Narins 1982, 1983; Schwartz and Wells 1983; Narins 1995).

Interference with the ability to hear predators and other important sounds.—In addition to communication, hearing is critical for detecting predators and other dangers and opportunities in the environment (Quinn et al. 2006, Slabbekoorn and Ripmeester 2008, Barber et al. 2010). If sounds made by predators, such as footsteps, breathing, and rustling leaves, are masked by noise, the immediate situation becomes considerably more risky for potential prey. Also, even in the absence of noise made

by predators (e.g., aerial predators; Leavesley and Magrath 2005), if noise masks warning calls (by conspecifics or heterospecifics), the perception of danger may be underestimated, resulting in inappropriate, perhaps lethal responses. Conversely, from a predator's perspective, many birds and other animals find food resources through listening (Goerlitz et al. 2008). For example, American Robins (Turdus migratorius) listen for sounds of worms underground (Montgomerie and Weatherhead 1997), and many raptors depend on noises made by their prey (Knudsen and Konishi 1979, Rice 1982). This seems a relatively unexplored topic.

Sounds are also critical for an animal's ability to determine its orientation and move across a landscape. The contribution of sounds to the environment is referred to as a "soundscape," and the use of perceived sounds for general orientation within a landscape is referred to as "soundscape orientation" (Slabbekoorn and Bouton 2008). For example, animals use sounds to find water sources and protected areas. Soundscapes are particularly important for nocturnal animals and animals that move through caves or dense vegetation.

CHALLENGES, NEEDS, AND OPPORTUNITIES

Isolating noise from confounding variables.—Determining effects of noise on free-ranging birds and other wildlife is particularly challenging because we rarely have the opportunity to isolate noise as a single testable variable. Numerous studies have suggested that human disturbances negatively affect birds and other wildlife species in a variety of ways. In many of these studies, noise is coupled with human disturbance, including snowmobiles (Creel et al. 2002, Seip et al. 2007), all-terrain vehicles (Barton and Holmes 2007), trails (Taylor and Knight 2003, Trulio and Sokale 2008), boating (Rodgers and Schwikert 2002, Peters and Otis 2006, Rojek et al. 2007), roads and traffic (Reijnen et al. 1995, Brotons and Herrando 2001), aircraft (Carney and Sydeman 1999, Giese and Riddle 1999, Goudie 2006, Rojek et al. 2007), and ski resorts (Ballenger and Ortega 2001).

However, none of these earlier studies separated noise from the effects of other disturbance. For example, studies on the effect of human noise (talking, laughing, etc.) are confounded with disturbance caused by physical presence of people (Burger and Gochfeld 1998) and with foraging opportunities provided by people (Fernández-Juricic 2001). Similarly, studies on the effects of

road or highway noise (Brotons and Herrando 2001) are confounded with effects of habitat fragmentation caused by the roads themselves, the physical movement of traffic, perceived risks of traffic and increased predators, and vehicular exhaust. A few studies have demonstrated that birds and other wildlife can also be negatively affected by nonmotorized human recreational activities for example, hiking with or without dogs on and off leash, horseback riding, cycling, and ski-slope activities—and some species are more disturbed by humans on foot than by motorized vehicles (Mallord et al. 2007, Patthey et al. 2008, Reed and Merenlender 2008, Stankowich 2008). The most definitive conclusion from most of these studies is that some aspect or several aspects of human disturbance negatively affect birds.

Our ability to detect birds with noise during surveys.—Ortega and Francis (2012) determined that sound pressure levels above 45 dB(A) significantly impaired our ability to detect birds; therefore, surveys in noisy areas likely underestimate bird occupancy. This is particularly relevant in studies aimed at comparing sites that differ in noise levels. For example, studies of fragmentation are often coupled with noisy activities, such as roads and other development. The effects of background noise clearly vary among observers' abilities to aurally detect birds, and species vary in their detectability. Pacifici et al. (2008) reported at 100 m, detection probabilities ranged from 0 to 1, and 3-99% of birdsongs were detected during a birdsong simulation experiment. They suggested that surveys focused on particular species might vield the best results. However, when the objective is to compare communities between or among sites, surveyors need to count all birds. In another simulated experiment, Simons et al. (2007) found that observers overcount within 50 m and undercount beyond that distance, and the mean number of birdsongs detected decreased by 41% with 10 dB(A) of added white noise.

Indirect effects that could change landscapes.—The indirect effects of noise, to my knowledge, have not been well studied, but at least one study has suggested potential effects on habitat because some birds that provide ecological services, such as pollination and seed dispersal, are affected either positively (e.g., Black-chinned Hummingbirds) or negatively (e.g., Western Scrub-Jays) by noise (Francis et al. 2009, 2012; Ortega and Francis 2012). Francis et al. (2009) reported on the potential of noise pollution from gas well compressors

to alter the future distribution of pinon–juniper (*Pinus edulis–Juniperus osteosperma*) forests because at least one of the main dispersers (Western Scrub-Jays) of pinons were notably absent from the noisy compressor sites. Currently, we do not know how noise indirectly affects other habitats.

