



INVITED PAPER

What is Known—and not Known—About Acoustic Communication in an Urban Soundscape

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Synopsis Urban environments have some of the most highly modified soundscapes on the planet, affecting the way many animals communicate using acoustic signals. Communication involves transmission of information via signals, such as bird song, between a signaler and a receiver. Much work has focused on the effects of urbanization on signalers and their signals, yet very little is known about how noise pollution affects receiver behaviors and sensory systems. Here, we synthesize key findings to date regarding avian acoustic communication in the urban environment and delineate key gaps in knowledge for future work. We leverage our own work comparing current and historical songs from urban and rural habitats for a subspecies of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*). We use this system, along with findings from other systems, to answer three key questions in the field: (1) Is song variation consistent with temporal and spatial variation in anthropogenic noise? (2) How are birds adjusting their song to the urban environment? (3) How does song ‘urbanization’ affect signal function? Our synthesis illustrates that the adjustments birds make to their songs in noisy environments can improve signal detection, but potentially at the cost of signal function. Many key gaps in knowledge need to be addressed to complete our understanding of how acoustic communication systems evolve in urban areas, specifically in regard to sexual selection and female preference, as well as how receivers perceive signals in an urban environment.

Introduction

Human activity has modified habitats and altered ecological and evolutionary processes around the world (Noss 1987; Bennett 1999; Shochat et al. 2006; Smith and Bernatchez 2008; McDonald et al. 2018; Díaz et al. 2019). Urban environments are some of the most highly modified habitats on the planet, as human density continues to increase in cities (Alberti 2015; Grimm et al. 2008; Seto et al. 2012; Rivkin et al. 2019). Many studies have documented the often negative effects of urbanization on species diversity and conservation implications (Hanski and Simberloff 1997; Gascon et al. 1999; McIntyre and Hobbs 1999; Bentley et al. 2000; Ricketts et al. 2001; Ibáñez-Álamo et al. 2017; Perillo et al. 2017; McDonald et al. 2018). However, many species persist in urban settings (McKinney 2006). A key question is how these populations are adapting (or not) to rapidly changing urban environments (Rivkin et al. 2019).

What is especially noteworthy are the evolutionarily unprecedented increases in environmental sound levels in high-density urban environments (Swaddle et al. 2015). This source of anthropogenic sensory pollution affects auditory signals for many animals (Brumm 2004; Shochat et al. 2006; Swaddle et al. 2015). Alteration of the ambient noise environment can affect the perception of acoustic mating signals and mask signal content (Patricelli and Bickley 2006; Slabbekoorn and den Boer-Visser 2006). For example, much of anthropogenic noise pollution in urban areas (e.g., vehicular and air traffic, HVAC systems) is high energy at low frequencies, which can mask frequencies found in many bird songs (Dooling and Popper 2007a). Because acoustic communication is a critical component of both male–male competition and female mate choice in many taxa including anurans, crickets, and birds (reviewed in Andersson 1994), the effects of urban ambient noise on signal detection might have significant

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consequences for mate choice and resource defense across a diversity of taxa (Halfwerk and Slabbekoorn 2015). Thus, the novel selective sound environment in urbanized areas provides an opportunity to examine contemporary and rapid evolution of acoustic communication in wildlife in response to human-caused environmental change (Swaddle et al. 2015).

Ambient noise is a component of all environments that shapes the evolution of acoustic communication (Wiley 2015). Because communication involves the transmission of information from a signaler to a receiver through the environment (Bradbury and Vehrencamp 2011), selection should act on 'signals, receptors and signaling behaviors' to maximize the signal to noise ratio in a given context to optimize the transmission of information during communication (Endler 1993; Cummings and Endler 2018). Signal Detection Theory generates testable predictions of how signals should vary with temporal and spatial variation in noise (Wiley 2015), providing a strong framework for addressing how anthropogenic noise affects communication in urban wildlife. Much work over the past 15–20 years has leveraged this framework to generate a strong understanding of how signals and signaling behaviors have adjusted to contemporary noise pollution (reviewed in Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006; Slabbekoorn 2013; Gilbert et al. 2017). However, there are many on-going debates, including how widespread such adjustments are geographically or across taxonomic groups (Berger-Tal et al. 2019; Hu and Cardoso 2010), whether adjustments of song to noise are in fact the result of changes over time (genetic or cultural evolution) or due solely to immediate flexibility (Nemeth and Brumm 2010; Reichard et al. 2020; Liu et al. 2021), as well as the extent to which these adjustments affect the function of song (Halfwerk and Slabbekoorn 2015).

Here, we organize current work into how it answers three fundamental questions: (1) Is signal variation consistent with temporal and spatial variation in anthropogenic noise? (2) How are animals adjusting their signals to the urban environment? (3) How have these signal adjustments affected song function? Because much of this work is centered on bird song, we focus on bird song studies to discuss what is and is not known in response to these questions. We then delve more deeply into our own study system—white-crowned sparrows (Box 1, Fig. 1)—because of the historical perspective that they provide and the opportunity they afford to address these questions with a new angle, namely how songs changed when the 'natural' experiment of the COVID-19 pandemic led to a reduction in noise pollution (Derrberry et al. 2020). Finally, we highlight that most work to date has focused almost exclusively on sig-

nals and signaling behaviors. There is a dearth of information on receptors and receiver thresholds, which we argue greatly limits our understanding of how sensory pollution affects communication. We end our synthesis by providing a road map for work on receivers to provide the other half of the story on how noise pollution shapes acoustic communication.

Box 1

In our work to date, we have examined how songs have evolved over generations in urban and rural areas for a songbird that persists in urban soundscapes, the white-crowned sparrow (*Zonotrichia leucophrys nuttallii*). Pioneering work by Luis Baptista, who extensively recorded white-crowned sparrow songs and breeding territories in and around San Francisco (Baptista 1975), enables our long-term comparisons (Fig. 1). His work in the 1960s and 1970s provides a baseline to which we have been comparing current variation in songs to test a number of hypotheses about the factors that drive song evolution. In 2020, we had the unprecedented opportunity to determine whether human movement restriction during the statewide COVID-19 shutdown in California alleviated noise pollution and whether birds responsively exploited newly emptied acoustic space by altering their songs to maximize communication to potential mates and competitors. This 'natural' experiment allowed us to re-assess our previous answers to the focal questions of this synthesis in the context of a dramatically altered soundscape.

Question 1: Is song variation consistent with temporal and spatial variation in anthropogenic noise?

