3-25-2016

Anthropogenic noise weakens territorial response to intruder's songs

Nathan J. Kleist
University of Colorado Boulder

Robert P. Guralnick
University of Florida

Alexander Cruz
University of Colorado Boulder

Clinton D. Francis
California Polytechnic State University, San Luis Obispo

Anthropogenic noise weakens territorial response to intruder's songs

NATHAN J. KLEIST,[1],† ROBERT P. GURALNICK,[2] ALEXANDER CRUZ,[1] AND CLINTON D. FRANCIS[3]

[1]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309-0334 USA
[2]University of Florida Museum of Natural History, University of Florida at Gainesville, Gainesville, Florida 32611-2710 USA
[3]Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, California 93407 USA

Abstract.   Noise pollution degrades natural acoustic conditions, potentially interfering with bird communication. However, exactly how noise impacts the ability of the signal receiver to detect and discriminate vocalizations from conspecifics remains understudied in field settings. We performed a natural experiment to determine the effect of noise pollution on the territory-defense behaviors of two emberizid sparrows exposed to carefully constructed playbacks of conspecific intruder songs. Although all birds reacted to the playbacks, response latency increased with noise levels. This suggests that noise interferes with signal reception and may indicate impaired signal discrimination. We place these results in the context of a receiver's "listening area" and the significant impact of noise pollution on this receiver-centric perceptual acoustic range. This work informs conservation efforts and provides a much needed field-based examination of the disruptive impact of noise pollution on behaviors directly related to reproduction and fitness.

† **E-mail:** nathan.kleist@colorado.edu

INTRODUCTION

Noise pollution is a habitat-degrading consequence of industrialization that is difficult to regulate, permeates physical boundaries and is increasing globally (Barber et al. 2010). Given the extent of the disturbance and the complexity of responses reported to noise, which range from the molecular to the community level, there remain many gaps in our understanding, especially field-based studies that explore the subject (Kight and Swaddle 2011). Consequently, it has become a target area for applied ecologists and conservationists who seek to better understand the environmental impact that results from wide-reaching noise stimuli, which differ, depending on production source, in their frequency, intensity, and timing (Francis and Barber 2013).

One way that high levels of ambient background noise can alter ecological process is through disruption of important vocal communications by way of acoustic masking, the obstruction of detection, and discrimination of sounds by other sounds. Birds' reliance on intricate, species-specific songs may increase their vulnerability to these disruptions and makes them a focal point of current vertebrate-based noise research (Patricelli and Blickley 2006, Slabbekoorn and Ripmeester 2008, Francis et al. 2009, Barber et al. 2010, Slabbekoorn 2013).

Recent studies largely explore the potential for certain bird species to adjust the frequency of

their vocalizations in response to the masking effects of low-frequency noise (Slabbekoorn 2013). Others have produced strong support for a relationship between the frequency of a species' song and habitat use with relation to noise, showing that birds with low-pitched vocalizations may experience more masking by low frequencies and are less common in loud areas relative to less noisy areas (Francis et al. 2011*a*, Goodwin and Shriver 2011, Proppe et al. 2013, Francis 2015). These studies show how producing signals that escape noise-masking might be important to successful communication. Equally important to these efforts is a bird's ability, as a receiver, to detect and discriminate song, which is the focal topic of the present study.

Receiver behavior in noise is relatively understudied compared to that of the signal producer, but efforts from some lab- and field-based experiments using simulated noise suggest that receivers might also make adjustments to account for the difficulties of communication in loud conditions. Results from laboratory-based behavioral studies of great tits (*Parus major*) show that noisy conditions increase the detection threshold of biologically relevant frequencies by up to 18 dB and that urban noise favors detection of high-frequency songs (Pohl et al. 2009, 2012). Other experiments in great tits have shown that low-frequency songs, which are most easily masked by noise pollution, are preferred by females and linked to reproductive success, and that female response latency to male songs within noise leads to alteration of male behavior (Halfwerk et al. 2011, 2012). Experiments with European robins (*Erithacus rubecula*) show that vocal responses to playbacks of conspecific songs paired with simulated traffic noise might change in complexity and pitch (McMullen et al. 2014). Finally, a "sound transmission" study using the song of the blackcap (*Sylvia atricapilla*), demonstrates how songs received at higher perches are less degraded, illustrating that receivers may alter perch height to improve communication (Mathevon et al. 2005). Results from these studies support the hypothesis that receivers must also modify behavior to cope with noise, but how these results transfer to free-living animals persisting within chronically noise polluted habitats, which are more indicative of real-world conditions, is a largely unanswered question.

We address this gap in our understanding by carrying out a playback experiment on two noise-tolerant species of songbird from the family *Emberizidae*, the spotted towhee (*Pipilo maculatus*) and the chipping sparrow (*Spizella passerina*). We focus on these two species because they are confamilial, common, and inhabit both quiet and noisy areas at our study site in northwestern New Mexico (see below). As well, these two relatively closely related species do differ in some aspects of song production. Specifically, spotted towhees are known to sing more frequently than chipping sparrows and may be better able to alter their vocal response (Marler and Isaac 1960, Greenlaw 1996). We examine if these differences in life-history may impact effect of noise on their responses.

