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Short notes

SHORT NOTES

Anthropogenic noise affects winter song structure of a long-distance migrant, Gambel's white-crowned sparrow

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Abstract

Many animals learn to produce acoustic signals that are used to attract mates and defend territories. The structure of these signals can be influenced by external features of the environment, including the anthropogenic soundscape. In many sedentary species, habitat features and soundscape appears to influence the cultural evolution of songs, often with tradeoffs for better transmission over sexually selected song structure. However, none have investigated whether noise on the wintering grounds affects song structure, which for long-distance migrants may result in an acoustic 'mismatch' when returning to a breeding ground. This study investigates urban noise effects on song structure in a long-distance migrant, *Zonotrichia leucophrys gambelii*, on the wintering grounds in the Fresno Clovis Metropolitan Area and in outlying non-urban areas. Songs and background noise levels were recorded concurrently, and song measurements of frequency and duration were examined differences across noise levels and habitats . We found that the buzz and trill decrease in bandwidth in the presence of noise. The length of the whistle and buzz portion of the song also tends to decreases with noise in urban habitats. This trend toward short, pure tones in noisy areas may transmit better in noisy urban winter habitats, but may not be adaptive on quieter breeding grounds. We suggest that future studies should consider whether winter auditory feedback and song learning environments have consequences for song crystallization and breeding success for long-distance migrants.

Key words: cultural evolution, song structure, urban noise, white-crowned sparrow, winter song

Introduction

Vocal communication plays an important role in contexts that affect fitness, such as male–male competition and female mate choice. Male birds sing to defend territories and attract mates, thus mating success is at least partly dependent on the effectiveness of the acoustic signal (Marler and Slabbekoorn 2004). Environmental conditions, such as background noise, can act as a selective force on acoustic signals and bias the evolution of animal behavior (Morton 1975; Endler 1992). Selection will favor individuals that produce vocalizations that transmit best in their environments (Katti and Warren 2004; Patricelli and Blickley 2006). Thus, background noise levels can have a profound effect on communication.

Background noise, also known as a soundscape, can be natural or anthropogenic. In natural settings, it is likely that a species has adapted over time to vocalize within background noise (Patricelli and Blickley 2006). For example, Martens and Geduldig (1990) found that several species across families of birds that lived near rushing rivers had loud, pure toned, high-pitched songs, ideal for standing out against that particular noisy background. Since the industrial revolution, urbanization has steadily increased. Urban development occurs at a much faster pace than the generation times of most species and therefore selection events, providing scientists an opportunity to study how animals will respond in their communication systems (Katti and Warren 2004). Traffic is a significant low frequency contributor to urban noise and studies have shown that motorways decrease biodiversity and breeding populations of birds (Reijnen and Foppen 1995; Reijnen, Foppen, and Meeuwsen 1996). Due to low frequency noise resonation in an anthropogenic landscape, many species of birds with urban breeding territories have higher-pitched minimum frequencies than conspecifics that live in quiet, non-urban areas (Luther and Derryberry 2012; Slabbekoorn 2013; Derryberry et al. 2016; Roca et al. 2016). Because song is often an indicator of fitness via phenotypic and genotypic mate quality (Nowicki, Peters, and Podos 1998), understanding how song changes in an urban environment may allow us to predict species adaptability in a changing world (Katti and Warren 2004).

Few studies have focused on bird species that migrate from a breeding ground to a wintering ground where young birds may practice their song. Most songbirds learn their song from neighboring birds during a critical learning period in the first months of their lives (Marler 1990). Juvenile passerines typically practice multiple songs in their first winter before crystallizing one song type (Baptista and Petrinovich 1986), and juveniles rely on auditory feedback for crystallization of a final song type (Konishi 1965). Therefore, if a juvenile practices lower song frequencies but cannot hear itself clearly or does not receive social reinforcement at those frequencies (King and West 1988), it is likely he will produce the song that transmits best in a noisy environment (Moseley et al. 2018, but see Potvin et al. 2016; Zollinger et al. 2017). If a species is migratory, the environment a bird winters in may be a significant factor in the type of song that is crystallized, and a recent study a recent study supports that migratory birds that sing on their wintering grounds are practicing for the breeding season, supporting the song improvement hypothesis (Sorensen, Jenni-Eiermann, and Spottiswoode 2016). To our knowledge, no studies have investigated whether winter song is adapted to soundscapes.

