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CHAPTER 4

BEHAVIORAL RESPONSES BY TWO SONGBIRDS TO NATURAL-GAS-WELL COMPRESSOR NOISE

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ABSTRACT.—Several urban-adapted species sing at a higher frequency in noisy urban areas than in quiet locations. Yet it remains unclear whether the ability to adjust signals in response to noise is related to an ability to persist in noisy areas, because signal change and habitat use are infrequently measured within a single study. We investigated occupancy and signal change in response to noise in the Blue-gray Gnatcatcher (*Poliioptila caerulea*) and the Spotted Towhee (*Pipilo maculatus*) using a study system that eliminates uncontrolled effects of habitat features that may influence song frequency or habitat use and controls for the negative effect of noise on bird surveys. We predicted that species that alter the frequency of their vocalizations in response to noise would use noisy and quiet areas similarly, and that species that do not adjust their vocalizations in response to noise may avoid noisy areas. Both study species were uninfluenced by noise in their habitat occupancy, but only Spotted Towhees sang at a higher frequency with increased noise exposure. This may be explained by low-frequency noise having a greater acoustic masking potential for low-frequency Spotted Towhee songs than for higher-pitched Blue-gray Gnatcatcher songs. These findings suggest that an ability to shift song frequency may not directly correspond to an ability to remain in noisy areas. Although many factors can influence habitat use by birds, habitat occupancy in noisy areas may depend on whether the noise has acoustic energy at frequencies that can mask a species' song; if so, signal flexibility may be important.

Key words: acoustic masking, anthropogenic noise, Blue-gray Gnatcatcher, frequency change, habitat occupancy, New Mexico, *Pipilo maculatus*, *Poliioptila caerulea*, Spotted Towhee.

Respuestas en el Comportamiento de Dos Aves Canoras al Ruido de los Compresores de Pozos de Gas Natural

RESUMEN.—Muchas especies adaptadas a ambientes urbanos cantan a una frecuencia más alta en áreas urbanas que en localidades silenciosas. Sin embargo, todavía no es claro si la habilidad de ajustar las señales como respuesta al ruido se relaciona con la habilidad de persistir en áreas ruidosas porque el cambio en las señales y el uso del hábitat frecuentemente no son medidos en un solo estudio. Investigamos la ocupación y el cambio en las señales como respuesta al ruido en *Poliioptila caerulea* y *Pipilo maculatus* usando un sistema de estudio que elimina los efectos no controlados de las características del hábitat que pueden afectar la frecuencia del canto o el uso del hábitat y controla el efecto negativo del ruido en los censos de aves. Predijimos que las especies que alteran la frecuencia de sus vocalizaciones en respuesta al ruido podrían usar áreas ruidosas y silenciosas de manera similar,

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y que las especies que no ajustan sus vocalizaciones en respuesta al ruido evitarían las áreas ruidosas. Las especies de estudio no estuvieron influenciadas por el ruido en términos de su ocupación del hábitat, y sólo *Pipilo maculatus* cantó a una frecuencia mayor con el incremento en la exposición al ruido. Esto puede ser explicado porque el ruido de baja frecuencia tiene un mayor potencial de enmascaramiento acústico de los cantos de baja frecuencia de *Pipilo maculatus* que de los cantos de alta frecuencia de *Poliophtila caerulea*. Estos resultados sugieren que la habilidad para cambiar la frecuencia del canto puede no corresponder directamente a la habilidad de permanecer en áreas ruidosas. Aunque muchos factores pueden influenciar el uso del hábitat por las aves, la ocupación del hábitat en áreas ruidosas puede depender de si el ruido tiene energía acústica a frecuencias que puedan enmascarar el canto de una especie; si es así, la flexibilidad de la señal puede ser importante

NOISE PERMEATES ALL landscapes. From continuous sounds generated by running water to anthropogenic noise from human activities, background sounds can interfere with animal acoustic communication through acoustic masking (Klump 1996). Masking may be most severe when the signal and background sound(s) share the same acoustic frequencies, reducing a receiver's ability to detect and discriminate relevant acoustic sounds (a signal) from irrelevant ones (unwanted background noise). Animals that rely on acoustic communication have evolved signal characteristics that minimize masking from background sounds in their natural habitats (Brumm and Slabbekoorn 2005). Yet anthropogenic noise is often markedly different in frequency, and often at much greater amplitudes, than sounds in most natural habitats (Slabbekoorn and Ripmeester 2008).