Who regulates noise, where, and how?—The federal Office of Noise Abatement and Control (under the authority of the Environmental Protection Act) closed in 1981 because they concluded that noise issues would be better handled at the local level. Currently, states, counties, and municipalities regulate noise from an anthropocentric perspective with little or no consideration for wildlife species, although some federal land management agencies set their own noise tolerance levels for the benefit of wildlife, but usually for charismatic species sensitive to disturbance. Local regulations are often very lenient, with many loopholes, exclusions, and exemptions that promote special interests (for links to state regulations, see www.epa.gov/epahome/ state.htm). For example, in Colorado, under Article 12, Noise abatement, section 25-12-103, Maximum permissible noise levels: "This article is not applicable to the use of property for the purpose of manufacturing, maintaining, or grooming machine-made snow." Other exclusions include athletic, entertainment, cultural, and patriotic events.

Sound pressure levels are also very lenient. For example, in Colorado, the limit set for motorized vehicles measured from 50 feet (15.2 m) from the center line of a road is 86 dB(A) and 90 dB(A) for speeds less than and exceeding, respectively, 35 mph (56.3 kph). Limits for off-road vehicles are almost as lenient, at 82 dB(A) and 86 dB(A) for below and above 35 mph (56.3 kph), respectively. Additionally, the same regulations state that

In all sound level measurements, consideration shall be given to the effect of the ambient noise level created by the encompassing noise of the environment from all sources at the time and place of such sound level measurement.

This does not take into account the cumulative effects of noise pollution and makes for regulation with little or no teeth, set within a framework of ambiguity.

Without more stringent and enforceable regulations, reducing noise pollution will require citizen consciousness and compliance. With increasing urban sprawl and its associated noise pollution, louder and more frequent noises throughout the world, and bird population declines, the responsibility rests with researchers to provide useful information on the effects of noise pollution on birds and other wildlife and how noise can best be mitigated.

What kind of mitigation is possible?—In order to plan mitigation for noise, we need to understand the major sources of noise. Anthropogenic noise is nothing new, but the sounds of outdoor markets and horses clopping along cobblestone streets have been traded for more contemporary noises that now dominate our soundscape. Noise can conveniently be categorized as (1) long-term and relatively constant, such as noise from industry and business as well as housing (e.g., air conditioning and exhaust fans); (2) regular but intermittent, such as air and road traffic; and (3) temporary noise, such as military activities, special events, and domestic conveniences (e.g., lawn mowers, chainsaws, weed trimmers, leaf blowers, snow blowers, cell phones, car horns and alarms). Many temporary noises, however, collectively produce a constant urban hum.

Most noises can be muffled better; others are unnecessary (e.g., car horns to confirm activated alarms). Noise from industry can also be muffled, but unless regulations require it, industries may not volunteer to pay the high cost of current mitigation technology, such as noise reduction barriers. Bayne et al. (2008) estimated that retrofitting a compressor station with sound reduction equipment would cost \$35,000-50,000. They also compared the estimated \$175-250 million cost to reduce noise by 4 dB(A) throughout the energy sector in boreal Alberta with the \$100 billion influx from the energy sector over the next 5 to 10 years (Habib et al. 2007, Bayne et al. 2008); they suggested that it would be a cost-effective best management practice.

Mitigation measures that have been suggested to reduce traffic noise include (1) using road surfaces that absorb more sound (Slabbekoorn and Ripmeester 2008, Blickley and Patricelli 2010); (2) reducing speed, especially during the breeding season (Makarewicz and Kokowski 2007, Parris and Schneider 2009, Slabbekoorn and Ripmeester 2008); (3) shuttle buses, especially in parks (Barber et al. 2010); and (4) seasonal road closures in important breeding areas to the extent feasible (Slabbekoorn and Ripmeester 2008). Parris and Schneider (2009) and Blickley and Patricelli (2010) pointed out that sound barriers for roads would reduce noise pollution but hinder wildlife movements. This is a management area in need of

further investigation. For many species, sound barriers make movement across roads difficult or impossible, but they may also prevent animal–vehicle collisions. Sound barriers do not necessarily have to extend to the ground and, coupled with wildlife overpasses, could be a potential solution, at least in some areas. Research on solutions as well as potential implementation might be funded by a noise tax (Sandberg 1991).

Mitigation measures will come with a financial burden; therefore, it is unlikely that industry will adopt them voluntarily or that citizens will willingly accept mitigation costs passed on by industry. As Blickley and Patricelli (2010) suggested, reduction of noise pollution will take policy action in terms of adjusted noise-level standards and mitigation measures to meet new standards. Before policy makers can make these important and perhaps controversial decisions, they will need compelling scientific evidence that noise negatively affects some species of birds and other wildlife, especially species of concern.

