

Spatiotemporal patterns of avian vocal activity in relation to urban and rural background noise

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Abstract

Background noise can interfere with and influence acoustic communication behavior. Signal interference is dependent on the amplitude and spectral characteristic of background noise, which varies over space and time. The likelihood of signal interference is greater when background noise is concentrated within the same frequency bands of an animal's vocalization, but even a partial masking effect can elicit signaling behavior modification. Relative to a rural landscape, background noise in an urban landscape is disproportionately comprised by anthropogenic sound, which fluctuates in amplitude throughout the day and occurs primarily in low frequencies (0–2 kHz). In this study, we examined if urban-rural differences in vocal activity patterns exist in a species *Zonotrichia leucophrys nuttalli* that communicates above the frequency range of anthropogenic noise (2–8 kHz). We tested whether vocal activity patterns changed in relation to sound in the high or low frequency bands within and between urban and rural locations. Automated acoustic recording devices (ARDs) continuously recorded throughout the morning song chorus, 0500 to 1,100 h, during the 2014 breeding season in San Francisco (urban) and Marin (rural) Counties, CA. Supervised learning cluster analysis was used to quantify vocal activity by totaling the number of songs. In general, vocal activity was greater in urban locations compared to rural locations. However, within rural and urban study sites, we found vocal activity decreased where low frequency noise levels were higher. There was not a relationship between vocal activity and high frequency, biotic sound. In both urban and rural locations, low frequency noise levels increased through the morning, while vocal activity remained relatively consistent. Our results demonstrate how patterns of vocal activity can change with low frequency, abiotic noise, even when there is no direct spectral overlap with the acoustic signal.

Introduction

Long distance acoustic communication involves the transmission and reception of signals that carry important messages, such as territory ownership, social status, mate attraction, and species identity (Catchpole and Slater, 2003; Bradbury and Vehrencamp, 2011). However, background noise can interfere with acoustic signal transmission, and reduce the active space of signals as well as signal detectability (Wiley and Richards, 1982; Klump, 1996; Lohr et al., 2003; Wiley, 2006). The chances of signal reception decrease as background noise amplitude increases, especially when the acoustic energy of the background noise is concentrated within the same frequency bands of an animal's vocalization (Egan and Hake, 1950; Parris and Schneider, 2008).

Animals can modify their acoustic behavior in ways that reduce signal interference from background noise and improve the active space of their signal, thus increasing the likelihood of signal detection by the receiver (Brumm and Slabbekoorn, 2005; Brumm and Zollinger, 2013; Shannon et al., 2015). Signal transmission and active space can be improved through modification of signal duration (Brumm et al., 2004; Foote et al., 2004), spectral structure (Slabbekoorn and Peet, 2003; Roca et al., 2016), and amplitude (Brumm, 2004; Brumm and Zollinger, 2011; reviewed in Luther and Gentry, 2013). The likelihood of successful communication can also be enhanced through increased repetition of vocalizations (Shannon and Weaver, 1949; Wiley, 2006). As a result, signaling rate and the amount of time spent vocalizing are predicted to increase relative to higher levels of background noise (Brumm and Slater, 2006; Slabbekoorn and den Boer-Visser, 2006; Hoskin and Goosem, 2010; Díaz et al., 2011).

Animals could also increase or decrease signaling rate or signaling effort temporally in response to shifts in background noise levels (Díaz et al., 2011; Cartwright et al., 2014). For instance, some animals vocalize less during brief fluctuations in background noise (Sun and Narins, 2005; Brumm, 2006; Parks et al., 2007; Halfwerk and Slabbekoorn, 2009; Potvin and Mulder, 2013; Lenske and La, 2014; Luís et al., 2014). In contrast, other animals increase call rate during higher levels of background noise (Potash, 1972; Lengagne et al., 1999; Penna et al., 2005). In addition, some avian species will shift the timing of their dawn chorus so that it starts earlier and prior to the daily rise in background noise levels (Arroyo-Solís et al., 2013; Gil et al., 2014; Dominoni et al., 2016; Dorado-Correa et al., 2016). The variation in signaling in response to noise may be due to a cost-benefit tradeoff in which increased signal redundancy improves communication without affecting the naturally selected structure of the vocalization. However, if intended receivers are paying attention throughout the morning, it would be more energy and time efficient to concentrate signaling effort during times with less background noise (Ward et al., 2003; Díaz et al., 2011).

Observable differences in acoustic signaling behavior between urban and rural locations are often ascribed to anthropogenic noise. Background noise in an urban landscape is disproportionately comprised by anthropogenic sound, which occurs at relatively high intensities and low frequencies, because human activity is denser and more frequent in urban landscapes (Slabbekoorn and Ripmeester, 2008; Naguib, 2013). In rural landscapes, the soundscape is generally dominated by high frequency biotic sounds, such as bird song and insect calls, and low frequency abiotic sounds, such as wind (Sueur et al., 2014). Still, the amplitude of biotic sound in urban locations can at times also be relatively high, especially if multiple species adjust the timing of their signaling effort so that it is concentrated during hours when anthropogenic noise is relatively reduced. Therefore, urban-rural differences in vocal activity and signal detectability might be related to an increase in biotic sound as well as or instead of just related to anthropogenic noise.