We conducted this experiment at our long term study site in the Bureau of Land Management's Rattlesnake Canyon Habitat Management Area (RCHMA) in San Juan County, New Mexico. The area is leased by the Bureau of Land Management to the oil and gas industry, and represents one of the highest densities of natural gas extraction activity in the United States. The piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands in RCHMA are spatially pockmarked by well pads that may or may not have active noise-producing compressor engines whose acoustic footprint can radiate through up to 650 m of habitat (Fig. 1; Francis et al. 2011*d*). The wells are situated in surrounding woodlands whose vegetation structure remains similar irrespective of location or presence of compressors (Francis et al. 2009, but see Francis et al. 2012*a*). Given these conditions, experiments run in this system have the exceptional advantage of isolating the effects of chronic anthropogenic noise for use as a controlled treatment variable (Francis et al. 2011*b*). This arrangement stands in contrast to many field systems where it is difficult to fully control for the confounding effects of urban environments. Previous results from this system show that not only do birds shift their songs in response to noise, they also amend occupancy patterns to avoid loud nest sites (Francis et al. 2009, 2011*c*).

Here, we utilize our unique study system to ask the following question about noise and its impact on male territorial defenses: Does an increase in ambient noise level alter territory-defense
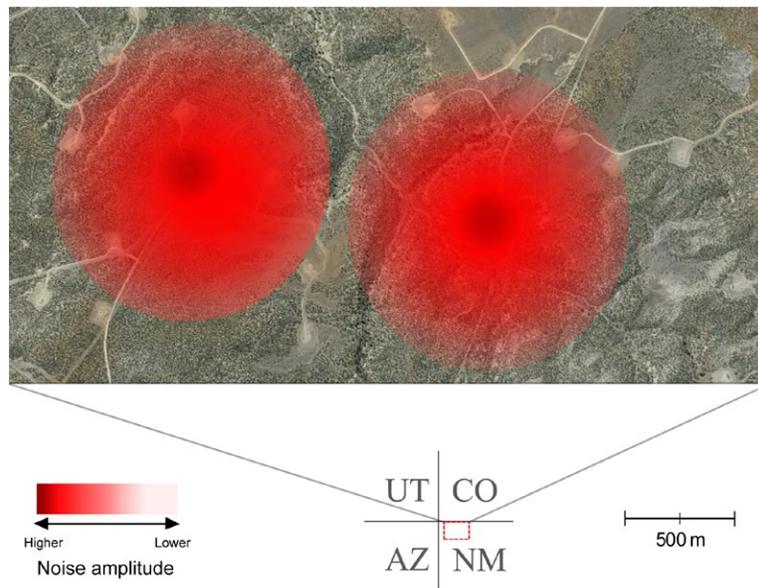
Fig. 1. Rattlesnake Canyon Habitat Management Area (red outline) is located in northwestern New Mexico, near the Colorado border in San Juan County. Noise increases in intensity near to the compressors and is represented by red spheres that extend 650 m from the point source.

behaviors in breeding males exposed to conspecific intruder songs? We predict that male birds in noisy areas will respond to an intruder in both voice and movement more slowly due to the masking effects of industrial noise on the song of the intruder, and that there may be variation in these responses related to the natural history of each species.

METHODS

We conducted all playback trials in RCHMA under a variety of background noise amplitudes. The noise produced by compressors at RCHMA is suitable for use as a masking agent in this experiment because it is continuous, high-amplitude, low-frequency industrial noise that overlaps the vocal range of both chipping sparrows and spotted towhees (Francis and Barber 2013, Fig. 2). The trial period was the second half of May 2010, and experiments were performed during morning hours (8 a.m.–12 p.m.). We chose early summer to ensure our trials would overlap a period of heightened territoriality associated with breeding behavior in males of both species (Davis 1957, Allaire and Fisher 1975).