Although variation exists among species, the difference in masking threshold is ~6 dB(A) less in humans than in birds; in other words, humans can detect sounds with 6 dB(A) greater background noise compared with the typical bird (Dooling and Popper 2007). This has important implications for potential mitigation. Sound pressure levels decrease by ~6 dB(A) for every doubling of distance from the sound source. This implies that at least some birds can no longer detect a sound at half the distance from the noise source as a human can hear it. Therefore, humans are poor judges of what masks sounds for birds. In other words, compared with humans, birds may be less disturbed by noise closer to the source (e.g., highway noise, compressor noise, etc.), but the masking effects are greater.

Future research needs.—The EPA identified a need for research in three major areas involving the effects of noise on wildlife: (1) effects of long-term exposure to moderate noise levels, (2) whether wild animals experience the same adverse reactions to noise as laboratory animals, and (3) the ecological consequences of masking and altered behavioral patterns (EPA 1980). Thirty years have passed since the agency made these suggestions; however, relatively few research efforts since have addressed these three areas of need.

More recently, Warren et al. (2006) also suggested three, albeit different, areas in need of research: (1) the relationship between spatial

distribution of noise and variation in communication, (2) potential relationship between timing of noise levels and the dawn chorus, and (3) the acoustics of canyons. They pointed out that, in addition to contributing to knowledge that benefits conservation and management planning strategies, these research topics would have the additional benefit of contributing to our overall knowledge of avian communication.

We are still on the forefront of our understanding of how at least some birds can adjust their vocalizations in response to noise pollution. But to my knowledge, in addition to the above research suggestions, we do not yet know the answers to many other critical questions (outlined below) and how all the information (known and unknown) interconnects.

- (1) We know that some species change frequency or loudness of their songs in response to noise, but our knowledge comes from relatively few species. In order to generalize about common responses of birds to noise, we must increase our understanding of species-specific responses, covering at least the major taxonomic groups of birds. It may also be useful to know whether species within the major taxonomic groups of birds respond to noise in similar ways.
- (2) Most research on effects of noise on bird communication has focused on song. However, other important vocalizations (e.g., alarm calls, contact calls, begging vocalizations, and invitation-to-copulation calls) have not been studied as much.
- (3) We know little about how females respond to changes in vocalization or whether noise interferes with their ability to orient themselves in a spatially appropriate manner. Most of our knowledge comes from a few studies of frogs. For example, Bee and Swanson (2007; cited in Barber et al. 2010) reported that female Gray Treefrogs (Hyla chrysoscelis) take longer to orient themselves to male signals in the presence of traffic noise playbacks. Parris et al. (2009) pointed out a tradeoff between audibility and mate attraction in frogs that may apply to at least some bird species. They suggested that female Common Eastern Froglets (Crinia signifera) prefer lower-frequency songs because they indicate larger males, yet males call at a higher frequency in areas of traffic noise.
- (4) In natural habitats, sound does not attenuate in a symmetrical spherical pattern because of permanent (e.g., topography) and temporary (e.g., atmospheric conditions) features. In general, lower frequencies degrade less in dense vegetation than

higher frequencies; however, lower frequencies attenuate more rapidly when emitted close to the ground (Boncoraglio and Saino 2007). Animals can spatially orient themselves to maximize hearing and vocalizing. For example, some birds directionally orient themselves in ways that maximize transmission of communication (Boncoraglio and Saino 2007, Patricelli et al. 2008). Therefore, one might expect that birds can change their position within the vegetation layers in addition to directional orientation to maximize their vocal transmissions.

- (5) There may be an interesting relationship between abundance of certain species in noisy areas and their song frequency; birds with higher dominant song frequency may be more abundant near roads and other noisy areas (Rheindt 2003). Further investigation would help us predict effects of noise, particularly with new roads, industry, and energy extraction activities.
- (6) Very little work has teased apart two major elements of noise masking: detection (signal not heard) and discrimination (signal heard but unintelligible). Distinction between these elements might be important if birds can still respond to certain components of a garbled song or call.
- (7) We do not have an understanding of how noise has affected, or might affect in the future, birds at the population level. A necessary component of this would be to gain a better understanding of the effects of noise on the communication system between nestlings and their parents. Potential population changes will likely have to be modeled using soundscape information in geographic information systems (GIS). This will open up opportunities for interdisciplinary collaboration with GIS experts, planners, architects, acoustical physicists, agencies, and biologists in various disciplines. Many workgroups are already working on soundscape maps; for example, noise contours are regularly mapped for airports (Warren et al. 2006), and the National Park Service is developing a soundscape program. GIS maps with context options (e.g., time of day, seasons, and when particular events such as train trips or sporting events occur) should be invaluable tools for predicting bird population changes due to noise.
- (8) We do not, to my knowledge, know how noise might affect competition for resources. For example, Ortega and Francis (2012) found that Violet-green Swallows (*Tachycineta thalassina*) are significantly more common on treatment sites (with noisy compressors) than on control sites (gas

