Temporal Modification of Songbird Singing Behavior in the Presence of Intermittent Noise Events

Emily Finch[a] and Darren S. Proppe[b]

[a]*Undergraduate student investigator, Biology Department, Calvin College*
[b]*Assistant professor of biology, Biology Department, Calvin College*

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Abstract

Anthropogenic noise can negatively affect wildlife species, including songbirds. The primary mechanism by which noise affects songbirds may be through acoustic obstruction to their systems of vocal communication. However, many species possess adaptations, such as increasing song amplitude or frequency, which allow them to cope with high levels of noise. Temporal modification of singing patterns is one behavioral adaptation that may provide substantial release from masking noise, but has been understudied and is poorly understood. Here we utilize playback experiments to investigate whether songbirds alter their pattern of singing to take advantage of quiet noise windows embedding within periods of elevated noise. Contrary to our hypothesis, birds significantly decreased their song output in gaps during noise playback. Daily point counts revealed that birds generally remained on site for the duration of the experiment, thus absence is unlikely to account for lower singing rates. Decreased song output may correlate with reduced fitness, but further work is needed to confirm this. Nonetheless, our results suggest that behavioral adaptation to utilize gaps in noise for communication is not occurring in many songbird species.

Introduction

As human development increases, anthropogenic noise is altering the soundscape of an increasingly large percentage of the biosphere. According to Forman (2000), almost twenty percent of the United States landmass is already affected by road noise, one particularly common source of anthropogenic noise. The spread of anthropogenic noise is not without consequences for wildlife; in some cases contributing to the loss of diversity (Proppe et al. 2013), reduced density (Bayne et al. 2008), lower reproductive success (Halfwerk et al. 2011), and altered age distribution and mating systems (Reijnen & Foppen 1995; Swaddle & Page 2007). Songbirds appear to be particularly vulnerable to noise, likely because they rely on acoustic forms of communication that become compromised when external noise is introduced (Slabbekoorn & Ripmeester 2008). Similarly, birds that sing at high frequencies often remain abundant in areas near roads (Rheindt 2003; Hu & Cardoso 2009). For these species communication may be less affected, because most of the energy in road noise is found in the lower frequencies (Skiba 2000), and thus, does not overlap their song frequencies.

Recently, several studies have examined why some songbird species are more tolerant of anthropogenic noise than others (Hu & Cardoso 2010; Barber et al. 2010; Francis et al. 2011). In additional to the native frequency of species-specific songs (mentioned above), flexibility also appears to be important. In the presence of high levels of noise, some songbirds increase the frequency (Slabbekoorn & Peet 2003) and/or amplitude (Brumm 2004) of their songs. Both of these adaptations increase the likelihood that the intended receiver will perceive the song, and thus, allow successful communication will occur. However, these adaptations become less useful as noise levels increase. In a review of the literature, Reijnen and Foppen (2006) revealed that as traffic levels increase near a roadway, an increasing number of songbird species are affected.

While this finding affirms the importance of song frequency and amplitude, the temporal adaptations have been largely ignored.

