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CHAPTER 5

ACOUSTIC SPACE IS AFFECTED BY ANTHROPOGENIC HABITAT FEATURES: IMPLICATIONS FOR AVIAN VOCAL COMMUNICATION

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ABSTRACT.—Human-altered landscapes often include structural features, such as higher levels of impervious surface cover (ISC) and less vegetation, that are likely to affect the transmission of avian vocalizations. We investigated the relationships between human habitat modifications and signal transmission by measuring four acoustic parameters—persistence, reverberation, and signal-to-noise ratio (SNR) of broadcast tones, as well as absolute ambient noise level—in each of 39 avian breeding territories across an anthropogenic disturbance gradient. Using a geographic information system, we quantified the amounts of different habitat features (e.g., ISC, grass, trees) at each site; a principal component analysis was used to identify which of these habitat features commonly co-occurred (e.g., "habitat suites"). Finally, we used a model selection process to explore whether the habitat suites predicted the acoustic parameters. Tone persistence was higher and reverberation was lower in more open, grassy habitats than in areas with more vertical anthropogenic structures. In more human-modified sites, ambient noise levels were higher, leading to lower SNR. In habitats with low levels of human modification, we found that even small increases in the total amount of open–grassy area will quickly improve the acoustic space of singing birds. However, our results also indicated that there may be a critical level of human habitat modification above which the addition of "natural" areas does not benefit avian communication. Thus, we recommend that managers focus their efforts on preserving pre-existing "natural" habitat, rather than attempting to introduce it into areas that have already received significant human modification.

Key words: bird song, disturbance, impervious surface, secondary cavity nester, sound propagation.

El Espacio Acústico es Afectado por Características Antropogénicas del Hábitat: Implicaciones para la Comunicación de Aves Locales

RESUMEN.—Generalmente, los paisajes afectados por el ser humano incluyen características estructurales, como altos niveles de cobertura de superficies impenetrables (CSI) y menor vegetación, que probablemente pueden afectar la transmisión de las vocalizaciones de las aves. Investigamos la relación entre las modificaciones humanas del hábitat y la transmisión de las señales midiendo cuatro parámetros acústicos –persistencia, reverberación, y el cociente señal-ruido (CSR) de tonos transmitidos, así como el nivel absoluto de ruido ambiental– en cada uno de 39 territorios reproductivos de aves a lo largo de un gradiente de disturbio antropogénico. Mediante sistemas de información geográfica, cuantificamos las cantidades de diferentes atributos del hábitat (e.g., CSI, pastos, árboles) en cada sitio. Hicimos un análisis de componentes

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principales para identificar cuáles de estas características del hábitat coexisten comúnmente (e.g., "compartimentos de hábitat"). Finalmente, usamos un proceso de selección de modelos para explorar si los compartimentos de hábitat predecían los parámetros acústicos. La persistencia de los tonos fue mayor y la reverberación fue menor en hábitats abiertos y dominados por pastos que en áreas con más estructuras antropogénicas verticales. En sitios con mayor modificación humana los niveles de ruido ambiental fueron mayores, lo que condujo a un menor CSR. En hábitats con bajos niveles de modificación humana encontramos que incluso pequeños incrementos en la cantidad total de áreas abiertas y con pastos podría mejorar rápidamente el espacio acústico de las aves canoras. Sin embargo, nuestros resultados también indican que podría haber un nivel crítico de modificación humana del hábitat, por encima del cual la adición de áreas "naturales" no beneficiaría la comunicación de las aves. Entonces, recomendamos que los administradores concentren sus acciones en preservar el hábitat "natural" preexistente, en vez de intentar introducirlo en áreas que ya hayan sufrido una modificación sustancial del hábitat.

Physical ecology plays an important role in shaping vocal signals (Wiley and Richards 1978). This stems predominantly from the ways in which ecological conditions—including temperature, humidity, air turbulence, and the presence or absence of structures with varying acoustic properties—affect sound degradation. Degradation is the process by which a signal undergoes changes while traveling from a signaler to a receiver (Morton 1975); it arises as a result of attenuation (the loss of intensity of a signal, such as occurs through absorption) and scattering (changes in the paths of sound waves due to reflection, refraction, and/or diffraction; Wiley and Richards 1978). Over time, the signals that propagate most efficiently despite degradation will be favored within populations (Hauser 1997, Wiley 2006) because they will be most effective at eliciting the intended response. However, as the environment continues to change, animals should also change their vocalizations in order to maintain their suitability within a given habitat (Derryberry 2007, 2009).

The primary ecological factors that affect signal design include habitat type (e.g., forest–closed or grassland–open; Morton 1975) and the height of and distance between signalers and receivers (Nemeth et al. 2001, Padgham 2004, Brumm and Naguib 2009). Both the presence and spectral characteristics of ambient noise will also influence signal design: Acoustically communicating organisms should evolve signals that reduce masking, the process by which a more intense sound (e.g., ambient noise) obscures a less intense sound (e.g., a song or call) occurring within the same frequency range.

In general, animals' vocalizations are tailored to environmental conditions in order to maximize signal efficacy (Morton 1975, Marten and Marler 1977, Marten et al. 1977, Wiley and Richards

1978); disruptions to the habitat may therefore affect vocal communication. One disruption that has received much recent attention is human disturbance—in particular, anthropogenic noise and human habitat (as reviewed in Rabin et al. 2003, Patricelli and Blickley 2006, Slabbekoorn and Ripmeester 2008). Despite the fact that human expansion is occurring at an unprecedented rate (Goines and Hagler 2007), little is known about sound propagation in these growing areas of anthropogenically modified habitat, though several studies have examined whether, and how, birds may modify their songs in response to the presence of human noise (Fernández-Juricic et al. 2005, Brumm 2006, Slabbekoorn and den Boer-Visser 2006, Wood and Yezerinac 2006, Bermúdez-Cuamatzin et al. 2009, Nemeth and Brumm 2009). Many authors have suggested management techniques for mitigating the impacts of anthropogenic noise (Katti and Warren 2004, Warren et al. 2006, Habib et al. 2007, Slabbekoorn and Ripmeester 2008). However, these proposals fail to address the possibility that physical habitat modifications may also place selective pressures on vocal parameters by altering the way in which sound propagates through the habitat, or the potential of sound propagation characteristics within human-altered areas to fall within the range of those occurring in more "natural" environments.