Currently, there is mixed evidence for noise affecting song learning, and whether noise affects song ontogeny may be species specific. For example, white-crowned sparrows (*Zonotrichia leucophrys*) crystallize songs less masked by noise (Moseley et al. 2018), but great tits (*Parus major*) do not (Zollinger et al. 2017). Zebra finches were also able to accurately copy adult tutors in noise, except for the order of syllables (Potvin et al. 2016). Based on these species by species differences, how noise affects the song learning process is still of great interest for evolutionary and behavioral biology.

Here we aim to understand the impact of urban noise on winter song structure, using the model system of Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*). *Zonotrichia leucophrys gambelii* is a long-distant migrant that defends a territory during the breeding season in subarctic North America and winters in the western USA in flocks composed of dominance hierarchies (Keys and Rothstein 1991; Ramenofsky and Wingfield 2017). Both sexes have the ability to sing (Baptista et al. 1993). White-crowned sparrows are a useful model because they have been the basis for our understanding of passerine song learning (Konishi 1965; Marler 1970), where auditory feedback from practicing during a plastic phase is essential to normal song development, as is the song of other singing conspecifics around them (Dewolfe, Baptista, and Petrinovich 1989; Bell, Trail, and Baptista 1998; Nelson, Khanna, and Marler 2001). White-crowned sparrows are close ended learners that go through a sensitive phase of song learning for 50–100 days, then typically practice, or overproduce, a series of song types during the winter (Baptista and Morton 1988; Dewolfe, Baptista, and Petrinovich 1989; Dewolfe and Baptista 1995; Nelson, Marler, and Morton 1996, Nelson, Khanna, and Marler 2001). Winter songs are less stereotyped than breeding songs (Dewolfe, Kaska, and Peyton 1974; Smith et al. 1995). Upon arrival to the subarctic breeding ground, *Z. l. gambelii* goes through a selective attrition process, eventually crystallizing one song type composed of a whistle, complex notes and trills (Nelson, Khanna, and Marler 2001). Because white-crowned sparrows have one song type, individual variation is relatively easy to capture; but because the songs have complex notes, practicing is likely an important winter behavior, especially in the first year when young males are learning more complex notes from the males around them (Marler and Tamura 1964).

White-crowned sparrows are abundant around human development, and therefore encounter anthropogenic noise. In a sedentary sub-species of white-crowned sparrow (*Zonotrichia leucophrys nuttalli*) breeding males sing songs with higher minimum frequencies, narrower bandwidth and faster trills in increasing noise (Luther and Derryberry 2012; Luther, Phillips, and Derryberry 2016). The rate and bandwidth of these complex notes and trills (hereafter, vocal performance) are assessed by male competitors (Phillips and Derryberry 2017a,b, 2018) and by females of similar species (Ballentine, Hyman, and Nowicki 2004). A recent study shows that white-crowned sparrow song development is affected by noise, where a captive experimental group of male birds crystallize songs with higher pitch and worse vocal performance, suggesting that noise is affecting the cultural evolution of sexually selected song traits (Moseley et al. 2018).

In this study, we investigated song differences of wintering *Z. l. gambelii* in non-urban and urban environments across a gradient of noise. We quantified variation in song length and frequency to determine whether or not songs vary in a predictable manner with the soundscape. We predicted that males in noisy urban soundscapes would tend to sing higher-pitched, narrow bandwidth and shorter songs than males in non-urban, quiet soundscapes. While it has been demonstrated that high-pitched song dialects outcompeted low-pitched dialects in San Francisco over a 30-year time period for the non-migratory subspecies *Z. l. nuttalli* (Luther and Baptista 2010), our study directly measures ambient noise levels concurrently with each song recording to assess whether song differences are associated directly with differences in the current soundscape. Ultimately, this study will provide an important first step to understanding which species of birds will be able to adapt to an increasingly urbanizing landscape, especially if wintering grounds and breeding grounds are a habitat or soundscape mismatch.

