

Soundscape Ecology of the Anthropocene

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Noisy human activities change natural soundscapes. This not only affects the health of people but also acoustic communication in animals.

Living the Anthropocene

“A picture is worth more than a thousand words and a soundscape is worth more than a thousand pictures” (Krause, 2013), but can we still enjoy those pictures today? It is a moment of joy for many to hear the first birds starting the dawn chorus in the dim light on a calm day in spring. It is the serenity of a quiet landscape gradually emerging from darkness and morning haze, against which the first bubbling notes and warbling melodies stand out so beautifully. However, today, many people who go outside early enough will likely hear something else: cars and trucks from nearby highways, noisy generators or air conditioners, street cleaners out sweeping the streets, construction sites gearing up for the day, or trains and planes transporting people to their destinations.

The Anthropocene is the current geological era, where natural habitats are increasingly affected and modified by the presence of human activities such as those that produce sound (McKinney, 2002; Slabbekoorn and Ripmeester, 2008). Indeed, many human activities are noisy and often cause a prominent acoustic modification of habitat, which may affect humans and animals alike (Barber et al., 2010; Brooks et al., 2014). Natural soundscapes without an acoustic trace of human presence have become increasingly difficult to find (Mennitt et al., 2015). Does it matter that people now only rarely experience moments of relative quiet? Does it matter to the birds that their environment has become noisier, often when they are at their daily peak of singing activity? Well, yes it does.

We know that people can get ill as a result of noisy conditions (Passchier-Vermeer and Passchier, 2000). The plethora of industrial and urban sounds or just one specific buzz or hum can annoy people and cause heart problems, sleeping disturbance, and all sorts of stress symptoms and hearing deficits. Moreover, human performance in precise tasks that require focus declines with rising levels of ambient sound. It has also been shown that cognitive development is impaired for children in schools near noisy airports.

How noisy conditions affect animals may be more difficult to grasp. However, birds are well studied and provide insights into how noise may impact their behavior and communication (Francis and Barber, 2013; Wiley, 2015), and how it may affect stress physiology, survival, and reproduction (Halfwerk and Slabbekoorn, 2014). All of this may translate into impacts on avian populations, communities, and ecosystems (Francis et al., 2009) and may provide critical understanding about how increased noise levels in the environment affect other species, from fishes to humans.

In this article, I focus on the scientific discipline of soundscape ecology (Slabbekoorn, 2004; Pijanowski et al., 2011) and the role of sound in the natural world of animals. I provide particular examples of insight gained from studies on birds. A picture of remarkable and informative acoustic diversity, shaped by natural se-

lection over an evolutionary time scale, will emerge. Unfortunately, this picture is being challenged by noise pollution, which is emerging over a much more rapid ecological time scale (Slabbekoorn and Ripmeester, 2008).

I start by addressing how animals have evolved in the context of their environment and how they are perceived by other animals who can affect their survival and reproductive success. This sets the stage for understanding how birds deal with the natural soundscape in which they live, through evolution and natural selection and through learning from experience and adjusting their behaviors accordingly. This clarifies the intricate acoustic relationship animals have with their environment that is now being modified in the industrializing and urbanizing world.

From Camouflage to Perceptual Contrast

The snow-white fur of an arctic hare (*Lepus arcticus*) makes it hard to find in a snow-covered landscape, but it is easily detected in a green meadow (Figure 1). This is true in general: if the spectrum of an object matches its background, it is well camouflaged, and if not, it stands out. Patterns of foreground-background matching have often evolved over time through natural selection when it is advantageous to not be seen, in both predators and prey. However, if it is beneficial for an animal to be seen, the opposite can be expected. For example, if transmitting a signal to conspecifics determines success in mate attraction, it is better to have contrasting rather than matching color spectra. The bright plumage and skin of many birds and frogs often stand out dramatically against their typically green and brown surroundings for this reason.

These phenomena of camouflage and perceptual contrast apply to audition as well as to vision (Figure 1). Sounds can blend in or stand out against the ambient background similar to visual objects (Handel, 1989; Endler, 1993). Acoustic events can match the ambient background “noise” in spectra, amplitude, and temporal patterns, thereby going unnoticed. In contrast, acoustic events can also have features that increase the perceptual salience of sounds relative to the ambient conditions, such as different frequencies or timing, high signal-to-noise ratios, and distinct temporal patterns.