- wells without compressors). One hypothesis is that the compressor noise eliminates bats that might overlap with swallows during the dawn and dusk hours, leaving more food resources for swallows.
- (9) In order to determine the role of noise in predator–prey relationships, we need to better understand how noise affects the success of predators by masking sounds of their prey. Conversely, we need to understand how noise affects the ability of prey to detect predators.
- (10) As mentioned above, noise is often difficult to study as a single testable variable. Several studies have used noise from gas well compressors because the noise can be turned off, and these sites can easily be compared with ecologically similar habitat adjacent to or surrounding gas wells without compressors. Conversely, adding noise is relatively easy but has both advantages and disadvantages of creating a situation that birds did not choose. It is easier to study human-created noise—at least in some situations, such as the energy sector-than to study the effects of noise in the natural world. However, it is not impossible to isolate naturally occurring noises. One opportunity to isolate naturally occurring noise as a single testable variable involves noise from flowing water. This may be logistically challenging but not impossible. Regulated streams can be "turned off" long enough to conduct bird surveys or experiments. These periods can be compared with times when streams flow and are noisy. Dam operators might be willing to cooperate as long as the requested times do not significantly interfere with water delivery. It could even be as simple as coordinating research activities with already scheduled dam operations.
- (11) Many birds provide ecological services, such as seed dispersal, pollination, and pest control. At this point in time, we have a poor understanding of how noise affects these birds and how these effects may, in turn, affect the future distribution of certain habitats.
- (12) Many birds incorporate songs of other species into their vocal repertoires. For example, David Attenborough hosted a revealing video of a Superb Lyrebird (*Menura novaehollandiae*) imitating sounds of camera shutters, car alarms, and chainsaws (www.youtube.com/watch?v=OFDdtRD5ED8). Similar accounts exist on the Internet of other birds, especially Northern Mockingbirds (*Mimus polyglottos*) and Eurasian Blackbirds (Stover 2009), imitating various cell phone rings and tones, ambulances, and other common urban noises. Presumably, incorporation of these anthropogenic

noises increases their overall repertoires, yet we do not know how females respond to these novel vocalizations.

The Future for Birds in a Noisier World

Noise is nothing new to many avian species, especially colonial species that collectively make deafening noises themselves. Some species have presumably lived with natural sound, such as streams, waterfalls, and wind, for a very long time. Anthropogenic noise pollution will continue to challenge many other species, and whether or not they can coexist with noise will depend on (1) the degree of sound spectrum overlap between anthropogenic noise and important acoustic cues in their world; (2) the degree to which other sensory forms can compensate for reduced hearing; (3) how other organisms (e.g., predators, competitors, parasites, seed dispersers, pollinators, and other organisms that provide ecological services) in the community respond to noise pollution; and (4) the extent to which males and females can coordinate their responses.

Sounds have always been an integral part of the environment, but changes by humans, resulting in noise pollution, have disturbed the integrity of natural ecosystems. Barber et al. (2010:8) suggested that "Taken collectively, the preponderance of evidence argues for immediate action to manage noise in protected natural areas." Management of noise will be necessary to maintain or restore the integrity of natural ecosystems. This will require numerous actions: (1) sound scientific research to better understand the complicated and sometimes seemingly underlying effects of noise pollution; (2) raising the collective consciousness of society about the harmful effects, including information on how citizens can reduce their contribution to noise pollution; and (3) working with policy makers to tighten regulations and enforcement of noise sources.

LITERATURE CITED

- Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten. 2002. Song Sparrow (*Melospiza melodia*). *In* The Birds of North America, no. 704 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- Badyaev, A. V., R. L. Young, K. P. Oh, and C. Addison. 2008. Evolution on a local scale: Developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. Evolution 62:1951–1964.