Methods

Survey design

Three methods were used to locate singing birds. First, we collected data along a 15 mile transect of Shaw Avenue from

October 2010 to late April 2011. Shaw Avenue is a major roadway that runs straight through the Fresno Clovis Metropolitan Area (FCMA) and continues into the countryside on both the east and west outskirts of town (Fig. 1). We began this transect outside of Sanger at the Zediker and Shaw intersection and ended outside of the CA-99 at Chateau Fresno Ave (Fig. 1). This allowed us to survey across the non-urban to urban gradient in both directions. In addition, we visited bird count points created for the Fresno Bird Count (www.fresnobirds.org; Schleder 2010; Katti et al. 2017; Hensley et al. 2019) and the Urban Long Term Research Area-Fresno and Clovis Ecological Survey project. These points were randomly generated within the FCMA (Schleder 2010). To locate non-urban birds, we surveyed random locations in accessible public and private lands where permitted by landowners, including agricultural lands, pasturelands and parks. These non-urban areas included the McKenzie Preserve at Table Mountain, private land in Quail Oaks, Pine Flat Campground, Hensley Lake Recreation Area and Millerton Lake State Recreation Area. Sites closer to town are typically fallow fields or active croplands, which transition to rolling grassland and oak woodland. While these non-urban areas are still used by humans, the density of human impact is much lower than within the city limits. Locations were categorized as urban if they fell within the boundaries of the FCMA, or non-urban if the location was beyond these boundaries (Fig. 1).

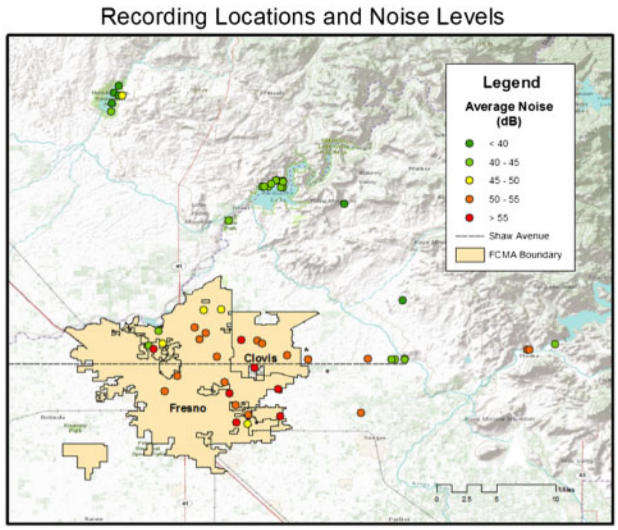

Figure 1: Map of recording locations. White-crowned sparrows were recorded throughout the FCMA, along Shaw Avenue and at random bird count points. Non-urban birds were recorded outside of the city limits and in the surrounding foothills. There are noticeably higher levels of noise within city limits compared to non-urban areas. Colors for each point represent dB(A). Map created in ArcMap 10 (ESRI, Redlands, CA, USA. Imagery Sources ESRI, CGIAR, USGS | Fresno County Dept. PWP, Esri, HERE, Garmin, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USDA).

Song recordings and ambient noise measures

Songs were recorded from 54 males using a Marantz PMD670 digital recorder and Sennheiser ME 66 directional microphone, pointed directly at the singing bird (WAV format, sampling rate = 48 kHz, 16-bit) in the winter of 2010 and 2011. Birds were detected by ear and located visually if possible. We began data collection at 7 AM each morning and continued as long as conditions allowed, with most recordings being taken between 7 AM and 11 AM. Songs were not recorded in rain or wind over category 2 on the Beaufort Wind Scale (4–7 mph), and a GPS location was noted for each location.