Whether we find patterns of camouflage or contrast in the acoustic mode of the natural world can usually be explained by natural selection (Brumm and Slabbekoorn, 2005). Sounds that are not produced with a purpose (e.g., just as a

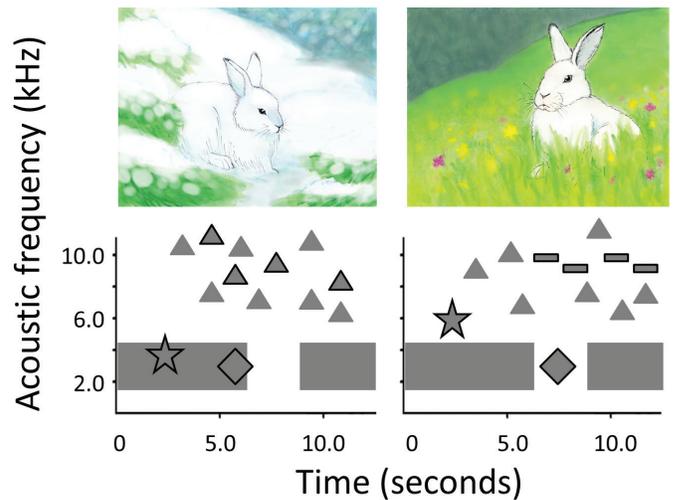


Figure 1. Top: visual camouflage and contrast illustrated with a snow hare in a snow-white landscape and against a green background after snow melt. **Bottom:** perceptual salience of sounds (see Handel, 1989; Endler, 1993) explained in two schematic spectrograms. **Left:** examples of how signals can blend into their acoustic surroundings. **Right:** signals that stand out against the ambient soundscape. **Stars** indicate how spectral overlap or deviation between signal and ambient noise may cause or avoid masking; **diamonds** reflect how timing can affect masking; **triangles** illustrate how similarity in shape and pattern make it hard to detect the presence of target sounds among nontarget sounds. The distinct repetitive pattern of the flattened squares of two different frequencies shows how sounds can also stand out against that background of triangles.

by-product of moving around) could become cues to third parties such as potential predators and prey. Consequently, such sounds have often become soft and low contrast so as not to be detected. Examples include the rustling sounds of potential prey insects and birds. Another example is hunting owls, which have evolved wing morphologies and flight skills that are very silent as the owls attack prey. If being heard has an advantage, evolution can take another direction; doves taking flight on alarm or snipes performing aerial acrobatics in nocturnal displays have evolved wing beats and special feathers to generate sounds during flight with their wings.

Some sounds (e.g., begging and contact calls) are usually relatively faint because they are only meant to be heard by a few nearby receivers. If the sounds were louder, they could become cues to third parties with negative consequences for the vocal animal. However, there are also examples of loud and raucous calls as well as vocal courtship interactions of high amplitude and intensity, which shows that natural selection pressures may vary across species and context. The specific evolutionary outcome is often the result of a trade-off between the costs and benefits of being detected, localized, and evaluated as worthwhile by different animals looking for prey or partners (Read et al., 2014).

Evolutionary Change

Acoustic signals can change over evolutionary time if variation in signal design is genetically determined, and it impacts lifetime reproductive success and, as a consequence, the genetic contribution of the signaler to the next generation (Slabbekoorn, 2013). Birds that sing songs that are detected easily or that convey acoustic details clearly should benefit by surviving longer or attracting more or better mates earlier or with less effort than birds that do not sing as well. This is the interpretation, for example, that helps explain the similarities in alarm calls of many songbirds, which are high-pitched long notes that fade in and out smoothly. In this way, callers warn each other about danger in the air. At the same time, the acoustic design of the signals is such that they are hard to hear and localize, making it difficult for predators to find the signaler. Sounds that are easier to detect and localize would obviously affect survival negatively.

The loud crows of roosters (*Gallus domesticus*), the elaborate songs of nightingales (*Luscinia megarhynchos*), and the varied trills of canaries (*Serinus canaria*) are all also thought to be the result of evolutionary adaptation (ten Cate, 2004). In the case of these advertisement signals, the benefits are positively correlated with being heard and found. These acoustic signals have become louder, more complex, and more broadband and rapid as a result of sexual selection. This is both for the perceptual salience of features that signal certain qualities of the sender and for standing out well against the background noise of the species-specific habitat.