Species that persist in urban soundscapes tend to have relatively high-frequency songs, which experience minimal masking from high-energy, low-frequency anthropogenic noise (Hu and Cardoso 2009; Cardoso et al. 2020). Even species with relatively high-frequency signals still experience some signal masking, and have a number of ways to reduce this masking (Hu and Cardoso 2010; Narango and Rodewald 2016). These behaviors include shifting to sing more often at less noisy times of day (Gentry and Luther 2017; Bermúdez-Cuamatzin et al. 2020), singing at higher amplitude (e.g., the Lombard effect; Zollinger and Brumm 2011; Brumm and Zollinger 2013; Hardman et al. 2017), moving to a new location to sing (Møller 2011; Halfwerk et al. 2012; Polak 2014), and/or changing the structure of their song to reduce masking (including increasing song

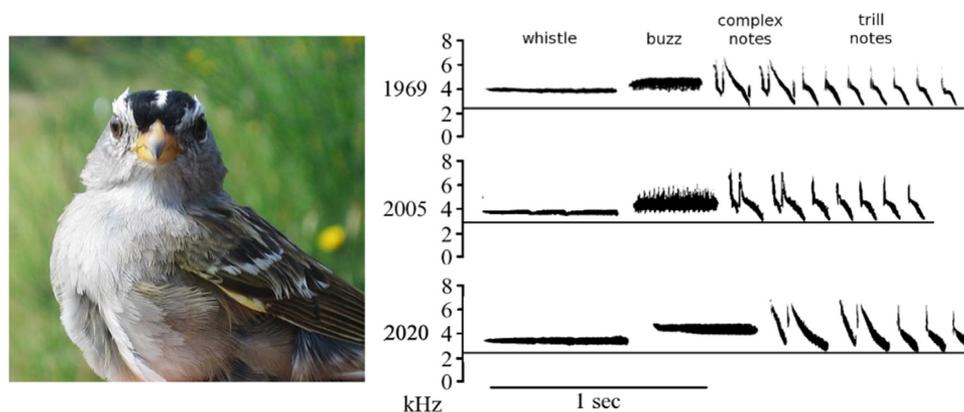


Fig. 1 A white-crowned sparrow and the San Francisco song dialect recorded in Battery area, Presidio in 1969, 2005, and 2020 naming parts of the song. Note few changes to syllable type or order over time but a 500 Hz increase in song minimum frequency between 1969 and 2005 and a similar decrease in song minimum frequency during the relative quiet of the pandemic in 2020.

minimum frequency, selectively singing less masked song types, and not singing low-frequency notes (Fig. 2) (reviewed in Slabbekoorn 2013).

All of these behaviors have been well-studied, but primarily by comparing songs produced in urban, ‘loud’ areas to rural, ‘quiet’ areas (Ripmeester et al. 2010; e.g., Slabbekoorn and den Boer-Visser 2006) or by experimentally increasing noise levels to measure real time shifts in song (e.g., Halfwerk and Slabbekoorn 2009; LaZerte et al. 2016). A powerful, but less used approach is to examine evolutionary trajectories of song over time across urban and rural areas to assess how songs are changing across generations and over urbanization gradients. We took this latter approach by leveraging the extensive history of recordings that exist for white-crowned sparrows (Box 1) (Luther and Baptista 2010; Luther and Derryberry 2012; Moseley et al. 2019).

We found that noise pollution has increased over time in areas where white-crowned sparrows breed in the city of San Francisco, such that sound pressure levels (SPLs) effectively doubled between 1974 and 2008 (Luther and Derryberry 2012). As predicted by this increase in low-frequency noise levels, white-crowned sparrow songs increased in minimum frequency over this same period of time (Luther and Baptista 2010; Luther and Derryberry, 2012). Given that white-crowned sparrows typically produce only one song type, and that most of the notes within their song occur within a similar frequency bandwidth, one of the few routes for them to adjust their songs in noise is to shift up the minimum frequency of their song. For example, songs recorded in 2005 in the Battery Area of the urban Presidio park had a significantly higher minimum frequency than songs recorded in the same area in 1969 (Luther and Derryberry, 2012). As most males within an area sing the same song type, these song neighborhoods are often referred to as song di-

alects (Marler and Tamura 1962). Notably, over decades, the urban song dialect with the highest minimum frequency has replaced one (and is in the process of replacing a second) song dialect with a lower frequency range in downtown San Francisco (Luther and Baptista 2010). Thus, shifts in song traits over generations are consistent with increasing noise levels over time in an urban environment.

Near the beginning of the 2020 breeding season for white-crowned sparrows, the state of California issued a strict shutdown associated with the COVID-19 pandemic that limited human movement. This limit on human movement resulted in a dramatic drop (~ 7 dB; note, 6 dB is a doubling in SPL) in ambient noise levels (Derryberry et al. 2020), effectively erasing a half-century of noise pollution. In response, white-crowned sparrows in urban areas produced songs with a lower minimum frequency and filled the sound space that had been occupied by traffic noise. In rural areas, minimum frequency remained unchanged, as there was minimal traffic prior to the pandemic and, for birds near the ocean, the noise of the ocean surf was still present. In addition, song amplitude dropped during the pandemic, such that birds were singing, on average, at a lower song amplitude (but higher relative to noise) than before the pandemic (Derryberry et al. 2017; Derryberry et al. 2020). These findings highlight that apparently gradual shifts in song traits over more than 50 generations in a population can disappear in one season, when the selective pressure that caused the shifts is abruptly removed. This finding is consistent with the prevailing hypothesis that ‘adaptations’ of song to urban environments are primarily the result of immediate flexibility of song in response to noise levels. In the next section, we discuss what is known and not known about how birds adjust their songs to urban environments.