To better understand the relationship between vocal activity and background noise, we passively recorded Nuttall's white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) (NWCS) and examined whether the vocal activity changed in relation to biotic or abiotic sources of background noise, such as anthropogenic activity. We also separately tested if the temporal patterns of abiotic noise changed across the urban-rural gradient, as the dominant sources of abiotic noise differ between our urban and rural locations. Because the NWCS communicates at higher frequencies, we did not expect to find a significant relationship between patterns of NWCS vocal activity and abiotic noise, which is concentrated

below 2,000 Hz (Sueur et al., 2014). Instead, we predicted that NWCS vocal activity would be more closely related to biotic noise.

Methods

Study species

We measured vocal activity of NWCS, as the reproductive success of birds is largely dependent on their ability to effectively secure territories and attract mates through song (Habib et al., 2007; Catchpole and Slater, 2003; Bradbury and Vehrencamp, 2011; Halfwerk et al., 2011). The NWCS is found throughout the coastal region of central California. NWCS are non-migratory and have only one song type, which spans across the 2,000–8,000 Hz frequency range (Blanchard, 1936; Blanchard, 1941; Brenowitz et al., 1998). NWCS are a model system for studying vocal behavior (Baptista, 1975; Petrinovich and Patterson, 1982; Petrinovich and Baptista, 1984; Dewolfe et al., 1989; Brenowitz et al., 1998; Slabbekoorn et al., 2003), with a rich history of studies specifically on the effects of anthropogenic noise on their vocal behavior (Luther and Baptista, 2010; Luther and Derryberry, 2012; Luther et al., 2015; Derryberry et al., 2016; Luther et al., 2016).

Study locations

We recorded songs in rural and urban locations in Marin and San Francisco Counties, California, respectively, and we coded location for categorical analysis (Marin County = 0, San Francisco = 1). The landscape of our rural locations is characterized by agricultural pasturelands and relatively undisturbed coastal scrub and chaparral habitat. In contrast, our urban recording sites, which were located throughout the Presidio National Park of San Francisco, are best described as fragmented green spaces. Portions of the Presidio landscape contain restored coastal scrub, dune, or serpentine grassland communities, but otherwise consists of unmanaged roadside vegetation, lawns, or invasive plants, including Monterey pine (*Pinus radiata*) stands.

We differentiated between rural and urban locations, because in contrast to our rural sites, anthropogenic activity is the dominant source of abiotic noise in our urban sites (Lee and MacDonald, 2011, 2013). The noise levels from anthropogenic activity are higher in the urban setting of San Francisco, as the percent of area developed and human population density is greater in comparison to a rural landscape (Marzluff, 2001). A Natural Sounds and Night Skies Division (NSNSD) acoustic monitoring report for Golden Gate National Recreational Area, which includes sites in San Francisco county, indicates an almost continuous stream of anthropogenic sound, including conversations, music, fog horns, air or ground vehicles, etc. (Lee and MacDonald, 2013). Road traffic in particular is a major source of abiotic noise in San Francisco: the annual average daily traffic (AADT) in 2014 (total yearly volume of vehicular traffic along a road divided by 365 days) reached up to 167,000 cars on roads near the urban locations.

In comparison, road traffic reached less than 4,000 cars on roads near the rural locations (CALTRANS, 2014). The NSNSD reports baseline and predicted acoustic conditions that confirm minimal influence of human activities to the acoustic environment in Point Reyes National Seashore (located in Marin County) (Lee and MacDonald, 2011). Thus, abiotic noise is attributable mostly to natural sources of low frequency sounds, like wind, shoreline surf, or rain in our rural locations. Both acoustic monitoring reports confirm that noise from anthropogenic activity tends to be highest during daylight hours.

Acoustic recording

NWCS songs and background noise were passively recorded for three weeks during a short window of high breeding activity (13 May 2014 to 1 June 2014) to minimize differences in breeding stages and subsequent changes in vocal activity (Hanski and Laurila, 1993). Recordings were taken with SM2+ song meters (Wildlife Acoustics, Concord, Massachusetts, USA), a type of automated ARD that has proven useful for monitoring vocal activity in other species (Colbert et al., 2015). Fifteen ARDs were



Figure 1: Map of study sites in San Francisco and Marin Counties.

All urban study sites are located within Presidio National Park of San Francisco, which is identified by dashed yellow box. The remaining points on the map (red, circular) are the rural study site locations, which are: Abbott's Lagoon (ABLA), Schooner's Bay (SCBA), and Commonweal (COMW). Distances in between rural study sites, as well as between Presidio National Park and the nearest rural study site, COMW, are labeled along white lines. The distance is measured between the two most proximal ARD locations between the nearest study sites.

mounted in three rural study sites and four urban study sites, two to three ARDs per site. ARD placement was based on prior NWCS sightings and observations so that we could confirm each location chosen for recording contained at least two male NWCSs territories. Each ARD was mounted to either a tree, shrub or fence post approximately 1.5 m from the ground. With one exception, the ARDs were separated by at least 200 m to ensure the same acoustic sounds were not recorded by more than one device (Figures 1–3). Two ARDs were separated from one another by 150 m due to spatial limitations, as we limited ARD placement in the urban locations to areas within each study site that were less accessible to the public. In that instance, the ARDs were mounted on opposite sides of a hill and the recordings were also later inspected to confirm the acoustic content that was recorded simultaneously in time differed between the two ARDs, which indicated that these were in fact independent samples.

The ARDs recorded continuously from 0500 to 1,100 h over a span of 3–12 days. Daily audio files were saved to internal memory as 16 bit, at a sampling rate of 22.05 kHz at 48.00 gain. The ARDs were set to record wav files on stereo channel using foam windscreen-covered SM2 microphones, which are weatherproof, omnidirectional and have a frequency response of flat 0.020–20 kHz and a sensitivity of -36 ± 4 dB, with a signal-to-noise ratio of > 62 dB (Wildlife Acoustics, 2011). We analyzed one morning of recordings (360 minutes) from each ARD (seven located in Marin County and eight located in San Francisco County [5,400 minutes total]).