We tested the response of both species to conspecific intruders by presenting playback recordings constructed from the songs of local males with average spectral and temporal features. The use of average songs was essential for two reasons. First, behavioral responses to song can change in response to differences in a variety of song features (Brumm and Ritschard 2011, Halfwerk et al. 2011, Moseley et al. 2013). Second, the two species included here are known to shift the minimum frequency of their songs in response to background noise (~500 and 400 Hz, respectively, for spotted towhee and chipping sparrow; Francis et al. 2012*b*, *unpublished data*) and our collection of local songs suitable for playback experiments reflected this variation. Thus, playback experiments using songs spanning the observed variation in song features have the potential to generate stronger or weaker responses solely due to specific song features or through an interaction between the song features and background sounds (e.g., Luther and Magnotti 2014). Here, the fundamental question we consider is the effect of the noise treatment under normative conditions, and not variation in song features of exemplar songs. This strategy helps inform how changing acoustic conditions impact
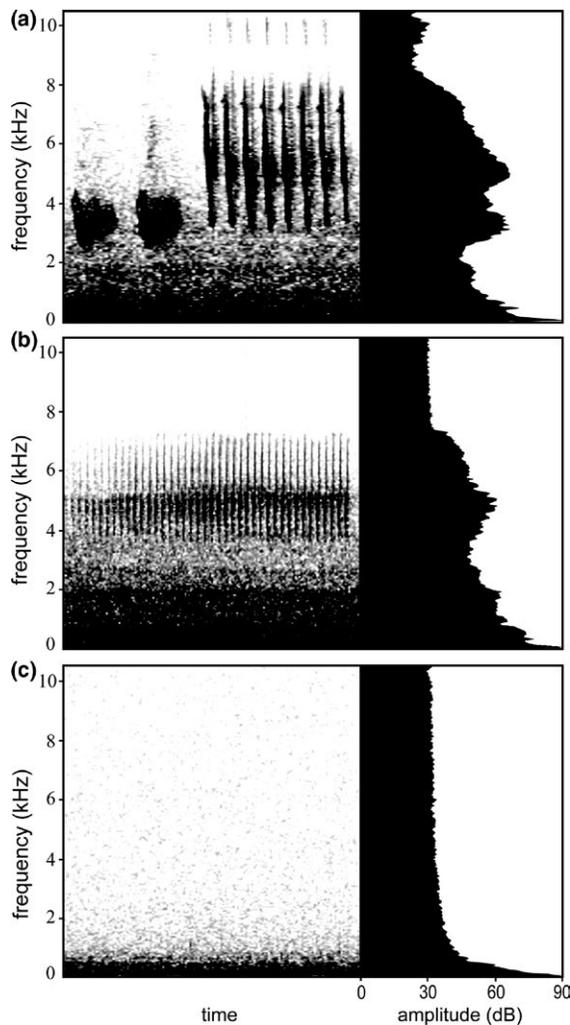
Fig. 2. Spectrograms (left portion of panel) and power spectra (right portion) at loud sites and spotted towhee (a) and chipping sparrow (b) songs embedded within high-amplitude, low-frequency background noise. In contrast, the spectrogram and power spectrum of background noise at a quiet site (c).

typical songs and may better generalize across species, because some species appear not to modify vocalizations in response to noise (Hu and Cardoso 2010, Francis et al. 2011*b*, 2012*b*).

We controlled for variation in stimulus by creating a set of averaged playbacks taken from field recordings of 51 spotted towhee individuals and 55 chipping sparrow individuals. The recordings used in this study were made in 2009 with a Marantz PMD 660 Digital Recorder with an Audio-

technica AT-815 directional shotgun microphone (Francis et al. 2012*b*). We then used principal components analysis (PCA) with varimax rotation (*principal* function in the *psych* library for R) to determine population-level average songs for each species from our recordings.

Average songs were constructed based on knowledge about songs for both species. Although detailed information is limited, seven to nine different song types are used per individual spotted towhee that can vary in composition, length, rate, and syllable count (Kroodsma 1971). Chipping sparrows, in contrast, are restricted to one primary song type with reported intraindividual variation for duration, syllables, inter-song interval, and min and max frequency (Marler and Isaac 1960). We highlighted ten individuals from the PCA results for both species that most closely matched the population average for song minimum frequency, maximum frequency, peak frequency, frequency bandwidth, number of notes, and song length (Table 1). From those ten individuals, we randomly chose five candidates with high-quality recordings (Fig. 3a, b). See Table 2 for song measurement data of the exemplar males used in this experiment. We then created five-minute loops from 5 to 10 different songs of each individual that were randomly arranged on the recording with average intersong intervals of 5.5 and 6.3 s for spotted towhee and chipping sparrow, respectively.

We selected male birds for use in the study by systematically searching our field sites within a gradient of noise to test birds under a variety of acoustic conditions. We only presented experimental playbacks to males at different sites, which are separated by at least 1 km, to ensure we did not resample individuals. Prior to the experiment, we made pretrial observations for five minutes to control for any singing or territorial behavior not solicited by experimental stimuli. We waited until the bird was stationary and not engaged in any obvious territorial disputes with nearby conspecifics, and then randomly selected one of the five exemplars for playback through a SME-AFS portable field speaker (response range = 0.1–12 kHz, uncompressed WAV files, amplitude = 80 dB(A) at one meter from the speaker (Brackenbury 1979)). The playback speaker was placed at an average initial distance of 17 m from the focal male and results were recorded with pen and paper by a hidden observer positioned at least 5 m from speaker.

Table 1. Principal component factor loadings for vocal characteristics of spotted towhees and chipping sparrows, as well as eigen values and proportion of variation explained for PC axes.

	Spotted towhee		Chipping sparrow	
Variables	PC1	PC2	PC1	PC2
Song Features				
Song length (s)	0.83	0.15	0.72	
Number of notes	0.88		0.85	−0.15
Peak frequency (Hz)	0.35	−0.48	0.17	0.75
Minimum frequency (Hz)	−0.42		0.73	0.38
Maximum frequency (Hz)	0.21	0.91	−0.40	0.83
Frequency bandwidth (Hz)	0.37	0.88	−0.72	0.54
Summary				
Eigenvalue	1.93	1.87	2.48	1.73
Proportion of variation explained	0.32	0.31	0.41	0.29

Note: Blank cells indicate no loading of a variable to an axis.