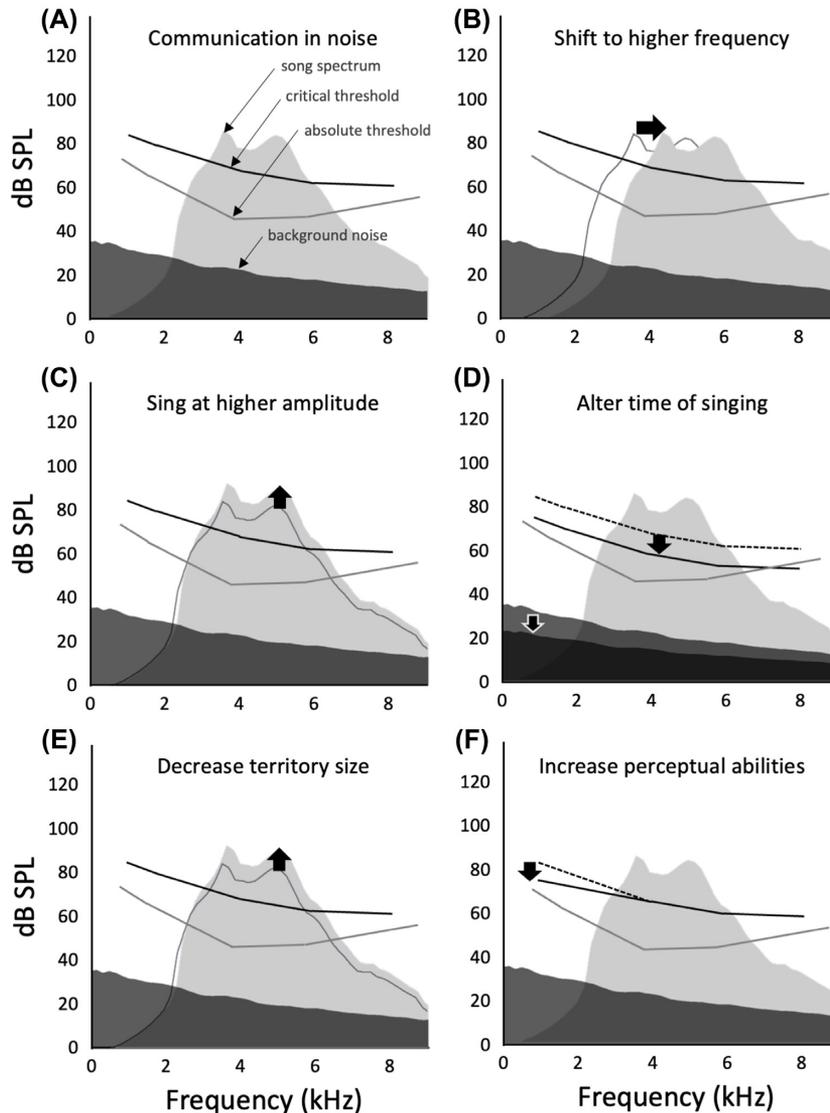


Fig. 2 Each plot illustrates distribution of sound energy (dB SPL) across frequencies (kHz) for typical urban noise (in black) and a typical white-crowned sparrow song (in gray) as well as the estimated critical threshold in noise (black line; the amplitude of noise that would mask other sounds at each frequency) for a closely related species (from [Dooling 2002](#)) and the audibility curve (gray line; the minimum sound amplitude that an animal perceives across its range of hearing) for white-crowned sparrows ([Vélez et al. 2015a](#)) as seen in (A). Essentially, white-crowned sparrows can detect the part of the song above the critical threshold and any adjustments that increase this area may increase the transfer of information. The remaining plots illustrate behavioral adjustments that could increase transmission of information in noise (direction of changes highlighted by solid black arrows). Well-described changes to singing behaviors or song traits include (B) shift to higher frequency song, (C) increase in song amplitude, and (D) sing at a time of day with lower noise levels, which would lower the critical threshold (dashed line). Less-well described behavioral adjustments include (E) reducing territory size to decrease communication distance between signaler and receiver, which would increase the signal as in (C) thus improving the signal to noise ratio and (F) adjustments to receiver perceptual abilities, such as an increased ability to detect songs at a lower signal to noise ratio, particularly at low frequencies.

Question 2: How are birds adjusting their song to the urban environment?

A central question in the field has been *how do birds adjust their songs to the urban environment?* Because many species of birds, and a majority of the urban species, learn their songs, most of the hypotheses developed in

response to this question focus on aspects of behavioral plasticity, namely plasticity during development (ontogenetic adjustments) or plasticity during adulthood (immediate flexibility). Far fewer studies examine the roles of cultural evolution (a form of developmental plasticity), selection on behavioral flexibility itself, or genetic evolution of singing behaviors.

The prevailing hypothesis is that song adjustment is the result of immediate flexibility (Box 2: Terminology). There is now extensive evidence across multiple bird species that males can alter their singing behavior in real time in response to low-frequency noise (e.g., Bermudez-Cuamatzin et al. 2009; Halfwerk and Slabbekoorn 2009; Nemeth and Brumm 2009; Gross et al. 2010; Verzijden et al. 2010; Cardoso and Hu 2011; LaZerte et al. 2016; Gentry et al. 2018; Courter et al. 2020). For example, great tit (*Parus major*) males selectively sing song types with higher minimum frequencies from their repertoire when noise levels are high (Halfwerk and Slabbekoorn 2009). However, not all species show immediate flexibility. For example, Vermilion flycatchers—who do not learn their song—do not show immediate flexibility of song in response to noise (Ríos-Chelén et al. 2018). Although at first it may appear that only birds that learn their song are capable of immediate flexibility, the Eastern wood-pewee (*Contopus virens*, another bird species that does not learn its song), does exhibit song plasticity (Gentry et al. 2018). Thus, it is probably safe to conclude that, although for many species, immediate flexibility can explain much of the association between noise levels and song traits, it does not explain it all.

Box 2 Terminology

Anthropogenic noise—Referring to environmental change in noise caused or influenced by people. Background noise is the maximum noise level experienced $\geq 90\%$ of the time (often measured as LAF90), which is biologically relevant to songbirds and humans (Dooling and Popper 2007a). Vehicular traffic is a common source of background noise in cities. Ambient noise also captures information about noise levels occurring $\leq 10\%$ of the time (often measured as LAeq), which often corresponds to short-term events (e.g., planes flying overhead, dogs barking).

Cultural selection—This selective process occurs when individuals choose which vocal models to learn, and so it is the individual that acts as the selective agent, with the selective value referring to the survival and spread of the vocal model not the Darwinian fitness of the individual (Hansen 1979). Because this process is a cultural analog of natural selection, it has been referred to as ‘psychological selection’ (Mundinger 1980) or ‘cultural selection’ (Lynch 1996).

Immediate flexibility—A context-dependent form of behavioral plasticity (*sensu*; Snell-Rood 2013) that allows animals to temporarily change their acoustic behavior in response to noise fluctuations and potentially improve the chances of successful communication in noisy environments.

Lombard effect—Noise-dependent regulation of vocal amplitude. As in humans, this is thought to be an involuntary response in birds and has been documented in a taxonomically diverse group of species (Brumm and Zollinger 2013).

Signal masking—The perception of a signal is limited by the presence of noise or other signals.

Signal salience—A measure of how potent a signal is in a functional context, such as mate choice or male-male competition. Often measured as the relative response of receivers to specific variation in signals.

Signal-to-noise ratio—Compares the level of a specific signal to the level of background noise.

