ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

Background Acoustics in Terrestrial Ecology

Clinton D. Francis,[1] Jennifer N. Phillips,[2,3] and Jesse R. Barber[4]

[1]Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, California, USA; email: cdfranci@calpoly.edu

[2]Department of Life Sciences, Texas A&M University–San Antonio, San Antonio, Texas, USA

[3]Current affiliation: School of the Environment, Washington State University, Pullman, Washington, USA

[4]Department of Biological Sciences, Boise State University, Boise, Idaho, USA

Keywords

behavior, community ecology, direct and indirect effects, hearing, masking, soundscapes

Abstract

The way in which terrestrial organisms use the acoustic realm is fundamentally important and shapes behavior, populations, and communities, but how background acoustics, or noise, influence the patterns and processes in ecology is still relatively understudied. In this review, we summarize how background acoustics have traditionally been studied from the signaling perspective, discuss what is known from a receiver's perspective, and explore what is known about population- and community-level responses to noise. We suggest that there are major gaps linking animal physiology and behavior to fitness; that there is a limited understanding of variation in hearing within and across species, especially in the context of real-world acoustic conditions; and that many puzzling responses to noise could be clarified with a community-level lens that considers indirect effects. Failing to consider variation in acoustic conditions, and the many ways organisms use and interact via this environmental dimension, risks a limited understanding of natural systems.

Review in Advance first posted on August 22, 2023. (Changes may still occur before final publication.)

1. INTRODUCTION

Noise: sound or sounds that interfere with the detection, discrimination, or processing of another sound or processing stimuli in another modality

The acoustic environment is of great functional significance to countless animal species (Bradbury & Vehrencamp 2011), but it has been narrowly perceived and studied by ecologists and evolutionary biologists. It is perhaps for this reason that acoustics have historically received relatively minor attention when seeking to explain ecological phenomena spanning distributions of species, interactions among them, or even their assembly into communities. Take, for example, the ecological niche. Ever since the debut of Hutchinson's (1957) *n*-dimensional hypervolume, ecologists have routinely used it to conceptualize and quantify the environmental conditions necessary for species survival. Notwithstanding the attention given to echolocating animals (reviewed in Page & ter Hofstede 2021), acoustic dimensions of the niche are rarely considered. However, research in the past two decades has begun to reveal profound consequences of variation in acoustic conditions across levels of biological organization. Given the immediacy of understanding the costs of human activities for natural systems, the vast majority of this research has focused on how anthropogenic noise influences animals (reviewed in Barber et al. 2010, Kight & Swaddle 2011, Francis & Barber 2013, Shannon et al. 2016). Yet the number of studies focused on natural acoustic conditions is growing, providing a fuller understanding of the role of acoustics in ecological systems (reviewed in Gomes et al. 2021a).

In this review, we articulate how acoustic conditions represent a fundamental niche axis and dimension of the environment that is relevant for organisms that utilize the acoustic realm, and how these effects can cascade through ecological communities and have consequences for organisms that do not sense sound. Although there is a long and rich history involving acoustics in the marine realm (reviewed in Duarte et al. 2021), we focus on terrestrial systems. Additionally, despite the use of acoustics by diverse animal taxa, most research has involved responses to noise by birds specifically (reviewed in Shannon et al. 2016). Our review reflects this strong taxonomic bias. Additional biases in the existing literature limit our current understanding of background acoustics in ecology. Current laboratory-based paradigms for studying hearing do not embrace the complexity of real-world listening conditions that include noise, and they are too narrowly framed by listening for communication rather than listening for other biologically informative acoustic cues.

We have structured this article around three themes we believe are critical for advancing and unifying our understanding of acoustics in ecology and evolution. Following a brief primer on acoustics and noise, we provide an overview of organismal responses to acoustic conditions. We emphasize how the predominant response measured to date, signaling behavior, needs to be explicitly linked to physiology and fitness. We then review what is known about the auditory sensory systems and hearing capabilities of terrestrial organisms, draw relationships between what is known about animals' hearing abilities and their ecology, and ultimately make the case that the dearth of intra- and interspecific information on hearing capabilities is a fundamental obstacle to understanding organismal responses and ecological patterns with respect to acoustic conditions. Finally, we review the state of our understanding of how acoustics influence the structure of communities and interspecific interactions. We point to key research needs at the community level, including a more holistic understanding of interactions among community members to fully understand responses to background acoustics.

2. WHAT IS NOISE?

Noise can have various definitions (reviewed in Brumm & Slabbekoorn 2005, Brumm & Naguib 2009). For the purpose of this review, we consider noise to be any ambient or background sound in a given landscape that interferes with the ability of an animal's auditory system to detect or

discriminate biologically meaningful acoustic cues or signals. Sources of acoustic stimuli in both natural and human-modified landscapes can be complex. Together, these sounds are considered a soundscape. In the context of ecology, behavior, and evolution, researchers are interested in noise that potentially disrupts acoustic signals between senders and receivers, affects animal behavior, and consequently affects ecological processes. Sources of noise can be natural, such as a babbling brook or windblown vegetation, and can include biological sources (reviewed in Gomes et al. 2021a). For instance, although insect or frog calls are signals dispatched for conspecifics, these sources, especially in choruses, serve as noise for other animals. Noise is most commonly used to describe sounds that are human-made or anthropogenic, such as sounds produced by moving vehicles, industrial equipment, airplanes, or stereo systems. Noise produced by humans is often called noise pollution, as it is an additional source of sound on top of nonhuman biotic and abiotic environmental sounds.

There are multiple ways to measure and describe features of noise, or any sound, and we define these terms as they appear in the text. To measure biologically relevant cues and signals, researchers use a variety of microphones and sound recorders. Most ecologists use a sound level meter to measure the amplitude and frequency of background noise. Amplitude can be measured via sound pressure level (SPL), which is similar to how animal ears detect sound. Additionally, every sound has a frequency spectrum, that is, a combination of frequencies at varying amplitudes. Anthropogenic noise often has the highest amplitudes at lower frequencies, whereas most biologically relevant cues and signals occur at higher frequencies (**Figure 1**).

3. THE PREDOMINANCE OF SIGNALING RESPONSES TO NOISE AND THE NEED TO LINK BEHAVIOR TO OTHER RESPONSES

The vast majority of our current knowledge involving animal responses to noise has focused on behavior and, most intensively, on acoustic signaling (reviewed in Shannon et al. 2016). That research involving vocal communication represents the majority of studies thus far is unsurprising for two reasons. First, compared with other responses, vocalizations can be easier to measure, quantify, and compare. Second, there is a long history of research focused on how acoustic signals may be tuned to environmental conditions (i.e., the acoustic adaptation hypothesis), including background noise (e.g., Morton 1975, Ryan & Brenowitz 1985). This history undoubtedly framed the focus of early studies seeking to understand behavioral responses to anthropogenic noise, such as Slabbekoorn & Peet's (2003) study demonstrating a correlation between background urban noise and song minimum frequency in great tits (*Parus major*) and Brumm's (2004) study reporting a positive correlation between background noise and song amplitude in nightingales (*Luscinia megarhynchos*). Indeed, early reviews involving the effects of noise involved only communication (Brumm & Slabbekoorn 2005, Patricelli & Blickley 2006, Brumm & Naguib 2009) and focused predominantly on signaling. This research has had a major impact on our knowledge and has increased awareness in the scientific community that variation in acoustic conditions can strongly influence animals. However, this focus may have prevented us from understanding the role of acoustics in many other aspects of the daily life of animals, which we discuss in Section 4. In the meantime, we provide an overview of the state of our understanding and argue for an integrated approach that explicitly examines links among behavior, physiology, and fitness in the context of noise.

3.1. Signaling Adjustments in Noise

Traditionally defined, communication between animals includes exchanging information between a sender and a receiver (Bradbury & Vehrencamp 2011). Anthropogenic noise represents a novel

Call: an animal's vocalization

Amplitude: the magnitude of sound, synonymous with sound pressure level, often measured in decibels

Frequency: the number of times that a sound pressure wave repeats per unit time, usually seconds, and expressed in hertz; colloquially referred to as pitch

Spectrum, power spectrum, and spectral profile: the distribution of acoustic energy in relation to frequency; in graphical presentations, the spectrum is often plotted as sound intensity against sound frequency

Acoustic adaptation hypothesis: posits that the environmental conditions and habitat features of given areas create a sonic environment that selects for efficient acoustic signals (i.e., less signal degradation and greater signal propagation)

Song: a vocalization often, but not always, used during the breeding season to compete with members of the same sex and to attract mates
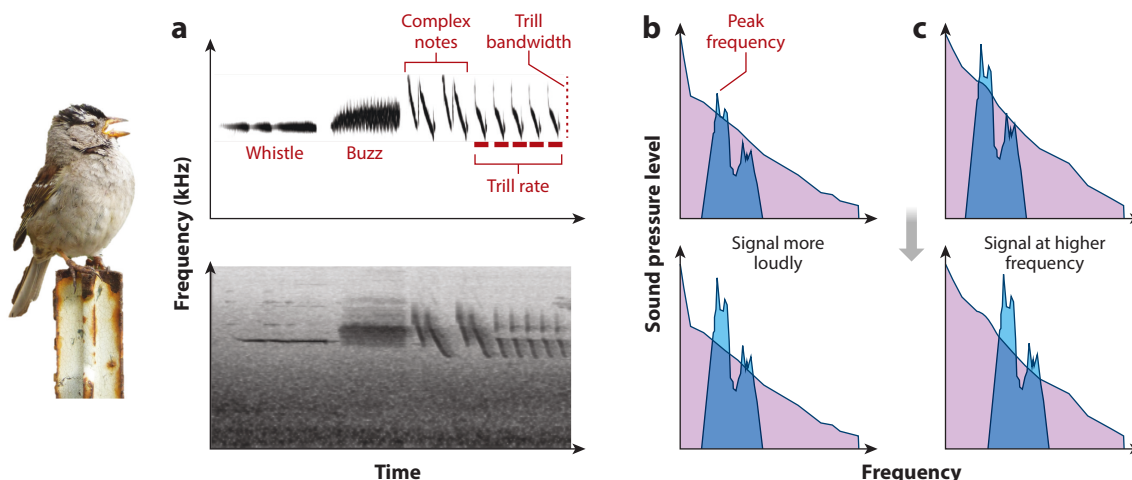
Figure 1