Measure of vocal activity

Recordings for analysis were selected after a preliminary inspection of acoustic content. Files were not used if it rained, as rain can affect temporal vocalization patterns (Keast, 1994). In addition, files were not selected for analysis if other uncharacteristic noise events were recorded, such as high wind, mowing or other non-routine, noisy, or maintenance-related events. The Kaleidoscope converter



Figure 2. ARD locations within rural study sites (scaled to 1 km).

The left, middle and right panels show the ABLA, SCBA, and COMW ARD locations, respectively.

utility of Wildlife Acoustics' acoustic analysis software, Kaleidoscope Pro 4.1.0a (Wildlife Acoustics, Maynard, Massachusetts), was used to split the collected data into files of one hour in length. We did not average the number of song detections per hour over multiple days per ARD, as we hypothesized that vocal activity could change directly with abiotic noise or acoustic richness throughout a given morning. Hourly measures of vocal activity were taken post-dawn (0600–1,059 h, 0500 h excluded), as the time when birds start to sing each morning (timing of the dawn chorus) is also related to many external variables in addition to anthropogenic noise, including anthropogenic light and weather (Bruni et al., 2014). Instead, the 5 am recording file (0500–0559 h) was utilized as training data to



Figure 3. Urban study site locations in Presidio National Park and the ARD locations within each study site (scaled to 1 km).

Distances in between urban study sites are labeled along white lines. The distance is measured between the two most proximal ARD locations between the nearest study sites.

create unique pairwise classifiers with the Cluster Analysis feature of Kaleidoscope Pro 4.1.0a, which we used to automatically detect NWCS songs in each of the remaining hours of recordings.

For each of the 0500 h recording files (1 per ARD unit), we ran the clustering algorithm to automatically detect and sort similar acoustic signals into clusters based on the following signal parameter settings: 1,250–10,000 Hz, 0.1–7.5 s duration, 0.35 s maximum inter-syllable gap. The FFT window was set to 5.33 ms (256 at 0–24 kHz). The maximum number of states for the target size of the Hidden Markov Model was set to 12, the maximum Euclidean distance to cluster center for building clusters was set to 0.5, and maximum Euclidean distance from cluster center to include in cluster file outputs was set to 1.0. To create pairwise classifiers, each of the detections in the cluster output file were manually reviewed through visual and auditory inspection of the spectrogram content using the Kaleidoscope Viewer feature, and then each detection was manually identified as “NWCS song” or “Not NWCS” (supervised learning; see [Wildlife Acoustics, Inc. \(2016\)](#) for further detail). The identification of “NWCS song” meant that a NWCS song was visible or audible in the spectrogram viewing window of the detection. The 0500 h recording file was then rescanned using the pairwise classifiers, and the number of correctly identified NWCS songs, false negatives, and false positives were manually reviewed and tallied. Pairwise classifier performance for each of the training hours is reported in [Appendix 1 \(S.1.docx\)](#).

Using the same settings in Kaleidoscope, the pairwise classifiers were used to batch sort and cluster acoustic signals in the remaining recording hours (0600–1,059 h, separate recording files for each hour). All acoustic signals automatically detected were manually reviewed, and although we created unique pairwise classifiers for recording files per ARD unit, we checked for false negative and false positive pairwise classifications to achieve a more accurate measure of song activity. We also estimated detection rates for each ARD by comparing the number of manual and automatic detections (see [Supplementary Material for detector performance analysis, results, and conclusion \[S.2.docx\]](#)). Manual detections were made using Raven 1.5 by randomly choosing either a 6 am, 7 am, 8 am, 9 am, or 10 am recording file from each ARD and noting the number of NWCS songs that were visually or audibly detectable in the spectrogram viewing window during that hour ([Bioacoustics Research Program, 2012](#)). In Raven 1.5, all audio files were transformed to the frequency domain and displayed as spectrograms along a frequency range between 0–11.025 kHz (Nyquist frequency) on the y-axis and 60 seconds on the x-axis using a Hann window with the following spectrogram settings: 679 sample (30.8 ms) window size, 50% overlapping, hop size 340 samples, and 2,048 DFT size with 10.8 grid spacing, 46.6 Hz 3 dB filter bandwidth, and a 680 spectrogram window size.

We measured vocal activity per hour by totaling the number of NWCS classifications for each hour, first subtracting the number of false positives and adding the number of false negatives. Because we defined vocal activity as the amount of time NWCS songs are detectable, we multiplied the final hourly total number of song detections by two (NWCS song duration is typically about 2 seconds ([Peterson, 1941](#); [Marler and Tamura, 1962](#))). For each site, a morning total of vocal activity was also calculated by adding up the vocal activity across hours.

Measure of noise and acoustic richness

We measured abiotic and biotic noise levels using Matlab based PAMGuide scripts ([Merchant et al., 2015](#)). Abiotic noise is concentrated in the spectral range below 2,000 Hz, and includes sound from anthropogenic activity (such as car traffic), and natural sources of low frequency noise, such as wind or shore surf. Biotic noise typically occurs in spectral bands above 2,000 Hz ([Sueur et al., 2014](#)). We measured the frequency ranges separately so that we could independently examine the effects of anthropogenic/abiotic noise and biotic noise. For each recording hour, the median unweighted band level (SPL_{median}) for abiotic noise (1–2,000 Hz) and biotic noise (2,000–11,025 Hz) was generated using manufacturer data calibration information and 1 s Hann window with 50% overlap. The temporal resolution was averaged to 10 s using the Welch method to improve computer processing capacity. We chose to measure SPL_{median} per hour rather than the mean or mode levels because, unlike the other two, the median is more robust and less influenced by intermittent high-amplitude events ([Merchant et al., 2015](#)). The hourly measures of median SPL were also averaged to obtain a mean

hourly SPL_{median} value per ARD. All reported sound pressure levels are in absolute units of dB re: 20 μ Pa for noted frequency bands.