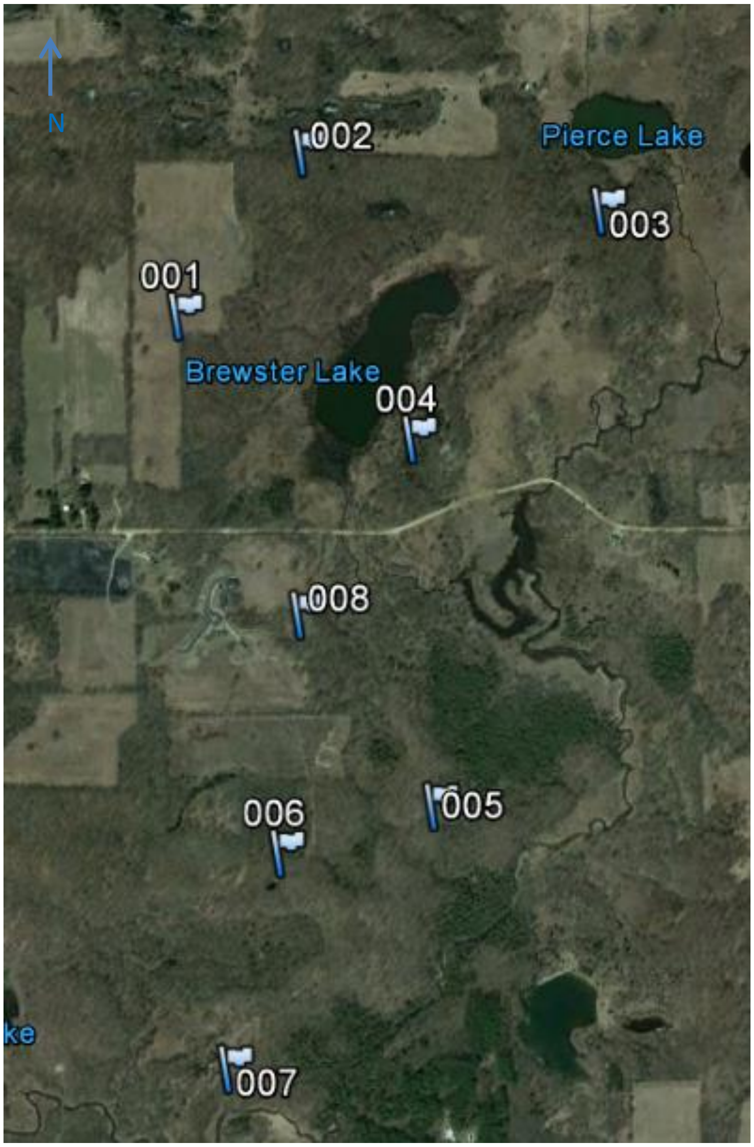
Near a roadway, noise production is generally limited to the period of time when a moving vehicle is present. Thus, at low traffic densities, periods of loud noise are punctuated with many relatively quiet time periods. In this scenario, birds could successfully communicate during these ‘windows’ of low noise levels. However, utilization of these windows between noise events is only advantageous if songbirds are able to alter the timing of their singing behavior accordingly. Two pieces of empirical data suggest that at least some species are capable of altering temporal characteristics of singing in response to external factors. First, European robins (*Erithacus rubecula*) that inhabit noisy urban areas sing significantly earlier in the morning (when traffic intensity is low) than their counterparts that inhabit quiet locations (Fuller et al. 2007). While this clearly represents a temporal modification to noise, whether this type of temporal adaptation translates to a fine-scale ability to utilize quiet windows in unknown. Second, great tits (*Paris major*; Slabbekoorn & Smith 2002) and black-capped chickadees (*Poecile atricapillus*; Proppe et al. 2011) that inhabit noisy roadside habitats produce shorter songs, potentially shortening songs to utilize the decreasing size of quiet windows between traffic events.

We investigated whether songbirds behaviorally alter their temporal patterns of song production to utilize periods of quiet embedded within elevated noise conditions. If temporal modification is an adaptation used to enhance communication in anthropogenic noise, we predict that songbirds will vocalize more often and with greater regularity during quiet periods of time embedded within experimentally elevated noise than during similar time intervals under control (non-noise) conditions.

Methods

Sites

Research was conducted from May 22 to August 9, 2013, on the premises of the Pierce Cedar Creek Institute in Hastings, Michigan. This property was ideal for the experimental approach utilized in this study because natural ambient noise levels were relatively low. As a result, the authors had a high degree of control over the types of noise present during each experiment. Eight sites (Map 1) were utilized to compare song production under control (non-noise) conditions, and under experimentally elevated noise conditions. All sites were forest or forest edge habitats to ensure that birds of the same species would be studied at each site. Each site served as both a control and experiment, being utilized as a control initially, and transitioning directly into experimental the following week. To minimize seasonal effects, two experimental and two control sites were run simultaneously each week for six weeks. Sites were separated by at least 350 m to reduce the potential for pseudoreplication. Nineteen species (Table 1) were selected for examination based on their known prevalence in previous bird inventories at Pierce Cedar Creek Institute (R. Keys, personal communication), timing of song production (overlapping the study period), and presence in initial experimental trials.



Map 1. A map of Pierce Cedar Creek Institute Property and the location of the eight forest and forest edge sites.