In urban areas, anthropogenic noise can be omnipresent, and several single-species studies suggest that at least some birds may change the frequency of their vocalizations in response to masking effects of urban noise (e.g., Slabbekoorn and Peet 2003, Nemeth and Brumm 2009, Gross et al. 2010). However, generalizations from findings for urban-adapted birds are limited, for several reasons. First, urban-adapted species may have greater behavioral, physiological, and ecological flexibility than nonurban species (Bonier et al. 2007); therefore, the ability to change acoustic signals in response to noise may not represent typical responses by most species. Second, it is difficult to separate the influence of noise from other influential habitat features in urban areas, such as foraging and nesting opportunities (Crocì et al. 2008), which may also explain urban habitat use by many urban-adapted birds. That is, it is unclear whether noise-dependent signal modification is a mechanism that permits urban-adapted birds to remain in noisy areas, or whether they flourish in urban habitats primarily because of other factors. Finally, in addition to an evolutionary predisposition to

occupy urban habitat and the confounding factors that may explain habitat use patterns, signal characteristics among urban-adapted birds that have been attributed to noise, such as higher-frequency songs, may also be due to other factors associated with human-altered landscapes, such as physical habitat features that favor higher-frequency vocalizations (Nemeth and Brumm 2009).

A separate line of research has focused on how areas exposed to noise may represent habitat lost for some species. Noise exposure can cause declines in densities (Bayne et al. 2008) and alter community diversity (Francis et al. 2009). The leading explanation suggested for these changes is that noise masks birds' acoustic communication (Brumm and Slabbekoorn 2005), thereby excluding some species from otherwise suitable areas (Slabbekoorn and Ripmeester 2008). However, few studies have examined acoustic signaling strategies and habitat use in response to noise within the same study. In one study involving the influence of traffic noise on two songbirds, Parris and Schneider (2009) found that Gray Shrike-thrushes (*Colluricincla harmonica*) near noisy roadways sang at a higher frequency, yet Gray Fantails (*Rhipidura fuliginosa*) in noisy areas did not sing higher-pitched songs than individuals in quiet areas. Detections of both species declined with increased traffic noise, but the authors were unable to determine whether this pattern reflected declines in abundance as a result of traffic noise or a reduced probability of detection with increased traffic noise; therefore, they were unable to link noise-dependent signal change with use of noisy areas. It is still unclear whether noise-dependent vocal plasticity may be a mechanism that permits species to remain in noisy areas. Stronger evidence for an association among anthropogenic noise, signal change, and occupancy of noisy areas would come from studies that (1) focus on non-urban bird species, (2) eliminate uncontrolled

effects of urban versus rural habitat features that may also influence song frequency and habitat use, and (3) control for negative effects of noise on bird surveys (Pacifci et al. 2008, Ortega and Francis 2012).

In the present study, we investigated changes in song and habitat occupancy in response to continuous anthropogenic noise in two songbirds that are not urban-adapted species (Burhans and Thompson 2006, Smith 2008): the Blue-gray Gnatcatcher (*Poliptila caerulea*; hereafter "gnatcatcher") and Spotted Towhee (*Pipilo maculatus*; hereafter "towhee"). In a previous nesting study, we isolated anthropogenic noise from other confounding variables often associated with noisy areas and controlled for habitat differences by using study sites located in areas adjacent to natural gas wells with and without noisy compressors (Francis et al. 2009). We found that towhees avoided areas with high noise amplitudes in their nest placement, but we lacked an adequate sample size of gnatcatcher nests to draw inferences about their response to noise in terms of nest-site selection. Here, we used the same study area to investigate these species' habitat use, as gauged through occupancy using point counts, and their vocal behavior in response to noise. On the basis of evidence that many urban-adapted species may modify their signals in response to urban noise (e.g., Slabbekoorn and Peet 2003, Nemeth and Brumm 2009, Gross et al. 2010), we hypothesized that if vocal frequency change is a mechanism that allows species to persist in noisy environments, then species capable of noise-dependent frequency changes would use noisy and quiet areas similarly, but those unable to change their signals in response to noise may have lower occupancy rates in noisy areas.