We collected data from 19 spotted towhees and 12 chipping sparrows on several measures of the subject's song and flight response behavior during the 5-min experimental period. Specifically, we measured song latency, maximum perch height, flight latency, latency to approach within 1 m and separately measured both overlapping and nonoverlapping songs to explore the potential effect of noise on signal jamming, which is a strategy used by birds to block information contained within the songs of rivals during competition for mates (Grafe and Bitz 2004, Tobias and Seddon 2009). See Table 3 for further description of these variables. We measured these variables, which include both movement and song production, because they are representative of typical responses to competitors (Moseley et al. 2013). Immediately after completion of the playback trial, we measured A-weighted background noise amplitudes (equivalent continuous noise levels [L_{eq}], fast response) for 1 min with NIST-certified sound pressure meters (Casella CEL320/CEL1002 converter) from the bird's original perch location at the beginning of the trial. Data were collected for both species within a gradient of noise on both control and treatment sites. Noise levels are reported as A-*weighted* decibels (dB(A)), because site designation as control or treatment is not a focus of this study as in other work in this system (Francis et al. 2009).

Due to potential multicollinearity of the responses measured, we used PCA to reduce the variables to two PC axes. PC1 and PC2 explained 38% and 23% of overall variance, respectively, and each loaded strongly to different behavioral responses; PC1, hereafter PC1$_{song}$, loaded with vocal responses and PC2, hereafter PC2$_{fly}$, with movement toward the speaker (Table 3). We used linear mixed effect models (LMMs) to determine how background noise amplitude influences receiver vocalization (PC1$_{song}$) and movement (PC2$_{fly}$) behaviors (see below). We included background noise amplitude, species identity, and their interaction as fixed effects. Julian date and initial speaker-to-bird distance were also included as fixed effects due to their potential influence on response behaviors. Whether the subject had sung during the 5-min pretrial observation period before we started the playback was treated as a random effect. We started with all candidate variables and used backwards elimination with likelihood ratio tests (LRT) in R to remove the least informative fixed effects to choose the best model. This model was then tested against the null with a LRT to check for goodness of fit.

Results

We ran playbacks on spotted towhees (*n* = 19) in noise conditions ranging from 33.9 to 52.2 dB(A), with an average ambient background noise of 42.12 dB(A) during all playbacks. All spotted towhee individuals responded with vocalizations and with flight toward the speaker during the 5-min playback. Spotted towhee song latency ranged from
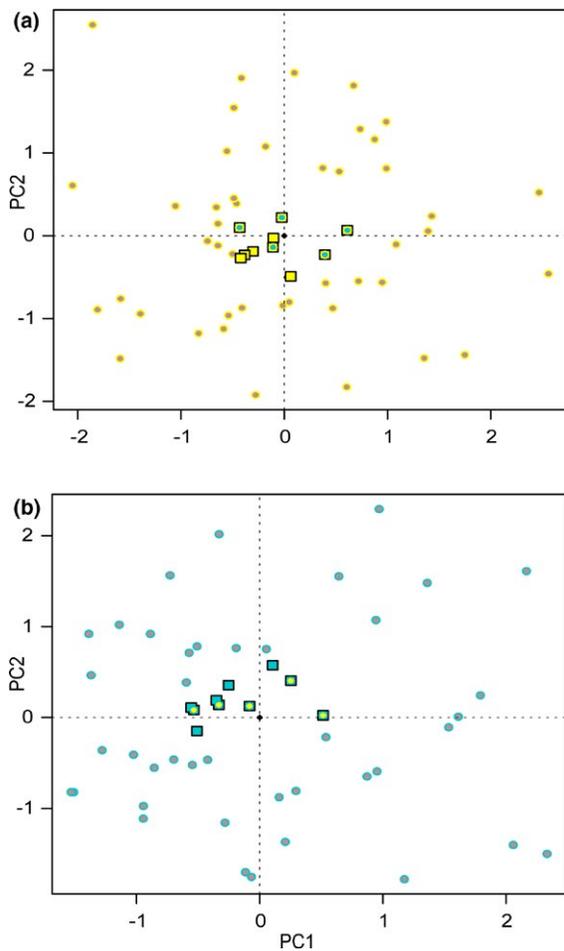
Fig. 3. Principal components of vocal characteristics for spotted towhee (a) and chipping sparrow (b). The ten individuals with the most average vocal characteristics among the birds sampled (Table 1), are marked with squares and surround the origin, representing the mean song. The songs of five of these individuals were chosen based on the suitability of recording quality for inclusion as playback stimuli in this study, and are shown on the plots as points within squares.

one-second at 34.6 dB(A) to 91 s at 52.2 dB(A), with an average of 33.68 s. Flight latencies in spotted towhees were recorded from 1 s at 42.58 dB(A) to 81 s at 50.7 dB(A), with an average of 18 s. Spotted towhees had a total song rate of 8.16 songs/min at the five quietest sites and 5.8 songs/min at the five loudest sites. We sampled chipping sparrows (n = 12) in acoustic conditions ranging from 34.6 to 52.4 dB(A), with an average noise level of 43 dB(A). All chipping sparrows responded vocally to the playback, and all but one responded with movement toward the speaker. Chipping sparrow song latency ranged from 4 s at 43.95 dB(A) to 270 s at 50.8 dB(A), with an average 42.75 s. Flight latency for chipping sparrows ranged from 1 s at 44.03 dB(A) to no response at 51 dB(A) with an average of 63.58 s. We recorded a song rate of 4.12 songs/min at the five quietest sites and 3.0 songs/min at the five loudest sites.