The Acoustic Richness Index (AR) was calculated using the R package Seewave (Sueur et al., 2008). AR is a ranked index that combines temporal entropy and intensity (the median of the recording's amplitude envelope) (Depraetere et al., 2012). Because AR is a ranked index, we did not compare hourly measures of acoustic richness and song activity between recordings from different ARDs. The index is minimally affected by background noise amplitude or the signal to noise ratio, and is especially applicable in temperate habitats where background noise is dominated by abiotic sound (Sueur et al., 2014; Gasc et al., 2015). Therefore, it is a reliable metric to determine if temporal shifts in vocal activity are associated with changes in acoustic diversity of biotic sound rather than abiotic noise (Towsey et al., 2013; Gasc et al., 2015).

To measure acoustic richness we used the converter utility in Kaleidoscope Pro 4.1.0a to divide each hour-long recording file into smaller files that were ten minutes in length. For each hour, we took the file that contained the first ten minutes of recording and divided it further, splitting it into files that were one minute in length. The one-minute file length was necessary due to limitations in computer processing capacity. Acoustic richness was then calculated for each of the first ten minutes of every hour (1–11,025 Hz; $T = 1$ min) (Acevedo and Villanueva-Rivera, 2006) with a Hilbert (default) amplitude envelope (Depraetere et al., 2012), which were then averaged together to obtain a single acoustic richness value for each hour.

Statistical analysis

All statistical analyses were performed in R (R Development Core Team, 2015). Linear mixed effect models were run using the *lmerTest* package (Kuznetsova et al., 2015) and the linear models were run using the *lme4* package (Bates et al., 2014). *P*-values and *F*-stats were computed using Satterthwaite's approximation for denominator degrees of freedom for linear mixed effect models. If there was a statistically significant interaction, we performed post hoc tests on the interaction term using *Post-hoc* interaction contrasts (function *testInteractions*) in "phia" package (De Rosario-Martinez, 2013). The linear mixed effect models were validated through visual inspection of QQ-plots of model residuals and linear models were validated through model assumption tests.

Temporal patterns of song activity

We tested whether vocal activity in urban and rural locations changed over the course of the morning in association with abiotic noise (SPL_{median} [1–2,000 Hz]; $T = 1$ h) and/or acoustic richness. To do so, we fit a model with a mixed effect linear model structure with "Hour," "Acoustic richness," and "Hourly Abiotic SPL_{median} " as fixed effect parameters, and we treated "ARD unit" and "Study site" as random effects. We found that model fit was not improved by an interaction term between "Location" (urban/rural) and "Hour" (AIC increased with addition of interaction term), such that differences in temporal vocal activity patterns were not observable at a large scale across the urban-rural gradient. Therefore, we decided to exclude "Location" from the model structure.

We included "Study site" in the final random effect structure, and a significant *p*-value ($P < 0.05$) from a likelihood ratio test indicated the model structure should include a hierarchical model structure with "ARD unit" and "Study site." We tested if the inclusion of "Study site" as a random effect in a hierarchical model structure improved model fit because variation in song activity can be attributable to between-site differences in acoustic signaling competition (Ripmeester et al., 2010), population density, or other population dynamics (Searcy and Beecher, 2009; Montague et al., 2013; Narango and Rodewald, 2016). The significant result of the likelihood ratio test indicated that variance in song activity was attributable to between-study site differences, which further supported the decision to exclude "Location" and consider the temporal patterns of vocal activity at a microscale. We treated "ARD unit" as a random effect because an intra-class correlation coefficient (ICC) calculation of 0.73 among hourly vocal activity measures coming from the same ARD provided evidence that data structure needed to be accounted for during analysis.

We also compared the residual variance, σ^2 , of the model with a fixed effect “Hour” with that of a model without “Hour” included in the fixed effect structure, and obtained a pseduo- R^2 of 0.049. Thus, only 5% of variability in hourly song activity recorded by each ARD unit was explained by a linear relationship with time. In addition, we inspected the ACF plot to determine if residual correlation was properly accounted for by the random effect structure or if there was significant autocorrelation at certain time lags. Based on the ACF plot and low pseduo- R^2 , we determined the correlation induced by the random effects sufficiently accounted for the serial correlation that might exist between observations and therefore did not fit the model with an autocorrelation term.

Temporal patterns of background noise

A mixed effect linear model was used to test how abiotic noise ($\text{SPL}_{\text{median}}$ [1–2,000 Hz]; $T = 1$ h) changed over the course of the morning in the rural and urban locations in Marin and San Francisco counties, respectively. For this model, we included an interaction term between “Hour” and “Location” in the fixed effect structure and kept “ARD unit” as a random intercept. A likelihood ratio test confirmed the model structure should also include “Hour” as a random slope ($P < 0.001$). Examination of the ACF plot revealed no apparent pattern, so we did not fit the model with an autocorrelation term. The “visreg” package was used to plot the fit of the model (Breheny and Burchett, 2012).