METHODS

Study species.—Both gnatcatchers and towhees breed in open woodlands of western North America. The gnatcatcher is the most widespread member of *Poliptila* in North America, ranging from Central America to Vermont, and they are found in a wide range of wooded habitats (Ellison 1992). The towhee is widespread in western North America and tends to breed in xeric shrubby habitats with and without emergent vegetation (Greenlaw 1996). Both species have songs that may be masked by low-frequency anthropogenic noise. Gnatcatchers sing between ≈ 2.0 and

9.5 kHz (Ellison 1992), and towhees sing between ≈ 1.5 and 8.0 kHz (Greenlaw 1996). Gnatcatchers produce high-frequency, complex songs that consist of continuous jumbles of phrases (Ellison 1992). Towhee song structure varies geographically from the Pacific coast, with mostly simple trills, to the mountains and Great Plains, with a short introduction phrase followed by trills (Greenlaw 1996).

Study area.—Our study area was in the San Juan Basin in northern New Mexico, within the Rattlesnake Canyon Habitat Management Area, which is managed by the Bureau of Land Management (BLM). This area is heavily developed by natural gas extraction (Francis et al. 2009), with >18,000 gas wells in the San Juan Basin (BLM 2003). Many gas wells are coupled with noisy gas-well compressors, which aid in gas extraction and transportation (for a complete description of the study area, see Francis et al. 2009, Ortega and Francis 2012). Because the compressors generate noise at frequencies ranging above 5 kHz and overlap the frequency ranges of both gnatcatchers and towhees (Fig. 1), compressor noise may impair receivers' abilities to detect and discriminate their songs through acoustic masking.

Point counts.—Point counts were conducted between 21 May and 4 July 2007 at eight quiet control sites that lacked gas compressors, five treatment sites with noisy compressors running during our surveys, and five treatment sites with compressors off during our surveys (for a detailed description of the point counts, see Ortega and Francis 2012). The data included here are only from point-count locations that were visited twice, and only from locations on control sites ($n = 125$) or from treatment sites where compressors were turned off during surveys ($n = 65$). We did not include locations where compressors were on during surveys because our ability to detect birds was severely impaired (Ortega and Francis 2012). Occurrence at a point-count location was defined as whether a species was detected within a 60-m fixed radius during either survey visit. We selected 60 m as a fixed radius because the habitat was relatively open, and we were confident that most birds were detected within this distance. Although detection probabilities can vary with observer experience, time of day, weather, and many other factors (e.g., Simons et al. 2009), here we assumed a constant detection probability on all surveys because compressors were turned off during surveys and we found no systematic

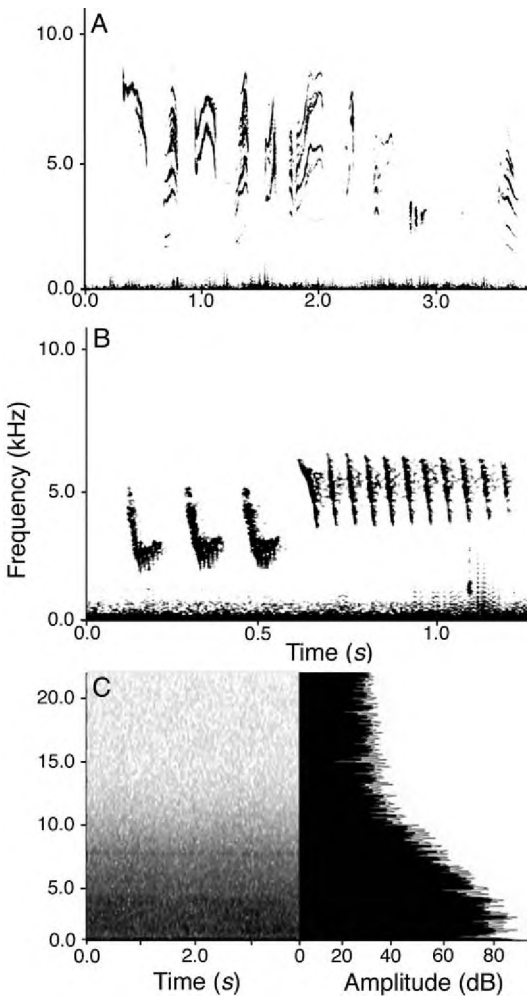


FIG. 1. Spectrograms of (A) Blue-gray Gnatcatcher and (B) Spotted Towhee songs. (C) Compressor noise, recorded at a distance of 100 m from the compressor exhaust, is displayed as a spectrogram (left) and power spectrum (right). Compressor noise is ~ 94 dB(A) at the source but may attenuate to ~ 55 dB(A) at a distance of 100 m (Francis et al. 2011c). Darker shades in the spectrogram indicate more acoustic energy located at those frequencies, which is reflected by higher amplitude values in the power spectrum. This illustrates that compressor noise has considerable acoustic energy up to 10 kHz, which overlaps frequencies used by gnatcatchers and towhees and may mask their acoustic signals.

differences in habitat characteristics on treatment and control sites (Francis et al. 2009).