The environment can affect signal evolution in various ways (Wiley and Richards, 1982). How well the message within an acoustic signal is transmitted from sender to receiver is a function of the propagation properties of the habitat and the perceptual interference from competing sounds (Figure 2). The competition for acoustic space depends on the timing and spectra of the local sound sources and also propagation properties, which may vary with height and angle of the typical transmission pathway through the vegetation (Slabbekoorn, 2004). Low frequencies, for example, penetrate better through dense vegetation than do high frequencies, and all sounds do better through relatively open forest layers. Furthermore, absorption and reflection by the ground may cause strong attenuation for low frequencies and sounds generated and received at low perches.

Environmental selection of bird song has led to many examples of habitat-dependent acoustic variation between and within species. Bird species in dense rainforests often

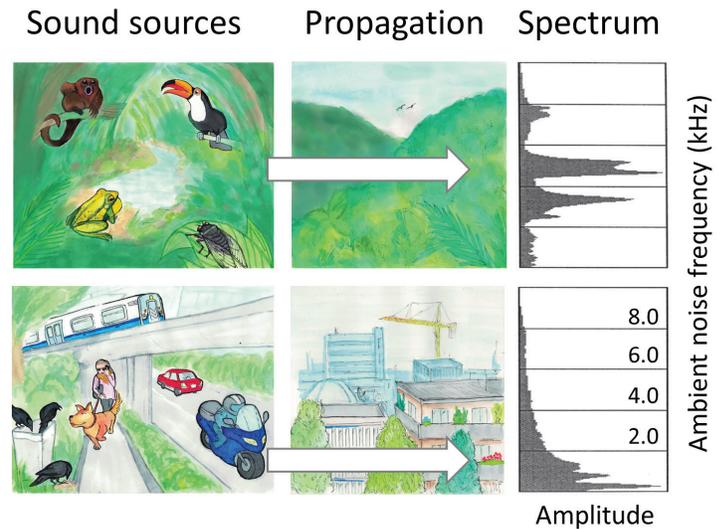


Figure 2. Ambient-noise profiles vary geographically and reflect habitat types (Slabbekoorn 2004, 2017). **Left:** each habitat has a characteristic set of sound sources, which can be of abiotic (wind, rain, forest streams) or biotic (vocal members of the local animal community) origin. **Center:** each habitat also has a characteristic filtering effect on sounds propagating from source to potential receivers. **Top:** dense vegetation favors low frequencies and slow, long-drawn-out notes; **bottom:** open urban habitat allows notes of wideband frequencies and favors brief, frequency-modulated notes that are relatively resistant to wind turbulence degradation. **Right:** power spectra illustrate examples of a diverse spectral pattern of a rain forest (**top**) and the simple urban pattern biased to low frequencies of traffic noise (**bottom**).

use relatively low-frequency sounds compared with species living in more open woodland spaces (Morton, 1975; Ryan and Brenowitz, 1985). The dense rainforest attenuates high frequencies more quickly than low frequencies and typically harbors rich and vocal animal communities that provide competition at high frequencies. Birds that favor breeding habitats close to noisy streams, with relatively high levels of low-frequency ambient noise, have been reported to sing relatively high-frequency songs. The spectral divergence between signal and noise renders the songs audible in such acoustically challenging environments (Figure 1).

A particularly nice and well-replicated example of noise-dependent song variation can be found in gray-breasted wood wrens (*Henicorhina leucophrys*) of South America (Dingle et al., 2008). These birds use low- and high-frequency notes when there are relatively low levels of acoustic interference across frequencies but refrain from using high frequencies when there is more high-frequency energy in the ambient noise (Figure 3). Consequently, wood wren populations living at high altitude in the Andes use a wide frequency range for singing because there is little competition from other sound-producing animals. Populations of low-altitude wood wrens, however, face severe competition for acoustic space due to the presence of a more diverse and abundant