Spatial patterns of song activity

We used a linear mixed effect structure to test if the morning total of vocal activity was greater where there were higher levels of mean abiotic $\text{SPL}_{\text{median}}$ values (1–2,000 Hz). “Location” (urban/rural) and the “Mean abiotic $\text{SPL}_{\text{median}}$ value” were included as fixed effects after checking that model fit was not improved by an interaction term (AIC increased with addition of interaction term), and “Study site” was included as a random intercept in the random effect structure. Although there was not a significant interaction, we decided to still include “Location” to account for the general differences in habitat quality that could influence song activity. A linear mixed effect structure was also used to test if the morning total of vocal activity was greater where there were higher levels of mean biotic $\text{SPL}_{\text{median}}$ values (2,000–11,025 Hz). Based on the same reasoning, “Location” and the “Mean biotic $\text{SPL}_{\text{median}}$ value” were included as fixed effects even after finding that model fit was not improved by an interaction term (AIC increased with addition of interaction term). Similarly, “Study site” was again included as a random intercept in the random effect structure.

In both models, we included “Study site” as a random intercept to account for variance in vocal activity due to between-site differences, allowing us to examine spatial patterns of vocal activity within study sites rather than across study sites. Within study sites, we assume population density, acoustic signaling competition, or other population dynamics remain constant, and thus do not explain any of the variation in song activity.

Results

From 6:00–10:59 am, there were between 1,668–3,264 songs a morning at urban study sites ($\bar{X} \pm \text{SE} = 2641.50 \pm 239.26$), and 506–2,156 songs a morning at rural study sites ($\bar{X} \pm \text{SE} = 1447.57 \pm 183.38$). The mean abiotic $\text{SPL}_{\text{median}}$ noise values ranged between 54.58–71.08 dB $\text{SPL}_{\text{median}}$ ([1–2,000 Hz]; $T = 1$ h) in urban study sites ($\bar{X} \pm \text{SE} = 64.11 \pm 2.03$), and 47.94–60.08 dB $\text{SPL}_{\text{median}}$ ([1–2,000 Hz]; $T = 1$ h) in rural study sites ($\bar{X} \pm \text{SE} = 52.84 \pm 1.80$). Biotic noise ranged between 32.72–48.66 dB $\text{SPL}_{\text{median}}$ ([2,000–11,025 Hz]; $T = 1$ h) in urban study sites ($\bar{X} \pm \text{SE} = 40.10 \pm 2.06$), and 27.68–31.06 dB $\text{SPL}_{\text{median}}$ ([2,000–11,025 Hz]; $T = 1$ h) in rural study sites ($\bar{X} \pm \text{SE} = 29.44 \pm 0.46$) (See Tables 1, 2 and 3 for summaries of vocal activity, abiotic noise, and biotic noise).

Table 1. Summary of Nuttall's white-crowned sparrow vocal activity, low frequency noise, and high frequency noise per recording point in urban and rural locations (2014).

Location	Study site*	ARD	Measures per ARD unit		
			Mean \pm SE Hourly vocal activity (sec)	Mean \pm SE Hourly SPL _{median} (0–2,000 Hz)	Mean \pm SE Hourly SPL _{median} (2,000–11,025 Hz)
San Francisco County (urban)	INPO	1	1272.4 \pm 118.0	56.6 \pm 0.7	32.7 \pm 0.5
		2	1241.6 \pm 67.6	59.2 \pm 0.7	38.5 \pm 0.3
	LODU	1	1061.2 \pm 138.1	60.9 \pm 0.6	35.1 \pm 0.2
		2	1305.6 \pm 37.6	60.3 \pm 0.9	34.5 \pm 0.5
	FWSC	1	1296.8 \pm 92.5	70.1 \pm 0.4	48.7 \pm 0.5
		2	932.8 \pm 70.1	64.1 \pm 1.2	42.2 \pm 0.6
	BATE-FOPO	1	675.2 \pm 40.5	70.6 \pm 0.4	46.3 \pm 0.2
		2	667.2 \pm 42.7	71.1 \pm 0.4	42.7 \pm 0.4
Marin County (rural)	ABLA	1	862.4 \pm 108.8	48.0 \pm 0.9	28.2 \pm 0.1
		2	582.4 \pm 104.8	60.1 \pm 1.9	30.2 \pm 0.3
	COMW	1	636.0 \pm 37.7	47.9 \pm 1.2	28.9 \pm 0.5
		2	590.8 \pm 111.8	55.6 \pm 4.0	31.1 \pm 1.1
		3	600.0 \pm 83.3	52.9 \pm 1.9	27.7 \pm 0.2
	SCBA	1	579.2 \pm 92.4	48.9 \pm 0.9	30.0 \pm 0.1
		2	202.4 \pm 58.3	56.4 \pm 0.9	30.1 \pm 0.6

Temporal and spatial patterns of noise and vocal activity

Vocal activity did not change temporally through the morning hours ($F_{163.392} = 2.329$, $P = 0.132$) (Figure 4) or in relation to acoustic richness or abiotic background noise (SPL_{median} [1–2,000 Hz]; $T = 1$ h) ($F_{1,58.669} = 1.025$, $P = 0.316$, $F_{1,54.166} = 0.083$, $P = 0.774$, respectively) in either urban or rural locations.

Abiotic SPL_{median} noise values ([1–2,000 Hz]; $T = 1$ h) increased through the morning hours in urban and rural locations, but to a greater extent in Marin County's rural locations ($\chi^2_1 = 4.217$, $P = 0.040$) (Figure 5). Acoustic richness did not change in relation to abiotic SPL_{median} noise values ([1–2,000 Hz]; $T = 1$ h) ($F_{1,69} = 1.25$, $P = 0.267$).