Amplitude measurements of background noise at control-site point-count locations were measured on the second of two visits, but because

the compressors were off during the second survey on treatment sites, noise measurements were completed on a third visit when compressors were turned on. For each point-count location, noise amplitude was measured with both A- and C-weighting (equivalent continuous noise level [L_{eq}], fast response time) with an NIST-certified sound pressure meter (Casella model CEL 320 and CEL 1002 converter). Measurements were taken only when there were no birds vocalizing within ≈ 30 m and when wind conditions were below category 3 (≈ 13 – 18 km h^{-1}) on the Beaufort Wind Scale. Here, we use A-weighted amplitude measurements (dB[A]) in all analyses because A-weighted values filter low-frequency (<0.5 kHz) compressor noise that most birds do not hear (Dooling and Popper 2007) and provide a better measurement of acoustic energy at frequencies that would mask vocalizations of the two species considered here (≈ 1.0 – 9.5 kHz; Fig. 1).

Song measurements.—Gnatcatcher and towhee vocalizations were recorded between 11 May and 2 July 2009 in woodlands surrounding 31 gas wells with and without compressors. Many sites were those used for point counts in 2007; however, to increase our sample size, we recorded individuals in areas surrounding other wells that had not been included in our study previously. We normally sampled one individual of each species per location (i.e., area surrounding a single well); however, when we sampled more than one individual of a species at a single site, only individuals with nonadjacent territories were included in the analysis.

We recorded full song bouts (i.e., duration that an individual vocalizes from a single perch) with a Marantz PMD 660 digital recorder using a directional shotgun microphone (Audio-technica AT-815) pointed directly at the vocalizing individual. After recording each song bout, background noise was measured for 2 min from as close to the singing perch as possible, using the same methods as for point counts. For each individual, the number of singing males at adjacent territories, distance to the individual measured, and cardinal direction of the projected vocalization were recorded. All measurements and recordings were made when wind speed was less than category 3 (≈ 13 – 18 km h^{-1}) on the Beaufort Wind Scale.

For each individual gnatcatcher and towhee sampled, we randomly sampled five songs from each recording and measured three frequency features in RAVEN PRO, version 1.3 (Charif

et al. 2008). We measured song peak frequency, the frequency of the song with the most acoustic energy, and peak frequency of the lowest note (the frequency of the lowest note with the most acoustic energy) automatically following placement of a selection box around the entire song and lowest note, respectively. We measured minimum frequency (lowest frequency of the entire song) manually using a selection box at the margin of notes on the spectrogram while refining box placement using the selection bars on the power spectrum view. Because compressor noise has more acoustic energy at lower frequencies, there was the potential for noise to completely mask low-frequency song features, making measurement of low-frequency signals impossible. In practice, however, all of our recordings had signal-to-noise ratios that were large enough to easily identify the minimum frequency amid the low-frequency noise (for examples from species with minimum song frequencies similar to that of the lower-pitched Spotted Towhee, see Francis et al. 2011b: fig. S3 or Francis et al. 2011a: fig. S1). All measurements were taken using a Hamming window and fast Fourier transformation (FFT) length of 1,024, which displayed a spectral resolution of 47 Hz. Frequency features from the five measured songs were averaged to obtain a single value representing each feature for each male.

Analysis.—For each species, we used generalized linear mixed-effect models to describe occupancy with the presence (treatment or control site-type) or amplitude (dB[A]) of noise, plus the interaction between the two. We treated gas-well site as a random effect in all models, including the null. For the acoustic analysis, we used generalized linear models to examine the influence of the same variables and interaction term included in the occupancy analysis on each of the spectral variables for gnatcatcher and towhee songs. Frequency data were log transformed prior to analysis to stabilize variances and to ensure normality.