The best model for $PC1_{song}$ included both background noise amplitude (β = −0.051 ± 0.020 SE; Fig. 4a) and species (β = 1.134 ± 0.269 SE; Fig. 4a) and fit the data better than the null model with random effects (χ^2 = 18.719, df = 2, P < 0.001). Specifically, increases in background noise were associated with increases in song latency, decreases in both overlapping and nonoverlapping songs and reduced relative maximum perch height (Fig. 4a) for both species. However, spotted towhees had a faster vocal response, more total songs, and higher relative perch height than chipping sparrows. The best model for $PC2_{fly}$ included a fixed effect for amplitude of background noise levels (β = 0.075 ± 0.024 SE; 4b) and performed better in the LRT than the null (χ^2 = 8.424, df = 1, P = 0.004). With increases in background noise, both species were slower in orienting to, and approaching within one meter of, the location of the playback speaker. For $PC2_{fly}$, we found no species-specific differences.

Discussion

Our results suggest that conspecific territorial defense behaviors for both species are impaired with increases in background noise levels and add to the body of evidence supporting noise-influenced shifts in bird behavior (Pohl et al. 2009, Francis et al. 2011*a*, *b*, 2012*b*, Slabbekoorn 2013). Our focus on the effects of acoustic masking from chronic noise at compressor sites in a natural system, as opposed to lab-based, intermittent, or experimentally introduced noise (Lohr et al. 2003, Slabbekoorn and Peet 2003, Pohl et al. 2009, Halfwerk et al. 2011) provides needed field-based evidence that auditory surveillance is impaired by chronic noise. As well, this study is the first to consider responses of

Table 2. Pooled descriptive song data for individuals included as exemplars in playback recordings.

Song features	Spotted towhee			Chipping sparrow		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Song length (s)	1.14	0.93	1.21	2.81	2.57	3.2
Number of notes	11.31	7.2	13.2	60.32	43.8	72
Peak frequency (Hz)	4276.71	3412.5	5137.5	5042.81	4518.76	5296.86
Minimum frequency (Hz)	2078.67	1857.64	2526.3	3182.83	2914.65	3581.62
Maximum frequency (Hz)	7855.32	7662.34	8104.54	6745.59	6511.24	6971.52
Frequency bandwidth	5776.67	5136.02	6246.9	3562.76	3077.18	3829.62
Songs per minute	7.86	6.59	9.63	5.18	4.11	6.12

receivers of two relatively closely related species found within the same environment.

Highly relevant to these findings is the concept of listening area, which is a receiver-centric approach to interpreting effects of masking noise. The area is represented as a circular zone centered on the receiver that represents the physical space of the perceptual range for detection of an acoustic signal. That is, listening area is a natural complement to the concept of "active space", which is the maximum distance from the sender that a signal is perceptible by the receiver (Lohr et al. 2003, Gall et al. 2012). Background noise can impact this perceptual range and might decrease detection distance by up to 50% with each increase in 3 dB (Barber et al. 2010). Even a conservative application of this estimate suggests a dramatic decrease in perceptual range for detecting intruder songs.

In our study, all individuals responded to the playback vocally and only one chipping sparrow individual failed to respond through movement, suggesting that detection was possible at the fairly close distances used in our experiments (16.8 m ± 1.1 SE); however, increased response latency with increases in noise level suggests that discrimination of the signal may have been impaired. Whether the birds had difficulty in discerning the information within the signal, or simply had trouble locating the source is unknown. However, both of these outcomes represent a reduced ability to respond to important acoustic information. Research suggests that the threshold for discrimination is approximately 3 dB higher than for detection (Lohr et al. 2003), and thus the physical space within which discrimination of a signal can occur may be much smaller than the previously

Table 3. Principal component loadings for behavioral responses across both species, with variables grouped by the axis to which they loaded most strongly.