The total morning vocal activity was greater at urban sites than rural sites ($F_{1,7.610} = 18.324$, $P = 0.003$), but also changed spatially amongst urban and rural sites in relation to the mean abiotic SPL_{median} value (1–2,000 Hz) ($F_{1,12.514} = 5.160$, $P = 0.041$). Specifically, the morning total of vocal activity was lower at sites with higher mean abiotic SPL_{median} values (1–2,000 Hz), in both urban and rural locations (Figure 6). The morning total of vocal activity did not change spatially between sites in

Table 2. Summary of Nuttall's white-crowned sparrow vocal activity, low frequency noise, and high frequency noise per study site in urban and rural locations (2014).

Location	Study site	ARD	Measures per study site		
			Mean \pm SE Hourly vocal activity (sec)	Mean \pm SE Hourly SPL _{median} (0–2,000 Hz)	Mean \pm SE Hourly SPL _{median} (2,000–11,025 Hz)
San Francisco County (urban)	INPO	1	1257.0 \pm 64.3	57.9 \pm 0.6	35.6 \pm 1.0
		2			
	LODU	1	1183.4 \pm 78.8	60.6 \pm 0.5	34.8 \pm 0.3
		2			
	FWSC	1	1114.8 \pm 81.7	67.1 \pm 1.2	45.4 \pm 1.1
		2			
	BATE-FOPO	1	671.2 \pm 27.8	70.8 \pm 0.3	44.5 \pm 0.6
		2			
Marin County (rural)	ABLA	1	722.4 \pm 85.1	54.1 \pm 2.2	29.2 \pm 0.4
		2			
	COMW	1	608.9 \pm 44.9	52.1 \pm 1.6	29.2 \pm 0.5
		2			
		3			
	SCBA	1	390.8 \pm 81.2	52.7 \pm 1.4	30.1 \pm 0.3
		2			

relation to the mean biotic SPL_{median} value (2,000–11,025 Hz) ($F_{1,10.199} = 0.589$, $P = 0.460$), and vocal activity was higher in urban locations ($F_{1,6.145} = 6.828$, $P = 0.039$).

Discussion

We found that there was less NWCS vocal activity where there were increased levels of abiotic noise within both urban and rural locations, but there was no relationship between vocal activity and biotic noise levels. Regardless of the urban or rural setting, abiotic background noise increased through the morning, but the vocal activity remained relatively constant. Overall, vocal activity was greater in urban locations relative to rural locations.

The temporal patterns of vocal activity did not change across the urban-rural gradient, even though the dominant source of abiotic background noise differed between our urban and rural locations. The dominant source of abiotic noise in our urban sites was anthropogenic noise, in contrast, wind-generated noise dominated the low frequencies at our rural sites (Lee and MacDonald, 2011, 2013). Wind-generated noise increases with wind speed throughout the day (Dabelsteen and Mathevon, 2002)

Table 3. Summary of Nuttall's white-crowned sparrow vocal activity, low frequency noise, and high frequency noise per hour in urban and rural locations (2014).

Location	Hour	Mean \pm SE Vocal activity (sec)	Mean \pm SE SPL _{median} (0–2,000 Hz)	Mean \pm SE SPL _{median} (2000–11025 Hz)
San Francisco County (urban)	0600	1104.0 \pm 109.3	63.0 \pm 2.2	40.3 \pm 1.9
	0700	1153.8 \pm 124.6	64.0 \pm 2.2	40.1 \pm 2.1
	0800	1025.0 \pm 88.5	64.7 \pm 2.0	40.2 \pm 2.2
	0900	1034.3 \pm 91.6	64.6 \pm 1.9	40.1 \pm 2.2
	1000	966.0 \pm 137.9	64.3 \pm 2.1	39.7 \pm 2.0
Marin County (rural)	0600	658.9 \pm 117.2	49.1 \pm 1.5	28.8 \pm 0.3
	0700	515.4 \pm 66.6	50.4 \pm 1.8	28.9 \pm 0.4
	0800	545.7 \pm 106.4	54.3 \pm 2.3	29.8 \pm 0.6
	0900	663.1 \pm 114.6	54.7 \pm 2.5	29.8 \pm 0.7
	1000	512.0 \pm 83.2	55.7 \pm 2.5	29.8 \pm 0.9