We used an information-theoretic approach to evaluate support for competing candidate models explaining occupancy and song features for both species (Burnham and Anderson 2002). We used Akaike's information criterion corrected for small sample sizes (AIC_c) for our model selection procedure. We ranked models on the basis of differences in AIC_c scores (ΔAIC_c). Models with ΔAIC_c scores within two of the best models were considered to have strong support. For

all candidate models within two ΔAIC_c of the best model, we calculated Akaike weights (w_i) to quantify the degree of support for each. We used all candidate models with Akaike weights to calculate model-averaged variable coefficients and unconditional 95% confidence intervals (CIs). We calculated odds ratios for the model-averaged coefficients and 95% CIs, and we concluded that there was little evidence for the effect of a predictor variable on occupancy when the odds ratios of the 95% CIs overlapped 1.0 (i.e., equal odds). We also weighted the evidence of importance of each variable included in candidate models with Akaike weights. To do so, we summed w_i scores for supported candidate models ($\Delta AIC_c < 2$) containing the variable of interest to calculate the relative variable importance (Burnham and Anderson 2002). All analyses were completed in the program R (R Development Core Team 2010). All means are reported \pm SE unless otherwise indicated.

RESULTS

Effect of noise on species occupancies.—Point-count location amplitudes ranged from 32.1 to 45.8 dB(A) on control sites and from 46.0 to 68.2 dB(A) on treatment sites, and we had previously found noise exposure to be significantly higher at treatment point-count locations than at control point-count locations (Francis et al. 2011b).

For gnatcatchers, the models including the presence of noise (treatment or control site) and noise amplitude and an interaction between the two were included among the models with strong support ($\Delta AIC_c < 2$; Table 1). However, all model-averaged variable coefficients resulting from supported models had odds ratios with 95% CIs overlapping 1.0 (i.e., equal odds), which suggests that neither presence of noise (site-type) nor its amplitude had a strong influence on gnatcatcher occupancy (Table 2). For towhee habitat occupancy, models with strong support included amplitude and site-type, but the null was also included (Table 1). Because their 95% CI of the odds ratios overlapped 1.0, there was also little evidence for a strong effect of amplitude or site-type on towhee occupancy.

Influence of noise on song features.—Noise amplitudes at the locations of singing gnatcatchers ranged from 33.4 to 55.0 dB(A) and were significantly higher on treatment sites than on control sites (two-tailed $t = 3.20$, $df = 20$, $P = 0.005$). We

TABLE 1. Mixed model results examining Blue-gray Gnatcatcher and Spotted Towhee occupancy in the Rattlesnake Canyon Habitat Management Area, northwest New Mexico, 2007. Models included treatment or control sites (site-type) and A-weighted noise amplitude (dB[A]) as fixed effects and well site as a random effect. K is the number of parameters in the model, AIC_c is Akaike’s information criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c values from the top-ranking model, and w_i is the Akaike weight, calculated for all models with strong support ($\Delta AIC_c < 2$).

Model ^a	K	AIC_c	ΔAIC_c	w_i
Blue-gray Gnatcatcher				
dB(A), site-type	4	178.4	0	0.52
Site-type		179.70	1.30	0.27
dB(A), site-type, dB(A)*site-type	5	180.24	1.84	0.21
Null ^b	2	182.34	3.94	
dB(A)	3	184.30	5.90	
Spotted Towhee				
Null ^b	2	124.59	0	0.56
dB(A)	3	126.46	1.87	0.22
Site-type	3	126.47	1.88	0.22
dB(A), site-type	4	128.54	3.95	
dB(A), site-type, dB(A)*site-type	5	129.65	5.06	

^a Site-type = a treatment vs. control site; dB(A) = amplitude in A-weighted decibels.

^b Null models included individual well sites as a random effect only.

recorded towhees singing in noise levels ranging from as low as 34.1 dB(A) to as high as 61.1 dB(A). As with the gnatcatchers, noise amplitude was significantly higher on treatment sites than on control sites (two-tailed $t = 5.56$, $df = 49$,

$P < 0.001$). We recorded towhee songs spanning a frequency range of 1.38 to 9.78 kHz, and with a peak frequency of ≈ 4.26 kHz. Gnatcatcher songs spanned 2.09 to 9.62 kHz, with a peak frequency of ≈ 5.73 kHz.

Noise had no influence on gnatcatcher song frequency features; the null model emerged as the only model with strong support ($\Delta AIC_c < 2$) for the analyses of song peak frequency, peak frequency of the lowest note, and minimum frequency. By contrast, towhee song features changed with noise exposure. Song peak frequency was best explained by models including noise amplitude and site-type, and noise amplitude was the only predictor variable for models with strong support explaining minimum song frequency (Table 3). Peak frequency of the lowest note was not explained by the presence or amplitude of noise; the null model was best supported by the data, and two other models were also supported (Table 3).