| Variables	Description	PC1$_{song}$	PC2$_{fly}$
Song axis			
Song latency	Time(s) from start of playback to first response song	−0.75	0.16
Nonoverlapping songs	Total number of songs in response to playback, nonoverlapping	0.81	0.06
Overlapping songs	Total number of songs that overlapped playback	0.69	0.11
Maximum perch height	Relative maximum perch ratio of "highest used" over "highest available"	0.68	−0.33
Flight axis			
Flight latency	Time(s) from start of playback to first movement towards speaker	0.17	0.83
Approach latency	Time(s) from start of playback to first approach within 1 m of speaker	−0.26	0.75
Summary			
Eigenvalue		2.26	1.39
Proportion of variation explained		0.38	0.23
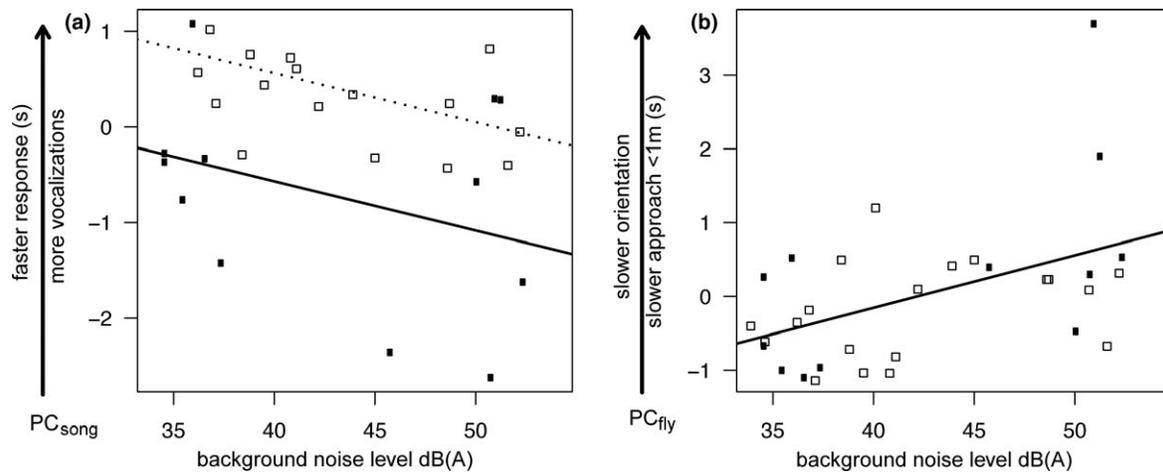
Fig. 4. (a) Chipping sparrows (black dots and line) and spotted towhees (white squares and dotted line) respond with vocalizations more slowly with increased noise levels. Spotted towhees exhibit a stronger vocal response. (b) Both species more slowly initiate movement toward, and approach the location of, the speaker with increases in background noise.

stated reduction in listening area. This small window for signal discrimination may partially explain how responses were affected even at the relatively short signal-receiver distance of our experiment.

It is not well known how vocal frequency and hearing range relates to listening areas in real-world contexts, but it is likely that the active space of acoustic signals is reduced by the high-energy, low-frequency sounds that are the byproducts of industry and infrastructure. We believe that the relationship between noise levels and flight and approach latency seen here in both species is evidence for reduced detection and discrimination of an acoustic signal and can be explained by the inability of the receiver to escape the masking effects of noise pollution. While *hearing range* may be fixed, birds can still gather more information by moving around in their environment to localize and assess the quality of the intruding males, as demonstrated by both species in this study. The lower relative perch heights with increases in background noise that we report, seem to contradict results reported for the Eurasian wren (*Troglodytes troglodytes*) and blackcap that show increases in perch height might help with signal detection (Mathevon et al. 1996, 2005, Holland et al. 1998). This might be an artifact of having the speaker on the ground during playbacks, yet it was still the birds in the noisiest habitats and

seemingly less capable of locating the source, that selected the lowest perches.

Decreased ability to locate the signaler might also explain decreases in pairing success reported in noisy environments (Habib et al. 2006, Gross et al. 2010). Disruption of acoustic signals, especially critical ones such as those produced by a competitor, can have direct and indirect negative effects for an organism relying on these cues. A noise-polluted environment, which reduces the signal-to-noise ratio and effectively dampens the amplitude of the intruder song, may sway the balance in favor of the intruder. In such a case, the male territory holder may not honestly discriminate the vigor of his competitor and may not allocate appropriate resources to territory defense. Even after mates and territory are won, noise pollution can impede reproduction. For example, zebra finch (*Taeniopygia guttata*) females are reported to lose preference for their pair-bonded mate with increases in background noise, as pair-reinforcing vocalizations may become more difficult to detect (Swaddle and Page 2007). Quantifying the potential for noise to reduce signal detection and discrimination, and then determining associated demographic consequences, is an important next step for understanding the conservation-relevant consequences of noise. Such field studies, as we have shown here, are tractable.

The importance of field-based systems to wholly test questions of detection and discrimination should not be understated. The quality of noise emanating directly from the source, and consequently, the effect that the noise has on experimental results may be drastically different in real world vs. lab-based or noise-simulated scenarios (Francis and Barber 2013). To illustrate, our results show how reception of the signal may be affected at a sender-receiver distance of only 17 m. Even at this relatively short distance, our data support a dampening of response to intruder song in two species as noise levels increase from 33.9 to 52.4 dB(A), suggesting that listening area for detection and, especially, discrimination might be drastically smaller for wild birds than previously thought. For instance, Lohr et al. 2003 estimate that receivers listening at 17 m should be able to detect and discriminate calls at traffic noise amplitudes in excess of 80 dB(A).

The discrepancy between results from the field and lab-based estimates suggests that there may be factors other than direct acoustic masking at biologically relevant frequencies affecting behavior. For example, it is possible that distraction from noise contributes to the observed changes in territorial behavior, and may work in concert with masking to further obscure the information contained within a signal (Chan et al. 2010). Although there is little information on this topic, a recent study on Brazilian free-tailed bats (*Tadarida brasiliensis*) in RCHMA showed how these animals, which vocalize above 24 kHz, shift aspects of their echolocation call in response to low-frequency compressor noise (Bunkley et al. 2015), which has very little acoustic energy above 20 kHz and should not result in energetic masking of echolocation signals. Our results here, taken in the context of the previously mentioned estimates, might be partly explained by degraded signal discrimination as a result of distraction. If distraction is indeed a driver of noise-related behavioral shifts, the spatial footprint of noise may be significantly larger than previously estimated from results based on masking alone.