Table 1. A list of the nineteen focal species by scientific name and common name**.**

Scientific Name	Common Name
Baeolophus bicolor	Tufted titmouse
Cardinalis cardinalis	Northern cardinal
Contopus virens	Eastern wood-pewee
Dendroica petechia	Yellow warbler
Dendroica virens	Black-throated green warbler
Dumetella carolinensis	Gray catbird
Empidonax virescens	Acadian flycatcher
Geothlypis trichas	Common yellowthroat
Hylocichla mustelina	Wood thrush
Melanerpes carolinus	Red-bellied woodpecker
Melospiza melodia	Song sparrow
Molothrus ater	Brown-headed cowbird
Myiarchus crinitus	Great crested flycatcher
Pipilo erythrophthalmus	Eastern towhee
Seiurus aurocapilla	Ovenbird
Spizella passerina	Chipping sparrow
Spizella pusilla	Field sparrow
Turdus migratorius	American robin
Vermivora pinus	Blue-winged warbler
Vireo olivaceus	Red-eyed vireo

Playback

Each site consisted of an area with a 35 m radius with a passive recording device (SM1: Wildlife Acoustics) attached to a small tree in center of the sampling area at 1.5 m above the ground (Figure 1). A portable sound production system (consisting of a Pyramid amplifier, timer, lead-acid battery, and Raspberry Pi computer) was placed in the center of the sample area and playback speakers (Pyle, PHSP6K) were placed 25 m from the center in each cardinal direction. Once a location was selected for inclusion in the study, two days of pre-experimental recordings were collected to establish baseline singing rates. Recording began 10 minutes prior to sunrise, and continued for 2 hours.

Following this collection of baseline vocal data, sites were either recorded for four additional days without noise presentation (control) or were exposed to four consecutive days of noise playback (experimental). Multiple days were recorded to assess whether changes in song production patterns became more or less evident as time progressed. Playback consisted of repeating presentation of pre-recorded noise from a high use highway near Edmonton, Alberta, Canada, and was free from very loud highway sounds (e.g., tractor-trailer) and animal noises. Playback amplitude was adjusted until its range was similar to what would be found near a busy roadway (65 ± 2 dB SPLa) at the center of the site (1 min Leq, Casella 633 Sound level meter; Skibba 2000). Amplitude at each speaker was consistently 90 ± 2 dB (SPLa). Although speakers were directional, sound levels remained > 65 dB for ~10 m beyond speaker placement (N = 8), justifying the 35 m radius sampling area comprised of 25 m from recorder to speaker and 10 m beyond the speaker. Noise playback began 30 minutes prior to sunrise, and increased slowly in amplitude (linear ramp, Audacity 2.02) to reduce the likelihood that birds would avoid the area due to the novel stimulus (Figure 2). Full noise levels were achieved by sunrise. Noise playback continued for one hour and contained three, one-minute periods of silence. Recording continued throughout playback and for 30 minutes after noise playback ceased. One additional day of vocal activity was recorded post-playback (day 5) to examine whether treatment differences were extinguished immediately after playback ceased.