Of all the model-averaged coefficient estimates, the presence of noise (site-type) did not have a strong effect on towhee song peak frequency, even though it was included in one of the models with strong support (Table 4). Instead, the amplitude of background noise appears to be more important. The effect of dB(A) on the log-transformed values for towhee song peak and minimum frequency had a strong, albeit small, effect (Table 4). It is important to note that these small effect sizes pertain only to single increases in A-weighted decibels for log-transformed frequencies. In terms of untransformed frequencies, for an order-of-magnitude increase in background noise acoustic power (+10 dB[A]), the peak frequency of towhee song was 314 Hz higher and minimum frequency was

TABLE 2. Influence of fixed effects influencing Blue-gray Gnatcatcher and Spotted Towhee occupancy in the Rattlesnake Canyon Habitat Management Area, northwest New Mexico, 2007. Presented are model-averaged effect sizes \pm SE, odds ratios with 95% confidence intervals, and relative variable importance for all variables in supported models ($\Delta AIC_c < 2$).

Predictor variable ^a	Effect size and direction	Odds ratio	95% CI	Relative importance
Blue-gray Gnatcatcher				
dB(A)	0.101 \pm 0.092	1.106	0.924–1.324	0.73
Site-typeT	-2.910 \pm 3.780	0.054	0.000–90.017	1.00
dB(A)*site-typeT	-0.015 \pm 0.072	0.985	0.856–1.133	0.21
Spotted Towhee				
dB(A)	0.003 \pm 0.020	1.003	0.965–1.044	0.22
Site-typeT	0.075 \pm 0.383	1.078	0.509–2.282	0.22

^a Site-typeT = effect of a noisy treatment site in relation to a quiet control site; dB(A) = amplitude in A-weighted decibels.

TABLE 3. Generalized linear model results pertaining to Spotted Towhee song features in the Rattlesnake Canyon Habitat Management Area, northwest New Mexico, 2009. K is the number of parameters in the model, AIC_c is Akaike's information criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c values from the top-ranking model, and w_i is the Akaike weight, calculated for all models with strong support ($\Delta AIC_c < 2$). All models with $\Delta AIC_c < 4$ are displayed, along with the null.

Model ^a	K	AIC_c	ΔAIC_c	w_i
Peak frequency				
dB(A)	3	-44.45	0.00	0.72
dB(A), site-type	4	-42.54	1.91	0.28
Null	2	-41.25	3.20	
dB(A), site-type, dB(A)*site-type	5	-41.25	3.20	
Site-type	3	-39.84	4.61	
Lowest note peak frequency				
Null	2	-42.72	0.00	0.45
dB(A)	3	-42.36	0.36	0.37
Site-type	3	-40.91	1.81	0.18
dB(A), site-type	4	-40.06	2.66	
dB(A), site-type, dB(A)*site-type	5	-38.35	4.37	
Minimum frequency				
dB(A)	3	-26.77	0.00	1.00
Null	2	-24.68	2.09	
dB(A), site-type	4	-24.54	2.23	
dB(A), site-type, dB(A)*site-type	5	-24.38	2.39	
Site-type	3	-23.94	3.34	

^a Variable abbreviations as in Table 1.

165 Hz higher (Fig. 2). Over the range of observed noise amplitudes (34–61 dB[A]), these effects correspond to an increase of ~950 Hz for peak frequency and ~500 Hz for minimum frequency.

DISCUSSION

Noise is an environmental stressor that now permeates much of the world (Barber et al. 2010), and our findings add to the growing body of evidence suggesting that noise influences animal distributions and behaviors. Although previous studies offer valuable insight into noise-dependent vocal change among birds in urban habitats (e.g., Slabbekorn and Peet 2003; Nemeth and Brumm 2009, 2010), our study system holds several key advantages. For instance, the nonurban environment allowed us to control for potentially confounding factors associated with studies of urban and road noise and the ability to turn off the noise source controlled for the influence of noise on detections (Pacifi et al. 2008, Ortega and Francis 2012). Additionally, we focused on two species that appear to be sensitive to urbanization (Burhans and Thompson 2006, Smith 2008), which holds particular relevance when compared with growing evidence suggesting that urban-adapted species may modify their songs in response to urban noise (e.g., Slabbekorn and Peet 2003, Brumm 2004, Wood and Yezerinac 2006, Nemeth and Brumm 2009).