Despite consistent findings that noise degrades ability to detect and discriminate conspecific intruders, we did find species-specific differences on $PC1_{song}$, but not on $PC2_{fly}$. During the breeding season, unpaired, male spotted towhees are known to allocate upwards of 80 percent of their time budget toward vocalizations (Greenlaw 1996), whereas the chipping sparrow, a "discontinuous" singer, has been reported to spend around 30% of its time vocalizing (Marler and Isaac 1960). Data from our system and others suggest that spotted towhees also have higher song rates during continuous singing bouts than chipping sparrows (Table 2; Greenlaw 1996). Accordingly, results for $PC1_{song}$ show that the intercepts are variable, with spotted towhees maintaining a stronger overall vocal response than the chipping sparrow across noise levels (Fig. 4a). Despite the overall stronger vocal response across noise levels by spotted towhees, we did not find any differences in *slope* of that response between the two species in increasingly noisy environments. We also found no difference between species on movement responses ($PC2_{fly}$) during our experiment. Spotted towhees and chipping sparrows are both known to show intolerance to conspecific intruders during the breeding season, and will respond aggressively to dissuade competitors. However, data on differences related to flight frequency or territorial flight response are lacking (Greenlaw 1996, Middleton 1998), precluding a more detailed look if the expectation of similar responses was an expected outcome.

One possible explanation for generally similar responses by these species is that they have similar vocal frequency ranges, which are known to correlate with hearing range (Dooling and Popper 2007). Although the exact critical ratio, which is the minimum amplitude necessary at a specific frequency for detection of an acoustic signal, is not known for either species, two other emberizids, the song sparrow (*Melospiza melodia*), and swamp sparrow (*Melospiza georgiana*), are reported to have maximum hearing sensitivity at 2–5 kHz (Okanoya and Dooling 1988, Gall et al. 2012). Therefore, weakened responses to intruder playbacks are likely, either directly or indirectly, due to noise from compressor fans overlapping frequencies used by both species for the sending and receiving of acoustic signals.

Our results demonstrate the importance of considering the receiver's role in communication in an increasingly loud world. Further exploration of how species in the wild not only detect, but discriminate, signals within noise gradients is an important next step in clarifying the true ecological impact of noise pollution. It

is therefore imperative to understand fully how noise pollution might act as a source of further habitat degradation for sensitive species already on the decline due to climate change and habitat loss and how ecological impacts from modification of the acoustic environment compare to anthropogenic impacts that have received more and longer attention by ecologists. Moving forward, we suggest designing experiments to tease apart the differences between masking and distraction, to explore how anthropogenic noise outside of an organism's vocal range might affect its behavior. We also suggest including exemplars with vocal features that fall outside of normative conditions (Fig. 3a, b), to investigate how a wider range of song types affect issues of detection and discrimination and to more fully understand demographic consequences. Future work, especially field-based experiments in suitable systems, will provide the means to better comprehend the full extent of the effects of anthropogenic noise on species and communities, how transformation of the acoustic environment compares to other well-studied human-induced habitat modifications and could potentially provide the means to mitigate such effects via conservation actions.

Acknowledgments

Literature Cited

Allaire, P. N., and C. D. Fisher. 1975. Feeding ecology of three resident sympatric sparrows in eastern Texas. Auk 92:260–269.

Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology and Evolution 25:180–189.

Brackenbury, J. 1979. Power capabilities of the avian sound-producing system. Journal of Experimental Biology 78:163–166.

Brumm, H., and M. Ritschard. 2011. Song amplitude affects territorial aggression of male receivers in chaffinches. Behavioral Ecology 22:310–316.

Bunkley, J. P., C. J. W. Mcclure, N. J. Kleist, C. D. Francis, and J. R. Barber. 2015. Anthropogenic noise alters bat activity levels and echolocation calls. Global Ecology and Conservation 3:62–71.

Chan, A. A. Y.-H., W. D. Stahlman, D. Garlick, C. D. Fast, D. T. Blumstein, and A. P. Blaisdell. 2010. Increased amplitude and duration of acoustic stimuli enhance distraction. Animal Behaviour 80:1075–1079.

Davis, J. 1957. Comparative foraging behavior of the spotted and brown towhees. Auk 74:129–166.

Dooling, R. J. and A. N. Popper. 2007. The effects of highway noise on birds. See http://www. dot. ca. gov/hq/env/bio/files/caltrans_birds_10-7-2007b. pdf.

Francis, C. D. 2015. Vocal traits and diet explain avian sensitivities to anthropogenic noise. Global Change Biology 21:1809–1820.

Francis, C. D., and J. R. Barber. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Frontiers in Ecology and the Environment 11:305–313.

Francis, C. D., C. P. Ortega, and A. Cruz. 2009. Noise pollution changes avian communities and species interactions. Current Biology 19:1415–1419.

Francis, C. D., C. P. Ortega, and A. Cruz. 2011a. Noise pollution filters bird communities based on vocal frequency. PLoS ONE 6:e27052.

Francis, C. D., C. P. Ortega, and A. Cruz. 2011b. Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. Proceedings. Biological Sciences/The Royal Society 278:2025–2031.