Soundscape—The sounds heard in a particular location and considered as a whole. The acoustic environment as perceived by humans.

Vocal performance—A measure of a motor constraint on song production used here *sensu* (Podos 1997).

A second hypothesis is that songs may evolve over generations in response to acoustic selection pressures via cultural selection, or preferential learning of song models that are less masked by low-frequency urban noise (Hansen 1979). There is some support for this hypothesis from song learning experiments in which juvenile male songbirds preferentially learn undegraded songs over songs that have been degraded during transmission through the environment (Morton et al. 1986; Peters et al. 2012). To understand the effects of noise specifically, several studies have now manipulated noise levels during critical song learning periods [e.g., in great tits (Zollinger et al. 2017) and in zebra finches (*Taeniopygia guttata*) (Liu et al. 2021)] and found that juveniles do not in fact reproduce adult songs at higher frequencies. Notably, these studies were not designed to test cultural selection for less-masked songs. A more explicit test of cultural evolution in response to noise pollution would come from testing whether there is a preference to copy the least masked song model if given only a choice of songs differently masked by urban noise.

Of course, these two hypotheses are not necessarily alternative hypotheses, as juvenile males may preferentially copy less masked songs and adult males may adjust songs in real time. There is limited knowledge of the relative importance of these two proximate mechanisms in explaining urban dependent song variation. Using the white-crowned sparrow system, we explored the relative roles of cultural evolution and behavioral plasticity, as well as the potential synergy between these two mechanisms.

Our work assessing correlations between song traits and noise levels at different spatial scales suggested

multiple potential mechanisms might generate a close association between noise levels and song traits. Using four urban sites, we tested whether mean site noise and/or territory noise predict an individual bird's minimum frequency (Derryberry et al. 2016). Support for site noise would suggest selection for higher minimum frequencies over time (i.e., cultural selection; Hansen 1979), whereas support for territory noise would suggest that males alter song minimum frequency in real time response to ambient noise (i.e., immediate flexibility; Snell-Rood 2013). We found strong support for a model that included an interaction between both mean site noise and territory noise, which indicated that males sang higher minimum frequencies when site noise was louder, suggesting cultural selection on song. In addition, males sang higher minimum frequencies when on noisier territories, suggesting individual immediate flexibility. The largest range in song minimum frequencies was in a subsite (Lobos Dunes) within the Presidio of San Francisco (an urban park), suggesting that immediate flexibility is most prevalent at intermediate noise levels.

We also tested the hypothesis of immediate flexibility using both observational data (Derryberry et al. 2017) and a noise-playback experiment, in which we manipulated noise levels on free-living male white-crowned sparrows territories (Gentry et al. 2017). We found that males readily adjust song amplitude in immediate response to natural variation in ambient noise levels, singing at higher amplitude when noise levels increase on their territories (Derryberry et al. 2017). However, we did not find significant changes to song minimum frequency, suggesting adult males of this species are in fact much less flexible in terms of frequency adjustments, at least in real time, than many other urban songbird species (Derryberry et al. 2017). We did have some conflicting experimental results however as adult males showed slight reductions in bandwidth in response to an experiment with relatively large increases in ambient noise levels (Gentry et al. 2017). Thus, the relative level as well as the degree of change in ambient noise levels are critical factors in determining the extent of immediate flexibility.

To test the role of cultural selection, we conducted an experimental test by manipulating noise levels during the critical learning period. We found that juvenile males preferentially learned songs that were less masked by urban noise (Moseley et al. 2018). Further, we discovered that juveniles made additional ontogenetic adjustments to these songs, such that the songs they produced as adults were even less masked by noise than their tutors' songs, with higher song minimum frequencies and narrower bandwidths. These findings provide strong support that cultural selection could explain in-

creases in song minimum frequency over time with increasing levels of noise pollution in the white-crowned sparrows system.

The extended period of low noise levels during shutdowns associated with the COVID-19 pandemic in San Francisco in 2020 allowed us to further test these hypotheses. We found that minimum frequency decreased and bandwidth increased significantly as compared to recordings made in 2016 (Derryberry et al. 2020). This dramatic change in song structure across the urban landscape suggests that adult males are capable of changing their song structure. Further, at least one song dialect (the Berkeley dialect in the East Bay area) exhibited song traits not heard since the 1960s (Derryberry et al. 2020). These findings appear to overturn our previous work and suggest that immediate flexibility may be a stronger driver of the close association between song minimum frequency and ambient noise levels than is cultural selection. However, we cannot draw a final conclusion based on these data because we do not have data from the same individual males from before and during the shutdown. It is possible that because the shutdown was at the start of the breeding season, males that had wider bandwidth, lower minimum frequency songs were more competitive than in the past at acquiring and maintaining territories in areas with high noise levels. Future work is needed to examine the songs of males that learned their song during the quiet of the shutdown. These second-year males may allow us to assess the extent to which adult males of this species are capable of immediate flexibility by determining whether they produce songs in 2021 that are more typical of the quiet period in 2020 or of the relatively louder period of 2016. Whether cultural selection or immediate flexibility is the primary mechanism underlying how birds are shifting their songs in response to noise, it is clear that songbirds have a striking capacity to exploit newly empty soundscapes following dramatic but ephemeral amelioration of noise pollution.

Beyond these two now well-explored hypotheses are a number of hypotheses that need to be tested. In particular, there is potential for genetic evolution of singing behaviors, not only in birds that do not learn their song, but also in learners. For example, a recent common garden experiment with an oscine (dark-eyed junco, *Junco hyemalis thurberii*) revealed that the higher song frequencies of an urban population are not a plastic response to noise (Reichard et al. 2020). There is also some evidence that urban populations may have evolved greater behavioral plasticity than more rural populations (Gentry et al. 2017), although more work is needed to tease apart the effect of experience on these findings. Thus, there is a clear need for more studies

Table 1 Known changes to signal traits in response to anthropogenic noise and how those changes affect receiver responses. See relevant references in the text

Adjustments to urban noise	Natural selection to increase signal detection in noise	Sexual selection to attract mates and deter rivals
Raise minimum frequency	+	–
Remove lowest notes	+	–
Lengthen song	+	?
Raise amplitude	+	+
Immediate singing flexibility	+	–

that investigate potential evolutionary, *genetic* behavioral adaptations to noise.

Question 3: How does song ‘urbanization’ affect signal function?