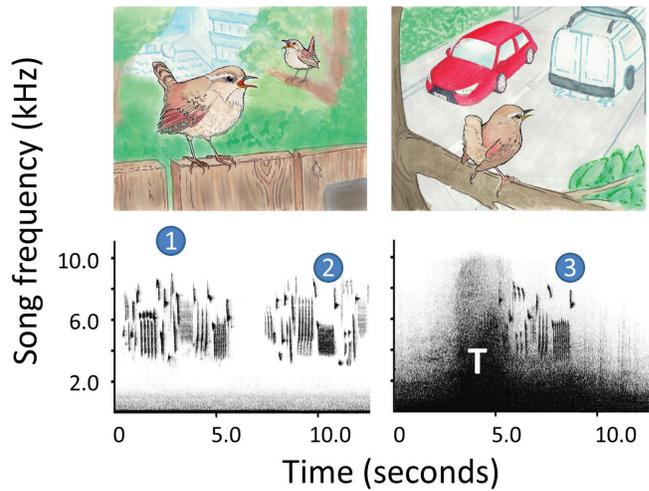
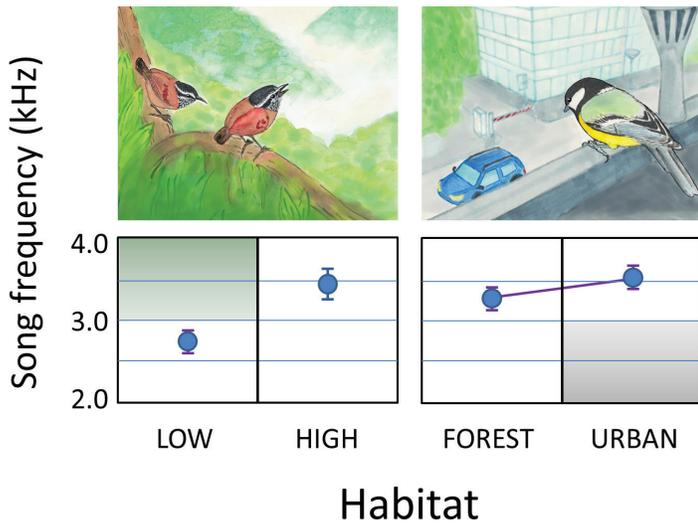


Figure 3. Spectral avoidance of ambient noise (based on Slabbekoorn and den Boer-Visser, 2006; Dingle et al., 2008). **Left:** South American wood wrens sing high notes at high altitudes in the Andes where there is little competition from the local animal community for high frequencies. They refrain from using high notes at low altitudes where they compete with the sounds from a more diverse and dense animal community that is also more active due to temperature-dependent vocal activity. **Right:** great tits across Europe have been found singing consistently higher frequency songs in urban populations compared to great tits of nearby forest populations. This pattern has been replicated in this species in several studies across Eurasia up to Japan and for several other bird species that are common in both urban and forest areas.

Figure 4. Timing ability in singing birds (based on Yang and Slabbekoorn 2014; Yang et al. 2014). **Left:** male winter wrens temporally avoid overlap with conspecific song (#1) by waiting for the other bird to finish a song before starting to sing themselves (#2). **Right:** winter wrens observed close to a road with fluctuating traffic noise levels and tested with experimental exposure were not found to avoid overlap by using their timing ability (song #3 masked by traffic noise [T]). Together, these two findings have been interpreted to mean that overlap avoidance is driven more by the need to hear competing sound than by the consequence of not being heard due to the competing sound (at least for this species).

community of invertebrates and amphibians who tend to be very active during large parts of the day in the lush and warmer habitat.

Flexibility for Fluctuating Conditions

Competition for acoustic space can be severe and may render the effort put into signaling a waste of time and energy if songs and calls are largely or completely masked by other sounds. Consequently, several counterstrategies have been found in birds to enable them to cope flexibly in fluctuating noise levels. Some species can, for example, sing roughly at the same time of day, but avoid each other at a smaller temporal scale; one species may start to sing as another stops (Figure 4). Winter wrens are a particularly loud singing species that alternates singing with neighboring birds of the same species and also avoids conspecific songs when played back during an experiment (Yang et al., 2014). Tested individuals shifted their timing by not starting a song during a playback song but initiated songs just after the playback. Another example of a noise-coping counterstrategy is found in blue-throated hummingbirds (*Lampornis clemenciae*), which sing louder when perched relatively close to noisy forest creeks or in response to playbacks of recorded stream noise (Pytte et al., 2003; Figure 5). This phenomenon is re-

ferred to as the Lombard effect and also occurs in people when ambient-sound levels rise, such as at a party (Brumm and Zollinger, 2011).