Here, we examine acoustic properties of avian breeding territories that surround nest boxes distributed across an anthropogenic disturbance gradient in Williamsburg, Virginia. These boxes have been occupied by a variety of secondary cavity-nesting passerines, most notably the Eastern Bluebird (*Sialia sialis*), Carolina Chickadee (*Poecile carolinensis*), and House Wren (*Troglodytes aedon*), which our research group has previously studied in the context of direct anthropogenic

disturbance (Kight 2005, Kight and Swaddle 2007) and land use (LeClerc et al. 2005). Focusing only on active nest boxes, we examined three propagation characteristics (specifically, tone persistence, reverberation, and signal-to-noise ratio, described in further detail below) at each of three frequencies, at four different distances, in each of the four cardinal compass directions within the nest-box territory. We also measured absolute noise levels at each distance in each direction. Further, we employed a geographic information system (GIS) to digitize orthorectified aerial photographs of each territory so that we could relate propagation measurements and ambient noise levels to specific suites of structures and materials found within the acoustic space of each habitat.

It is our intention that the data from this study serve two purposes. First, it will illuminate whether, and how, human habitat modifications can affect the sound environment of birds. This information is essential not only for understanding the ways in which human activities might shape further evolution of avian communication, but also for developing adequate management plans, because birds often rely on vocal communication for maintenance of breeding, social, territorial, foraging, and anti-predatory activities. Second, we hope to promote the view that habitat types should be considered along a continuous gradient, rather than as dichotomous endpoints (traditionally "closed" vs. "open," or "urban" vs. "rural"). To understand the impact of noise on avian populations, we need to develop questions and studies that encompass an entire rural–urban gradient, because many avian habitats will lie between the currently studied extremes.

Methods

"Study species" and site description.—Our study was designed to investigate the acoustic properties of nest-box territories that were distributed across a disturbance gradient around Williamsburg; more detailed geographic information can be found elsewhere (Kight 2005, LeClerc et al. 2005, Kight and Swaddle 2007). Since 2003, we have studied three secondary cavity-nesting species breeding in these boxes: Eastern Bluebirds, Carolina Chickadees, and House Wrens. Although the research presented here has no study species, per se, the protocols were designed with these species in mind, with the goal of examining the sound propagation results within the context of these birds' life histories and, therefore, making our results more biologically meaningful. In cases where life-history differences precluded the possibility of choosing a methodology that allowed broad application to each of the "study species," we chose protocols based on the behaviors of Eastern Bluebirds, our primary species of interest.

Territories were located in a variety of sites, including parks, golf courses, campuses, cemeteries, and roadsides. Accordingly, habitat features and layouts differed greatly; there was much variation in the openness of the habitat, the number and type of anthropogenic features, and the distance to the nearest acoustically significant structure (Kight 2005, LeClerc et al. 2005, Kight and Swaddle 2007). This variation is typical of our study species' territories, which, historically, have been found along habitat edges and in areas undergoing rapid succession (Gowaty and Plissner 1998, Johnson 1998, Mostrom et al. 2002).

Sound propagation recordings.—We conducted playback recordings at 39 nest boxes during the 2007 breeding season (March–August). All recordings were collected between 0800 and 1800 hours on days with little or no wind. Recordings were collected either prior to nest-box occupation or after completion of breeding, thus minimizing disturbance to the animals. Because the acoustic characteristics evaluated here are influenced by permanent physical structures in the environment, differences in collection date, in relation to box occupation date, should not substantially alter our ability to interpret how sound propagation might affect resident breeding birds. This includes natural structures, such as trees and shrubs that were fully leaved at the time of all recordings. Although we originally intended to record weather conditions associated with each collected recording, we had technical problems midway through the season and were not able to resume measurement of temperature, wind speed, or humidity thereafter. However, we devised an alternative way of measuring, and therefore controlling for, variations in weather conditions (see below).

We used NCH TONE GENERATOR (NCH Software, Greenwood Village, Colorado) to create 0.1-s clips of pure tones at 3, 5, and 7 kHz. These tones were arranged into a master playback file consisting of 10 repeats of the following sequence: 3 kHz tone, 2 s silence, 5 kHz tone, 2 s silence, 7 kHz tone, and 2 s silence. Using a decibel meter (model 407727; Extech Instruments, Waltham, Massachusetts) and RAVEN PRO, version 1.3,

acoustic software (Cornell Lab of Ornithology, Ithaca, New York), we calibrated our recording instruments (Sennheiser ME65 directional microphone with windscreen, Marantz PMD 660 solid state recorder, Sony SRS T70 personal travel speakers, and an Apple iPod). We also determined and marked an appropriate volume setting on the iPod in order to consistently play tones at 65 dB at 1 m from the speakers, because a random sampling of singing males in our territories showed this to be the median amplitude of vocal performances (Kight 2010).

Because individuals of all three focal species actively defend at least a 50-m-radius area around their nest boxes, and because behaviors during the breeding season are focused around frequent nest visits, we assumed that the box location would be a fairly accurate representation of the center of the birds' acoustic space. Therefore, this was the point of broadcast for the sequence of pure tones, which we delivered via the speakers after mounting them at the top of a 3-m pole in order to simulate an average perch height (Gowaty and Plissner 1998). Likewise, we recorded the playback with the microphone mounted at the top of an identical pole. Recordings were collected along a transect at distances of 20, 40, 60, and 80 m from the nest. These values reflect typical distances to a nearby mate, an intruding bird, the edge of a neighbor's territory, and halfway into a neighbor's territory, respectively. We made recordings at each set of distances in each of the four cardinal compass directions, beginning at east and working clockwise through north. The broadcasting speakers always pointed directly at the receiving microphone.

Although we attempted to position the microphone as accurately as possible, we occasionally encountered environmental barriers such as trees or parked cars. In order to accommodate these structures, we allowed ourselves ±5 m of flexibility at each recording point. In eight sites, we could not position the microphone within the intended areas at all directions and distances around the nest box (because of bodies of water, large buildings, and busy roads); hence, these eight sites had incomplete sound-propagation data sets.