(*a*) A white-crowned sparrow produces a song, visualized here via a spectrogram, which displays sound frequency over time. (*Top*) A band-pass-filtered song, where environmental noise has been filtered out of the recording. (*Bottom*) A white-crowned sparrow song vocalized in a noisy environment where the noise has more energy at lower frequencies (*darker shading*). This pattern of declining energy toward higher frequencies is typical of noise from many natural and anthropogenic sources. Both subpanels display a song consisting of an introductory whistle, a buzz, complex notes, and a trill. One way to compare song or vocal performance among or within individuals singing in different contexts is to measure the trill rate (notes per second) and bandwidth of the trill (its maximum frequency minus its minimum frequency). There is a physical trade-off between the trill rate and the bandwidth such that fast trills typically have a narrow bandwidth and trills with a broad bandwidth are sung more slowly. (*b,c*) White-crowned sparrow song and background noise via power spectra that indicate the sound pressure level across the frequency spectrum. (*Top*) Conditions where the song cannot be detected by a receiver because the signal-to-noise ratio is too small to be audible. (*Bottom*) Two documented responses by signalers to mitigate masking effects by noise. In panel *b* the song is sung with greater intensity, and in panel *c* the song is sung at a higher frequency. In both cases the song adjustments improve the signal-to-noise ratio. White-crowned sparrow photo by Jennifer N. Phillips. Panels *b* and *c* adapted from Gomes et al. (2021a) with permission from Oxford University Press.

Acoustic masking: when noise impairs the ability of an animal to hear a biologically relevant signal or cue; in other words, when a nontarget sound increases the detection or discrimination threshold (measured in decibels) of a target sound

evolutionary pressure that can interfere with communication (Patricelli & Blickley 2006). The loss of information in noise can potentially drive the evolution of vocalizations (Swaddle et al. 2015), following acoustic adaptation theory. Many different animals use vocal communication and have been documented to respond to noise, including invertebrates (Lampe et al. 2014, Orci et al. 2016), anurans (reviewed in Lee et al. 2023), primates (Duarte et al. 2018), bats (e.g., Hage et al. 2013, Bunkley et al. 2015), and birds (reviewed in Slabbekoorn 2013). Although noise can interfere with acoustic communication via several mechanisms (Dominoni et al. 2020), acoustic masking has been the best documented. Acoustic masking occurs when background noise (i.e., nontarget sounds) reduces or eliminates the detection of sounds of interest (Moore 2012). Signaling animals respond to masking in several ways, for instance, by shifting their signal frequencies, amplitude, or temporal patterning.

3.2. Altering Amplitude, Frequency, and Temporal Patterning

Perhaps the most intuitive response to avoid having vocalizations masked by noise is for animals to increase the signal amplitude (**Figure 1b**), known as the Lombard effect (reviewed in Brumm & Zollinger 2011). Increasing signal amplitude in background noise has been documented in mammals, birds, and anurans (Brumm & Zollinger 2011). Compared with other signal features, amplitude is more difficult to measure in wild animals, as the distance and angle of the recorder, motivation of the focal subject, and lateral head movements when signaling can influence

measurements. Thus, signal amplitude change in response to noise is typically studied in the lab. However, using careful field recordings, researchers have documented increasing amplitude with increasing noise and decreasing amplitude with relief from noise (e.g., Brumm 2004; Derryberry et al. 2017, 2020). However, amplitude, like other signal features, can be constrained by body size and other morphological features, and some animals may be incapable of vocalizing more loudly to mitigate acoustic masking. Additionally, changes in amplitude can positively or negatively covary with other signal features, such as the involuntary increase in vocal frequency with vocal amplitude (reviewed in Brumm & Zollinger 2011). Detailed amplitude recordings from microphone arrays or microphones attached to animals in the wild may enable us to fully understand whether and when animals shift the amplitude of their signals in response to noise and whether other signal features change as well.

Frequency alterations to signals in response to noise have been widely documented (reviewed in Slabbekoorn 2013). Well-studied alterations are changes in notes or entire song types vocalized by birds (Slabbekoorn & Peet 2003) (**Figure 1c**) as well as direct shifting of notes upward in minimum frequency and/or down in maximum frequency in birds and anurans (reviewed in Roca et al. 2016). Although some small frequency changes in response to noise may simply reflect an epiphenomenon of the Lombard effect (Nemeth & Brumm 2010) or measurement error (Brumm et al. 2017), mounting evidence suggests that some species can shift signal frequencies through immediate behavioral flexibility in response to noise conditions (e.g., Gross et al. 2010, Gentry et al. 2017). Other changes to frequency may be the result of learning and cultural evolution (e.g., Luther & Baptista 2010, Moseley et al. 2018, Brumm et al. 2021) and/or potential genetic effects (Reichard et al. 2020). However, the evidence is mixed. Both great tits (*P. major*) and zebra finches (*Taeniopygia guttata*) do not sing higher-frequency songs following noise exposure during development (Zollinger et al. 2017, Liu et al. 2021), but white-crowned sparrows (*Zonotrichia leucophrys*) do (Moseley et al. 2018). In the case of white-crowned sparrows, nestlings were collected from the same population in San Francisco and tutored with song types from different populations, indicating that the shift to higher frequencies is a learned behavior rather than explained by genetic differences (Moseley et al. 2018). Indeed, genetic comparisons between populations within close geographic range show little differentiation, despite major song differences (Lipshutz et al. 2017). Thus, the white-crowned sparrow system provides key experimental evidence for song change through cultural evolution and bolsters research showing an increase in minimum frequency over the last 50 years in San Francisco birds through the loss of lower-frequency song types (Luther & Baptista 2010, Luther & Derryberry 2012).

White-crowned sparrows also respond to background acoustics with immediate flexibility. Urban males exposed to experimental noise playback reduce maximum frequencies, concentrating the power of their song; however, rural males do not change their songs when faced with experimental noise playbacks (Gentry et al. 2017), prompting important questions about prior exposure and behavioral flexibility. During the COVID-19 shutdowns, when urban noise levels plummeted with human movement restrictions, white-crowned sparrow song bandwidth increased relative to prepandemic recordings (Derryberry et al. 2020). However, the mechanisms driving the change are unknown. High-performance males could have outcompeted low-performance males in the now quieted soundscape, or males could have exhibited immediate flexibility.

A third mechanism is altering the timing of acoustic communication, such as signaling during quiet temporal windows or signaling more frequently in noisy conditions to increase signal redundancy when conditions for communication are difficult. Examples include the vermilion flycatcher (*Pyrocephalus rubinus*), a species that does not learn song, which exhibits longer song bouts with increased noise (Ríos-Chelén et al. 2013); a tree cricket (*Oecanthus pellucens*) that shortens calls and pauses calling more frequently with elevated noise levels (Orci et al. 2016); and the black-fronted

<div style="float:right; border:1px solid; padding:5px;">
Cultural evolution:
a change in a socially learned behavior within a population, independent of heritable genetic variation or change
</div>

titi monkey (*Callicebus nigrifrons*), which produces shorter vocalizations with altered temporal patterning when exposed to mining noise (Duarte et al. 2018). Ultimately, temporal changes appear widespread and diverse. However, we do not know whether calling more or less, or otherwise altering temporal features of signals, is an adaptive or maladaptive behavior. Insights into when these changes have physiological costs or influence mate attraction will be key to answering this question.

Vocal performance:
a trade-off between sound production rate and spectral bandwidth (minimum to maximum frequency range) in animal vocalizations

3.3. Do Noise-Dependent Signal Changes Matter?

Signal adjustments in noise outwardly appear to be adaptive, but they may have costs. In great tits, females prefer low- and high-frequency male songs equally in control conditions, but with experimental exposure to low-frequency traffic noise, females prefer higher-frequency songs (Halfwerk et al. 2011a). While this finding suggests an adaptive benefit to high-frequency songs, other evidence suggests that males that sing higher-frequency songs suffer greater rates of cuckoldry, presumably because females use song frequency as an indication of male quality (Halfwerk et al. 2011a). Importantly, however, research establishing the link between cuckoldry and male song frequency did not explicitly consider noise. Whether increases in extrapair paternity is indeed a consequence of plastic signal changes in noise needs to be studied directly, as does understanding the role of song frequency on lifetime fitness.

In another example, documented changes in frequency and amplitude (Derryberry et al. 2020) should help white-crowned sparrows transmit songs in noise by concentrating the power of the song within a more narrow frequency. Yet the loss of signal bandwidth (i.e., range of song frequencies) in response to noise decreases vocal performance (Luther et al. 2016), a physically limited measure between bandwidth and trill rate used to assess competitors in this and other trilling species (**Figure 1**). For instance, in quiet parts of San Francisco, male white-crowned sparrows react more aggressively to high- relative to low-performance songs. However, as noise increases, this differentiation disappears and males respond aggressively to both high- and low-performance songs (Phillips & Derryberry 2018). Physically attacking conspecifics indiscriminately could increase energetic costs, cause stress hormone dysregulation, and lead to lost mating opportunities or mating with lower-quality partners, all of which could reduce reproductive success. However, these relationships have not been explicitly tested in the species known to alter songs due to noise.