When birds adjust their songs in response to urban noise, this could affect signal salience as songs are used to repel rivals and attract mates (Catchpole and Slater 2003). Changes to certain song traits may improve signal detection in noise (e.g., increased song minimum frequency, higher amplitude songs), but reduce potency in the context of mate choice and male–male competition. In other words, natural and sexual selection may be acting in opposition on song traits. In contrast, both selective pressures may act in concert when changes to song traits both improve detection and increase potency. In Table 1, we summarize known changes to song in response to noise and how those changes affect receiver response.

Two of the most commonly studied song traits in noise are song minimum frequency and song amplitude. Increased amplitude and higher minimum frequencies increase communication distance in at least two species of birds, the great tit and the common blackbird (*Turdus merula*) (Nemeth and Brumm 2010). For song frequency, there is a strong positive correlation between frequency and signaler size (Davies and Halliday 1978) within and among most species examined. Females choosing mates and males assessing competitors may respond more strongly to songs that contain lower frequencies as these songs may indicate larger (and potentially better quality) signalers. Thus, for this song trait, sexual selection may act in opposition to noise-dependent selection. In urban female great tits intended female receivers give stronger responses to songs with lower minimum frequencies, even though urban males produce songs with higher minimum frequencies (Halfwerk et al. 2011a). Similarly, white-crowned sparrow male song adjustments to noise affect signal salience in the context of male competition (Luther and

Derryberry 2012); however, we later discovered that males were not attending to the shift in song minimum frequency, instead they were responding to the simultaneous narrowing of song bandwidth (Luther et al. 2016; Luther et al. 2017; Phillips and Derryberry 2017a). Reduction in song bandwidth reduced the overall ‘vocal performance’ of the song, a performance trait of acoustic signals that is salient in a number of taxonomic groups (Podos et al. 2009). In other words, male white-crowned sparrows on noisier territories produce narrower bandwidth songs, which transmit more effectively in noise but are less salient in the context of male–male competition (Phillips and Derryberry 2017b; 2018). Male song structure thus reflects a balance of opposing selection pressures—urban noise selecting for narrower bandwidth songs and sexual selection selecting for wider bandwidth songs.

Song amplitude may also be under sexual selection (Gil and Brumm 2014) as both males and females appear to respond more strongly to louder songs (Searcy 1996; Ritschard et al. 2010; Brumm and Ritschard 2011; Luther et al. 2017). In terms of song amplitude, sexual selection and noise-dependent selection appear to act in concert. Further, if higher song amplitude increases response, then an increase in amplitude relative to background noise may compensate for the effect of an increase in minimum frequency on receiver response. To test this idea, we used a 2 × 2 factorial design of playback experiments to measure male territorial responses to songs that were relatively quiet or loud in relation to typical white-crowned sparrow songs and with lower or higher minimum frequencies within the range of natural white-crowned sparrow songs. Males responded more strongly to relatively louder songs than to quieter songs and more strongly to relatively lower than to higher minimum frequency songs, with the strongest responses to louder songs with relatively lower minimum frequencies. These results indicate that increases in signal amplitude increase signal salience in male–male interactions whether or not increases in amplitude or minimum frequency are more effective at

increasing signal transmission distance in anthropogenic noise (Nemeth and Brumm 2010; Nemeth et al. 2013). Thus, in the context of territoriality and sexual selection, an increase in song amplitude can compensate for losses in signal salience due to higher minimum frequency (Luther et al. 2017). Similar studies are needed to fully ascertain the functional consequences of ‘urbanization’ of songs. In the next section, we highlight the many gaps that still remain to be addressed.

Communication in noise: gaps in knowledge

A complete picture of how anthropogenic noise shapes communication systems requires understanding how signalers and receivers adapt to this new sound environment (Wiley 2013; Wiley 2015). The greatest gap in knowledge in this field is understanding how receivers may be adjusting or evolving in terms of their sensory capabilities and thresholds in noise (Fig. 2). Auditory processing abilities in songbirds vary among species, seasons, sexes, and individuals (Henry et al. 2016). Among species, signal frequency range correlates with the frequency range of best auditory sensitivity (Dooling 1982). Furthermore, species differences in auditory processing can be explained by differences in habitat and in signal complexity (Lucas et al. 2015). Within species, hearing abilities may vary among sexes to the extent that males and females resemble different species (Gall et al. 2013). Moreover, individuals vary on how they hear across seasons (Vélez et al. 2015b; Henry et al. 2016). For example, auditory sensitivity differs between breeding and non-breeding white-crowned sparrow males (Caras et al. 2010). White-crowned sparrows also have remarkable hearing capacity with strong fine-structure processing as well as a broad range of frequencies that they can detect (Lucas et al. 2015; Vélez et al. 2015a), suggesting an ability to adjust to variation in noise levels. The great variation and plasticity of the avian auditory system sets the stage for research on variation in auditory processing across soundscapes. An important first step would be to quantify how auditory processing abilities vary across urban and rural landscapes.

In noisy environments, communication is compromised because the distance over which information in the song can be detected or discriminated is reduced by masking with likely fitness consequences for both signalers and receivers (Bradbury and Vehrencamp 2011). Communication distance is determined by the level and spectral composition of ambient noise, the SPL of the song, song transmission properties in a given soundscape, and the hearing capabilities of the organism in noise (Dooling and Popper 2007b). The most signifi-

cant limiting factor in calculating communication distance is lack of knowledge of individual variation in hearing capabilities across soundscapes. We also know very little about the thresholds receivers set for detections and how they vary in relation to ambient noise. We also do not know how easy it is for individuals to alter their detection thresholds, the range of those alterations, or any associated costs to altering detection thresholds. Generating information about variation in hearing capabilities and detection thresholds will provide a better understanding of how communication systems are responding to soundscape variation and expand our knowledge of adaptations and adjustments by receivers.

There is also much to learn about how and why song traits and signaling behaviors vary with urban noise. For example, other key signaler behaviors still need to be examined, including how birds might adjust their territory size and shape in response to decreases in communication distance in urban areas (Fig. 2). Do birds with shorter communication distances defend smaller territories or have more song posts? Understanding the interplay between signaling behavior, territory size and communication distance would be a fruitful area of exploration. Recent work also clearly demonstrates the high fitness costs of sensory pollutants, including noise, for birds (Halfwerk et al. 2011b; Senzaki et al. 2020), but we still have limited knowledge regarding the extent to which adjustments of signals or signaling behaviors in noise mitigate these fitness costs. There is a clear need to map variation in signaling traits, such as song minimum frequency, onto variation in reproductive success to understand the extent to which these adjustments are adaptive (Rivkin et al. 2019). Similarly, work is needed to understand the potential cross-modal and multimodal effects of sensory pollution along multiple sensory channels, such as chemical pollution, light pollution and noise pollution (Halfwerk and Slabbekoorn 2015). Each of these modes of pollution has the potential to cross into other sensory channels and influence signaling and response behavior. Given these ongoing gaps in knowledge, we foresee many fruitful avenues of future work, even on well-studied phenotypes such as bird song.