We also collected near-field recordings in an open, grassy area of habitat near the center of each territory, with the speakers positioned 3 m from the microphone. Because signal amplitude and distance were held constant across all sites, any differences among these recordings should

be due to atmospheric conditions (e.g., temperature and humidity). We used this measure as a covariate to control for weather in further analyses (see below).

All recordings were analyzed in RAVEN PRO. We quantified three values to describe environmental degradation of tones. (1) "Persistence" is the ratio of the strength of tone at each distance versus the strength of the reference tone recorded at 3 m. Higher values of persistence indicate better maintenance of the signal as it travels through the environment and, therefore, an increased likelihood that the signal will reach its intended target. (2) "Reverberation" is the ratio of the strength of the "tail" (or echo) after each tone and the strength of the preceding tone. Higher values of reverberation indicate that the signal is encountering more reflective surfaces as it travels through the environment. This may overlap with elements of longer signals, which may obscure them or join with them to make the signal seem artificially strong (Slabbekoorn et al. 2002). (3) Signal-to-noise ratio (SNR) is the ratio of the strength of the tone and the strength of the background noise (Dabelsteen et al. 1993, Blumenrath and Dabelsteen 2004, Slabbekoorn et al. 2007; Fig. 1). Higher values of SNR indicate signals that are easier to differentiate from the background noise, which means that they are more likely to elicit responses from receivers.

In all cases, "strength" denotes RMS amplitude that we converted into dB SPL (hereafter "dB"), for easier interpretation in a real-world context (Brumm et al. 2009). Additionally, we used the values of noise calculated while determining SNR to investigate whether absolute ambient noise level was related to specific suites of microhabitat features.

For the analyses, all recordings were bandpass filtered at values 1 kHz below and above the focal tone; in other words, for a 3-kHz tone, all sounds between 2 and 4 kHz passed through the filter unchanged, whereas all frequencies <2 kHz and >4 kHz were attenuated. Environmental noise was evaluated across a 0.03-s selection of ambient noise preceding the focal tone by 0.05 s. This value was then used to calculate the strength of the tone itself. In order to measure the strength of the focal tone, we measured RMS amplitude within a 0.05-s recording selection taken from the middle of the 0.1-s tone. Finally, we measured the strength of the tone's reverberation within another 0.03-s selection beginning 0.03 s after
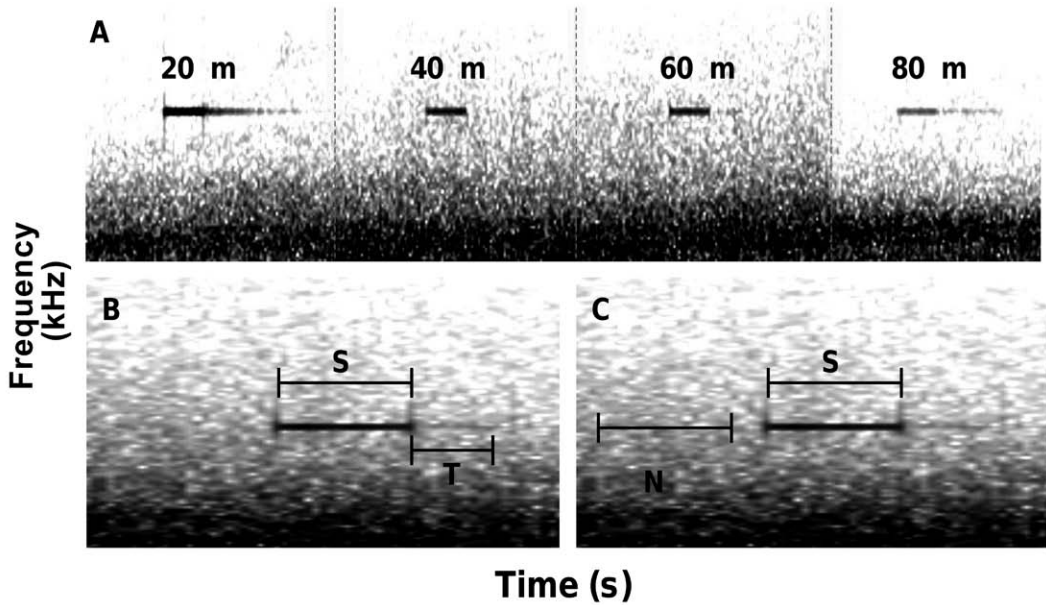
Fig. 1. Illustrations of sound information generated in our study. (A) Reverberation at different distances between the transmitting speaker and receiving microphone. (B) An example of the tone signal (S) and the tail of this signal (T). (C) An example of ambient noise (N) in relation to S.

the end of the tone. The two 0.03-s lengths were chosen because this is approximately the average length of an Eastern Bluebird song syllable (Kight 2010); thus, this is the period over which a bird might have the opportunity to evaluate its acoustic environment and adjust its song accordingly, as well as the period after which reverberations might affect song performance (Slabbekoorn et al. 2002). The 0.05-s selection length was chosen to avoid distortions present at either end of the tone, which was not ramped.

Habitat evaluation.—We used ARCGIS, version 9.3.1 (ESRI, Redlands, California), to digitize recently photographed and orthorectified aerial images of each habitat, according to the following categories: short impervious surface (including roads, sidewalks, and short walls <3 m in height), short vegetation (including shrubs and grass), tall impervious surface (including structures such as buildings and lamp posts >3 m), trees (forest and ornamental), and water (Korte 2001). Habitat features were ground-truthed in all territories. Because sound propagates spherically, sound waves can be attenuated or reflected by habitat features placed outside of the direct line between the broadcasting speakers and receiving microphone. Therefore, for each directional set of recordings, we evaluated habitat within a 90°

wedge centered on the cardinal direction. At each recording distance, we measured the amount of each type of habitat present between the speaker and the microphone; thus, evaluations of the 40-, 60-, and 80-m wedges are cumulative. Furthermore, an additional 10 m of habitat was evaluated at each distance in order to account for the fact that sound travels fast enough to bounce off objects behind the microphone before being recorded. This means, for instance, that habitat values for the 20-m wedge actually reflect features that occurred within 30 m of the nest box.