The habitat-dependent and natural noise-related variation in frequency use between and within species can also result from a flexible response to current noise conditions (Patricelli and Blickley, 2006; Slabbekoorn, 2013). Because juvenile songbirds learn the songs of conspecifics, any masking will impact adult song development; juveniles will not copy what they cannot hear and are therefore likely to end up with adult songs that are well-audible given local noise conditions. Similarly, immediate feedback may yield even more rapid adjustments. If birds get no response from others when using a song type that is heavily masked but they get a response from another, they may continue to repeat the latter. These kinds of signal adjustments are not evolutionary changes, although the flexibility itself may be the result of an evolutionary adaptation.

The Anthropocene

Human settlement, the exploitation of natural resources, and the building of all sorts of infrastructure induce habitat destruction, degradation, habitat fragmentation, and a variety of noise pollution effects. As suggested in *Living the*

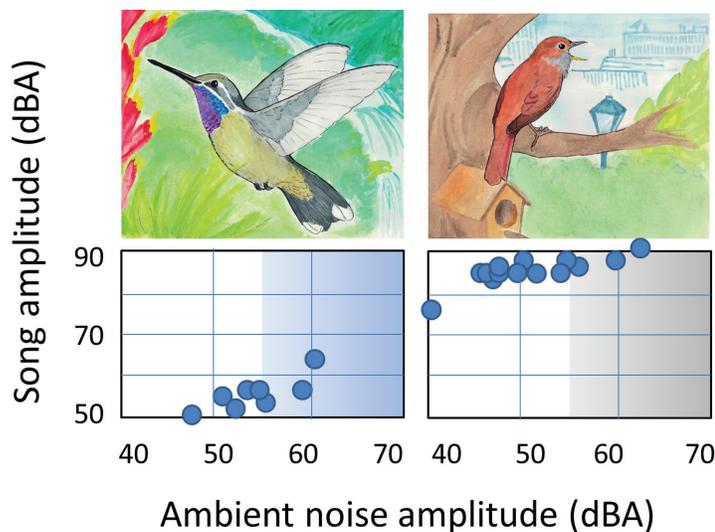


Figure 5. Flexible singing amplitude with fluctuating ambient-noise levels (based on Pytte et al., 2003; Brumm, 2004). **Left:** blue-throated hummingbirds sing louder when their territorial song perches are noisier due to relative proximity to a noisy forest stream. **Right:** urban nightingales in Berlin sing louder in territories that are noisier due to relative proximity to noisy street sections. Birds recorded on multiple days sing louder on noisy weekdays than on relatively quiet weekend mornings.

Anthropocene, human-altered landscapes have the potential to have a big impact on animal communities. Some species disappear or decline, whereas others may enter a habitat and thrive. Consequently, avian communities in urban environments can still be relatively diverse. However, the species that inhabit urban communities are typically the same in cities over large geographic ranges, whereas the species that occur in the original and replaced natural habitats vary much more from place to place. Therefore, although local diversity may not decline, large-scale diversity does. This phenomenon is known as urban homogenization (McKinney, 2002).

Acoustically, the Anthropocene is changing natural soundscapes in several ways (Warren et al., 2006). Rachel Carson (1962) alluded to the potential of human pollution to detrimentally affect the presence of singing birds in her influential book *Silent Spring*. The turning of natural habitats into large-scale monocultures for agricultural crops and the use of pesticides indeed results in quieter mornings due to a decline in bird diversity and density. Although habitats have not become totally silent, changes in vocal animal communities change the sounds that are filling the air. Dropouts and new arrivals change the competition and the patterns of acoustic interference for local communities (Slabbekoorn, 2017).

Another prominent acoustic change of the Anthropocene is the emergence of increasing human activities that make loud and low-frequency sounds (Klump, 1996; Slabbekoorn and Peet, 2003). Road, rail, and air traffic is spreading in space and time and adds noise in large parts of the world. There is an almost continuous presence of man-made sound in urban areas and along many highways. Even in natural areas and wildlife reserves, far-reaching sounds of traffic, pile driving, seismic surveys, or airplanes are more common. Elevated ambient-noise levels resulting from human activities have been shown to negatively affect birds in many ways, as discussed in **Anthropogenic Noise Impact on Birds** (Halfwerk and Slabbekoorn, 2014).