A small, but growing, body of evidence in birds suggests that noise exposure may have various physiological costs, such as telomere attrition (Injaian et al. 2019) or stress hormone dysregulation (Kleist et al. 2018). Outwardly, many changes to acoustic signals in response to noise should also be linked to physiology via energetics. Although limited by a small sample size, Zollinger et al. (2011) found no evidence that singing more loudly in response to noise increased metabolic costs in zebra finches. Instead, metabolic costs increased in birds exposed to noise whether they were singing or not, suggesting that physiological consequences resulting from noise exposure may not be mediated by altered signals. However, in a follow-up study, the same group found that, compared with those raised in control conditions, zebra finches raised with exposure to traffic noise playback took longer to learn and crystallize their songs and had suppressed immune function. Songs sung as adults were also poor copies of their tutors' songs in comparison to individuals raised in control conditions (Brumm et al. 2021).

More broadly, documented direct effects of noise on fitness have been mixed. For example, great tits have smaller clutch sizes in noise and fewer fledglings (Halfwerk et al. 2011b), but whether these differences are related to the well-documented noise-dependent changes in song in this species is unknown. Similarly, eastern bluebirds (*Sialia sialis*) adjust the frequency and amplitude of vocalizations in noise (Kight & Swaddle 2015), but it is unclear whether these changes

are responsible for lower breeding success in noise (Kight et al. 2012). Huet des Aunay et al. (2014, 2017) provide the closest link to signal changes and fitness consequences. In one study, they demonstrated that low-frequency noise degrades the well-established preference for low-frequency songs among female domestic canaries (Huet des Aunay et al. 2014). In another, they demonstrated that noise that specifically masks male advertisement signals, and not noise in general, reduces female sexual receptivity and decreases female investment through a reduction in clutch size (Huet des Aunay et al. 2017). This reduction in clutch size is supported by a multi-species study that also found noise to reduce clutch size and overall nest success in forest-dwelling birds across North America (Senzaki et al. 2020a). However, as we illustrate in Section 5, relationships between noise exposure and fitness become less straightforward once other species within a community are explicitly considered. For now, we shift away from signalers and explore the consequences of noise from a receiver's perspective.

4. BEYOND THE SIGNALING PARADIGM: USING HEARING TO UNDERSTAND DIRECT RESPONSES

4.1. The Importance of Hearing

With the overwhelming focus on signaling in noise, it is easy to lose sight of the broader role that acoustics can play in the daily lives of animals. A return to first principles is in order to understand the complete function of hearing in animals. Ears originated to extract information from the acoustic environment. The earliest forms of acoustic information were likely adventitious sounds (e.g., movement and breathing sounds) produced by animals and geophysical sounds produced by moving water and wind. This acoustic information reduces uncertainty regarding the presence and spatial location of habitat features, predators, prey, competitors, and mates and thus likely shaped the transduction properties of early hearing organs.

Broad evolutionary patterns indicate that hearing evolved before the capacity to produce sounds for conspecific communication or echolocation [vertebrate inner ear (400 Mya; Popper et al. 1992), orthopteran ears (150–300 Mya; Song et al. 2020), lepidopteran ears (90 Mya; Kawahara et al. 2019)]. Furthermore, all species studied, from vertebrates to invertebrates, hear a broader range of frequencies than they are capable of producing (Popper et al. 1992, Bradbury & Vehrencamp 2011). It seems clear that auditory systems have been and are under selection to detect myriad types of acoustic stimuli.

The fact that hearing continues to function during sleep (Rabat 2007) and hibernation (Lyman & Chatfield 1955) reinforces the importance of auditory surveillance for survival and fitness. Perhaps the most convincing evidence supporting the assertion that hearing is central to animal fitness is that while several species appear to have evolved reduced hearing at certain frequencies (Fullard & Yack 1993, Yager & Svenson 2008), none has completely lost the sense of hearing, in contrast to common losses in other modalities such as vision (Fong et al. 1995). The information available across the acoustic spectrum has selected for the ability to hear an extraordinary range of frequencies, with some species transducing astonishingly quiet sounds.

Human hearing abilities provide a reference point to appreciate the diversity of hearing capabilities among animals. Elephants (*Elephas maximus*) and pigeons can detect sound below the spectral limit of human hearing (human limit ∼20 Hz, infrasound), and a menagerie of animals can hear frequencies above human limits (∼18–20 kHz, ultrasound), including rodents, bats (Geipel et al. 2021), cetaceans, canids, felids, and insects (at least 18 independent origins; ter Hofstede & Ratcliffe 2016, Heffner & Heffner 2018). Within the spectral hearing range of humans, many animals are capable of detecting sounds that are considerably below the threshold of human hearing (0 dB at 1 kHz). For instance, barn owls (*Tyto alba*) have behaviorally measured

by the audiogram are limiting signal or cue detection. Instead, acoustic perception is constrained by the spectrum and level of the background acoustic environment via masking. If the masking noise is in the same frequency band as the target sound, the threshold for detecting the target sound is elevated. This phenomenon is called energetic masking because it relies on the energetic overlap of the nontarget masking sound and target sound within the same frequency band. If, however, the noise is outside of the frequency range of the target sound, the threshold for detecting the target sound will not be elevated (i.e., there will be no energetic masking). Energetic masking can be estimated by calculating the ratio between the sound level of a pure tone to that of noise. The ratio that occurs when the tone becomes inaudible due to masking by noise is called the critical ratio (Scharf 1970). Thus, when a target sound has a signal-to-noise ratio that is smaller than the critical ratio, the target sound cannot be detected.

Critical ratios have been quantified in several mammal and bird species and tend to increase monotonically with frequency at 3 dB per octave (Dooling & Popper 2007). For all species measured, the critical ratio most often changes with frequency but remains constant across a wide range of noise levels. On the basis of averages from 14 bird species investigated to date, a pure tone of 3 kHz must be ~27 dB (±3 dB) above the spectrum level of noise to be detected (Dooling & Popper 2007). Birds, and all groups of animals measured, show substantial variation in their critical ratios (e.g., 21 dB for budgerigar, 32 dB for canary; measured at 3 kHz). The differences in critical ratios between animal species can be larger than the variation in absolute thresholds (i.e., audiograms). To be redundant, the critical ratio is more informative than the audiogram to understand the ability of animals to extract information from noisy acoustic backgrounds. Thus, quantifying this property across species is a powerful, but unrealized, approach to understanding the strength of selection on hearing in noise.

4.3. Auditory Filters and the Upward Spread of Masking

Acoustic perception in vertebrates is shaped most basally by the basilar membrane in the cochlea, where different frequencies resonate strongly at different points along this structure. This tonotopic organization can be modeled by an array of overlapping band-pass filters called auditory filters (Moore 2012). In birds, narrow auditory filters offer greater spectral resolution, whereas wider filters allow greater temporal resolution (Henry et al. 2011), mirroring mathematical constraints found in the computational analysis of sounds by bioacoustics software. Assuming equal energy across frequencies, as noise levels increase, higher frequency regions are affected more by masking than lower frequency regions, because auditory filter bandwidths usually become increasingly wider as frequency rises. Furthermore, background acoustic energy distant from the signal or cue, but still within the same filter, can have some masking effect. Additionally, the effects of masking are asymmetrical, spreading more from low to high frequencies than the reverse (Moore 2012). Thus, lower-frequency acoustic backgrounds (the most common spectral profile) can influence the detection and discrimination of higher-frequency signals and cues. Interestingly, auditory filters in birds are more symmetrical than in mammals (Fontaine et al. 2015), which may be an adaptation to listening in noisy acoustic environments. Understanding the size and shape of auditory filters is an important frontier in modeling how different animals listen in noise and will allow broad predictions of the ecological costs of noise, including disambiguating direct versus indirect effects.

4.4. Hearing Real Sounds in Real Acoustic Backgrounds

Decades of auditory physiological and psychoacoustic research have produced a comparative foundation of how animals hear in noise (reviewed in Dooling & Popper 2007). Yet, essentially

Pure tone: a sound that consists of a single frequency

Critical ratio: ratio of the sound level (measured in decibels) of a tone or target sound to the sound level of noise at the threshold of detection/audibility; a simplified metric that uses fundamental acoustic signals to probe the function of the auditory system

Tonotopic: refers to a pattern in the cochlea and brain where ascending frequencies are spatially represented in adjacent tissues

Band-pass filter: a function that excludes acoustic frequencies above and below set values

everything we know about hearing has been quantified using the laboratory paradigms described above. For instance, the use of tones and white noise (equal energy across frequencies) to understand basic properties such as critical ratios and auditory filter shape allows researchers to cleanly compare hearing abilities between disparately related animals. However, white noise does not exist in nature, and the spectral shape of real acoustic environments can be quite variable (Gomes et al. 2021a).

One operant conditioning study conducted by Lohr et al. (2003) disrupted these common paradigms by using natural bird vocalizations and background noise from roadway traffic to better understand hearing conspecific signals in real-world listening conditions. Relevantly, traffic noise is similar in spectral shape to wind-generated noise in multiple habitats (reviewed in Gomes et al. 2021a). The results supported the idea that bird vocalizations are masked mainly by energy in the spectral region of the signals, not by energy distant from these target auditory objects, and that the effect of different noise types on masking magnitude can be predicted by the spectral band having the greatest signal-to-noise ratio.