The responses by the two species examined here did not match our hypothesis that species with equivalent occupancies in noisy and quiet areas would also have noise-dependent signal change. Gnatcatchers altered neither the frequencies of their signals with increased noise exposure, nor their occupancy patterns with increased noise amplitudes. Occupancy of noisy areas and presence of noise-dependent frequency change was observed for the towhee, but this result was counter to our expectation that towhee occupancy would decline with noise exposure given the past result of noise avoidance in towhee nest

TABLE 4. Influence of variables influencing Spotted Towhee song features in the Rattlesnake Canyon Habitat Management Area, northwest New Mexico, 2009. Presented are model-averaged effect sizes \pm SE, odds ratios with 95% confidence intervals, and relative variable importance for all variables in supported models ($\Delta AIC_c < 2$). Bold denotes variables considered to have a strong effect.

Predictor variable ^a	Effect size and direction	Odds ratio	95% CI	Relative importance
Peak frequency				
dB(A)	0.010 \pm 0.004	1.012	1.005–1.164	1.00
Site-typeT	-0.010 \pm 0.033	0.99	0.928–1.057	0.28
Minimum frequency				
dB(A)	0.017 \pm 0.008	1.017	1.002–1.033	1.00

^a Variable abbreviations as in Table 2.

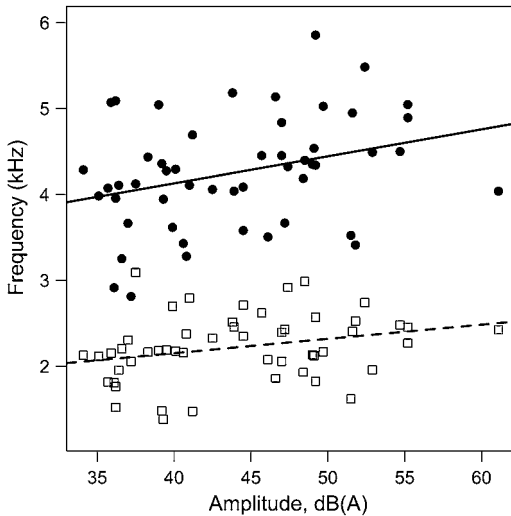


FIG. 2. Relationship between Spotted Towhee vocal frequency (kHz) and background noise amplitude (dB[A]) measured at the location of the individual. Peak frequency of Spotted Towhee song (black circles and solid line) and minimum frequency (open squares and dashed line) increased with increases in dB(A). Data displayed as untransformed frequencies.

placement (Francis et al. 2009). We explore this discrepancy between towhee habitat occupancy and nest placement below, but we must first acknowledge that habitat occupancy is influenced by many factors, some of which may explain why we did not find a relationship between occupancy rates and the presence and amplitude of noise. In our study area, noise changes the composition of the nesting community such that fewer species nest in noisy areas and key nest predators are less common (Francis et al. 2009, Francis et al. 2012). It is possible that some towhees and gnatcatchers settle in noisy areas following cues indicative of decreased nest predation or the absence or reduced densities of key heterospecific competitors. Yet if this were true, one might expect to see a noise-dependent increase in habitat occupancy rates by towhees and gnatcatchers.

It is also plausible that species-specific song frequency influences occupancy and acoustic behavioral responses to noise. That towhee song increases in frequency with increased noise exposure and that the gnatcatcher's song does not may be due to a different degree of acoustic masking experienced by each species. Because towhee song occupies lower frequencies than gnatcatcher song, it follows that towhee song should suffer from greater acoustic masking from compressor

noise than gnatcatcher song; thus, one might expect towhees to have a stronger behavioral response to noise, whether by avoiding noisy areas or by noise-dependent signal change. By contrast, the gnatcatcher's higher-pitched song may be masked less by compressor noise; thus, signal modification may be unnecessary. A recent study involving two Australian songbirds supports this possibility: the Gray Shrike-thrush, which sings at relatively low frequencies (1.5–4.0 kHz), sang at a higher frequency with increased noise exposure, but the Gray Fantail, which has a higher-pitched song (4.0–7.5 kHz), did not (Parris and Schneider 2009). This absence of noise-dependent frequency adjustments in the high-pitched gnatcatcher and Gray Fantail, and the presence of noise-dependent frequency adjustments in the lower-pitched songs of towhees and Gray Shrike-thrushes, is consistent with the hypothesis that acoustic masking by anthropogenic noise should be more severe for species with lower-frequency vocalizations.