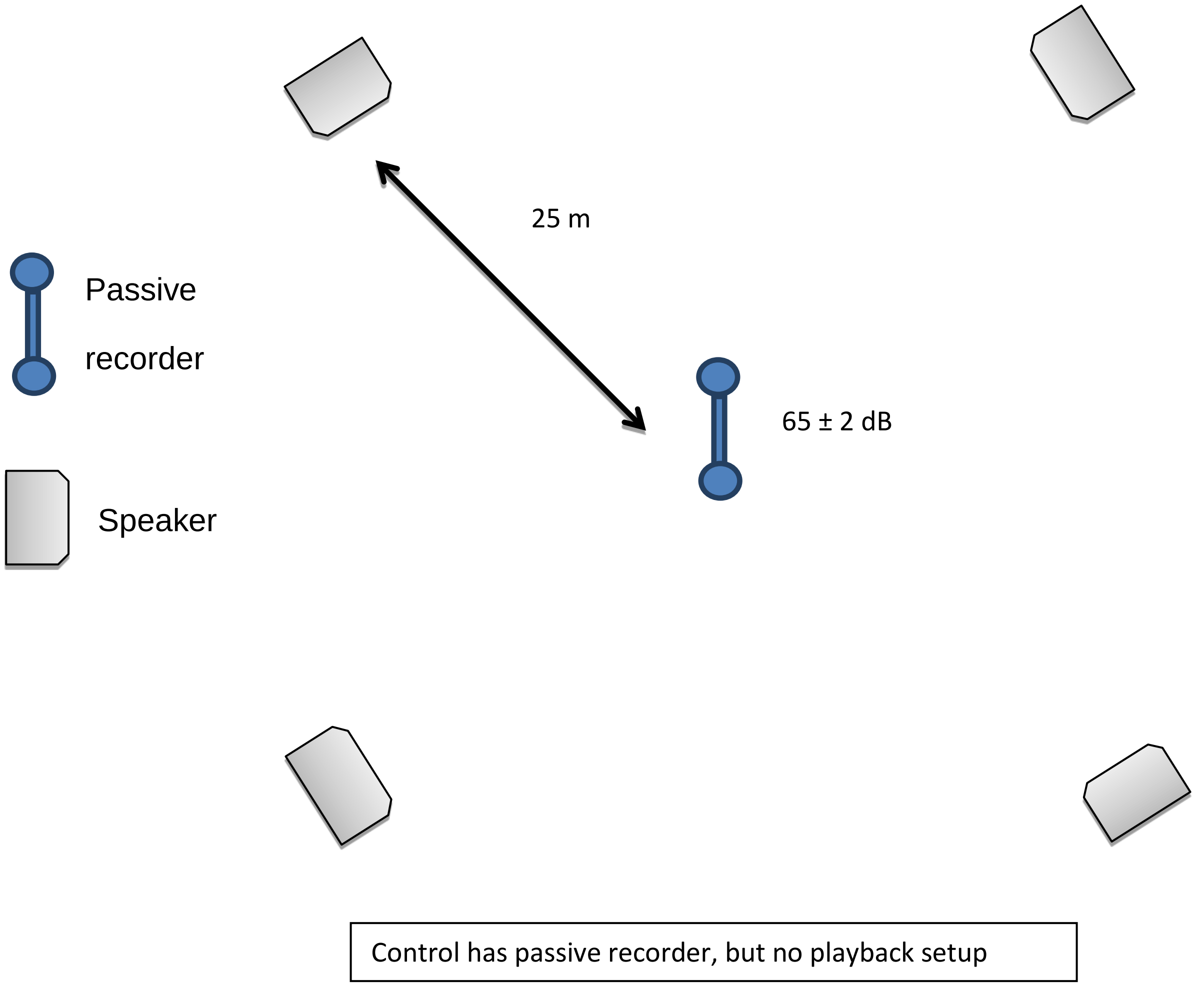


Figure 1. Experimental setup for the test sites includes speakers placed at the four cardinal directions, a passive recorder in the center and a distance of 25 m from recorder to speaker. Control sites only had the recorder, not the speakers. Also, all locations were used for both control and experimental tests.