Importantly, Lohr et al. (2003) also tested both budgerigars (*Melopsittacus undulatus*) and zebra finches (*T. guttata*) on their ability to not only detect but also discriminate the contact calls of both species. Overall, discrimination thresholds were higher than detection thresholds by an average of ∼3 dB, indicating that it is more difficult to discriminate among sounds in the presence of masking noise than it is to detect the presence of those same stimuli. Also, birds were no better at discriminating their own species-specific calls compared with those of conspecifics in the presence of noise. Yet, different noise profiles (white noise versus traffic noise) did affect discrimination performance (Lohr et al. 2003). These same stage-dependent (i.e., detection or discrimination stage) findings have been found in humans with speech discrimination requiring a higher signal-to-noise ratio than simple detection and comprehension requiring even greater ratios (Moore 2012).

Much work remains to be done to understand how natural signals are masked in natural backgrounds. When signals span multiple auditory filters (which is usually the case) and acoustic backgrounds are complex, more sophisticated models of auditory processing will be necessary to predict the magnitude of masking. Laboratory studies that can carefully measure hearing thresholds within ±1 dB will remain essential for understanding the precise tuning of auditory systems, yet substantial and important progress can be made toward answering this question by studying animal behavior in the field. In particular, a focus on understanding the effect of noise on all stages of perception (i.e., detection, discrimination, and identification/comprehension) is critical for understanding the evolutionary pressures that shape the perception of signals and cues.

4.5. Plasticity in Hearing

Sound transduction abilities are known to decrease with high-intensity sound exposure (Dooling & Popper 2007), but variation in sound transduction abilities between sexes or across seasons is less appreciated. Seasonal changes in auditory processing have been documented in frogs (Goense & Feng 2005) and birds (Lucas et al. 2007). Sex differences exist in Carolina chickadees (*Poecile carolinensis*; Henry & Lucas 2010), and Gall et al. (2013) showed an interaction between sex and season in house sparrows (*Passer domesticus*): Females exhibited enhanced frequency selectivity and reduced temporal resolution during the breeding season, while males showed no seasonal plasticity in auditory processing. The lack of difference in male (versus female) hearing across seasons suggests a more general role for hearing than simply transducing song. In fact, auditory properties seem to be shaped by habitat as well.

In a study of nine New World sparrows (Passeriformes: Passerellidae) that spanned habitat types (open, scrub, and forest) and song types with diverse acoustic features, such as trills, tones,

and other features, Vélez et al. (2015) found that high-frequency song content was unrelated to high-frequency audiogram shape. However, species that produce complex songs showed higher sensitivity to high-frequency sounds than other species tested, indicating a complicated interaction between audiogram shape and signaling strategies. Perhaps most interestingly, scrub species had higher thresholds at low frequencies than species from open or forested habitats and forest species had lower thresholds at higher frequencies than open-habitat species. These results fit poorly with predictions based on how song propagates through different habitats (i.e., the acoustic adaptation hypothesis) and indicate that a signaling-based communication paradigm is too myopic to fully understand how animals hear. This is underscored by the fact that differences in sensitivities at low frequencies persist despite variation in song type. Could variation be related to the background acoustic environment?

That seasonal and sex differences exist in hearing sensitivities, and that variation occurs across broad habitat categories, suggests that the peripheral auditory system is evolutionarily labile and plastic, and thus capable of change to meet different hearing demands. Understanding how pressures to extract information change across animals' annual cycles and habitat affiliations, for example, is an important future research direction. Equally important is knowing how background acoustics shape how animals extract auditory information from noise. For example, do animals that evolved in loud natural acoustic environments, such as near cacophonous rivers and crashing surf, show special auditory adaptations for hearing in noise (i.e., better critical ratios)?

4.6. Background Acoustics as a Selective Force

It is evident that auditory systems are adapted to extract meaningful acoustic information in noisy backgrounds. The sender–receiver matching hypothesis (Gall et al. 2012)—the idea that auditory systems are adapted specifically, and primarily, to receive the acoustic signals that conspecifics produce—has received mixed support (Lohr et al. 2003, Henry et al. 2016). However, it is clear that some acoustic features of signals are reflected in the properties of the peripheral auditory system (Gall et al. 2012).

Many animals have best intensities/frequencies in spectra well outside of their vocalizations. Barn owls, for example, have average thresholds in quiet below 0 dB for frequencies between 1 and 10 kHz, with a lowest mean threshold around −13 dB at 8 kHz, yet their mating call has peak energy at ∼2 kHz (Krumm et al. 2017). Barn owls are specialists at detecting and localizing the movement sounds of their prey, and the ability to phase-lock up to 8 kHz to provide precise interaural time difference cues for sound localization seems to be a primary selective force shaping such auditory responses. Similarly, phyllostomid gleaning bats that passively listen for prey-generated sounds (e.g., walking, rustling, calling) when hunting have audiograms with broad and similar sensitivities between 9 and 70 kHz, even though sonar and communication calls in this group are primarily ultrasonic (Geipel et al. 2021). Interestingly, the echolocation calls of all 12 bat species for which Geipel and colleagues quantified hearing thresholds lie outside of these species' best hearing ranges.

Clearly, selection to detect both signals (e.g., conspecific acoustic signals) and cues (e.g., adventitious sounds, abiotic cues reflective of habitat features) has shaped hearing sensitivities. Background acoustics also exert concomitant selection on hearing properties (reviewed in Gomes et al. 2021a, Lee et al. 2023) and a rich literature has investigated how animals cope with noise. As reviewed in Section 3, animals reduce masking using a variety of approaches, but most documented approaches involve changes to signal properties within a sender to improve auditory function in a receiver. Yet, for acoustic cues—the rustling sounds of a prey animal, the rush of running water indicating riparian habitat—the receiver cannot modify the acoustic target of interest. To

Sender–receiver matching hypothesis: predicts that hearing systems are optimized primarily for acoustic communication to detect and process conspecific vocalizations

Phase lock: an auditory system response in which neurons respond to a particular phase of an ongoing periodic sound wave

Interaural time difference: disparity in time arrival of a sound between two ears

maximize the reception of many sounds, animals must modify basic properties of the auditory system itself.

One way animals can shape the reception of acoustic information is to elevate hearing thresholds in spectral bands that contain chronic high levels of noise where information extraction engenders substantial attentional costs or high risk of false alarms. Swordtail crickets (Gryllidae: Trigoniinae) have reduced acoustic sensitivity (thresholds near 80 dB) to high-frequency sounds (the same frequencies as their communication calls) compared with most other insects tested (thresholds between 40 and 70 dB), perhaps as a protection mechanism against false alarms from the nearly ubiquitous high-frequency katydid noise in their rainforest environments (Römer & Holderied 2020). It is possible that vertebrates might also shield the low-frequency end of their hearing range from similar costs. A transitional evolutionary state in this process might indeed be a mismatch between signal properties and receiver characteristics, as has been shown in a frog (*Amolops torrentis*) where best hearing is at 2 kHz but whose males vocalize above 4 kHz, pushing the signal out of the background stream noise in their habitat (Zhao et al. 2017). Mapping auditory traits across taxa on dated phylogenies will be important to reveal the evolutionary forces structuring hearing. It is also probable that the intense contemporary pressure from low-frequency anthropogenic noise is currently shaping hearing properties across animals.

Most limiting to our understanding of inter- and intraspecific variation in hearing, and the forces that contribute to it, are data from more species and more individuals within species. We predict that quantifying audiogram shapes, critical ratios, and other hearing attributes across gradients of natural and anthropogenic noise exposure will produce important data about the lability of auditory systems in the face of natural and anthropogenic soundscapes. Techniques such as auditory evoked potentials will allow high-throughput quantification of hearing properties. Calibrated acoustic monitors will permit careful characterization of the acoustic environment (e.g., Gomes et al. 2021a), and on-animal recording will enable quantification of received sound characteristics in the wild. Understanding whether and how human-caused noise is altering the reception of acoustic information will allow for a deeper understanding of selective pressures and provide a powerful measure of the strength of contemporary selection.

5. ALTERED COMMUNITIES AND CHANGING INTERACTIONS IN RESPONSE TO NOISE

5.1. Noise Filtering by Traits

Recent studies have provided compelling evidence that ambient noise can filter communities nonrandomly. For instance, low-frequency stream noise appears to shape the distributions of neotropical anurans, such that smaller-bodied frogs with higher-frequency calls tend to reside alongside streams while larger species with lower-frequency calls do not (Vargas-Salinas & Amézquita 2014). Multispecies studies and meta-analyses have revealed similar patterns of habitat filtering based on acoustic signal characteristics for bird distributions in response to anthropogenic noise (Francis 2015, Cardoso et al. 2020). In these cases, the most prominent pattern is that low-frequency noise tends to decrease habitat use most strongly among birds with low-frequency vocalizations, a pattern that has been dubbed the noise filter hypothesis (Cardoso et al. 2020). More recently, an experimental study that implemented landscape-scale playback of sounds of rushing rivers identified a strong link between the strength and direction of species changes in abundance in response to background sounds and vocal frequency (Gomes et al. 2021c). Interestingly, higher-amplitude background noise resulted in a weaker connection with song frequency, indicating that masking of vocalizations may no longer be a primary mechanism above amplitude thresholds. This study not only provides strong experimental evidence matching the observational studies reviewed

above but also suggests that there may be nothing unique about anthropogenic noise that causes shifts in animal distributions. Indeed, from the perspective of a listening or signaling individual animal, the source of noise may matter little (Gomes et al. 2021a).