Our finding that towhees shift their minimum song frequencies in response to increased noise exposure is supported by the majority of studies documenting noise-dependent signal shifts, which have found shifts in low-frequency song features (e.g., Slabbekoorn and Peet 2003, Wood and Yezerinac 2006, Gross et al. 2010; but see Francis et al. 2011a). However, in the present study, peak frequency of towhee song, which is not a low-frequency song feature, also increases with noise exposure, and this suggests that some species may need to adjust multiple song features located at various frequencies to improve signal transmission. Yet these observed frequency shifts may do little to improve signal transmission in noisy areas. For example, Nemeth and Brumm (2010) suggested that the small frequency increases (≈ 200 – 500 Hz) observed in urban Great Tits (*Parus major*) and European Blackbirds (*Turdus merula*) may only slightly improve communication in noisy urban environments. Although towhee minimum frequency may shift by 500 Hz, peak frequency appears to shift by nearly 1,000 Hz across the range of background noise amplitude values observed in the present study. This magnitude is similar to the shifts observed for the Gray Vireo (*Vireo vicinior*) and Plumbeous Vireo (*V. plumbeus*) in the same study area (Francis et al. 2011a) and greater than shifts observed for Great Tits and European Blackbirds. Although these large frequency changes may decrease the

acoustic masking potential from low-frequency noise, potentially improving communication in one way, higher frequencies attenuate over shorter distances, so increases in frequency may only marginally improve long-distance communication (Nemeth and Brumm 2010).

Frequency change in noise: Adaptive, a byproduct, or costly?—Evolutionary, ontogenetic, or behavioral modifications may represent mechanisms responsible for many correlative patterns of higher song frequencies with increased background noise (Patricelli and Blickley 2006). However, several recent studies have shown that short-term behavioral modifications are responsible for frequency shifts in at least three oscine species—the Great Tit (Halfwerk and Slabbeboom 2009), House Finch (*Carpodacus mexicanus*; Bermúdez-Cuamatzin et al. 2010), and Reed Bunting (*Emberiza schoeniclus*; Gross et al. 2010)—and the shifts observed for towhees may also be short-term adjustments. Nevertheless, identification of the precise mechanism responsible for frequency shifts remains unresolved. For example, noise-dependent frequency shifts may be a side effect of increases in vocal amplitude in response to noise (the “Lombard effect”). The coupled increases in vocal amplitude and frequency have been documented in frogs (Lopez et al. 1988), nonpasserine birds (Beckers et al. 2003), and even humans (Junqua 1993, Traunmüller and Eriksson 2000). Unfortunately, because an accurate field measurement of vocal amplitude is often infeasible, we were unable to determine whether towhees also increase amplitude with the documented frequency increases. Careful studies that standardize distance between the microphone and a vocalizing individual, while simultaneously controlling for the directional radiation of vocal sound waves (e.g., Brumm 2004), will be needed to determine whether amplitude and frequency covary among freelifving birds.

Regardless of why pitch shifts are observed among birds singing in noisy areas, the consequences for these adjustments are still poorly understood. Song is used to attract mates and repel rivals (e.g., Collins 2004), and small changes to signal structure may have serious consequences for the signaler. For example, male Reed Buntings increased the pitch of their songs in noisy areas, but more males in noisy areas remained unpaired throughout the breeding season than males in quiet areas (Gross et al. 2010). Decreased pairing rates were also observed for territorial male

Ovenbirds (*Seiurus aurocapilla*) in noisy areas, though changes to their vocalizations were not examined (Habib et al. 2007). These findings suggest that noise-dependent frequency adjustments may come with a cost. It is possible that male towhees holding territories in noisy areas were also experiencing decreased pairing success. This explanation would be consistent with the discrepancy between our finding that towhee occupancy was unchanged with increases in noise exposure and the previous finding that towhees avoid noise in their nest placement (Francis et al. 2009). Interestingly, Gray Vireo occupancy and nesting data show the same discrepancy (Francis et al. 2009, 2011a). It may be that our previous interpretation of avoidance of noisy areas in nest placement actually represented patterns of pairing success, with lower pairing rates with increased noise exposure.

Of course, additional explanations for noise-dependent decreases in pairing success are plausible; a higher proportion of lower-quality males defending territories in noisy areas than in quiet areas could explain the same pattern. Additionally, signal adjustments made by males in noisy areas may be insufficient to overcome the masking effects of noise such that females cannot discriminate among their signals, again possibly leading to lower pairing success. Future efforts are needed to sort out which, if any, of these mechanisms may explain reduced pairing success in noise and to determine whether noise-dependent signal adjustments come with costs.

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