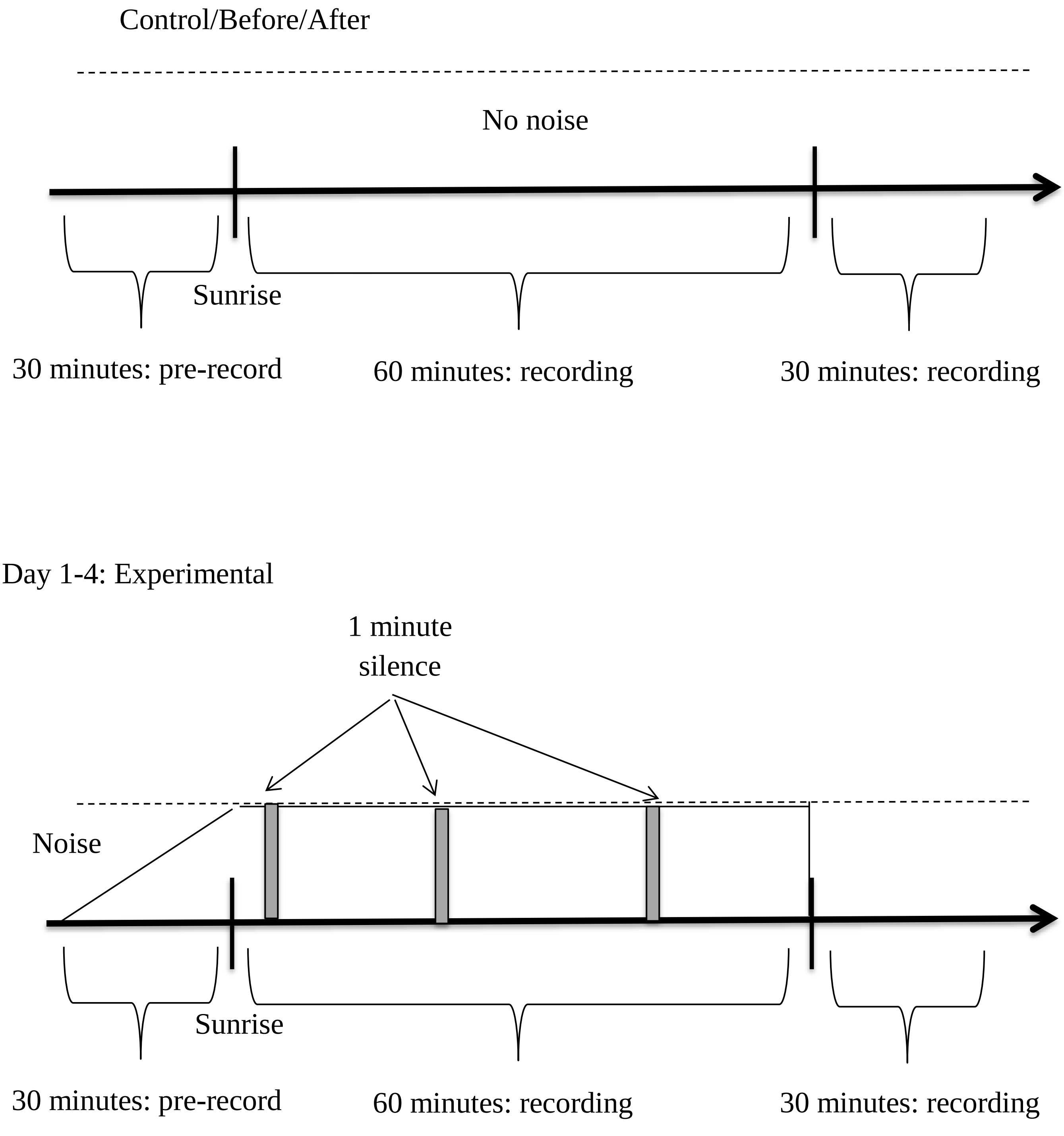


Figure 2. Recording schedule in control and experimental sites. Pre-experimental recording mirrored the control schedule for all sites.

Point Counts

Changes in observed singing rates may be due to differences in bird presence rather behavior. To control for this potential confound, we conducted point counts each site daily during experimental and control periods after the conclusion of the recorded testing period. Ten-minute point counts were conducted between 0800-1000 hours, and each focal species was identified by site or sound within a 100 m radius.

Analysis

To assess whether males of focal species were altering the timing of their song production in response to quiet events embedded within elevated noise, we compared song rate within one minute gaps in noise for experimental sites, and the corresponding one minute windows of time in the control condition. We used only one minute gaps because they most closely resemble the length of actual gaps in traffic noise. To increase the likelihood that we utilized only songs that were produced by individuals within our experimental plot, we played back pre-recorded yellow warbler, veery, and red-eyed vireo songs at the edge of our experimental area (amplitude = 80 dB at 1 m, N = 8). These songs were re-recorded and imported into Audacity 2.02. Songs were viewed on a non-normalized FFT spectrogram with settings adjusted (Hanning, window size = 2048, frequency range = 1-10 kHz, range = 75 dB, gain = 20) such that songs were on the edge of visibility. Thus most songs produced beyond the range of our plots were not visible to the observer. These standardized settings were used for the duration of the experiment, and all visible songs were counted within the one-minute windows. Songs were identified by species for the 19 focal species, and categorized as other for non-focal species. With one exception (Red-bellied woodpecker), calls and vocalizations from non-passerines were not utilized.

For our analysis we utilized only the total song count, which included all songs produced by all species, and have analyzed eight sites. Because we were interested in changes in song rate over time, we determined baseline singing rates via recordings before experimental conditions were implemented, and subtracted the baseline rate from additional days. Thus, increases in singing were positive, and decreases in singing were negative. We utilized ANOVA to compare total song count between treatment (control/experimental), day (1-5) and the interaction between treatment and day. Because singing was expected to decrease over time each morning, we added an additional dependent variable (order) designed to parse out variance due to the timing of gaps. To test whether birds remained in our plots during experimentation we used a MANOVA to test for abundance differences between treatments, day, and the interaction between the two. Each species (N = 19) was included as a dependent variable. Results are presented as means ± standard error (SE). *P* values < 0.05 were considered to be significant.