The abovementioned studies provide considerable evidence that acoustics, whether natural or anthropogenic, can shape species distributions. In some cases, metrics that quantify the acoustic environment are better at explaining distributions than more conventional measures, such as land cover (Kleist et al. 2017). Still, other studies have failed to document shifts. In many studies, acoustics were not measured or were quantified in a manner that may not reflect the hearing capabilities of target species. For example, the authors of a study focused on the effects of traffic noise on bird abundance concluded that the positive relationship between distance from road and bird species richness was likely the result of mortalities due to collisions with vehicles (Summers et al. 2011). Aside from the problem that mortalities were not quantified in order to reach this conclusion, the authors restricted sound measurements to between 0.3 and 2.0 kHz, which fall outside of the range at which many birds communicate and encompass spectra poorly heard by some species (**Figure 2**). Given this failure to quantify sounds in a way that is relevant to the study species, it is unsurprising that the sound metric measured did not explain richness patterns. Of course, explicitly considering responses among each community member in the context of how it uses the acoustic environment may also clarify patterns. For instance, modeling changes in abundance between areas exposed to traffic noise and quiet areas as a function of vocal frequency, while controlling for the influence of body size, mirrors the repeated patterns supporting the noise filter hypothesis (**Figure 3a**).
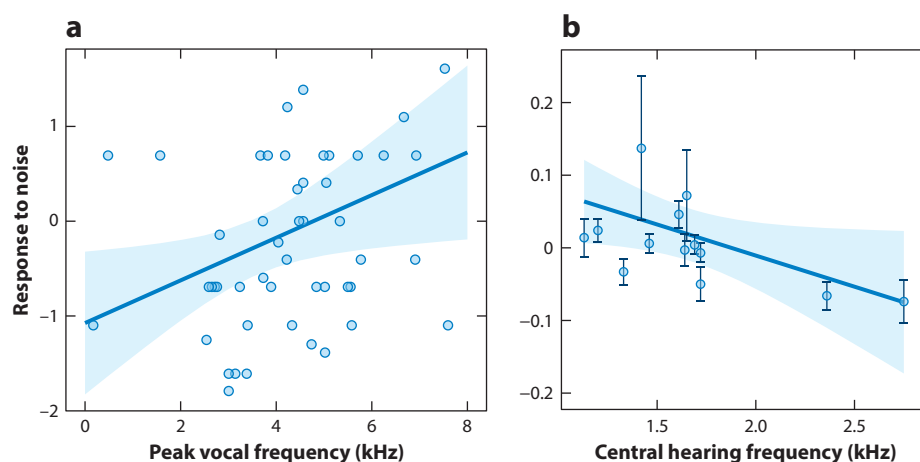

Figure 3

(*a*) After accounting for the influence of mass (natural logarithm), the peak frequency of birdsong is strongly related to distributional response to noise in the Summers et al. (2011) data set (β = 0.22; 95% CI, 0.02, 0.43). Individual point distance from zero on the *y* axis reflects the magnitude of difference in abundances near and far from the roadway. Negative values reflect greater abundance away from the roadway and positive reflect greater abundance near the roadway. (*b*) Central hearing frequency is related to the strength and direction of responses to noise as measured in terms of changes in nonbreeding abundance (β = −0.086; 95% CI, −0.16, −0.01) with increases in anthropogenic noise. Error bars denote the standard error of the effect of noise on response from spatially explicit mixed-effect models that also accounted for several other environmental gradients (for details, see Wilson et al. 2021). Both panels display results from phylogenetic generalized least squares using a consensus phylogeny based on class-wide phylogenies (Jetz et al. 2012) and, in panel *b*, using the standard error of responses in a weighting function to account for variation in the precision of estimates. Data in panel *a* are from Francis (2015). Response data in panel *b* are from Wilson et al. (2021).

Other studies report negligible effects of noise on bird abundance, particularly among grassland birds (e.g., Raynor et al. 2017, Nenninger & Koper 2018). Although it is unclear whether sources of noise in these studies elevated sounds above ambient conditions at a scale relevant to breeding birds, unchanged distributions with respect to noise exposure could be explained by habitat filtering by vocal frequency. Several studies suggest that birds that inhabit grasslands and other open environments have higher-frequency vocalizations than would be expected on the basis of allometric scaling alone (Francis & Wilkins 2021) or in comparison to birds in more densely vegetated environments (Weir et al. 2012; but see Mikula et al. 2021). Whether this vocal trait could explain the absence of responses among grassland birds is an open question; however, high-frequency singing as a preadaptation to areas characterized by noise has support elsewhere. For instance, Hu & Cardoso (2009) found that species that live in urban areas have higher-frequency songs than rural congeners. Still other studies report no change in distributions in response to noise, even among species that outwardly appear to be especially sensitive to changes in acoustics, such as owls (Shonfield & Bayne 2017). Understanding these contrasting responses may come from a more holistic lens in which responses to noise of other interacting species (e.g., competitors and prey) are also explicitly quantified.

Additional studies have sought to explain distributional changes in responses to noise with other traits, such as foraging location, diet, habitat affiliations, or nest type, but evidence is mixed (Francis 2015, Wilson et al. 2021), and the link between vocal characteristics and responses remains the most well documented and robust. This is unsurprising, because vocal traits are directly relevant to how animals use acoustics. However, as we emphasize in Section 4, acoustic communication represents only one way organisms use the sonic world. Given the high reliance of acoustics for passive surveillance for both threats and opportunities, it is likely that better characterization of what organisms can hear, and how well they can hear in difficult listening conditions, will greatly improve our understanding of distributional changes to noise. For instance, hearing sensitivities correlate with the strength and direction of changes in abundance in response to noise among species using bird feeders (**Figure 3b**).

5.2. Indirect Responses to Noise

Direct effects of noise that change the behavior or distribution of one or more species can indirectly influence other species in a community. Indeed, consideration of the community context can help make sense of otherwise puzzling distributions. Take, for example, the pattern of black-chinned hummingbirds (*Archilochus alexandri*) nesting almost exclusively in noise-exposed areas within piñon/juniper woodlands of New Mexico (92% of nests; Francis et al. 2009). Likely interpretations of this apparent preference for nesting in noisy locations emerge only through an understanding that Woodhouse's scrub jay (*Aphelocoma woodhouseii*), a key nest predator in this system, strongly avoids noisy areas (Francis et al. 2009) and that black-chinned hummingbirds are known to exploit areas avoided by jays in other contexts. For instance, Greeney et al. (2015) demonstrate that black-chinned hummingbirds capitalize on enemy-free space by nesting in areas avoided by jays due to predation risk from hawks. The precise cues that hummingbirds use to locate and exploit areas of lower nest predation risk are unknown. However, songbirds regularly parasitized by the brown-headed cowbird (*Molothrus ater*) avoid nesting in areas exposed to cowbird song and call playback during settlement (Forsman & Martin 2009), suggesting that acoustic cues reflective of risk are used by some species for nest site selection. It is probable that black-chinned hummingbirds do the same. However, changes in acoustics could also mislead individuals in settlement decisions (Dominoni et al. 2020). In other communities, predators may not alter distributions in response to noise, but acoustic cues reflective of their presence could be masked to listening prey.
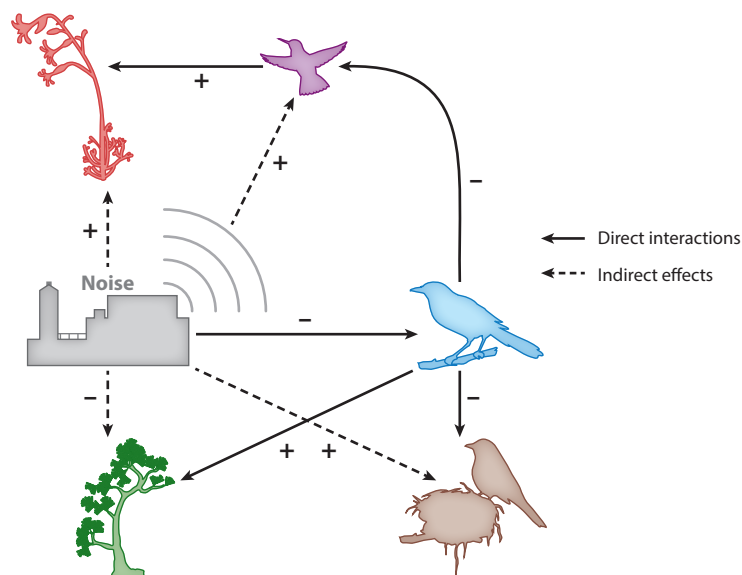
Figure 4

Simplified ecological interaction web demonstrating several indirect effects of noise. Avoidance of noise (*gray*) by Woodhouse's scrub jays (*blue*) increases nest success in songbirds (*brown*) via lower rates of nest predation by jays (Francis et al. 2009) and increases densities of black-chinned hummingbirds (*purple*), which strongly avoid jays when nesting (Greeney et al. 2015). Elevated densities of hummingbirds increase pollination of hummingbird-pollinated plants (*red*) (Francis et al. 2012), yet the avoidance of noise by jays negatively affects recruitment of piñon pine (*green*) (Francis et al. 2012, Phillips et al. 2021), a woodland foundational species that receives seed dispersal services from jays.