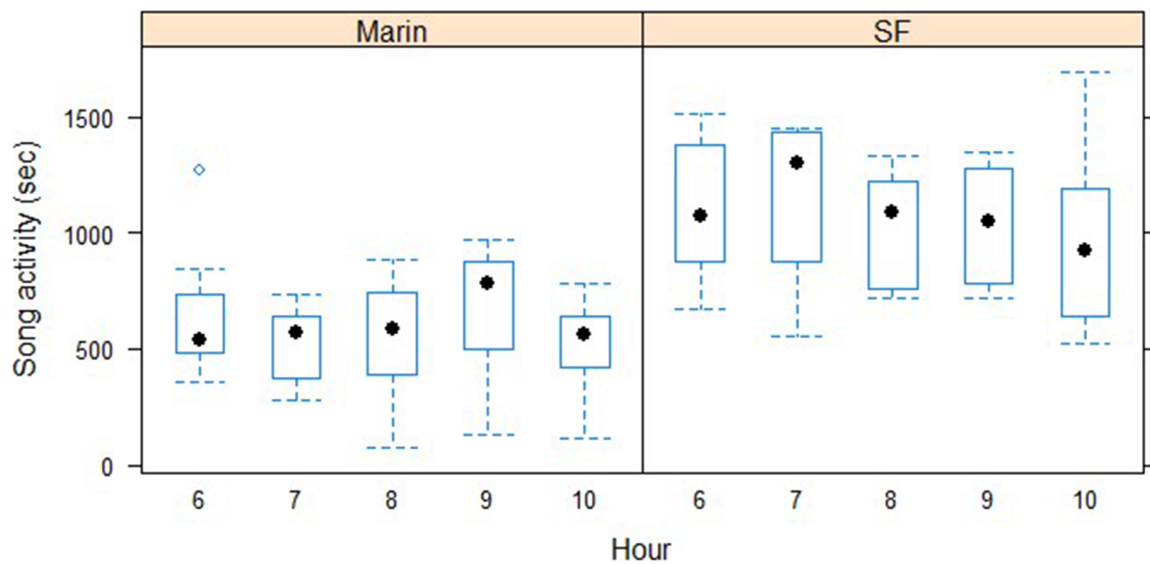


Figure 4. Hourly vocal activity for Nuttall's white-crowned sparrows.

Vocal activity remained relatively constant throughout the morning in both rural and urban locations (shown in "Marin" and "SF" panels, respectively).

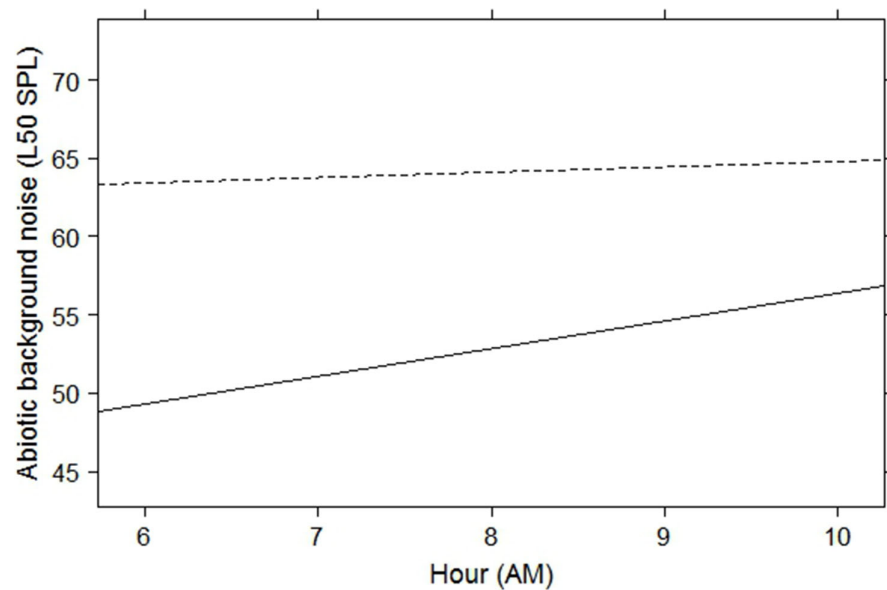


Figure 5. Abiotic noise levels increased in rural and urban locations between 0600 and 1,100 h. Abiotic noise levels tended to be higher in urban locations (dotted trend line) in comparison to rural locations (solid trend line).

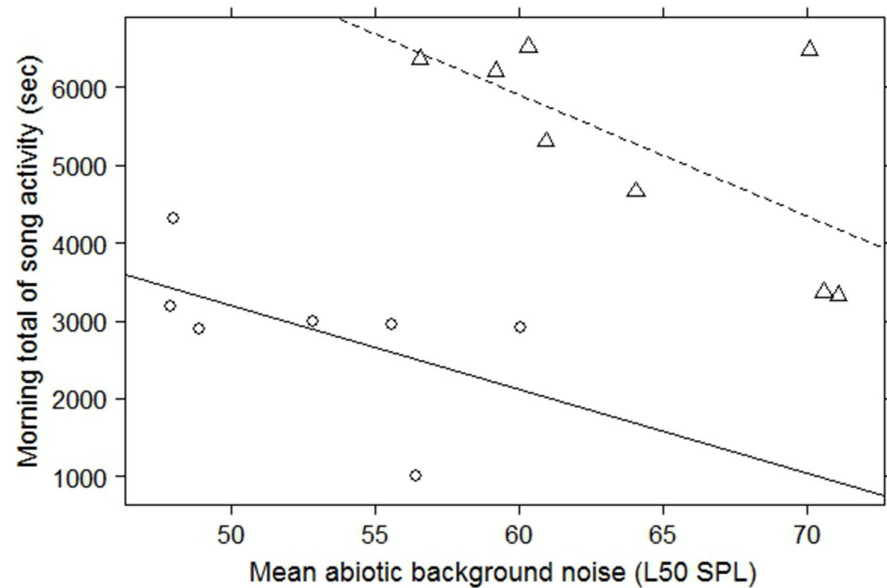


Figure 6. Total morning vocal activity for Nuttall's white-crowned sparrows. Vocal activity was greater in urban sites of San Francisco County than rural sites of Marin county (dotted trend line and solid trend line, respectively). Total morning activity was decreased at sites with higher abiotic noise levels in both counties (rural sites represented by circles, urban sites represented by triangles).

and is greater in open habitats (Morton, 1975; Ryan and Brenowitz, 1985). Like anthropogenic noise, the energy of wind-generated noise is also concentrated in the lower frequency range, occurring mostly below 200 Hz and usually not above 2,000 Hz (Ellinger and Hödl, 2003). It is likely that the temporal patterns of vocal activity did not change across the urban-rural gradient because the amplitude of abiotic noise increased throughout the morning at both urban and rural sites. Otherwise, our results might have

been more similar to those of Cartwright et al., (2014), who found that red-winged blackbird (*Agelaius phoeniceus*) vocal activity fluctuates more in rural marshes than in urban marshes.