There is also a great need for integration among the different questions regarding changes in song such that evolutionary and mechanistic questions can be answered and inform each other. Integration should also incorporate the other senses and proximate cues, such as physiology and pollution to assess how all of these factors affect the behavior, song production and responses of intended receivers. Integrative studies that assess the physiology, behavior, ecology, and evolutionary implications of behavioral adjustments to

urban landscapes will be especially helpful in advancing our knowledge. A potential framework for further advances involves a multipronged approach that includes computer simulations, field experiments, laboratory experiments, an integrative approach to research questions, and a coordinated effort among multiple research teams.

While a plethora of studies have observed that birds, and other taxonomic groups, adjust their vocalizations in the presence of anthropogenic noise (Blickley and Patricelli 2010; Slabbekoorn et al. 2010; Slabbekoorn 2013; Roca et al. 2016), only a small fraction of studies have designed experiments to assess the implications of the song adjustments. In this paper, we highlighted several experiments that get at the function and consequences of these adjustments, but further experiments are required to assess the true cost, if any, of vocal adjustments in urban landscapes. These include operant or copulation solicitation display experiments with females to measure response to variation in song associated with song urbanization; hand-rearing experiments to further understand how noise affects learning and development in general; speaker removal experiments to test more directly the effect of vocal adjustments on song's function as a 'keep out' signal; and playback experiments that test effects of noise on eavesdropping by both intended conspecifics as well as unintended receivers such as conspecific eavesdroppers and predators. For example, increases in song amplitude in the presence of anthropogenic noise could attract more predators, which might put the signaler at greater risk of predation. Further, as we discovered, replicating the same experiments in both urban and rural areas can reveal potential population-level differences in behavioral responses and in the degree of behavioral plasticity within a population (Gentry et al. 2017).

Finally, assessments of the evolution of acoustic communication in urban environments provide an opportunity to test fundamental predictions of signal detection theory such as evolution of a joint optimum, namely a point of coincidence between optimal exaggeration of signals to increase detectability and optimal receiver response thresholds to the exaggerated signals (Wiley 2017). In terms of receivers, signal detection theory also predicts fundamental tradeoffs for receivers in the presence of noise, where errors should increase when ambient noise is louder (Wiley 2004, 2017). For signalers, signal detection theory predicts that they should increase the predictability and redundancy of signals and contrast signals with ambient noise in noisier environments. Signal detection theory also predicts that higher redundancy of signal expression should lead to less exaggeration in signals (Wiley 2017), which could man-

ifest itself through lower vocal performance, or song traits, as well as lead to incipient divergence from signals in less noisy environments. This brings to bear the point that in ecology, noise has come to be viewed as a critical axis of the ecological niche (Senzaki et al. 2020), and more work is needed to assess whether it may also be an important driver in evolutionary processes as well.

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References

- Alberti M. 2015. Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol Evol* 30:114–26.
- Andersson M. 1994. Sexual selection. Princeton, NJ: Princeton University Press.
- Baptista LF. 1975. Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). *Univ Calif Publ Zool* 105:1–52.
- Bennett AF. 1999. Linkages in the landscape: the role of corridors and connectivity in wildlife conservation. Gland, Switzerland and Cambridge, UK: IUCN.
- Bentley JM, Catterall CP, Smith GC. 2000. Effects of fragmentation of araucarian vine forest on small mammal communities. *Conserv Biol* 14:1075–87.
- Berger-Tal O, Wong BB, Candolin U, Barber J. 2019. What evidence exists on the effects of anthropogenic noise on acoustic communication in animals? A systematic map protocol. *Environ Evid* 8:1–7.
- Bermúdez-Cuamatzin E, Delamore Z, Verbeek L, Kremer C, Slabbekoorn H. 2020. Variation in diurnal patterns of singing