Noise-dependent changes in predator distributions or behaviors should have a variety of consequences for communities through changes in top-down control (Estes et al. 2011). For instance, avoidance of noise among Woodhouse's scrub jay, and possibly other opportunistic nest predators, results in increases in songbird nest success with noise exposure (Francis et al. 2009) (**Figure 4**). Elsewhere, field and lab-based studies suggest that noise impairs hunting success among owls and bats (Siemers & Schaub 2011, Bunkley & Barber 2015, Mason et al. 2016, Senzaki et al. 2016), potentially explaining declines in abundance of these taxa with respect to noise (Fröhlich & Ciach 2018, Gomes et al. 2021c). However, both noise avoidance by predators and declines in hunting efficiency could indirectly benefit prey species. Using bill marks on artificial prey (clay caterpillars) as an index of predation on insects among gleaning songbirds, Gomes et al. (2021c) demonstrated that, even after accounting for declines in bird densities in response to experimental playback of natural sounds, attacks on artificial prey declined strongly with increases in background sound levels. One likely explanation for this functional response among foraging birds is an increase in visual vigilance at the expense of foraging. Indeed, as we emphasize in Section 3, listening for a variety of sounds, including those from predators and other threats, may be underappreciated. Lab studies across several species demonstrate that when passive acoustic surveillance is impaired by traffic or natural noise, individual birds respond by increased visual scanning for threats and decreased foraging (Ware et al. 2015, Sweet et al. 2022). An increase in vigilance at the expense of foraging when exposed to noise has also been documented in the dwarf mongoose (*Helogale parvula*), California ground squirrel (*Otospermophilus beecheyi*), and white-tailed prairie dog (*Cynomys leucurus*) (Shannon et al. 2014, Morris-Drake et al.

2017, Le et al. 2019), suggesting that functional responses to noise among these and other species have the potential to indirectly influence a variety of organisms and community processes.

Avoidance of noise among predators can have broader consequences not only for communities exposed to noise but also for communities located in quiet areas, where predators displaced by noise have moved. In their study aiming to understand direct and indirect effects of traffic noise, Senzaki et al. (2020b) measured relative abundance in birds, orthopterans, and odonates among locations near and far from experimental traffic noise playback, plus ambient conditions. Importantly, both birds and orthopterans can hear and use acoustic signals for communication, whereas odonates have no organs for sound detection. Birds were in lower abundance and represented by fewer species in sites near traffic playback, suggestive of direct effects. Interestingly, another prominent pattern was lower abundance or richness of odonates and orthopterans in quieter areas further from noise exposure, suggesting that displacement of birds, or at least shifts in their spatial foraging patterns toward quiet locations, intensified predation pressure on prey species in quiet locations. The extent to which similar patterns could arise in nature due to natural and anthropogenic noise remains unknown; however, there are many plausible scenarios. For instance, in temperate regions, breeding birds may settle adjacent to rivers or roadways in protected areas in spring, when river water levels and traffic on roadways are relatively low. However, in early summer, snowmelt at high elevations and human visitors in protected areas could fundamentally alter acoustics (reviewed in Gomes et al. 2021a). Studies are needed to capitalize on these seasonal fluctuations in acoustic regimes to determine to what extent they cause regular displacement of animals with links to the acoustic world and whether there are consequences for nearby communities where sound levels are lower.

Although less common than for vertebrates, evidence for noise effects among terrestrial arthropods is growing. Studies have documented altered abundance of arthropod families in areas exposed to industrial noise (Bunkley et al. 2017) and changes in arthropod orders with changes to the amplitude and spectral content of experimental noise playback (Gomes et al. 2021b). Although useful in demonstrating potential consequences of noise for invertebrates, these studies were limited by their use of higher-level taxonomy and by the limited state of knowledge regarding hearing abilities across arthropods. For these reasons, the authors could only speculate about the extent to which responses were due to direct or indirect effects of noise. Elsewhere, studies focused on host–parasite interactions have provided additional evidence for indirect effects. Experimental playback of anthropogenic noise and both traffic and ocean surf noise disrupts the ability of eavesdropping frog-biting midges (Diptera: Corethrellidae) to locate Túngara frogs (*Engystomops pustulosus*) (McMahon et al. 2017) and the obligate parasitoid *Ormia ochracea* to locate its host, the variable field cricket (*Gryllus lineaticeps*) (Phillips et al. 2019). In an observational study, McMahon et al. (2017) also documented declines in midge abundance with noise, suggesting that noise creates parasite-free space for hosts. Because parallel research has shown that low-frequency frog calls are most attractive to frog-biting midges (Virgo et al. 2019), anthropogenic noise, which has the highest energy at low frequencies, has the strong potential to broadly shape midge–frog interactions.

The effects of noise exposure can also cascade through responses by animals to affect plants and, potentially, feed back on acoustic conditions. In addition to its role as a key nest predator in the piñon/juniper woodlands of New Mexico, Woodhouse's scrub jay provides the key ecological service of dispersing seeds of the foundational woodland tree, the Colorado piñon pine (*Pinus edulis*). Through a series of experiments and observations, Francis et al. (2012) provided evidence that scrub jay avoidance of noisy areas results in a decline in piñon pine seed dispersal, which is consistent with lower recruitment of this species to the woodland in noisy areas compared with quiet locations (**Figure 4**). Scrub jay avoidance of noise is likely indirectly linked to responses

among other plants via other species. For instance, the black-chinned hummingbird's exploitation of noisy areas results in more visits to, and more pollen transfer among, artificial flowers constructed to mimic the hummingbird-pollinated flower *Ipomopsis aggregata* (Francis et al. 2012) (**Figure 4**). The full range of indirect consequences of noise due to responses of this single species is unknown, as is the persistence of these effects over time. These, however, are dwarfed by the sheer number of ecological changes that likely occur via documented responses among the many other species known to respond to noise in this system (Francis et al. 2009, Bunkley et al. 2017, Kleist et al. 2017).

Phillips et al. (2021) provide a glimpse of the breadth of possibilities and longevity of effects. They resurveyed vegetation 12 years after Francis et al. (2012) and showed that the decline in piñon pine persists in the long term. Importantly, lack of recruitment appears to persist even after the removal of noise for many years, likely a signature of piñon pine's infrequent masting strategy, continued avoidance of formally noisy areas by scrub jays and other seed dispersers, or both. The authors also found other prominent responses to noise by vegetation, such as declines in Utah juniper (*Juniperus osteosperma*) and declines in the evenness of woody vegetation with noise level. Sound level was also a strong predictor of community turnover in animal-pollinated plants, implicating widespread indirect effects not considered previously. Collectively, the few responses documented in this system suggest broad ecological consequences of noise exposure via direct and indirect effects. However, research in additional systems is critical, including those based in urban environments where noise may function additively, synergistically, or antagonistically with other dimensions of human activities.

Although it has been more than 10 years since the first evidence for indirect effects of noise was published (Francis et al. 2009, 2012), relatively little research has followed. Those researchers who have adopted a community-level lens have documented widespread, and sometimes surprising, responses. Many other studies provide strong evidence that community-level consequences are likely, but they remain untested empirically. To fully understand the role of acoustics in structuring ecological systems, more ecologists need to consider the role of noise, whether natural or anthropogenic, in their own study systems.

6. CONCLUSION

The weight of evidence points to acoustic conditions as an underappreciated dimension of the environment that alters animal behavior and shapes animal and plant distributions and communities through a variety of pathways. However, our understanding of noise as a structuring force has been limited by a narrow focus on conspecific communication and signaling in general; a rudimentary understanding of hearing across animals, especially in the context of real acoustic conditions; and a near absence of research involving indirect consequences of noise exposure. Incorporating this environmental dimension more broadly in ecology and evolution will provide stronger inference for both basic and applied questions. With that in mind, we list several areas of research ripe for attention in the Future Issues section. A renewed focus on animal sensory worlds will help refine how we assess drivers in natural systems, expanding our lens past those limited by our own sensory biases.

FUTURE ISSUES

1. Does noise select for a consistent phenotype across species?
2. Are acoustic thresholds and critical ratios a target of selection within and across species?
3. Does noise alone have consequences for population dynamics?

4. How do animals move through noise-fragmented landscapes?

5. How does noise affect ecosystem engineers and animal mutualists, and what are the cascading consequences of these effects?

6. Will a focus on noise as a continuous variable rather than quiet/noisy treatment categories help identify nonlinear patterns and thresholds?

7. Will future research clarify the relative importance of energetic versus informational masking? Informational masking has been demonstrated in humans in whom central processing deficits occur even when the spectra of the signal and noise do not overlap. How common is it in animals?

8. Does hearing loss via temporary threshold shifts occur in nature? What are the ecological consequences?

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

LITERATURE CITED

Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* 25:180–89

Bradbury JW, Vehrencamp SL. 2011. *Principles of Animal Communication*. Sunderland, MA: Sinauer. 2nd ed.

Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* 73:434–40

Brumm H, Goymann W, Derégnaucourt S, Geberzahn N, Zollinger SA. 2021. Traffic noise disrupts vocal development and suppresses immune function. *Sci. Adv.* 7:eabe2405

Brumm H, Naguib M. 2009. Environmental acoustics and the evolution of bird song. *Adv. Study Behav.* 40:1–33

Brumm H, Slabbekoorn H. 2005. Acoustic communication in noise. *Adv. Study Behav.* 35:151–209

Brumm H, Zollinger SA. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behavior* 148:1173–98

Brumm H, Zollinger SA, Niemelä PT, Sprau P. 2017. Measurement artifacts lead to false positives in the study of birdsong in noise. *Methods Ecol. Evol.* 8:1617–25

Bunkley JP, Barber JR. 2015. Noise reduces foraging efficiency in pallid bats (*Antrozous pallidus*). *Ethology* 121:1116–21

Bunkley JP, McClure CJW, Kawahara AY, Francis CD, Barber JR. 2017. Anthropogenic noise changes arthropod abundances. *Ecol. Evol.* 7:2977–85

Bunkley JP, McClure CJW, Kleist NJ, Francis CD, Barber JR. 2015. Anthropogenic noise alters bat activity levels and echolocation calls. *Glob. Ecol. Conserv.* 3:62–71

Cardoso GC, Klingbeil BT, La Sorte FA, Lepczyk CA, Fink D, Flather CH. 2020. Exposure to noise pollution across North American passerines supports the noise filter hypothesis. *Glob. Ecol. Biogeogr.* 29:1430–34

Derryberry EP, Gentry K, Derryberry GE, Phillips JN, Danner RM, et al. 2017. White-crowned sparrow males show immediate flexibility in song amplitude but not in song minimum frequency in response to changes in noise levels in the field. *Ecol. Evol.* 7:4991–5001

Derryberry EP, Phillips JN, Derryberry GE, Blum MJ, Luther D. 2020. Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science* 370:575–79

Dominoni DM, Halfwerk W, Baird E, Buxton RT, Fernández-Juricic E, et al. 2020. Why conservation biology can benefit from sensory ecology. *Nat. Ecol. Evol.* 4:502–11

Dooling RJ, Popper AN. 2007. *The effects of highway noise on birds*. Rep., Jones & Stokes Assoc., Sacramento, CA. **https://www.dot.ca.gov/hq/env/bio/files/caltrans_birds_10-7-2007b.pdf**

Duarte CM, Chapuis L, Collin SP, Costa DP, Devassy RP, et al. 2021. The soundscape of the Anthropocene ocean. *Science* 371:eaba4658

Duarte M, Kaizer M, Young R, Rodrigues M, Sousa-Lima R. 2018. Mining noise affects loud call structures and emission patterns of wild black-fronted titi monkeys. *Primates* 59:89–97

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, et al. 2011. Trophic downgrading of Planet Earth. *Science* 333:301–306

Fong DW, Kane TC, Culver DC. 1995. Vestigialization and loss of nonfunctional characters. *Annu. Rev. Ecol. Syst.* 26:249–68

Fontaine B, Köppl C, Peña JL. 2015. Reverse correlation analysis of auditory-nerve fiber responses to broadband noise in a bird, the barn owl. *J. Assoc. Res. Otolaryngol.* 16:101–19

Forsman JT, Martin TE. 2009. Habitat selection for parasite-free space by hosts of parasitic cowbirds. *Oikos* 118:464–70

Francis CD. 2015. Vocal traits and diet explain avian sensitivities to anthropogenic noise. *Glob. Change Biol.* 21:1809–20

Francis CD, Barber JR. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Front. Ecol. Environ.* 11:305–13

Francis CD, Kleist NJ, Ortega CP, Cruz A. 2012. Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. *Proc. R. Soc. B* 279:2727–35

Francis CD, Ortega CP, Cruz A. 2009. Noise pollution changes avian communities and species interactions. *Curr. Biol.* 19:1415–19

Francis CD, Wilkins MR. 2021. Testing the strength and direction of selection on vocal frequency using metabolic scaling theory. *Ecosphere* 12:e23733

Fröhlich A, Ciach M. 2018. Noise pollution and decreased size of wooded areas reduces the probability of occurrence of tawny owl *Strix aluco*. *Ibis* 160:634–46

Fullard JH, Yack JE. 1993. The evolutionary biology of insect hearing. *Trends Ecol. Evol.* 8:248–52

Gall MD, Brierley LE, Lucas JR. 2012. The sender–receiver matching hypothesis: support from the peripheral coding of acoustic features in songbirds. *J. Exp. Biol.* 215:3742–51

Gall MD, Salameh TS, Lucas JR. 2013. Songbird frequency selectivity and temporal resolution vary with sex and season. *Proc. R. Soc. B* 280:20122296

Geipel I, Lattenkamp EZ, Dixon MM, Wiegrebe L, Page RA. 2021. Hearing sensitivity: an underlying mechanism for niche differentiation in gleaning bats. *PNAS* 118:e2024943118

Gentry KE, Derryberry EP, Danner RM, Danner JE, Luther DA. 2017. Immediate signaling flexibility in response to experimental noise in urban, but not rural, white-crowned sparrows. *Ecosphere* 8:e01916

Goense JB, Feng AS. 2005. Seasonal changes in frequency tuning and temporal processing in single neurons in the frog auditory midbrain. *J. Neurobiol.* 65:22–36

Gomes DG, Francis CD, Barber JR. 2021a. Using the past to understand the present: coping with natural and anthropogenic noise. *BioScience* 71:223–34

Gomes DG, Toth CA, Bateman CC, Francis CD, Kawahara AY, Barber JR. 2021b. Experimental river noise alters arthropod abundance. *Oikos* 130:2001–14

Gomes DG, Toth CA, Cole H, Francis CD, Barber JR. 2021c. Phantom rivers filter birds and bats by acoustic niche. *Nat. Commun.* 12:3029

Greeney HF, Meneses MR, Hamilton CE, Lichter-Marck E, Mannan RW, et al. 2015. Trait-mediated trophic cascade creates enemy-free space for nesting hummingbirds. *Sci. Adv.* 1:e1500310

Gross K, Pasinelli G, Kunc HP. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *Am. Nat.* 176:456–64

Hage SR, Jiang T, Berquist SW, Feng J, Metzner W. 2013. Ambient noise induces independent shifts in call frequency and amplitude within the Lombard effect in echolocating bats. *PNAS* 110:4063–68

Halfwerk W, Bot S, Buikx J, van der Velde M, Komdeur J, et al. 2011a. Low-frequency songs lose their potency in noisy urban conditions. *PNAS* 108:14549–54

Halfwerk W, Holleman LJM, Lessells CM, Slabbekoorn H. 2011b. Negative impact of traffic noise on avian reproductive success. *J. Appl. Ecol.* 48:210–19

Heffner HE, Heffner RS. 2018. The evolution of mammalian hearing. *AIP Conf. Proc.* 1965:130001

Henry KS, Gall MD, Bidelman GM, Lucas JR. 2011. Songbirds tradeoff auditory frequency resolution and temporal resolution. *J. Comp. Physiol. A* 197:351–59

Henry KS, Gall MD, Vélez A, Lucas JR. 2016. Avian auditory processing at four different scales: variation among species, seasons, sexes, and individuals. In *Psychological Mechanisms in Animal Communication*, ed. MA Bee, CT Miller, pp. 17–55. Berlin: Springer

Henry KS, Lucas JR. 2010. Auditory sensitivity and the frequency selectivity of auditory filters in the Carolina chickadee, *Poecile carolinensis*. *Anim. Behav.* 80:497–507

Hu Y, Cardoso GC. 2009. Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behav. Ecol.* 20:1268–73

Huet des Aunay G, Grenna M, Slabbekoorn H, Nicolas P, Nagle L, et al. 2017. Negative impact of urban noise on sexual receptivity and clutch size in female domestic canaries. *Ethology* 123:843–53

Huet des Aunay G, Slabbekoorn H, Nagle L, Passas F, Nicolas P, Draganoiu TI. 2014. Urban noise undermines female sexual preferences for low-frequency songs in domestic canaries. *Anim. Behav.* 87:67–75

Hutchinson GE. 1957. Concluding remarks. In *Proceedings of the 22nd Cold Spring Harbor Symposia on Quantitative Biology*, pp. 415–27. Cold Spring Harbor, NY: Cold Spring Harbor Lab. Press

Injaian AS, Gonzalez-Gomez PL, Taff CC, Bird AK, Ziur AD, et al. 2019. Traffic noise exposure alters nestling physiology and telomere attrition through direct, but not maternal, effects in a free-living bird. *Gen. Comp. Endocrinol.* 276:14–21

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* 491:444–48

Kawahara AY, Plotkin D, Espeland M, Meusemann K, Toussaint EF, et al. 2019. Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. *PNAS* 116:22657–63

Kight CR, Saha MS, Swaddle JP. 2012. Anthropogenic noise is associated with reductions in the productivity of breeding eastern bluebirds (*Sialia sialis*). *Ecol. Appl.* 22:1989–96

Kight CR, Swaddle JP. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecol. Lett.* 14:1052–61

Kight CR, Swaddle JP. 2015. Eastern bluebirds alter their song in response to anthropogenic changes in the acoustic environment. *Integr. Comp. Biol.* 55:418–31

Kleist NJ, Guralnick RP, Cruz A, Francis CD. 2017. Sound settlement: Noise surpasses land cover in explaining breeding habitat selection of secondary cavity-nesting birds. *Ecol. Appl.* 27:260–73

Kleist NJ, Guralnick RP, Cruz A, Lowry CA, Francis CD. 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *PNAS* 115:E648–57

Krumm B, Klump G, Köppl C, Langemann U. 2017. Barn owls have ageless ears. *Proc. R. Soc. B* 284:20171584

Lampe U, Reinhold K, Schmoll T. 2014. How grasshoppers respond to road noise: developmental plasticity and population differentiation in acoustic signalling. *Funct. Ecol.* 28:660–68

Le M-LT, Garvin CM, Barber JR, Francis CD. 2019. Natural sounds alter California ground squirrel, *Otospermophilus beecheyi*, foraging, vigilance and movement behaviors. *Anim. Behav.* 157:51–60

Lee N, Vélez A, Bee M. 2023. Behind the mask(ing): how frogs cope with noise. *J. Comp. Physiol. A* 209:47–66

Lipshutz SE, Overcast IA, Hickerson MJ, Brumfield RT, Derryberry EP. 2017. Behavioural response to song and genetic divergence in two subspecies of white-crowned sparrows (*Zonotrichia leucophrys*). *Mol. Ecol.* 26:3011–27