Results

ANOVA results revealed that song count varied significantly by treatment ($F_{1, 152} = 9.43$, $p = 0.003$) and by order ($F_{2, 152} = 6.57$, $p = 0.002$), but did not vary significantly by day ($F_{4, 152} = 0.33$, $p = 0.854$) or the interaction between treatment and day ($F_{4, 152} = 2.17$, $p = 0.075$). Pre-experimental baseline singing rates were 47.63 ± 3.69 songs/minute under control conditions and 56.44 ± 3.77 songs/minute under experimental conditions. Overall song rates at control sites increased by 6.01 ± 2.59 songs/minute, but decreased by 2.07 ± 2.36 songs/minute in experimental sites which were observed in the following days. While not significant, song rates generally decreased with additional days of noise playback (interaction term), reaching an average decrease of 9.00 ± 5.32 songs/minute on the first day post-playback and 11.22 ± 10.06 songs/minute on the final playback day, (Figure 3). This represents an average decrease of 16% and 20% in song output on these days, respectively; however both days have high levels of variation. MANOVA results show that the absence of focal species was unlikely to account for these differences. Neither treatment, day, nor the interaction was significant (Wilks lamba $F > 1.078$, $p < 0.330$). Within each day, singing in gaps decreased as time proceeded (order: 1 = 61.45 ± 2.92 songs/minute; 2 = 50.89 ± 2.24 songs/minute; 3 = 46.90 ± 2.02 songs/minute).