Because previous studies have already examined the effects of particular environmental features on signal propagation, we were interested in focusing on the effects of entire habitats (e.g., "more human-disturbed" or "less human-disturbed"). This is also more realistic, because there is multicollinearity among the ecological variables recorded here. Thus, we used a principal component analysis (PCA) to determine which suites of habitat features commonly co-occur across the disturbance gradient examined here. These are reflected in the principal components (PCs) generated by the analysis. Principal component analysis also reduces the number of variables that need to be considered when determining the best-fit model, which not only saves time when analyzing

the models, but also decreases the chance of finding significant results simply because a large number of variables was entered into the analysis.

Our PCA generated two PCs with λ > 1.0, cumulatively explaining 61.4% of the total variance (Table 1). Habitat PC1, which explained 35.8% of the variance, loaded strongly positively for total area of short vegetation, and strongly negatively for total area of trees. This combination of characteristics, which is common among the more "natural" territories of our three focal species, are hereafter referred to as "total area open–grassy habitat." Habitat PC2, which explained 28.3% of the variance, loaded strongly positive for both tall and short impervious surface. Because impervious surface is a product of human construction, we have called this variable "total area human-modified habitat."

Statistical analyses.—We utilized an information-theoretic model selection approach (Burnham and Anderson 2002) to evaluate how suites of habitat characteristics affect sound propagation. For each dependent variable, a candidate set of models was determined *a priori*. Because several breeding territories were within a single, larger breeding site, all analyses included "site" as a random variable in order to minimize pseudoreplication. "Weather" was also included in all analyses in order to control for the effects of temperature and humidity on sound propagation. "Distance" was included only in models intended to explain persistence and reverberation, because neither SNR nor ambient noise was measured in comparison to a baseline near-field recording and, thus, would not be expected to change with increasing distance from the speakers. All models contained terms for habitat characteristics, as well as two-way and three-way interactions between habitat, frequency, and distance, as appropriate. We predicted that signal persistence would be highest for lower-frequency tones, over shorter distances, and in open environments with relatively

more soft surfaces (e.g., habitat PC1). We expected to find the highest levels of reverberation among lower-frequency tones, over shorter distances, and in environments with more hard surfaces (e.g., habitat PC2). Finally, we predicted that SNR would be lowest in territories with the most anthropogenic (hard) features (e.g., habitat PC2). Likewise, these are the environments where we also expected to find the highest levels of ambient noise.

Prior to statistical analyses, distributions of all variables were checked for normalcy and transformed, where appropriate. We used SPSS, version 15 (SPSS, Chicago, Illinois), to run generalized linear mixed models in order to determine Akaike's information criterion (AIC) for each model. These values were used to calculate AIC_c (which adjusts AIC for small sample sizes) and ΔAIC_c (the difference between the model with the lowest AIC_c and each subsequent model). Models with ΔAIC_c scores within 4.0 of the nearest model were considered to have strong support and were assigned Akaike weights (w_i) to quantify the degree of support for each model (Burnham and Anderson 2002). We used all candidate models with Akaike weights to calculate model-averaged variable coefficients (Mitchell 2008). We also calculated the standard error (SE) associated with each model parameter, which allowed us to visualize the likely range of values that our estimated parameters could take; where this range overlapped with 0, we concluded there was little evidence for the effect of a predictor variable. This is similar to calculating 95% confidence intervals (CIs) and evaluating odds ratios. However, CIs are generally used in conjunction with *P* values, which we did not generate as part of our information-theoretic approach. Thus, we determined that it was more appropriate to use SE in the current analysis.

In order to visualize the relationships between sound propagation variables and interaction terms, we categorized one variable in the interaction term

TABLE 1. Loading factors for principal component analysis of habitat features around each territory's nest box (PC = principal component in the principal component analysis).

Variable	PC1 (35.8% of variance)	PC2 (28.3% of variance)
Short impervious surface (<3 m)	0.183	0.777
Short vegetation (grass, shrubs)	0.882	−0.352
Tall impervious surface (>3 m)	0.157	0.733
Trees (forest and ornamental)	−0.974	−0.85
Water	0.080	−0.375

as "high" or "low," in relation to median values. This allowed us to plot separate trend lines (e.g., persistence in open–grassy habitats with low levels of human modification vs. persistence in open–grassy habitats with high levels of human modification) in order to compare the direction and strength of each relationship. These categories were not used in any statistical analyses but are useful for illustrating the effects of the interaction terms.

Results

We sampled the relationships between acoustics and habitat at a total of 1,872 points across 39 breeding territories. Considering our data from the perspective of a male Eastern Bluebird, whose songs occur at ~3 kHz and whose vocal signals are used to defend a territory that extends ≥50 m in radius from his nest box, the following are the average acoustic conditions (in absolute, unitless values): signal persistence falls between a minimum of 6.0×10^{-5} and a maximum of 1.4×10^{-3}, with an average of 4.6×10^{-4}. The expected reverberation of a vocal signal ranges from zero to 1.3×10^{-3}, with an average of 2.1×10^{-4}. The SNR falls between zero and 1.17, with an average of 3.4×10^{-2}. Finally, environmental noise ranges from 18.4 dB (comparable to rustling leaves or a quiet conversation) to 67.4 dB (comparable to street noise caused by passenger cars, when heard from ~25 m away), with an average amplitude of 38.1 dB (comparable to a quiet home or office).

Associations between habitat and signal persistence.—Two models were within 4 ΔAIC$_c$ units of each other and best explained the effects of environment on the persistence of tone strength (Table 2).

Table 2. Models constructed to explore the association between habitat (PC = principal component in the principal component analysis) and persistence of pure tones. K is the number of parameters in the model, including the intercept and the residual; AIC$_c$ is Akaike's information criterion corrected for small sample size; ΔAIC$_c$ is the difference in AIC$_c$ value when compared with the top-ranking model; and w_i is the Akaike weight.