Liu Y, Zollinger SA, Brumm H. 2021. Chronic exposure to urban noise during the vocal learning period does not lead to increased song frequencies in zebra finches. *Behav. Ecol. Sociobiol.* 75:3

Lohr B, Wright TF, Dooling RJ. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Anim. Behav.* 65:763–77

Lucas JR, Freeberg TM, Long GR, Krishnan A. 2007. Seasonal variation in avian auditory evoked responses to tones: a comparative analysis of Carolina chickadees, tufted titmice, and white-breasted nuthatches. *J. Comp. Physiol. A* 193:201–15

Luther DA, Baptista L. 2010. Urban noise and the cultural evolution of bird songs. *Proc. R. Soc. B* 277:469–73

Luther DA, Derryberry EP. 2012. Birdsongs keep pace with city life: Changes in song over time in an urban songbird affects communication. *Anim. Behav.* 83:1059–66

Luther DA, Phillips J, Derryberry EP. 2016. Not so sexy in the city: Urban birds adjust songs to noise but compromise vocal performance. *Behav. Ecol.* 27:332–40

Lyman CP, Chatfield PO. 1955. Physiology of hibernation in mammals. *Physiol. Rev.* 35:403–25

Mason JT, McClure CJW, Barber JR. 2016. Anthropogenic noise impairs owl hunting behavior. *Biol. Conserv.* 199:29–32

McMahon TA, Rohr JR, Bernal XE. 2017. Light and noise pollution interact to disrupt interspecific interactions. *Ecology* 98:1290–99

Mikula P, Valcu M, Brumm H, Bulla M, Forstmeier W, et al. 2021. A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. *Ecol. Lett.* 24:477–86

Moore BC. 2012. *An Introduction to the Psychology of Hearing.* Leiden, Neth.: Brill

Morris-Drake A, Bracken AM, Kern JM, Radford AN. 2017. Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls. *Environ. Pollut.* 223:476–83

Morton ES. 1975. Ecological sources of selection on avian sounds. *Am. Nat.* 109:17–34

Moseley DL, Derryberry GE, Phillips JN, Danner JE, Danner RM, et al. 2018. Acoustic adaptation to city noise through vocal learning by a songbird. *Proc. R. Soc. B* 285:20181356

Nemeth E, Brumm H. 2010. Birds and anthropogenic noise: Are urban songs adaptive? *Am. Nat.* 176:465–75

Nenninger HR, Koper N. 2018. Effects of conventional oil wells on grassland songbird abundance are caused by presence of infrastructure, not noise. *Biol. Conserv.* 218:124–33

Orci KM, Petróczki K, Barta Z. 2016. Instantaneous song modification in response to fluctuating traffic noise in the tree cricket *Oecanthus pellucens*. *Anim. Behav.* 112:187–94

Page RA, ter Hofstede HM. 2021. Sensory and cognitive ecology of bats. *Annu. Rev. Ecol. Evol. Syst.* 52:541–62

Patricelli GL, Blickley JL. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* 123:639–49

Phillips JN, Derryberry EP. 2018. Urban sparrows respond to a sexually selected trait with increased aggression in noise. *Sci. Rep.* 8:7505

Phillips JN, Ruef SK, Garvin CM, Le M-LT, Francis CD. 2019. Background noise disrupts host–parasitoid interactions. *R. Soc. Open Sci.* 6:190867

Phillips JN, Termondt SE, Francis CD. 2021. Long-term noise pollution affects seedling recruitment and community composition, with negative effects persisting after removal. *Proc. R. Soc. B* 288:20202906

Popper AN, Platt C, Edds PL. 1992. Evolution of the vertebrate inner ear: an overview of ideas. In *The Evolutionary Biology of Hearing*, ed. DB Webster, AN Popper, RR Fay, pp. 49–57. Berlin: Springer

Rabat A. 2007. Extra-auditory effects of noise in laboratory animals: the relationship between noise and sleep. *J. Am. Assoc. Lab. Anim. Sci.* 46:35–41

Raynor EJ, Whalen CE, Brown MB, Powell LA. 2017. Grassland bird community and acoustic complexity appear unaffected by proximity to a wind energy facility in the Nebraska Sandhills. *Condor Ornithol. Appl.* 119:484–96

Reichard DG, Atwell JW, Pandit MM, Cardoso GC, Price TD, Ketterson ED. 2020. Urban birdsongs: Higher minimum song frequency of an urban colonist persists in a common garden experiment. *Anim. Behav.* 170:33–41

Ríos-Chelén AA, Quirós-Guerrero E, Gil D, Macías Garcia C. 2013. Dealing with urban noise: Vermilion flycatchers sing longer songs in noisier territories. *Behav. Ecol. Sociobiol.* 67:145–52

Roca IT, Desrochers L, Giacomazzo M, Bertolo A, Bolduc P, et al. 2016. Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behav. Ecol.* 27:1269–74

Römer H, Holderied M. 2020. Decision making in the face of a deadly predator: High-amplitude behavioral thresholds can be adaptive for rainforest crickets under high background noise levels. *Philos. Trans. R. Soc. B* 375:20190471

Ryan MJ, Brenowitz EA. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* 126:87–100

Scharf B. 1970. Critical bands. In *Foundations of Modern Auditory Theory*, ed. JV Tobias, Vol. 1, pp. 159–202. New York: Academic

Senzaki M, Barber JR, Phillips JN, Carter NH, Cooper CB, et al. 2020a. Sensory pollutants alter bird phenology and fitness across a continent. *Nature* 587:605–9

Senzaki M, Kadoya T, Francis CD. 2020b. Direct and indirect effects of noise pollution alter biological communities in and near noise-exposed environments. *Proc. R. Soc. B* 287:20200176

Senzaki M, Yamaura Y, Francis CD, Nakamura F. 2016. Traffic noise reduces foraging efficiency in wild owls. *Sci. Rep.* 6:30602

Shannon G, Angeloni LM, Wittemyer G, Fristrup KM, Crooks KR. 2014. Road traffic noise modifies behavior of a keystone species. *Anim. Behav.* 94:135–41

Shannon G, McKenna MF, Angeloni LM, Crooks KR, Fristrup KM, et al. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol. Rev. Camb. Philos. Soc.* 91:982–1005

Shonfield J, Bayne E. 2017. The effect of industrial noise on owl occupancy in the boreal forest at multiple spatial scales. *Avian Conserv. Ecol.* 12:13

Siemers BM, Schaub A. 2011. Hunting at the highway: Traffic noise reduces foraging efficiency in acoustic predators. *Proc. R. Soc. B* 278:1646–52

Slabbekoorn H. 2013. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* 85:1089–99

Slabbekoorn H, Peet M. 2003. Birds sing at a higher pitch in urban noise. *Nature* 424:267–67

Song H, Béthoux O, Shin S, Donath A, Letsch H, et al. 2020. Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. *Nat. Commun.* 11:4939

Summers PD, Cunnington GM, Fahrig L. 2011. Are the negative effects of roads on breeding birds caused by traffic noise? *J. Appl. Ecol.* 48:1527–34

Swaddle JP, Francis CD, Barber JR, Cooper CB, Kyba CM, et al. 2015. A framework to assess evolutionary responses to anthropogenic light and sound. *Trends Ecol. Evol.* 30:550–60

Sweet K, Sweet B, Gomes D, Francis C, Barber J. 2022. Natural and anthropogenic noise increase vigilance and decrease foraging behaviors in song sparrows. *Behav. Ecol.* 33:288–97

ter Hofstede HM, Ratcliffe JM. 2016. Evolutionary escalation: the bat–moth arms race. *J. Exp. Biol.* 219:1589–602

Vargas-Salinas F, Amézquita A. 2014. Abiotic noise, call frequency and stream-breeding anuran assemblages. *Evol. Ecol.* 28:341–59

Vélez A, Gall MD, Fu J, Lucas JR. 2015. Song structure, not high-frequency song content, determines high-frequency auditory sensitivity in nine species of New World sparrows (Passeriformes: Emberizidae). *Funct. Ecol.* 29:487–97

Virgo J, Ruppert A, Lampert KP, Grafe TU, Eltz T. 2019. The sound of a blood meal: acoustic ecology of frog-biting midges (*Corethrella*) in lowland Pacific Costa Rica. *Ethology* 125:465–75

Ware HE, McClure CJW, Carlisle JD, Barber JR. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *PNAS* 112:12105–9

Weir JT, Wheatcroft DJ, Price TD. 2012. The role of ecological constraint in driving the evolution of avian song frequency across a latitudinal gradient. *Evolution* 66:2773–83

Wilson AA, Ditmer MA, Barber JR, Carter NH, Miller ET, et al. 2021. Artificial night light and anthropogenic noise interact to influence bird abundance over a continental scale. *Glob. Change Biol.* 27:3987–4004

Yager DD, Svenson GJ. 2008. Patterns of praying mantis auditory system evolution based on morphological, molecular, neurophysiological, and behavioral data. *Biol. J. Linn. Soc.* 94:541–68

Zhao L, Wang J, Yang Y, Zhu B, Brauth SE, Tang Y, Cui J. 2017. An exception to the matched filter hypothesis: a mismatch of male call frequency and female best hearing frequency in a torrent frog. *Ecol. Evol.* 7:419–28

Zollinger SA, Goller F, Brumm H. 2011. Metabolic and respiratory costs of increasing song amplitude in zebra finches. *PLOS ONE* 6:e23198

Zollinger SA, Slater PJ, Nemeth E, Brumm H. 2017. Higher songs of city birds may not be an individual response to noise. *Proc. R. Soc. B* 284:20170602

Review in Advance first posted on
August 22, 2023. (Changes may
still occur before final publication.)