Noise levels were recorded using an Extech 407764 Sound Level Meter with a RS232 Data Logger, sampling fast response time (every 2 s) in A-weighted amplitude measurements [dB(A)]. A-weighting was used because it approximates the hearing of birds (Dooling, Lohr, and Dent 2000). At each site, we recorded each singing bird and the ambient noise concurrently. We recorded multiple songs from each individual. Ambient noise was measured by holding the noise meter at chest height (~1.5 m) for 10 min, and noise measurements were averaged at each site for each recording.

Song analysis

Gambel's white-crowned sparrow songs typically consist of five parts: a whistle, a note complex, two buzzes and a terminal trill (Fig. 2; Dewolfe, Kaska, and Peyton 1974). The buzzes typically contain the highest frequencies, although some birds have a similar maximum frequency in the note complex. The terminal trill contains the lowest pitches of the song. For this study, a note is considered as a continuous tracing on a spectrogram, separated from other notes by at least 1 ms (Nelson 1999). For each bird sampled, one song was chosen at random from high signal to noise ratio recordings to measure frequency and temporal features in Raven Pro 1.3 (http://ravensoundsoftware.com/). Two birds only sang songs lacking a terminal trill, so all trill calculations were from the remaining 52 birds recorded. All spectrograms analyzed were high-pass filtered at 1500 Hz (Derryberry 2009). Because adult male song is stereotyped, one song per bird should be sufficient for comparing between individuals (Nelson, Whaling, and Marler 1996; Derryberry 2009).

We measured dominant frequency, minimum frequency, maximum frequency and bandwidth of the individual notes of the song (whistle, complex notes, buzzes and terminal trill; Fig. 2). Minimum and maximum frequency measurements were made using a selection spectrum at −24 dB below maximum amplitude (Podos 1997). This method ensures that frequency measurements are taken at the same relative amplitude to avoid bias in comparisons across songs, as the 'by-eye' method for frequency measures is subject to error (Brumm et al. 2017; Ríos-Chelén et al. 2017). Bandwidth was calculated as the difference between the values measured with the threshold method. We also measured the length(s) of the whole song, whistle, note complex, two buzzes and the terminal trill using the delta time function in Raven Pro, which calculates the duration of each selection (Billings 2018). While narrow bandwidth low frequency syllables also may be prone to error using this method (Ríos-Chelén et al. 2017), white-crowned sparrow song elements measured here largely are broadband, except for the introductory whistle (Fig. 2). Nonetheless, we consider this information when interpreting our duration results. Dominant frequency was calculated in Raven Pro using the peak frequency function around each variable.

Statistical analyses

Statistical analyses were conducted using SPSS v.20 and R 3.1.3 (R Development Core Team 2015). Exploratory analysis showed a high level of collinearity among the 16 dependent frequency variables, as bandwidth is naturally related to minimum and maximum frequency. Thus, we conducted a principal components analysis (PCA) (correlation matrix, varimax rotation) for all frequency measures, resulting in five PC axes with an

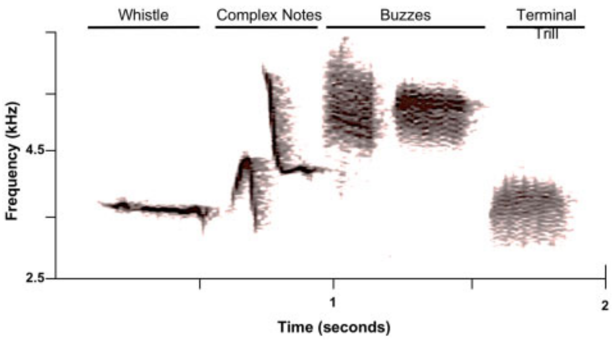

Figure 2: Typical Gambel's white-crowned sparrow song in spectrogram using Raven Pro 1.3. A full song consists of five parts: a whistle, complex notes, two buzzes and a terminal trill. The buzzes are usually the highest note, although some birds have a similar maximum frequency in the note complex. The terminal trill contains the lowest pitches of the song. A typical song is about 2 s long

eigenvalue above one (see Table 1 for eigenvalues and variable loadings). The first PC is loaded positively with whistle measures, while the second is loaded positively with trill dominant frequency and whistle bandwidth and negatively with note complex minimum frequency (Table 1). PC3 is loaded negatively with buzz bandwidth and positively with buzz minimum frequency, PC4 is loaded positively with all note complex measures, buzz maximum frequency and buzz dominant frequency. PC5 is loaded with all trill measures (Table 1).