Model	K	Parameters	AIC$_c$	ΔAIC$_c$	w_i	Likelihood
1	8	Frequency, weather, distance, PC1, PC2, PC1*PC2	1,166.3	0	0.773	1
2	9	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1	1,168.7	2.48	0.224	0.289
3	10	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2	1,177.3	11.07	0.0031	0.0040
4	11	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1	1,184.2	17.97	9.7×10^{-5}	0.0001
5	12	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance	1,191.1	24.81	3.2×10^{-6}	4.1×10^{-6}
6	13	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2	1,198.5	32.26	7.7×10^{-8}	9.9×10^{-8}
7	14	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2	1,209.6	43.33	3×10^{-10}	3.9×10^{-10}
8	15	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2, frequency*distance* PC2	1,222.2	56.00	5.4×10^{-13}	6.9×10^{-13}
9	16	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2, frequency*distance* PC2, frequency*distance*PC1	1,235.7	69.48	6.3×10^{-16}	8.2×10^{-16}
10	17	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2, frequency*distance* PC2, frequency*distance*PC1, frequency*PC1*PC22	1,242.8	76.53	1.9×10^{-17}	2.4×10^{-17}

Frequency, distance, PC1 (total area open–grassy habitat), PC2 (total area human-modified habitat), and the interaction term PC1*PC2 appeared in both models; the second-most-supported model also included the interaction term PC1*distance. In the final, averaged model, the SEs for all terms were <0.001 and none of the SE ranges overlapped with zero (Table 3).

Persistence was highest at lower frequencies and shorter distances, as expected. There was a positive relationship between PC1 (total area open–grassy habitat) and persistence, indicating that the power of tones was better preserved in increasingly open areas with fewer obstacles in the habitat. There was a corresponding negative relationship between persistence and PC2 (total area human-modified habitat), indicating higher attenuation in sites with more impervious surface.

As indicated by the presence of two interaction terms in the final model, signal persistence is influenced by complex interactions of multiple environmental variables. In our territories, persistence increased slightly more rapidly over shorter distances (20 and 40 m) than over longer distances (60 and 80 m) as the amount of PC1 (total area open–grassy habitat) increased (Fig. 2A). Additionally, increases in the amount of open–grassy habitat in areas with less human modification leads to more rapid increases in persistence than in territories where there are higher levels of human-modified habitat (Fig. 2B).

Associations between habitat and signal reverberation.—Three models were within 4 ΔAIC_c units of each other and best explained the effects of environment on reverberation (Table 4). Both distance and PC1 (total area open–grassy habitat) appeared in all three models, and PC2 (total area human-modified habitat) appeared in two

of three models. In the final, averaged model, the SEs for all habitat terms were <0.003 and none of the ranges overlapped with zero (Table 5).

As expected, reverberation increased with increasing distance between the microphone and the sound source. Reverberation decreased in territories with more total area open–grassy habitat (PC1). However, it increased in human-modified habitats (PC2), which contained more vertical structures and acoustically harder surfaces.

Reverberation was also influenced by an interaction between the two habitat types. Where there were low levels of human modification (PC2), even small increases in the amount of open–grassy habitat (PC1) led to substantial decreases in reverberation. However, in areas with high levels of human modification, reverberation remained fairly stable regardless of how much open–grassy habitat was present (Fig. 2C).

Associations between habitat and SNR.—Two models were within 4 ΔAIC_c units of each other and best explained the effects of habitat on SNR (Table 6). Both models included frequency and the two habitat PCs. In the final, averaged model, the SEs for all habitat and acoustic terms were <0.01 and none of the ranges overlapped zero (Table 7).

Signal-to-noise ratio was positively related to frequency, with 7-kHz tones possessing the greatest SNR, and was also positively related to PC1 (total area open–grassy habitat), indicating that signals are most detectable to receivers in open, grassy territories. On the other hand, SNR was negatively related to PC2 (total area human-modified habitat), which suggests that signals are least detectable to receivers that spend time in territories with higher quantities of human modifications.

TABLE 3. Parameters included in the final, averaged model explaining the relationship between tone persistence and environment (PC = principal component in the principal component analysis). B is slope of the relationship between each explanatory variable and persistence.

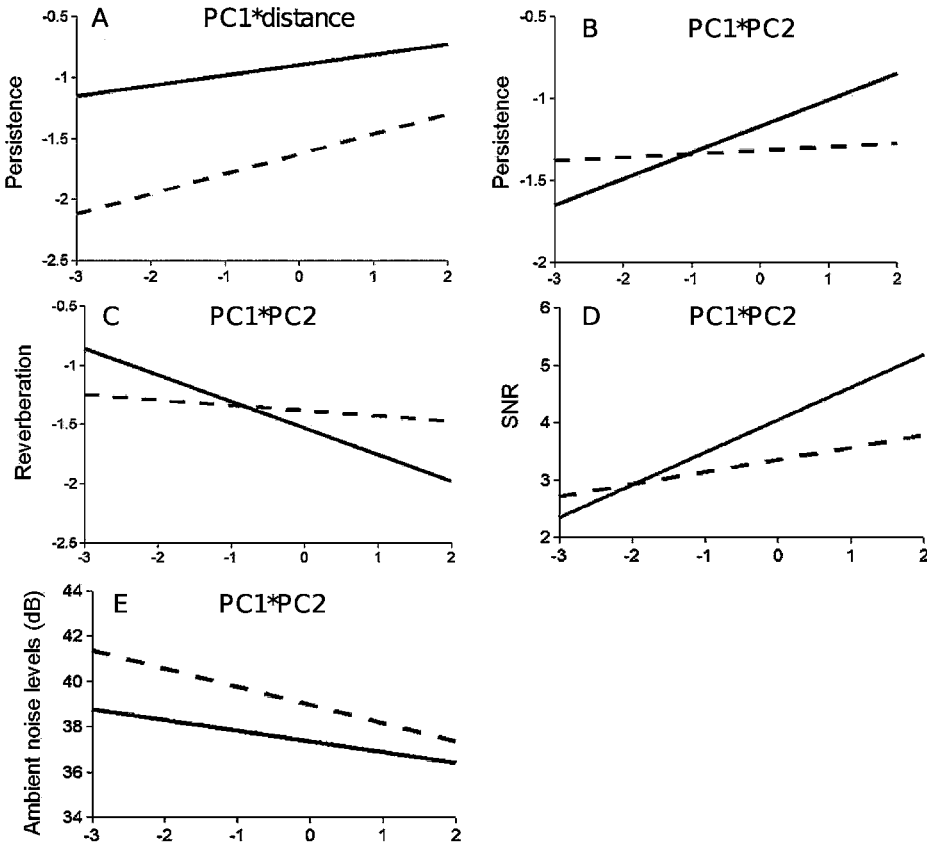| Parameter	B	SE	$B \pm SE$	
			Lower	Upper
PC1 (total area open–grassy habitat)	0.081	0.001	8.03×10^{-2}	8.25×10^{-2}
Frequency	–0.060	0.0002	-5.95×10^{-2}	-5.91×10^{-2}
PC1*PC2	–0.046	0.0004	-4.60×10^{-2}	-4.52×10^{-2}
Distance	–0.017	1.55×10^{-5}	-1.58×10^{-2}	-1.68×10^{-2}
PC2 (total area human-modified habitat)	–0.015	0.0004	-1.55×10^{-2}	-1.47×10^{-2}
Distance*PC1	0.0005	2.14×10^{-5}	4.49×10^{-4}	4.91×10^{-4}
Weather	2.2×10^{-5}	5.02×10^{-7}	2.15×10^{-5}	2.25×10^{-5}