The absence of a relationship between NWCS vocal activity and sound in the higher frequencies suggests that their communication is not limited or influenced by biotic noise. In tropical forests, where species richness is much greater, there has been evidence of temporal partitioning of acoustic space due to competition (Sueur, 2002; Chek et al., 2003; Luther, 2008, 2009). In contrast, acoustic diversity and acoustic niche partitioning is predicted to decrease in areas with relatively low biodiversity (Pijanowski et al., 2011). It is possible that species in temperate latitudes, such as the NWCS, are not under the same pressure, at least in terms of their vocal activity. In fact, biotic noise in our study locations was primarily comprised by bird vocalizations (rather than vocalizations from birds, insects, and anurans).

In general, we observed more vocal activity at urban sites relative to rural sites. For species that can survive in cities, population densities can be greater than in rural areas and territory size decreases (Marzluff et al., 2001). Thus, the relative increase in vocal activity at urban sites could result from more males singing within recording range of the ARDs mounted in urban locations. Alternatively, male NWCS in the city could sing more often with greater vocal activity than rural males if noise levels tend to fluctuate more frequently at the urban recording locations. Other studies have found animals respond to brief fluctuations in background noise levels by temporarily elevating their signaling rate (Potash, 1972; Lengagne et al., 1999; Penna et al., 2005; Dominoni et al., 2016; Sierro et al., 2017).

The observed negative relationship between vocal activity and abiotic noise within urban and rural study sites could result from a higher degree of signal masking and thus a shorter detection range at noisier sites, where the signal to noise ratio is reduced by elevated levels of background noise (Lohr et al., 2003). The NWCS song occurs in the higher frequencies (2,000–8,000 Hz) and does not directly overlap with abiotic noise; however, even without direct spectral masking, a reduction in the signal to noise ratio can limit an animal's ability to detect vocalizations- especially those emitted from greater distances (Lohr et al., 2003; Wiley, 2006). A reduced ability to detect the songs of rivals could influence the perception of intraspecific competition, and diminish the impetus to sing as often (Kleist et al., 2016).

In a previous study, NWCS were found to elevate song amplitude in response to increased noise levels (Derryberry et al., 2017). Therefore, it is also possible that NWCS sing fewer songs where abiotic noise is greater within urban and rural study sites because it is difficult to maintain relatively high amplitude songs for longer periods of time (Oberweger and Goller, 2001). In this scenario, a reduction in vocal activity might be attributable to energetic constraints related to male fitness and habitat quality (Reid, 1987; Strain and Mumme, 1988; Díaz et al., 2011). Although males can improve the chance of signal detection through increased repetition of songs (Shannon and Weaver, 1949; Wiley, 2006), more energy is required to increase song production (Nowicki et al., 1998). A significant increase in singing can incur fitness costs when less time and energy is allocated to foraging, nestling feedings, and/or other vigilance-related activities (Gil and Gahr, 2002; Barber et al., 2010).

In the studies of the effects of anthropogenic noise on acoustic behavior of animals, there is no one way in which animals improve communication in the presence of noise (Luther and Gentry, 2013; Shannon et al., 2015). Thus, if the greater vocal activity needed to optimize signal detection in relatively loud locations is not energetically sustainable, an overall reduction in vocal activity could lead NWCS to modify their vocal behavior in other ways in the noisiest locations. In fact, we know NWCS increase their trill rate (Luther et al., 2016), decrease their maximum frequency and bandwidth (Gentry et al., 2017), and increase the amplitude of their songs as anthropogenic noise increases (Derryberry et al., 2017). In addition, the minimum song frequency of NWCS has increased over time, reducing the masking effect of abiotic noise (Luther and Baptista, 2010; Luther and Derryberry, 2012). Although currently unknown, it is also possible that they start to sing their dawn chorus earlier, as an earlier dawn chorus would give them a window of opportunity to concentrate their singing before the daily rise in abiotic background noise (Arroyo-Solís et al., 2013; Gil et al., 2014; Dominoni et al., 2016; Dorado-Correa et al., 2016). Because the NWCS can modify their signaling behavior in multiple ways, they seem to be especially well adapted to communicate in noisy environments. To

improve our understanding of how other animals communicate over anthropogenic noise, future research should examine the spatiotemporal vocal activity patterns of species with less plastic vocal behavior as well.

In conclusion, we found a relationship between vocal activity and abiotic noise, but not biotic noise, such that there was less vocal activity where abiotic noise was greater within urban and rural locations. We did not find a temporal relationship between vocal activity and abiotic noise or acoustic richness. By isolating abiotic and biotic background noise from full spectrum background noise and continuously recording vocal activity through the morning, we were able to examine the spatiotemporal patterns of vocal activity across an urban-rural gradient and show how vocal activity changes with different spectra of background noise. Our results demonstrate how spatial patterns of vocal activity can change with abiotic noise, including anthropogenic noise, even when there is not direct spectral overlap with the acoustic signal.

Supporting material

S1. Appendix. ([DOCX](#))

S2. Detector performance for *Zonotrichia leucophrys nuttalli* song. ([DOCX](#))

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Competing interests

Katherine Gentry and David Luther declare that they have no conflict of interest.

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