We used the 'qqp' function in packages 'car' and 'MASS' to confirm our data were normally distributed (Venables and Ripley 2002; Fox and Weisberg 2011), and examined plots to identify then drop outliers. Therefore, two outliers were dropped from PC3 analyses to meet model assumptions. To test the effects of average background noise, we first ran linear regressions against each dependent variable. Next, independent samples t-tests were used to see if habitat (urban or non-urban) correlates with background noise level, song frequencies and temporal differences in song. Finally, we assessed linear model fit of additive effects of background noise and habitat (habitat + noise) and interactive models (habitat*noise) to predict patterns of frequency and temporal structure using package 'lme4' in R (Bates et al. 2015; R Development Core Team 2015).

Results

Buzz and trill bandwidth decrease as noise increases

No significant linear relationships were found between noise and PC1 ($R^2 = 0.02$, $\beta = -0.02$, $F_{1,50} = 1.33$, $P = 0.25$), PC2 ($R^2 = 0.01$, $\beta = -0.02$, $F_{1,50} = 1.33$, $P = 0.44$) or PC4 ($R^2 = 0.002$, $\beta = 0.007$, $F_{1,50} = 0.11$, $P = 0.74$). PC3, which is loaded negatively with buzz bandwidth and positively with buzz minimum frequency, increases with increasing noise ($R^2 = 0.09$, $\beta = 0.03$, $F_{1,48} = 4.86$, $P = 0.03$; Fig. 3A). Noise negatively correlates with PC5 ($R^2 = 0.08$, $\beta = -0.04$, $F_{1,50} = 4.34$, $P = 0.04$; Fig. 3B), indicating a decrease in trill bandwidth with lower maximum trill frequency and higher minimum trill frequency as noise increases (see loadings in Table 1).

When each principal component is compared between habitats, there is not a significant difference in means for PC1 ($t_{50} = 0.64$, $P = 0.52$), PC2 ($t_{50} = -0.53$, $P = 0.60$), PC3 ($t_{48} = -1.03$, $P = 0.31$) or PC4 ($t_{50} = -0.34$, $P = 0.73$). PC5 is significantly different between urban and non-urban birds, where non-urban songs have higher maximum trill frequencies and wider trill bandwidths than urban songs (mean ± SD; Urban PC5 $= -0.03 \pm 0.92$, non-urban PC5 $= 0.28 \pm 1.01$, $t_{50} = 2.19$, $P = 0.03$, Fig. 4). For biologically relevant context, we compared means of the individual measurements, where trill bandwidth is narrower and trill maximum frequency is lower in urban areas compared to non-urban areas (mean ± SD; urban trill bandwidth $= 2047.85 \pm 789.57$, non-urban trill bandwidth $= 2634.15 \pm 978.74$, $t_{50} = -2.37$, $P = 0.02$; urban trill maximum frequency $= 4708.26 \pm 637.4$, non-urban trill maximum frequency $= 5117.28 \pm 804.5$, $t_{50} = 2.04$, $P = 0.04$; urban trill minimum frequency $= 2660.41 \pm 591.79$, non-urban trill minimum frequency $= 2483.13 \pm 480.68$, $t_{50} = -1.18$, $P = 0.24$). The interaction between noise and habitat is significant for PC3 ($R^2 = 0.17$, SE $= 0.55$, $F_{3,46} = 3.09$, $P = 0.03$, Table 2; Fig. 5A), but the additive model is not ($R^2 = 0.11$, SE $= 0.56$, $F_{2,47} = 2.92$, $P = 0.06$). The additive and interactive effects between habitat and noise are not significant for PC1, PC2, PC4 or PC5 (all $P > 0.05$, Supplementary Appendix A).