FIG. 2. Visualization of the interactions between acoustic variables and environmental interaction terms in principal component analysis. (A) Persistence regressed against principal component 1 (PC1, total area open–grassy habitat) at low (solid lines) and high (dashed lines) levels of habitat PC2 (total area human-modified habitat). (B) Persistence regressed against PC1 over short (20 and 40 m; solid lines) and long (60 and 80 m; dashed lines) distances. (C) Reverberation regressed against PC1 at low (solid lines) and high (dashed lines) levels of habitat PC2. (D) Signal-to-noise ratio regressed against PC1 at low (solid lines) and high (dashed lines) levels of PC2. (E) Ambient noise levels regressed against PC1 at low (solid lines) and high (dashed lines) of PC2. Values for all acoustic variables except ambient noise levels have been transformed to meet normalcy requirements and therefore do not reflect absolute values.

To our surprise, SNR varied much more in open–grassy areas with low levels of human modification (median = 17.2, range: 0–611.2) than in areas with high levels of human modification (median = 10.5, range: 0.33–412.9). As a result, increases in total area of open–grassy habitat (PC1) were associated with more dramatic increases in SNR in territories with fewer human modifications (PC2) than in territories with more human modifications (Fig. 2D).

Associations between habitat and ambient noise.— The global model best explained the effects of habitat on ambient noise level (Table 8). In the

final, averaged model, the SEs for all three habitat terms were <0.009 and none of their SE ranges overlapped with zero (Table 9).

As implied by the SNR results (above), lower environmental noise was recorded in territories with higher levels of open–grassy habitat (PC1), whereas louder noise was recorded in areas with more human-altered habitat (PC2). A visualization of ambient noise regressed against PC1 (total area open–grassy habitat) at low and high levels of PC2 (total area human-modified habitat) (Fig. 2E) indicates that the decline in noise associated with increasingly open–grassy areas

Table 4. Models constructed to explore the association between habitat (PC = principal component in the principal component analysis) and reverberation of pure tones. K is the number of parameters in the model, including the intercept and the residual; AIC_c is Akaike's information criterion corrected for small sample size; ΔAIC_c is the difference in AIC_c value when compared with the top-ranking model; and w_i is the Akaike weight.

Model	K	Parameters	AIC_c	ΔAIC_c	w_i	Likelihood
1	5	Weather, distance, PC1	1,993.6	0	0.4340	1
2	6	Weather, distance, PC1, PC2	1,993.7	0.08	0.417	0.961
3	7	Weather, distance, PC1, PC2, PC1*PC2	1,995.8	2.15	0.148	0.341
4	8	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1	2,002.4	12.13	0.0010	0.0023
5	9	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency	2,007.2	18.79	3.6×10^{-5}	8.310^{-5}
6	10	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1	2,012.9	23.53	3.4×10^{-6}	7.8×10^{-6}
7	11	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2	2,018.9	29.21	2×10^{-7}	4.5×10^{-7}
8	12	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2	2,031.4	40.99	5.4×10^{-10}	1.3×10^{-9}
9	13	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2	2,043.2	52.11	2.1×10^{-12}	4.8×10^{-12}
10	14	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance	2,053.2	64.55	4.2×10^{-15}	9.6×10^{-15}
11	15	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance, frequency*distance*PC2	2,064.3	77.02	8.2×10^{-18}	1.9×10^{-17}
12	16	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance, frequency*distance*PC2, frequency*PC1*PC2	2,076.8	83.13	3.9×10^{-19}	8.9×10^{-19}
13	17	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance, frequency*distance*PC2, frequency*PC1*PC2, frequency*distance*PC1	2,089.7	96.07	6×10^{-22}	1.4×10^{-21}

TABLE 5. Parameters included in the final, averaged model explaining the relationship between reverberation and environment (PC = principal component in the principal component analysis). B is slope of the relationship between each explanatory variable and reverberation.

| | | | $B \pm SE$ | |
Parameter	B	SE	Lower	Upper
PC1 (total area open–grassy habitat)	–0.167	0.003	–0.170	–0.163
PC2 (total area human-modified habitat)	0.030	0.0007	0.029	0.030
PC1*PC2	0.008	0.0005	0.007	0.008
Distance	0.006	9.25×10^{-5}	0.006	0.006
Weather	0.0001	0.0001	-1.02×10^{-5}	0.0002

TABLE 6. Models constructed to explore the association between habitat (PC = principal component in the principal component analysis) and signal-to-noise ratio (SNR) of pure tones played. K is the number of parameters in the model, including the intercept and the residual; AIC_c is Akaike's information criterion corrected for small sample size; ΔAIC_c is the difference in AIC_c value when compared with the top-ranking model; and w_i is the Akaike weight. Distance was not included as a covariate in this model because SNR was calculated using paired signal and noise recordings taken at each distance and, therefore, was distance-independent.