- Ballenger, N., and C. P. Ortega. 2001. Effects of ski resort fragmentation on wintering birds in southwest Colorado. Journal of the Colorado Field Ornithologists 35:122–128.
- Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology & Evolution 25:180–189.
- BARTON, D. C., AND A. L. HOLMES. 2007. Off-highway vehicle trail impacts on breeding songbirds in northeastern California. Journal of Wildlife Management 71:1617–1620.
- BAYNE, E. M., L. HABIB, AND S. BOUTIN. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology 22:1186–1193.
- Bee, M. A., and E. M. Swanson. 2007. Auditory masking of anuran advertisement calls by road traffic noise. Animal Behaviour 74:1765–1776.
- BLICKLEY, J. L., AND G. L. PATRICELLI. 2010. Impacts of anthropogenic noise on wildlife: Research priorities for the development of standards and mitigation. Journal of International Wildlife Law and Policy 13:274–292.
- Boncoraglio, G., and N. Saino. 2007. Habitat structure and the evolution of bird song: A meta-analysis of the evidence for the acoustic adaptation hypothesis. Functional Ecology 21:134–142.
- BOWLES, A. E. 1995. Responses of wildlife to noise. Pages 109–156 in Wildlife and Recreationists: Coexistence through Management and Research (R. L. Knight and K. J. Gutzwiller, Eds.). Island Press, Washington, D.C.
- Brotons, L., and S. Herrando. 2001. Reduced bird occurrence in pine forest fragments associated with road proximity in a Mediterranean agricultural area. Landscape and Urban Planning 57:77–89.
- Brown, A. L. 1990. Measuring the effect of aircraft noise on sea birds. Environment International 16:587–592.
- Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73:434–440.
- Brumm, H. 2006. Signalling through acoustic windows: Nightingales avoid interspecific competition by short-term adjustment of song timing. Journal of Comparative Physiology A 192:1279–1285.
- Brumm, H., and M. Naguib. 2009. Environmental acoustics and the evolution of bird song. Advances in the Study of Behavior 40:1–33.
- Brumm, H., R. Schmidt, and L. Schrader. 2009. Noisedependent vocal plasticity in Domestic Fowl. Animal Behaviour 78:741–746.
- Brumm, H., and H. Slabbekoorn. 2005. Acoustic communication in noise. Advances in the Study of Behavior 35:151–209.
- BRUMM, H., AND P. J. B. SLATER. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behavioral Ecology and Sociobiology 60:475–481.

- Brumm, H., and D. Todt. 2002. Noise-dependent song amplitude regulation in a territorial songbird. Animal Behaviour 63:891–897.
- Burger, J. 1998. Effects of motorboats and personal watercraft on flight behavior over a colony of Common Terns. Condor 100:528–534.
- Burger, J., and M. Gochfeld. 1998. Effects of ecotourists on bird behaviour at Loxahatchee National Wildlife Refuge, Florida. Environmental Conservation 25:13–21.
- CANADAY, C., AND J. RIVADENEYRA. 2001. Initial effects of a petroleum operation on Amazonian birds: Terrestrial insectivores retreat. Biodiversity and Conservation 10:567–595.
- CARNEY, K. M., AND W. J. SYDEMAN. 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22:68–79.
- COATES, P. A. 2005. The strange stillness of the past: Toward an environmental history of sound and noise. Environmental History 10:636–665.
- Conomy, J. T., J. A. Dubovsky, J. A. Collazo, and W. J. Fleming. 1998. Do Black Ducks and Wood Ducks habituate to aircraft disturbance? Journal of Wildlife Management 62:1135–1142.
- CREEL, S., J. E. FOX, A. HARDY, J. SANDS, B. GARROTT, AND R. O. PETERSON. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809–814.
- Dooling, R. J. 1982. Auditory perception in birds. Pages 95–130 *in* Acoustic Communication in Birds, vol. 1 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.
- Dooling, R. J., and A. N. Popper. 2007. The Effects of Highway Noise on Birds. [Report prepared for the California Department of Transportation, Sacramento; Jones and Stokes Associates.] [Online.] Available at www.dot.ca.gov/hq/env/bio/files/caltrans_birds_10-7-2007b.pdf.
- ENDLER, J. A. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139 (Supplement):S125–S153.
- Environmental Protection Agency. 1980. Effects of noise on wildlife and other animals: Review of research since 1971. EPA 550/9-80-100.
- Feare, C. J., E. Henriette, and S. E. A. Feare. 2003. Variation in sound levels produced within a Sooty Tern colony. Waterbirds 26:424–428.
- Fernández-Juricic, E. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. Biodiversity and Conservation 10:1303–1316.
- 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.
- FORMAN, R. T. T. 2000. Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology* 14:31–35.
- FORMAN, R. T. T., AND L. E. ALEXANDER. 1998. Roads and their major ecological effects. Annual Review of Ecology & Systematics 29:207–231.