Table 1: Eigenvalues, percentages and variable loadings of rotated PCA with varimax rotation for all frequency variables (whistle, note complex, buzzes and terminal trill)

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.49	2.89	2.2	1.80	1.46
% variance	21.80	18.08	13.76	11.24	9.10
Loadings					
Whistle maximum	**0.92**	0.121	−0.12	0.10	
Whistle minimum	**0.90**	−0.15		0.12	
Whistle dominant	**0.72**		−0.11		0.13
Trill dominant		**0.88**			0.12
Whistle bandwidth	0.16	**0.72**	−0.29		
Note complex minimum	0.38	**−0.52**	0.50		
Buzz bandwidth	0.17	0.20	**−0.91**	0.12	
Buzz minimum	−0.17		**0.87**	0.18	
Note complex maximum	0.28		0.36	**0.70**	−0.25
Note complex dominant	0.24	−0.13	0.30	**0.67**	
Buzz dominant		−0.17		**0.66**	
Buzz maximum		0.37	−0.40	**0.57**	
Note complex bandwidth	−0.15	0.55	−0.20	**0.56**	−0.20
Trill bandwidth		0.23			**0.96**
Trill minimum		0.31	0.23	−0.22	**−0.70**
Trill maximum		0.50	0.14	−0.26	**0.69**

Loadings below 0.1 are suppressed from the table, and strongest loadings per variable are bolded.

Urban birds tend to sing shorter buzz notes as noise increases

The lengths of the note complex and trill had no linear relationships to noise, habitat, noise + habitat or noise*habitat (all $P > 0.05$, Supplementary Appendix A). Whistle duration tends to be shorter in urban habitats as compared to non-urban habitats ($R^2 = 0.05$, SE $= 0.02$, $F_{1,52} = 3.25$, $P = 0.08$). Buzz duration is not predicted by noise alone ($R^2 = 0.10$, SE $= 0.07$, $F_{1,52} = 0.01$, $P = 0.46$) or habitat alone ($R^2 = 0.001$, SE $= 0.06$, $F_{1,52} = 0.08$, $P = 0.78$). However, the interactive model suggests that buzz length tends to be shorter as noise increases in urban areas only ($R^2 = 0.10$, SE $= 0.06$, $F_{3,50} = 1.8$, $P = 0.16$, Table 3; Fig. 5B). Subsequently, overall song length tends to shorten in urban habitats as compared to non-urban habitats ($R^2 = 0.03$, SE $= 0.11$, $F_{1,52} = 1.84$, $P = 0.18$, Supplementary Appendix A). An independent samples t-test revealed that average noise is significantly higher in urban areas than in non-urban areas [mean ± SD dB(A); urban noise $= 51.87 \pm 3.77$, non-urban noise $= 42.75 \pm 5.05$, $t_{52} = 8.57$, $P < 0.001$].