Model	K	Parameters	AIC_c	ΔAIC_c	w_i	Likelihood
1	6	Frequency, weather, PC1, PC2	4,057.3	0	0.793	1
2	7	Frequency, weather, PC1, PC2, PC1*PC2	4,060.3	2.97	0.180	0.227
3	8	Frequency, weather, PC1, PC2, frequency*PC1, PC1*PC2	4,064.3	7.03	0.024	0.030
4	9	Frequency, weather, PC1, PC2, frequency*PC1, frequency*PC2, PC1*PC2	4,068.7	11.4	0.0026	0.0033
5	10	Frequency, weather, PC1, PC2, frequency*PC1, frequency*PC2, PC1*PC2, frequency*PC1*PC2	4,072.7	15.4	0.0004	0.0005

TABLE 7. Parameters included in the final, averaged model explaining the relationship between signal-to-noise ratio (SNR) and environment (PC = principal component in the principal component analysis). B is slope of the relationship between each explanatory variable and SNR.

| | | | $B \pm SE$ | |
Parameter	B	SE	Lower	Upper
PC1 (total area open/grassy habitat)	0.578	0.002	0.576	0.580
Frequency	0.528	0.006	0.522	0.534
PC2 (total area human-modified habitat)	–0.396	0.010	–0.406	–0.386
PC1*PC2	–0.005	0.0004	–0.005	–0.005
Weather	–0.0003	0.005	–0.005	0.005

was more marked in areas with relatively more anthropogenic features (median dB = 39.0, range: 18.4–62.0) than in areas with fewer anthropogenic features (median dB = 37.2, range: 18.7–67.4). In other words, increasing grassy, open areas in human-altered habitats has a larger (negative) influence on ambient noise levels than does increasing grassy, open areas in habitats that are not particularly human-altered.

DISCUSSION

We found that signal transmission was influenced by both tone frequency and distance between the transmitting speakers and the receiving microphone. Lower-frequency tones persisted more strongly and all tones became more degraded at greater distances from the point of origin, as we hypothesized. Furthermore, in open–grassy

TABLE 8. Models constructed to explore the association between habitat (PC = principal component in the principal component analysis) and ambient noise levels in Eastern Bluebird breeding territories. *K* is the number of parameters in the model, including the intercept and the residual; AIC_c is Akaike's information criterion corrected for small sample size; ΔAIC_c is the difference in AIC_c value when compared with the top-ranking model; and w_i is the Akaike weight.

Model	*K*	Parameters	AIC_c	ΔAIC_c	w_i	Likelihood
1	6	Weather, PC1, PC2, PC1*PC2	6,757.0	0	0.99347	1
2	5	Weather, PC1, PC2	6,767.3	10.29	0.0058	0.0058
3	4	Weather, PC1	6,771.4	14.40	0.0007	0.0008
4	4	Weather, PC2	6,784.0	27.01	1.4×10^{-6}	1.4×10^{-6}

TABLE 9. Parameters included in the final (global) model explaining the relationship between environment and ambient noise levels (PC = principal component in the principal component analysis). *B* is slope of the relationship between each explanatory variable and ambient noise.

			$B \pm SE$	
Parameter	*B*	SE	Lower	Upper
PC1 (total area open–grassy habitat)	–1.75	0.009	–1.76	–1.74
PC1*PC2	–1.17	0.009	–1.18	–1.16
PC2 (total area human-modified habitat)	1.04	0.008	1.04	1.05
Weather	0.0005	0.003	–0.002	0.003

habitats (PC1), persistence declined more rapidly at larger distances (60 m and 80 m) from the signal source. Given what is known about the physics of sound propagation, none of these results is surprising: All sound waves are expected to decrease in power as they propagate through the environment, because their energy is increasingly absorbed by air (Berg and Stork 2004). This is particularly true for higher frequencies, whose waves are composed of shorter periods and are therefore more likely to be scattered and absorbed (Wiley and Richards 1978, 1982). For management and conservation purposes, it is comforting to confirm that these expected relationships hold true in anthropogenically modified environments utilized by breeding birds, and that manmade materials and habitat configurations do not produce complex or unexpected effects on acoustics.

Perhaps more importantly, we found that habitat type was an important predictor of all three sound propagation characteristics measured here (signal persistence, reverberation, and SNR), and that it is strongly associated with the absolute level of ambient noise. The general effects of habitat type on tone persistence fit with established

theory: Tones persisted more in environments that were more open and possessed fewer vertical obstructions (habitat PC1), but attenuated more in areas that possessed more vertical anthropogenic structures. This latter pattern may have occurred as a result of buildings acting as barriers to sound or the deflection of sound waves off buildings and away from the microphone.

As with persistence, we made several predictions about reverberation based on our knowledge of the physics of sound. We were slightly surprised that there was no relationship between tone frequency and reverberation. This result suggests that the ratio between wavelength and the size of the obstructing habitat feature (which determines strength of reverberation) was more similar across the three frequencies than we expected. However, the associations we found between reverberation and habitat structure were as predicted: Reverberation decreased in areas that were more open and had fewer trees, resulting from the fact that these sites had fewer vertical objects off which the sound waves could reflect. Similarly, reverberation increased in areas with more human-modified habitat. This is

likely related to the presence of more vertical objects (buildings) and the presence of more acoustically "hard" features (impervious surface) that reflect sound waves more intensely (Warren et al. 2006). Future work will be required to differentiate between these two possibilities—a distinction that might have important management implications.

Predictions for our analyses investigating the relationships between habitat and both SNR and noise levels were closely related. Specifically, habitats with higher noise levels should have lower SNR, given that the amplitude of our tones (the signal) was kept constant while the ambient noise levels increased. Indeed, this is the relationship we found. Across nest-box territories, more open–grassy habitats had lower levels of ambient noise and, thus, higher SNR. Correspondingly, more anthropogenic habitats had higher levels of ambient noise and lower SNR. We also found that SNR improved at higher frequencies, confirming previous observations that the bulk of environmental noise (particularly anthropogenic noise) occurs at lower frequencies, and that higher-frequency signals are less susceptible to acoustic masking (Slabbekoorn and Peet 2003, Brumm 2004) even though they are less likely to persist over long distances (Nemeth and Brumm 2010).