Anthropogenic Noise Impact on Birds

The bird communities in noisy areas of otherwise suitable breeding habitats are less diverse and less dense compared with naturally quieter areas in equivalent habitats (Francis et al., 2009). Species that sing relatively low-frequency songs were more affected by the typically low-frequency sounds of generators or road traffic than were high-frequency singers (reviewed in Slabbekoorn, 2013). More spectral overlap between song and noise sources means more masking and more birds avoiding an area. Some species with high-pitched songs or calls may benefit indirectly from the presence of low-frequency noise due to the negative effects on competitors with lower pitches, a phenomenon called competitive release. Breeding may be affected, along with migration and survival, because birds foraging under relatively noisy conditions have a lower food intake rate (Francis and Barber, 2013). Foragers in noisy conditions are less efficient in pecking seeds from the ground because they need to look up more often to scan for potential predators that cannot be heard due to auditory masking.

There are also examples of male birds that persist in singing at noisy breeding sites but achieve a significantly lower pairing success compared with males at quieter sites (Halfwerk and Slabbekoorn, 2014). Potential mates in the noisy environment apparently do not hear the singing males or are not able to get sufficient detail from the song to evaluate their quality. It is also possible that females do not like to settle in a noisy territory and thus ignore the calling males. Finally, birds that do breed in noisier territories have significantly smaller clutch sizes and fledglings with lower body weights. This may be due to chronic stress causing reduced chick growth or to the masking of parent-offspring or parent-parent communication, leading to less efficient feeding patterns by the parents.

Another effect of man-made sounds on birds that has been reported for many common urban areas all over the world is vocal adjustment. The flexible song features that are found in natural settings with fluctuating noise levels apparently also allow many species to adjust to noisy human habits in the city. Urban great tits (*Parus major*) use more high-frequency song types in the presence of low-frequency traffic noise (Figure 3), in comparisons both among individuals within a single population (Slabbekoorn and Peet, 2003) and among populations in urban and forested areas across Europe (Slabbekoorn and den Boer-Visser, 2006). Playback experiments suggest that the spectral shifts in urban great tits have the potential to be adaptive. Male great tit communication toward females is negatively affected by the overlapping spectrum of traffic noise in the case of low-frequency songs but not for high-frequency songs (Halfwerk et al., 2011).

Coping Flexibly in Urban Settings

The level-dependent use of different frequencies in great tit songs can be explained by relatively fast masking-dependent switches between low- and high-frequency song types within individual repertoires (Halfwerk and Slabbekoorn, 2009). If great tits sing low-frequency songs and the ambient-noise level is experimentally elevated by playing back an urban noise spectrum, the birds switch more quickly to another song type than if they are singing a high-frequency song type. Interestingly, a recent repeat of the experimental exposure test in black-capped chickadees (*Poecile atricapillus*) revealed that birds may have to learn to cope in such a flexible way; an upward shift in song frequency use on the elevating ambient-noise level depended on whether local territories were more or less urban and thus whether territorial birds had more or less experience with conditions of fluctuating levels of traffic (LaZerte et al., 2016).

At airports, birds can be exposed intermittently to very high levels of broadband noise from which there is no spectral escape. In such cases, singing birds stop and temporally avoid the periods of noisy takeoff and nearby overflights (Dominoni et al., 2016). The fluctuation in ambient-noise level at the scale of minutes is also typical for the heterogeneous cacophony of busy traffic on city roads along which birds may breed in urban shrubs and trees. Winter wrens, for example, are often found defending their territories acoustically at places that can be very noisy when cars and trucks are passing by. Although I previously discussed in **Flexibility for Fluctuating Conditions** the capability of timing song production neatly into relatively quiet slots of neighboring conspecifics, males of this species did not temporally avoid masking (Figure 4), ei-

ther from actual traffic noise or from an experimental broadband and intermittent noise exposure (Yang et al., 2014). Apparently, the task is either too difficult or not beneficial in this particularly loud-singing bird species.