- activity between urban and rural great tits. *Front Ecol Evol* 8:246.
- Bermudez-Cuamatzin E, Rios-Chelen AA, Gil D, Garcia CM. 2009. Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use? *Behaviour* 146:1269–86.
- Blickley JL, Patricelli GL. 2010. Impacts of anthropogenic noise on wildlife: research priorities for the development of standards and mitigation. *J Int Wildl Law Policy* 13:274–92.
- Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. Sunderland, MA: Sinauer.
- Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J Anim Ecol* 73:434–40.
- Brumm H, Ritschard M. 2011. Song amplitude affects territorial aggression of male receivers in chaffinches. *Behav Ecol* 22:310–6.
- Brumm H, Slabbekoorn H. 2005. Acoustic communication in noise. *Adv Study Behav* 35:151–209.
- Brumm H, Zollinger SA. 2013. Avian vocal production in noise. In: Brumm H, editor. *Animal communication and noise*. Seewiesen, Germany: Springer Berlin Heidelberg. p. 187–227.
- Caras ML, Brenowitz EA, Rubel EW. 2010. Peripheral auditory processing changes seasonally in gambel's white-crowned sparrow. *J Comp Physiol A Sens Neural Behav Physiol* 196:581–99.
- Cardoso GC, Hu Y. 2011. Birdsong performance and the evolution of simple (rather than elaborate) sexual signals. *Am Nat* 178:679–86.
- 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. *Global Ecol Biogeogr* 29:1430–4.
- Catchpole CK, Slater PJ. 2003. *Bird song: biological themes and variations*. Cambridge: Cambridge University Press.
- Courter JR, Perruci RJ, McGinnis KJ, Rainieri JK. 2020. Black-capped chickadees (*Poecile atricapillus*) alter alarm call duration and peak frequency in response to traffic noise. *PLoS One* 15:e0241035.
- Cummings ME, Endler JA. 2018. 25 years of sensory drive: the evidence and its watery bias. *Curr Zool* 64:471–84.
- Davies NB, Halliday TR. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 274:683–5.
- Derrberry EP, Danner RM, Danner JE, Derrberry GE, Phillips JN, Lipshutz SE, Gentry KE, Luther DA. 2016. Patterns of song across natural and anthropogenic soundscapes suggest that white-crowned sparrows minimize acoustic masking and maximize signal content. *PLoS One* 11:e0154456.
- Derrberry EP, Gentry KE, Derrberry GE, Phillips JN, Danner RM, Danner JE, Luther DA. 2017. White-crowned sparrow males show immediate flexibility in song amplitude but not in song minimum frequency in response to changes in ambient noise levels in the field. *Ecol Evol* 7:4991–5001.
- Derrberry EP, Phillips JN, Derrberry 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* 370:575–9.
- Díaz S, Settele J, Brondízio ES, Ngo HT, Guèze M, Agard J, Arneeth A, Balvanera P, Brauman K, Butchart SH. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. In: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
- Dooling RJ. 1982. Auditory perception in birds. In: Kroodsma DE, Miller EH, editors. *Acoustic communication in birds*. New York: Academic Press. p. 95–130.
- Dooling RJ. 2002. Avian hearing and the avoidance of wind turbines. In: Laboratory NRE, editor. Golden, CO: U.S. Department of Energy Laboratory.
- Dooling RJ, Popper AN. 2007a. The effects of highway noise on birds. Vol. 74. The California Department of Transportation Division of Environmental Analysis. p. 1–74.
- Dooling RJ, Popper AN. 2007b. The effects of highway noise on birds. In: Analysis TCDotDoE, editor. Sacramento, CA: Environmental BioAcoustics LLC. p. 1–74.
- Endler JA. 1993. Some general comments on the evolution and design of animal communication systems. *Phil Trans R Soc B: Biol Sci* 340:215–25.
- Gall MD, Salameh TS, Lucas JR. 2013. Songbird frequency selectivity and temporal resolution vary with sex and season. *Proc R Soc Lond B*. 280:20122296.
- Gascon C, Lovejoy TE, Bierregaard Jr RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S. 1999. Matrix habitat and species richness in tropical forest remnants. *Biol Conserv* 91:223–9.
- Gentry KE, Derrberry EP, Danner RM, Danner JE, Luther DA. 2017. Immediate signalling flexibility in response to experimental noise in urban, but not rural, white-crowned sparrows. *Ecosphere* 8:e01916.
- Gentry KE, Luther DA. 2017. Spatiotemporal patterns of avian vocal activity in relation to urban and rural background noise. *J Ecoacoustics* 1:Z9TQHU.
- Gentry KE, McKenna MF, Luther DA. 2018. Evidence of suboscine song plasticity in response to traffic noise fluctuations and temporary road closures. *Bioacoustics* 27:165–81.
- Gil D, Brumm H. 2014. Acoustic communication in the urban environment: patterns, mechanisms, and potential consequences of avian song adjustments. In: Gil D, Brumm H, editors. *Avian urban ecology*. Oxford: Oxford University Press.
- Gilbert EA, Sompud J, Sompud CB. 2017. A review on the impact of anthropogenic noise on birds. *Borneo Sci* 38:28–35.
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008. Global change and the ecology of cities. *Science* 319:756–60.
- Gross K, Pasinelli G, Kunc HP. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *Am Nat* 176:456–64.
- Halfwerk W, Bot S, Buix J, van der Velde M, Komdeur J, ten Cate C, Slabbekoorn H. 2011a. Low-frequency songs lose their potency in noisy urban conditions. *Proc Natl Acad Sci* 108:14549–54.
- Halfwerk W, Bot S, Slabbekoorn H. 2012. Male great tit song perch selection in response to noise-dependent female feedback. *Funct Ecol* 26:1339–47.
- Halfwerk W, Holleman LJ, Lessells CM, Slabbekoorn H. 2011b. Negative impact of traffic noise on avian reproductive success. *J Appl Ecol* 48:210–9.
- Halfwerk W, Slabbekoorn H. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Anim Behav* 78:1301–7.
- Halfwerk W, Slabbekoorn H. 2015. Pollution going multimodal: the complex impact of the human-altered sensory envi-

- ronment on animal perception and performance. *Biol Lett* 11:20141051.
- Hansen P. 1979. Vocal learning: its role in adapting sound structures to long-distance propagation and a hypothesis on its evolution. *Anim Behav* 27:1270–1.
- Hanski I, Simberloff D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. *Metapopul Biol* 5–26.
- Hardman SI, Zollinger SA, Koselj K, Leitner S, Marshall RC, Brumm H. 2017. Lombard effect onset times reveal the speed of vocal plasticity in a songbird. *J Exp Biol* 220:1065–71.
- Henry KS, Gall MD, Vélez A, Lucas JR. 2016. Avian auditory processing at four different scales: variation among species, seasons, sexes, and individuals. *psychological mechanisms in animal communication*. Berlin: Springer. p. 17–55.
- Hu Y, Cardoso GC. 2009. Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behav Ecol* 20:1268–73.
- Hu Y, Cardoso GC. 2010. Which birds adjust the frequency of vocalizations in urban noise? *Anim Behav* 79:863–7.
- Ibáñez-Álamo JD, Rubio E, Benedetti Y, Morelli F. 2017. Global loss of avian evolutionary uniqueness in urban areas. *Global Change Biol* 23:2990–8.
- LaZerte SE, Slabbekoorn H, Otter KA. 2016. Learning to cope: vocal adjustment to urban noise is correlated with prior experience in black-capped chickadees. *Proc R Soc B: Biol Sci* 283:20161058.
- 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* 75:1–9.
- Lucas JR, Velez A, Henry KS. 2015. Habitat-related differences in auditory processing of complex tones and vocal signal properties in four songbirds. *J Comp Physiol A Sens Neural Behav Physiol* 201:395–410.
- Luther D, Baptista L. 2010. Urban noise and the cultural evolution of bird songs. *Proc R Soc B: Biol Sci* 277:469–73.
- Luther DA, Danner RM, Danner JE, Gentry KE, Derryberry EP. 2017. The relative response of songbirds to shifts in song amplitude and song minimum frequency. *Behav Ecol* 28:391–7.
- Luther DA, Derryberry EP. 2012. Birdsongs keep pace with city life: changes in song over time in an urban songbird affect 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 performance and potency in communication. *Behav Ecol* 27:332–40.
- Lynch A. 1996. The population memetics of birdsong. In: Kroodsma DE, Miller EH, editors. *Ecology and evolution of acoustic communication in birds*. Ithaca, NY: Comstock Pub. p. 181–97.
- Marler P, Tamura M. 1962. Song “dialects” in three populations of white-crowned sparrows. *Condor* 64:368–77.
- McDonald RI, Güneralp B, Huang C-W, Seto KC, You M. 2018. Conservation priorities to protect vertebrate endemics from global urban expansion. *Biol Conserv* 224:290–9.
- McIntyre S, Hobbs R. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conserv Biol* 13:1282–92.
- McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–60.
- Møller AP. 2011. Song post height in relation to predator diversity and urbanization. *Ethology* 117:529–38.
- Morton ES, Gish SL, van der Voort M. 1986. On the learning of degraded and undegraded songs in the Carolina Wren. *Anim Behav* 34:815–20.
- Moseley DL, Derryberry GE, Phillips JN, Danner JE, Danner RM, Luther DA, Derryberry EP. 2018. Acoustic adaptation to city noise through vocal learning by a songbird. *Proc R Soc B* 285:20181356.
- Moseley DL, Phillips JN, Derryberry EP, Luther DA. 2019. Evidence for differing trajectories of songs in urban and rural populations. *Behav Ecol* 30:1734–42.
- Munding PC. 1980. Animal cultures and a general theory of cultural evolution. *Ethol Sociobiol* 1:183–223.
- Narango DL, Rodewald AD. 2016. Urban-associated drivers of song variation along a rural–urban gradient. *Behav Ecol* 27:608–16.
- Nemeth E, Brumm H. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *Anim Behav* 78:637–41.
- Nemeth E, Brumm H. 2010. Birds and anthropogenic noise: are urban songs adaptive? *Am Nat* 176:465–75.
- Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Miranda AC, Brumm H. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proc R Soc B: Biol Sci* 280:20122798.
- Noss RF. 1987. Corridors in real landscapes: a reply to simberloff and cox. *Conserv Biol* 1:159–64.
- Patricelli GL, Blickley JL. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* 123:639–49.
- Perillo A, Mazzoni LG, Passos LF, Goulart VD, Duca C, Young RJ. 2017. Anthropogenic noise reduces bird species richness and diversity in urban parks. *Ibis* 159:638–46.
- Peters S, Derryberry EP, Nowicki S. 2012. Songbirds learn songs least degraded by environmental transmission. *Biol Lett* 8:736–9.
- Phillips JN, Derryberry EP. 2017a. Equivalent effects of bandwidth and trill rate: support for a performance constraint as a competitive signal. *Anim Behav* 132:209–15.
- Phillips JN, Derryberry EP. 2017b. Vocal performance is a salient signal for male–male competition in white-crowned sparrows. *Auk* 134:564–74.
- Phillips JN, Derryberry EP. 2018. Urban sparrows respond to a sexually selected trait with increased aggression in noise. *Sci Rep* 8:7505.
- Podos J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51:537–51.
- Podos J, Lahti DC, Moseley DL. 2009. Vocal performance and sensorimotor learning in songbirds. *Adv Study Behav* 40:159–95.
- Polak M. 2014. Relationship between traffic noise levels and song perch height in a common passerine bird. *Transport Res D: Transport Environ* 30:72–5.
- Reichard DG, Atwell JW, Pandit MM, Cardoso GC, TD Price, Ketterson ED. 2020. Urban birdsongs: higher minimum song frequency of an urban colonist persists in a common garden experiment. *Anim Behav* 170:33–41.