Each of our acoustic variables was associated with the interaction term between our two habitat types (PC1*PC2). These relationships show that, in habitats with low levels of human modification, even small increases in the total amount of open–grassy area will quickly improve the acoustic space of singing birds (e.g., by increasing persistence, decreasing reverberation, and improving the SNR by decreasing ambient noise levels; Fig. 2B–E). However, the relatively flat relationships between the acoustic variables and PC1 at high levels of human modification suggest that there may be a critical level of human modification above which the addition of "natural" features is no longer beneficial for communication (though these features might be valuable for providing habitat for other activities, such as nesting and feeding). If this is the case, further research should be focused on identifying this limit so that it can be used as a guideline when designing cities, parks, and animal refugia. Our current results suggest that land management plans that utilize cluster developments and include nature preserves would be beneficial to preserving the integrity of birds' acoustic space. A further

benefit of these techniques is the emphasis on allowing only minimal ISC to be installed within current breeding habitat, rather than on trying to create new habitats by introducing vegetation into a pre-existing matrix of impervious surfaces. However, it is also important to keep in mind that, in highly anthropogenic sites, the absolute levels of persistence and SNR were consistently higher, whereas the absolute levels of reverberation and ambient noise were consistently lower. In other words, the presence of impervious surface was almost always associated with decreases in the quality of the acoustic environment. Thus, although we can improve the acoustic space of animals that attempt to communicate in such areas, their optimal habitat is likely one in which there is no impervious surface at all.

Another interesting implication of our data is that species with different song characteristics or territory size preferences (or both) may be differentially affected by these relationships between habitat and sound propagation. For instance, species singing at higher frequencies are less likely to experience transmission problems that stem from low SNR but may have more difficulties communicating in anthropogenically altered environments where attenuation is more likely to occur. Similarly, species that maintain larger territories are likely to have evolved signals that are more persistent over longer distances and less likely to be obscured by their own reverberations (but see Slabbekoorn and Smith 2002). Individuals of these species may therefore have a harder time signaling effectively in more human-altered environments, where persistence tends to be lower and reverberation tends to be higher.

Unfortunately, these life-history-specific relationships make it hard to generalize and predict how the effects of habitat on sound propagation are likely to affect all the avian species across an anthropogenic disturbance gradient. This is particularly true given the amount of behavioral flexibility that has been observed in the way in which birds learn both song and song preferences, as well as the variety of spontaneous vocal adjustments they may make in real time in response to current environmental conditions (Bermúdez-Cuamatzin et al. 2009, Brumm et al. 2009). However, our models clearly indicate that specific suites of habitat features can be used to predict the acoustic characteristics of particular territories, and this information can, in turn, be combined with life-history information in order to make educated predictions

about whether and how species may cope with the acoustic environment.

It is important to remark that the habitats we studied did not include extremely "rural" and "urban" areas, such as purely agrarian sites, areas with no remaining natural habitat, or areas that receive nonstop noise pollution. Additionally, because our focal sites are located on the Coastal Plain of Virginia, they had very little topographic variation. The presence of hills and mountainsides, particularly those with large amounts of exposed rock, is likely to add an interesting element to sound propagation analyses, as would large areas of water, denser forests, and acoustically soft features >3 m in height (including ornamental plants such as tall grasses or ferns). Each of these latter habitat features has been underrepresented in previous work on sound propagation and signal design, let alone within an anthropogenic-disturbance context. Furthermore, future work should attempt to more directly compare anthropogenic features with analogous "natural" features in order to develop a more fine-grained understanding of how specific habitat elements affect sound propagation. For instance, one interesting question might be whether trees and buildings have similar effects on signal persistence and reverberation, or whether anthropogenic materials differ sufficiently in acoustic hardness to interact significantly differently with sound waves.

A major assumption of the many recent studies on anthropogenic noise and signal design is that more urban habitats are uniformly louder than rural habitats, or in some other way offer "worse" acoustic environments. However, across the habitats we studied, the average amplitude of ambient noise is only marginally higher in human-altered habitats than in "natural" habitats, and, in fact, there is considerable overlap in the ambient noise levels observed in these two types of site. Additionally, all habitats across our anthropogenic disturbance gradient offer their own acoustic challenges: Individuals in more human-modified habitats may be more susceptible to lower SNR and reduced persistence of signals, but individuals in more open–grassy sites are likely to experience more reverberation. Taken together, these relationships underline the importance of evaluating sites on the basis of their own intrinsic acoustic or structural characteristics, as opposed to assigning them to categories based on subjective assumptions.

On the whole, our findings indicate that small amounts of impervious surface cover can have a disproportionately large effect on signal efficacy, which suggests that wildlife managers should be cautious about installing structures such as paved access roads, boardwalks, or observation huts into relatively unaffected breeding habitats. Our results also indicate that acoustically communicating wildlife, including birds, would benefit from the presence of buffers (e.g., strips of unmodified land, or acoustically neutral barriers) that shield their territories from nearby anthropogenic structures. Conversely, the inclusion of buffers around new development projects in otherwise "natural" areas might help mitigate the effects of introducing anthropogenic features to the environment.

Although previous research has used field correlations to show that SNR is highest at higher signal frequencies (Morton 1975, Marten and Marler 1977, Marten et al. 1977, Brown and Handford 2000), our results are the first, to our knowledge, to confirm this with experimental methods performed on active breeding territories. This observation suggests that increases in ambient noise levels may place more intense selection pressures on species with lower-frequency vocalizations. This could lead to a number of frequency-related song adaptations, such as preferential performance of higher-frequency notes (Bermúdez-Cuamatzin et al. 2009), omission of lower-frequency portions of song elements, and upward shifts of frequency characteristics (Slabbekoorn and Peet 2003, Wood and Yezerinac 2006, Nemeth and Brumm 2009). Alternatively—or additionally—birds may alter behaviors associated with their vocal performances. We found that signaler-to-receiver distance affected both persistence and reverberation of signals. By altering perch characteristics, such as height and location within the territory, birds could improve their signal transmission. It would be particularly interesting to see whether these signal design and delivery adaptations follow divergent routes in open–grassy habitats and human-altered habitats. Although such processes have often been theorized after the fact, they have not been investigated in real time (Slabbekoorn and Smith 2002, Leader et al. 2005, Slabbekoorn et al. 2007, Kirschel et al. 2009). Anthropogenic environments can therefore be thought of as "natural experiments" that not only can yield important

evolutionary insights, but also can facilitate more informed management decisions.

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