Finally, urban nightingales in Berlin, Germany, sing louder in noisy than in quiet territories (Figure 5), and a few males that were recorded at multiple occasions were reported to sing louder during noisy weekdays than during the quieter weekends (Brumm, 2004). These urban birds thus seem to respond in the same way as hummingbirds at noisy rain-forest streams and humans at noisy cocktail parties: raise your voice to cope with noise. Interestingly, for some bird species, it has also been found that singing louder is inherently related to singing at higher frequencies (Brumm and Zollinger, 2011). This increase in frequency has likely to do with the mechanistic challenges of producing sound at both low frequencies and high amplitudes. The human voice also raises in pitch when shouting or calling to reach someone at a distance. This implies two changes in acoustic design that could benefit auditory perception under noisy urban conditions: improvement of the signal-to-noise ratio by increasing volume and spectral avoidance.

Conclusions

In conclusion, the diversity in the animal kingdom is reflected in the diversity of acoustic communication systems, which is shaped by diversity in the environment. Species-specific evolution of acoustic repertoires allows each species to stand out when needed for mate attraction or deterrence of competitors and to blend in when predators are among the potential eavesdroppers. The species-specific acoustic design or elaboration of signals is driven by sexual and natural selection, given the sensory performance of receivers of sounds that are filtered during sound propagation and affected by noise interference in their habitat. This phenomenon is referred to by evolutionary ecologists as “sensory drive,” although “environmental drive” may be a better term because it is the environment that determines the direction of the drive.

Acoustic diversity and evolutionary shaping is particularly true and well studied for birds. However, other taxa using acoustic signals are affected by the same aspects of environmental selection (Francis and Barber, 2013; Wiley, 2015; Slabbekoorn, 2017). Some frog species have evolved the use of ultrasonic frequencies when living close to fast-flowing streams that produce low-frequency noise. Many fish species produce sounds that propagate well in the aquatic envi-

ronment. There are also reports of matches between a gap in the ambient-noise spectrum and the sound spectrum used by fish for communicating to mates and competitors. Many taxa also exhibit flexible coping strategies for fluctuating ambient-noise levels. Tamarin monkeys (*Saguinus oedipus*), for example, avoid noisy periods and call preferentially in windows of relative quiet, whereas some bat species raise the amplitude of their echolocation calls in response to a rise in ambient-sound levels (Brumm and Slabbekoorn, 2005).

The widespread importance of sounds taxonomically and the critical role of the acoustic environment in their functionality and evolution means that changes to the soundscapes in the Anthropocene may also have widespread consequences. Conservation is, in that respect, an odd term because almost all ecosystems are dynamic and changes are inherent to nature. We should, therefore, not necessarily aim to stop all changes. Furthermore, we have also seen that many species are able to cope with flexible responses in cases of novel environmental factors such as elevating noise levels. However, we often lack insight into the energetic costs of adjusting signals and whether or not there are positive fitness consequences for the animals. As a result, the link between flexibility and breeding success is not yet confirmed and may turn out to be just a temporary solution for the individual. Persistence of the species in an increasingly noisy environment is therefore by no means guaranteed.

The best advice at the moment should therefore be: do not make sounds when it is not essential. Many of our activities only produce sound as a by-product of their function. Noise mitigation is, therefore, often a reasonable solution. Another sensible thing is to make use of soundscapes for monitoring, as discussed in an article in this issue of *Acoustics Today* by Miksis-Olds, Martin, and Tyack. Recordings tell more than a thousand pictures and not only report which species are present but potentially also whether they are breeding, whether they were able to get a mate, what condition they are in, and whether they have an acoustic strategy to cope flexibly with fluctuating noise conditions. Changes over time in the presence and relative prominence of anthropogenic noise can be quantified and matched with alterations in the soundscape spectrum due to changes in the vocal animal community. Hopefully, more recordings and more studies will improve both our understanding and appreciation for the acoustic world around us and make such efforts not just for the record.

Acknowledgments

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Biosketch



Hans Slabbekoorn is an associate professor at the Institute of Biology, Faculty of Science, Leiden University, The Netherlands. His expertise is in animal behavior, evolutionary ecology, and bioacoustics in air and water. His core research theme is the function and evolution of acoustic signals and natural and anthropogenic noise impact on animals. He integrates this field with studies on animal personality, stress physiology, dynamic energy budget models, and a population consequences of acoustic disturbance framework. He believes it is critical to listen to nature and that sound science can benefit decision making about the balance between ecology and economy.

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