- Ricketts TH, Daily GC, Ehrlich PR, Fay JP. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conserv Biol* 15: 378–88.
- Ríos-Chelén AA, Cuatrecasas-Lima C, Bautista A, Martínez-Gómez M. 2018. No reliable evidence for immediate noise-induced song flexibility in a suboscine. *Urban Ecosyst* 21:15–25.
- Ripmeester EAP, Kok J, van Rijssel J, Slabbekoorn H. 2010. Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European blackbirds. *Behav Ecol Sociobiol* 64:409–18.
- Ritschard M, Riebel K, Brumm H. 2010. Female zebra finches prefer high-amplitude song. *Anim Behav* 79:877–83.
- Rivkin LR, Santangelo JS, Alberti M, Aronson MF, de Keyser CW, Diamond SE, Fortin MJ, Frazee LJ, Gorton AJ, Hendry AP. 2019. A roadmap for urban evolutionary ecology. *Evol Appl* 12:384–98.
- Roca IT, Desrochers L, Giacomazzo M, Bertolo A, Bolduc P, Deschesnes R, Martin CA, Rainville V, Rheault G, Proulx R. 2016. Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behav Ecol* 27: 1269–74.
- Searcy WA. 1996. Sound-pressure levels and song preferences in female red-winged blackbirds (*Agelaius phoeniceus*) (Aves, Emberizidae). *Ethology* 102:187–96.
- Senzaki M, Barber JR, Phillips JN, Carter NH, Cooper CB, Ditmer MA, Fristrup KM, McClure CJ, Mennitt DJ, Tyrrell LP. 2020. Sensory pollutants alter bird phenology and fitness across a continent. *Nature* 587:605–9.
- Seto KC, Güneralp B, Hutyra LR. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc Natl Acad Sci* 109:16083–8.
- Shochat E, Warren PH, Faeth SH, McIntyre N, Hope D. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol Evol* 21:186–91.
- 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, Bouton N, van Opzeeland I, Coers A, ten Cate C, Popper AN. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends Ecol Evol* 25: 419–27.
- Slabbekoorn H, den Boer-Visser A. 2006. Cities change the songs of birds. *Curr Biol* 16:2326–31.
- Smith TB, Bernatchez L. 2008. Evolutionary change in human-altered environments. *Mol Ecol* 17:1–8.
- Snell-Rood EC. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim Behav* 85:1004–11.
- Swaddle JP, Francis CD, Barber JR, Cooper CB, Kyba CCM, Dominoni DM, Shannon G, Aschehoug E, Goodwin SE, Kawahara AY et al. 2015. A framework to assess evolutionary responses to anthropogenic light and sound. *Trends Ecol Evol* 30:550–60.
- Vélez A, Gall MD, Fu J, Lucas JR. 2015a. 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.
- Vélez A, Gall MD, Lucas JR. 2015b. Seasonal plasticity in auditory processing of the amplitude envelope and temporal fine structure of sounds in three songbirds. *Anim Behav* 103:53–63.
- Verzijden M, Ripmeester E, Ohms V, Snelderwaard P, Slabbekoorn H. 2010. Immediate spectral flexibility in singing chaffinches during experimental exposure to highway noise. *J Exp Biol* 213:2575–81.
- Wiley RH. 2013. A receiver-signaler equilibrium in the evolution of communication in noise. *Behaviour* 150:957–93.
- Wiley RH. 2015. *Noise matters: the evolution of communication*. Cambridge, MA: Harvard University Press.
- Wiley RH. 2017. How noise determines the evolution of communication. *Anim Behav* 124:307–13.
- Zollinger SA, Brumm H. 2011. The Lombard effect. *Curr Biol* 21:R614–5.
- Zollinger SA, Slater PJB, Nemeth E, Brumm H. 2017. Higher songs of city birds may not be an individual response to noise. *Proc R Soc B: Biol Sci* 284:20170602.