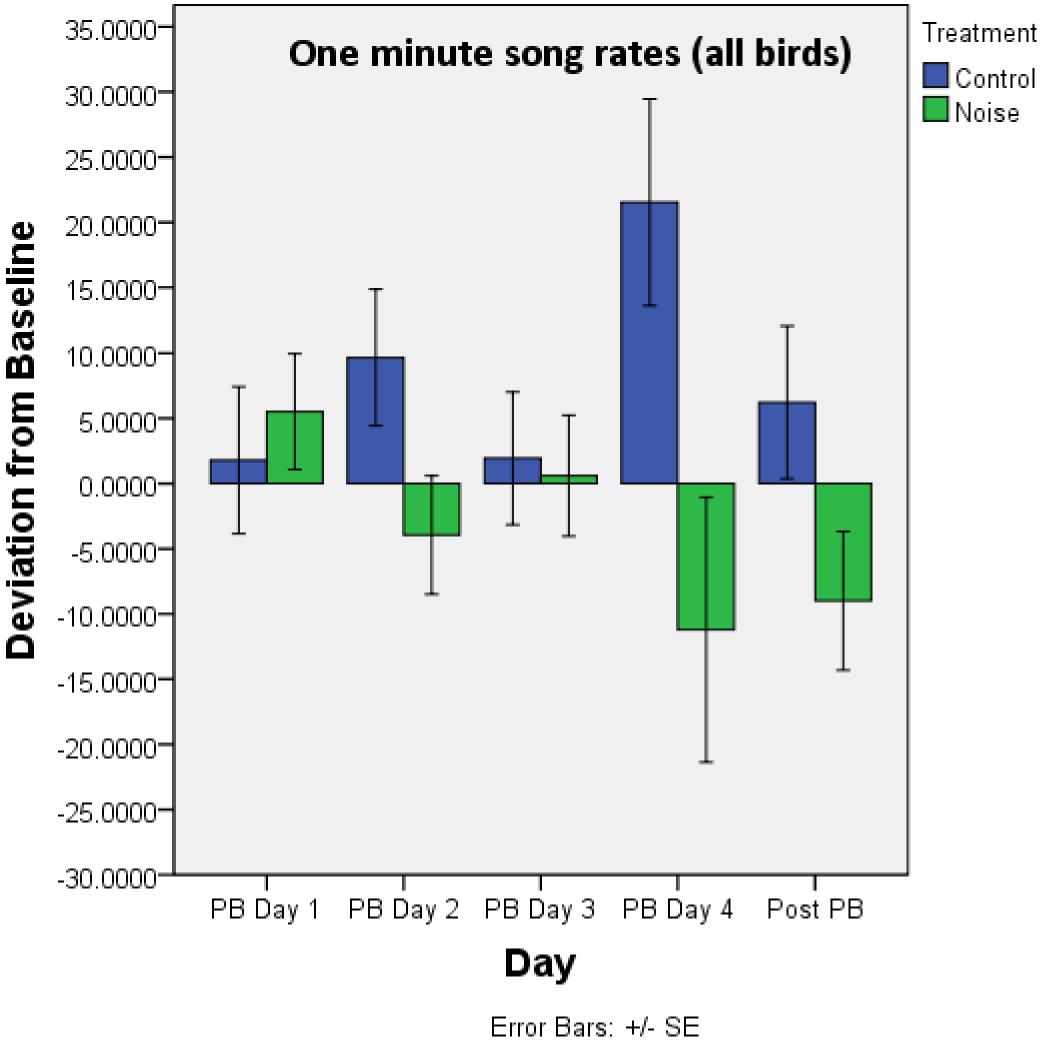


Figure 3. Daily mean deviation from baseline song counts in the control and experimental (noise) condition for all passerine species. Error bars are standard error.

Discussion

Our study demonstrated that the songbirds did not leave noise-affected areas, but that noise did have a significant effect on their vocalization patterns. Specifically, birds sang less in 1-minute gaps embedded in noise than during the same periods of time in control sites. While a trend towards reduced singing in noisy sites is visible as days progress, neither day nor the interaction between day and treatment were significant. As expected, order was also significant, demonstrating a general reduction in singing rates as morning progressed.

By using point counts to determine if the songbird population remained the same with or without the noise playback, we were able to show that established songbirds remain in an area when anthropogenic noise is introduced. The somewhat surprising finding that birds did not leave the area, despite the introduction of the novel road noise stimulus, suggest that either a) they do not perceive this novel stimulus as threatening, (Sih 2013) or b) site fidelity overrules a potential flight response (Hoover 2003). A number of studies have demonstrated a reduction in bird abundance and richness in similar noise conditions (Proppe et al. 2013, Bayne et al. 2008), but further research is needed to determine the point at which birds are most susceptible to noise. Nonetheless, our results suggest that susceptibility is unlikely to occur after to establishment.

The finding that focal species of songbirds did not depart suggests that lower recorded song rates were not due to songbird absence, but are a result of altered vocal behavior. We found that birds sang less when the noise was played in their habitats. This result contradicted our hypothesis, but suggests that noise does alter the rate at which birds produce their songs. Birds may vocalize less frequently in response to the addition of low-frequency road noise because it masks some if not all of their songs (Mockford and Marshall 2009). This decreased song rate, however, raises questions such as the impact on fitness if male songbirds are unable to communicate as effectively with potential mates (Parris and McCarthy 2013).

It cannot be assumed that all species of songbirds will react similarly to those we studied, and there may even be variation among the focal species used in our study. Nineteen forest and forest edge species were chosen for their relative abundance at Pierce Cedar Creek Institute, but analyses were not conducted on individual species. Therefore, our results cannot address the behavior of any particular species, but do offer a general observation about common songbirds in our study area. Our results suggest that the general reaction of songbirds is such that there is a need to investigate species-specific reactions. Data for all nineteen species were recorded separately and may be analyzed separately in the future.

In our our study, we played noise for a maximum of four consecutive days. This was primarily due to the limited amount of time (song production occurs from May to July) in which we could study these birds and apply noise disturbance to their environments. We were able to obtain the initial reaction of songbirds to road noise. We used noise playback for four consecutive days to overcome the initial response to novelty, however this does not provide long-term data on adaptability. By demonstrating that birds sing less, but remain in an affected area, we provide information that suggests there is potential for long-term adaptability. Thus we have addressed our objective which was to study songbird reactions to newly introduced road noise, such as might occur with a new road paved in a previously undisturbed area. A long term study that aims to determine the effects of road noise on bird fitness is needed.

In summary, we demonstrated that established songbirds do not vacate an area in response to introduced road noise. We also showed that birds sing less under noisy conditions than under control conditions, even when noise is punctuated with silent gaps. This demonstrates that noise does not induce evacuation, but it does alter singing behavior. Because singing behavior is tied to mating and reproduction, this may fitness implications. While studies on fitness consequences are still somewhat ambiguous (Halfwerk 2011; Crino et al. 2013), mitigation of anthropogenic noise may be beneficial for songbird communication.

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