- Forman, R. T. T., and R. D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conservation Biology 14:36–46.
- FRANCIS, C. D., C. P. ORTEGA, AND A. CRUZ. 2009. Noise pollution changes avian communities and species interactions. Current Biology 19:1415–1419.
- FRANCIS, C. D., C. P. ORTEGA, AND A. CRUZ. 2011. Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. Proceedings of the Royal Society of London, Series B 278:2025–2031.
- FRANCIS, C. D., C. P. ORTEGA, R. I. KENNEDY, AND P. J. NYLANDER. 2012. Are nest predators absent from noisy areas or unable to locate nests? Pages 99–108 in The Influence of Anthropogenic Noise on Birds and Bird Studies (C. D. Francis and J. L. Blickley, Eds.). Ornithological Monographs, no. 74.
- FULLER, R. A., P. H. WARREN, AND K. J. GASTON. 2007. Daytime noise predicts nocturnal singing in urban robins. Biology Letters 3:368–370.
- GIESE, M., AND M. RIDDLE. 1999. Disturbance of Emperor Penguin *Aptenodytes forsteri* chicks by helicopters. Polar Biology 22:366–371.
- GOERLITZ, H.R., S. GREIF, AND B.M. SIEMERS. 2008. Cues for acoustic detection of prey: Insect rustling sounds and the influence of walking substrate. Journal of Experimental Biology 211:2799–2806.
- GOUDIE, R. I. 2006. Multivariate behavioural response of Harlequin Ducks to aircraft disturbance in Labrador. Environmental Conservation 33:28–35.
- Habib, L., E. M. Bayne, and S. Boutin. 2007. Chronic industrial noise affects pairing success and age structure of Ovenbirds *Seiurus aurocapilla*. Journal of Applied Ecology 44:176–184.
- HAFF, T. M., AND R. D. MAGRATH. 2010. Vulnerable but not helpless: Nestlings are fine-tuned to cues of approaching danger. Animal Behaviour 79:487–496.
- HALFWERK, W., AND H. SLABBEKOORN. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. Animal Behaviour 78:1301–1307.
- HANSEN, I. J. K., K. A. OTTER, H. VAN OORT, AND C. I. HOLSCHUH. 2005. Communication breakdown? Habitat influences on Black-capped Chickadee dawn choruses. Acta Ethologica 8:111–120.
- HASKELL, D. G., 2000. Effects of forest roads on the macroinvertebrate soil fauna of the southern Appalachian mountains. Conservation Biology 14:57–63.
- HILL, B. G., AND M. R. LEIN. 1987. Function of frequencyshifted songs of Black-capped Chickadees. Condor 89:914–915.
- Knudsen, E. I., and M. Konishi. 1979. Mechanisms of sound localization in the Barn Owl (*Tyto alba*). Journal of Comparative Physiology A 133:13–21.
- Kreithen, M. L., and D. Quine. 1979. Infrasound detection by the homing pigeon: A behavioral audiogram. Journal of Comparative Physiology A 129:1–4.
- Kryter, K. D. 1994. The Handbook of Hearing and the Effects of Noise: Physiology, Psychology, and Public Health. Academic Press, San Diego, California.

- LARKIN, R. P., L. L. PATER, AND D. J. TAZIK. 1996. Effects of military noise on wildlife: A literature review. Technical Report 96/21. U.S. Army Construction Engineering Research Laboratory, Champaign, Illinois.
- Leavesley, A. J., and R. D. Magrath. 2005. Communicating about danger: Urgency alarm calling in a bird. Animal Behaviour 70:365–373.
- Leonard, M. L., and A. G. Horn. 2008. Does ambient noise affect growth and begging call structure in nestling birds? Behavioral Ecology 19:502–507.
- LOMBARD, É. 1911. Le signe de l'élévation de la voix. Annales des maladies de l'oreille et du larynx 37:101–119.
- Magrath, R. D., B. J. Pitcher, and A. H. Dalziell. 2007. How to be fed but not eaten: Nestling responses to parental food calls and the sound of a predator's footsteps. Animal Behaviour 74:1117–1129.
- MAKAREWICZ, R., AND P. KOKOWSKI. 2007. Prediction of noise changes due to traffic speed control. Journal of the Acoustical Society of America 122:2074–2081.
- MALLORD, J. W., P. M. DOLMAN, A. F. BROWN, AND W. J. SUTHERLAND. 2007. Linking recreational disturbance to population size in a ground-nesting passerine. Journal of Applied Ecology 44:185–195.
- MAURER, G., R. D. MAGRATH, M. L. LEONARD, A. G. HORN, AND C. DONNELLY. 2003. Begging to differ: Scrubwren nestlings beg to alarm calls and vocalize when parents are absent. Animal Behaviour 65:1045–1055.
- MOCKFORD, E. J., AND R. C. MARSHALL. 2009. Effects of urban noise on song and response behaviour in Great Tits. Proceedings of the Royal Society of London, Series B 276:2979–2985.
- Montgomerie, R., and P.J. Weatherhead. 1997. Howrobins find worms. Animal Behaviour 54:143–151.
- MORTON, E. S. 1975. Ecological sources of selection on avian sounds. American Naturalist 109:17–34.
- NARINS, P. M. 1995. Frog communication: In striving to be heard by rivals and mates, these amphibians have evolved a plethora of complex strategies. Scientific American 273(2):78–83.
- Nemeth, E., and H. Brumm. 2009. Blackbirds sing higher-pitched songs in cities: Adaptation to habitat acoustics or side-effect of urbanization? Animal Behaviour 78:637–641.
- Nemeth, E., and H. Brumm. 2010. Birds and anthropogenic noise: Are urban songs adaptive? American Naturalist 176:465–475.
- NIEMIEC, A. J., Y. RAPHAEL, AND D. B. MOODY. 1994. Return of auditory function following structural regeneration after acoustic trauma: Behavioral measures from quail. Hearing Research 75:209–224.
- Ortega, C. P., and C. D. Francis. 2012. Effects of gaswell-compressor noise on the ability to detect birds during surveys in northwest New Mexico. Pages 78–88 *in* The Influence of Anthropogenic Noise on Birds and Bird Studies (C. D. Francis and J. L. Blickley, Eds.). Ornithological Monographs, no. 74.