Francis, C. D., C. P. Ortega, and A. Cruz. 2011c. Different behavioural responses to anthropogenic noise by two closely related passerine birds. Biology Letters 7:850–852.

Francis, C. D., J. Paritsis, C. P. Ortega, and A. Cruz. 2011d. Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. Landscape Ecology 26:1269–1280.

Francis, C. D., N. J. Kleist, C. P. Ortega, and A. Cruz. 2012a. Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. Proceedings. Biological Sciences/The Royal Society 279:2727–2735.

Francis, C., N. Kleist, B. Davidson, C. Ortega, and A. Cruz. 2012b. Behavioral responses by two songbirds to natural-gas-well compressor noise. Ornithological Monographs 74:36–46.

Gall, M. D., K. L. Ronald, E. S. Bestrom, and J. R. Lucas. 2012. Effects of habitat and urbanization on the active space of brown-headed cowbird song. Journal of the Acoustical Society of America 132:4053–4062.

Goodwin, S. E., and W. G. Shriver. 2011. Effects of traffic noise on occupancy patterns of forest birds. Conservation Biology 25:406–411.

Grafe, T. U., and J. H. Bitz. 2004. Functions of duetting in the tropical boubou, *Laniarius aethiopicus*: territorial defence and mutual mate guarding. Animal Behaviour 68:193–201.

Greenlaw, J. S. 1996. Spotted Towhee (*Pipilo maculatus*). The Birds of North America Online.

Gross, K., G. Pasinelli, and H. P. Kunc. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. American Naturalist 176:456–464.

Habib, L., E. M. Bayne, and S. Boutin. 2006. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. Journal of Applied Ecology 44:176–184.

Halfwerk, W., S. Bot, J. Buikx, M. van der Velde, J. Komdeur, C. ten Cate, and H. Slabbekoorn. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proceedings of the National Academy of Sciences of the United States of America 108:14549–14554.

Halfwerk, W., S. Bot, and H. Slabbekoorn. 2012. Male great tit song perch selection in response to noise-dependent female feedback. Functional Ecology 26:1339–1347.

Holland, J., T. Dabelsteen, S. B. Pedersen, and O. N. Larsen. 1998. Degradation of wren *Troglodytes troglodytes* song: implications for information transfer and ranging. Journal of the Acoustical Society of America 103:2154–2166.

Hu, Y., and G. C. Cardoso. 2010. Which birds adjust the frequency of vocalizations in urban noise? Animal Behaviour 79:863–867.

Kight, C. R., and J. P. Swaddle. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecology Letters 14:1052–1061.

Kroodsma, E. 1971. Song variations and singing behavior in the rufous-sided towhee, *Pipilo erythrophthalmus oregonus*. Condor 73:303–308.

Lohr, B., T. F. Wright, and R. J. Dooling. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Animal Behaviour 65:763–777.

Luther, D., and J. Magnotti. 2014. Can animals detect differences in vocalizations adjusted for anthropogenic noise? Animal Behaviour 92:111–116.

Marler, P., and D. Isaac. 1960. Physical analysis of a simple bird song as exemplified by the chipping sparrow. Condor 62:124–135.

Mathevon, N., T. Aubin, and T. Dabelsteen. 1996. Song degradation during propagation: importance of song post for the wren *Troglodytes troglodytes*. Ethology 102:397–412.

Mathevon, N., T. Dabelsteen, and S. H. Blumenrath. 2005. Are high perches in the blackcap *Sylvia atricapilla* song or listening posts? A sound transmission study. Journal of the Acoustical Society of America 117:442–449.

McMullen, H., R. Schmidt, and H. P. Kunc. 2014. Anthropogenic noise affects vocal interactions. Behavioural Processes 103:125–128.

Middleton, A. L. A. 1998. Chipping Sparrow (*Spizella passerina*). The Birds of North America Online.

Moseley, D. L., D. C. Lahti, and J. Podos. 2013. Responses to song playback vary with the vocal performance of both signal senders and receivers. Proceedings. Biological sciences/The Royal Society 280:20131401.

Okanoya, K., and R. J. Dooling. 1988. Hearing in the swamp sparrow, *Melospiza georgiana*, and the song sparrow, *Melospiza melodia*. Animal Behaviour 36:726–732.

Patricelli, G., and J. J. L. Blickley. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk 123:639–649.

Pohl, N. U., H. Slabbekoorn, G. M. Klump, and U. Langemann. 2009. Effects of signal features and environmental noise on signal detection in the great tit, *Parus major*. Animal Behaviour 78:1293–1300.

Pohl, N. U., E. Leadbeater, H. Slabbekoorn, G. M. Klump, and U. Langemann. 2012. Great tits in urban noise benefit from high frequencies in song detection and discrimination. Animal Behaviour 83:711–721.

Proppe, D. S., C. B. Sturdy, and C. C. St. Clair. 2013. Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. Global Change Biology 19:1075–1084.

Slabbekoorn, H. 2013. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Animal Behaviour 85:1089–1099.

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

Slabbekoorn, H. and E. A. P. Ripmeester. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17:72–83.

Swaddle, J. P., and L. C. Page. 2007. High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. Animal Behaviour 74:363–368.

Tobias, J. A., and N. Seddon. 2009. Signal jamming mediates sexual conflict in a duetting bird. Current Biology 19:577–582.