- PACIFICI, K., T. R. SIMONS, AND K. H. POLLOCK. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. Auk 125:600–607.
- Parris, K. M., and A. Schneider. 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecology and Society 14:29.
- PARRIS, K. M., M. VELIK-LORD, AND J. M. A. NORTH. 2009. Frogs call at a higher pitch in traffic noise. Ecology and Society 14:25.
- PATER, L. L., T. G. GRUBB, AND D. K. DELANEY. 2009. Recommendations for improved assessment of noise impacts on wildlife. Journal of Wildlife Management 73:788-795.
- Patricelli, G. L., and J. L. Blickley. 2006. Avian communication in urban noise: Causes and consequences of vocal adjustment. Auk 123:639–649.
- PATRICELLI, G. L., M. S. DANTZKER, AND J. W. BRADBURY. 2007. Differences in acoustic directionality among vocalizations of the male Red-winged Blackbird (Agelaius phoeniceus) are related to function in communication. Behavioral Ecology and Sociobiology 61:1099–1110.
- PATRICELLI, G. L., M. S. DANTZKER, AND J. W. BRADBURY. 2008. Acoustic directionality of Red-winged Blackbird (Agelaius phoeniceus) song relates to amplitude and singing behaviours. Animal Behaviour 76:1389–1401.
- Patthey, P., S. Wirthner, N. Signorell, and R. Arlettaz. 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of Applied Ecology 45:1704–1711.
- Peters, K. A., and D. L. Otis. 2006. Wading bird response to recreational boat traffic: Does flushing translate into avoidance? Wildlife Society Bulletin 34:1383–1391.
- Pohl, N. U., H. Slabbekoorn, G. M. Klump, and U. Langemann. 2009. Effects of signal features and environmental noise on signal detection in the Great Tit, *Parus major*. Animal Behaviour 78:1293–1300.
- Quinn, J. L., M. J. Whittingham, S. J. Butler, and W. Cresswell. 2006. Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. Journal of Avian Biology 37:601–608.
- Ratcliffe, L., and R. G. Weisman. 1985. Frequency shift in the fee bee song of the Black-capped Chickadee. Condor 87:555–556.
- REED, S. E., AND A. M. MERENLENDER. 2008. Quiet, nonconsumptive recreation reduces protected area effectiveness. Conservation Letters 1:146–154.
- REIJNEN, R., AND R. FOPPEN. 2006. Impact of road traffic on breeding bird populations. Pages 255–274 in The Ecology of Transportation: Managing Mobility for the Environment (J. Davenport and J. L. Davenport, Eds.). Springer-Verlag, Heidelberg, Germany.
- 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.
- 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.
- RICE, W. R. 1982. Acoustical location of prey by the Marsh Hawk: Adaptation to concealed prey. Auk 99:403–413.
- RIPMEESTER, E. A. P., J. S. KOK, J. C. VAN RIJSSEL, AND H. SLABBEKOORN. 2010. Habitat-related birdsong divergence: A multi-level study on the influence of territory density and ambient noise in European blackbirds. Behavioral Ecology and Sociobiology 64:409–418.
- Rodgers, J. A., Jr., and S. T. Schwikert. 2002. Bufferzone distances to protect foraging and loafing waterbirds from disturbance by personal watercraft and outboard-powered boats. Conservation Biology 16:216–224.
- ROJEK, N. A., M. W. PARKER, H. R. CARTER, AND G. J. McChesney. 2007. Aircraft and vessel disturbances to Common Murres *Uria aalge* at breeding colonies in central California, 1997–1999. Marine Ornithology 35:61–69.
- Rosen, G. 1974. A backward glance at noise pollution. American Journal of Public Health 64:514–517.
- Ryals, B. M., R. J. Dooling, E. Westbrook, M. L. Dent, A. MacKenzie, and O. N. Larsen. 1999. Avian species differences in susceptibility to noise exposure. Hearing Research 131:71–88.
- Ryan, M. J. 1986. Environmental bioacoustics: Evaluation of a commonly-used experimental design. Animal Behaviour 34:931–933.
- 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.
- SANDBERG, U. 1991. Abatement of traffic, vehicle and tire/road noise—A global perspective. Noise Control Engineering Journal 49:170–181.
- SCHERMULY, L., AND R. KLINKE. 1990. Infrasound sensitive neurones in the pigeon cochlear ganglion. Journal of Comparative Physiology A 166:355–363.
- SCHWARTZ, J. J., AND K. D. WELLS. 1983. An experimental study of acoustic interference between two species of Neotropical treefrogs. Animal Behaviour 31:181–190.
- SEIP, D. R., C. J. JOHNSON, AND G. S. WATTS. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71:1539–1544.
- SIMONS, T. R., M. W. ALLDREDGE, K. H. POLLOCK, AND J. M. WETTROTH. 2007. Experimental analysis of the auditory detection process on avian point counts. Auk 124:986–999.
- SLABBEKOORN, H., AND N. BOUTON. 2008. Soundscape orientation: A new field in need of sound investigation. Animal Behaviour 76:e5–e8.

- SLABBEKOORN, H., AND A. DEN BOER-VISSER. 2006. Cities change the songs of birds. Current Biology 16:2326–2331.
- SLABBEKOORN, H., AND M. PEET. 2003. Birds sing at a higher pitch in urban noise—Great Tits hit the high notes to ensure that their mating calls are heard above the city's din. Nature 424:267.
- SLABBEKOORN, H., AND E. A. P. RIPMEESTER. 2008. Birdsong and anthropogenic noise: Implications and applications for conservation. Molecular Ecology 17:72–83.
- SLABBEKOORN, H., AND T. B. SMITH. 2002. Habitatdependent song divergence in the Little Greenbul: An analysis of environmental selection pressures on acoustic signals. Evolution 56:1849–1858.
- SLABBEKOORN, H., P. YEH, AND K. HUNT. 2007. Sound transmission and song divergence: A comparison of urban and forest acoustics. Condor 109:67–78.
- Southern, L. K., and W. E. Southern. 1979. Absence of nocturnal predator defense mechanisms in breeding gulls. Proceedings of the Colonial Waterbird Group 2:157–162.
- STANKOWICH, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141:2159–2173.
- STOVER, D. 2009. Not so silent spring. Conservation Magazine 10 (1). [Online.] Available at www.conservationmagazine.org/articles/v8n2/not-so-silent-spring/.
- Swaddle, J. P., C. R. Kight, S. Perera, E. Davila-Reyes, and S. Sikora. 2012. Constraints on acoustic signaling among birds breeding in secondary cavities: The effects of weather, cavity material, and noise on sound propagation. Pages 63–77 *in* The Influence of Anthropogenic Noise on Birds and Bird Studies (C. D. Francis and J. L. Blickley, Eds.). Ornithological Monographs, no. 74.
- SWADDLE, J. P., AND L. C. PAGE. 2007. High levels of environmental noise erode pair preferences in Zebra Finches: Implications for noise pollution. Animal Behaviour 74:363–368.
- TAYLOR, A. R., AND R. L. KNIGHT. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications 13:951–963.
- TRIMPER, P. G., N. M. STANDEN, L. M. LYE, D. LEMON, T. E. CHUBBS, AND G. W. HUMPHRIES. 1998. Effects of low-level jet aircraft noise on the behaviour of nesting Osprey. Journal of Applied Ecology 35:122–130.
- TRULIO, L. A., AND J. SOKALE. 2008. Foraging shore-bird response to trail use around San Francisco Bay. Journal of Wildlife Management 72: 1775–1780.
- WARCHOL, M. E., AND P. DALLOS. 1989. Neural response to very low-frequency sound in the avian cochlear nucleus. Journal of Comparative Physiology A 166:83–95.

- WARD, D. H., R. A. STEHN, W. P. ERICKSON, AND D. V. DERKSEN. 1999. Response of fall-staging brant and Canada Geese to aircraft overflights in southwestern Alaska. Journal of Wildlife Management 63:373–381.
- Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: It's not just noise. Animal Behaviour 71:491–502.
- Wood, W. E., and S. M. Yezerinac. 2006. Song Sparrow (*Melospiza melodia*) song varies with urban noise. Auk 123:650–659.
- Yodlowski, M. L., M. L. Kreithen, and W. T. Keeton. 1977. Detection of atmospheric infrasound by homing pigeons. Nature 265:725–726.
- Zelick, R. D., and P. M. Narins. 1982. Analysis of acoustically evoked call suppression behaviour in a Neotropical treefrog. Animal Behaviour 30:728–733.
- Zelick, R. D., and P. M. Narins. 1983. Intensity discrimination and the precision of call timing in two species of Neotropical treefrogs. Journal of Comparative Physiology A 153:403–412.