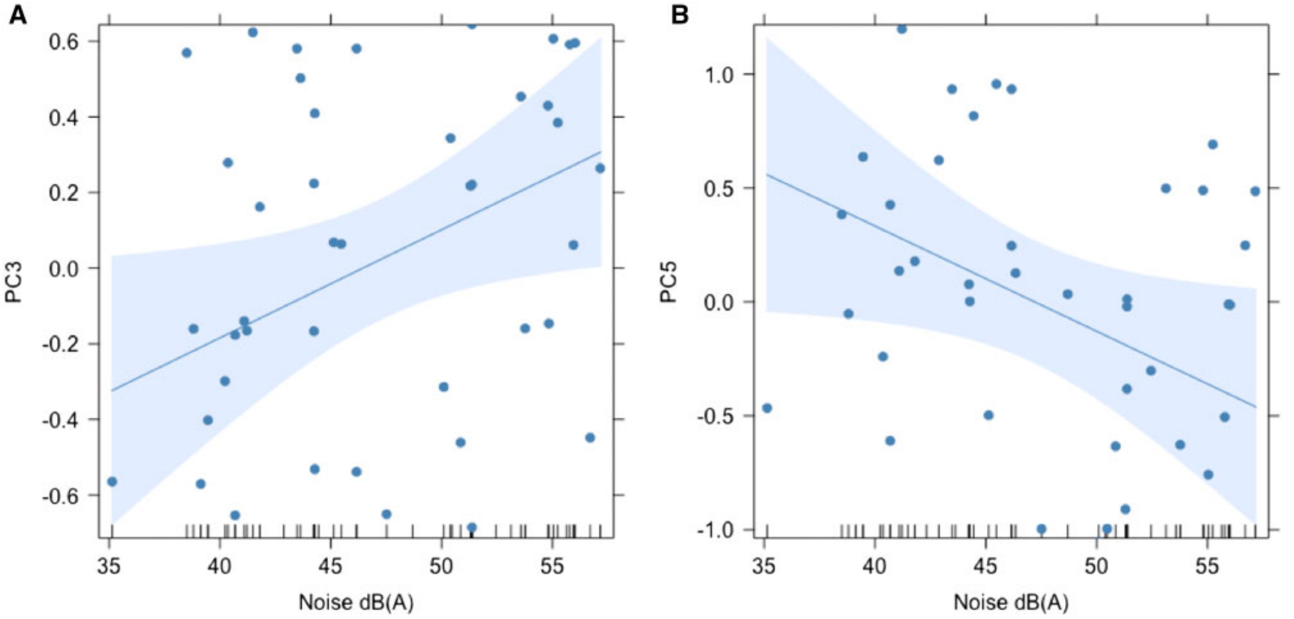

Figure 3: Effects plots with raw data of (**A**) PC3, loaded with buzz frequency measures and (**B**) PC5 loaded with trill frequency measures, indicate that as noise increases, minimum frequency increases, maximum frequency decreases and bandwidth decreases

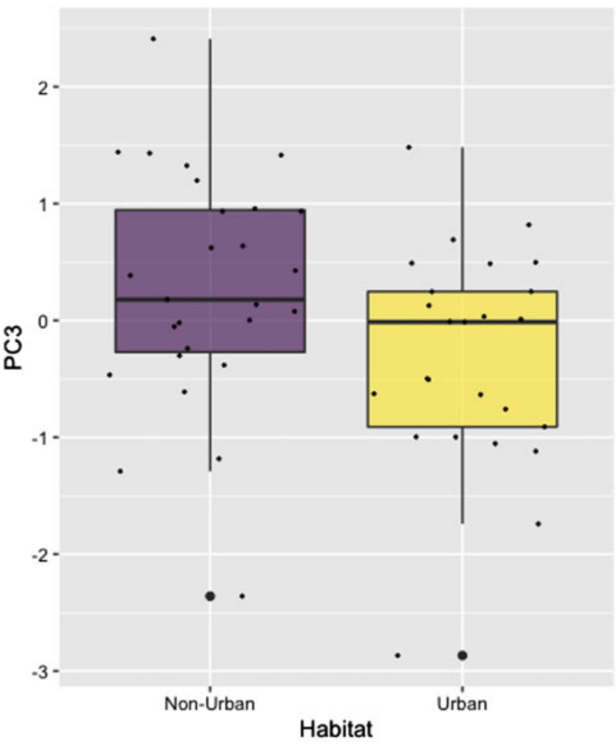

Figure 4: PC5 has larger values in non-urban areas compared to urban areas

Discussion

Our results show that winter song frequency, namely bandwidth, does vary with background noise. While many studies have found that only minimum frequency shifts in response to noise (reviewed in Slabbekoorn 2013), that is not the case here. Rather, our results show that songs exhibit narrower bandwidth near noisy areas as measured by two of the five principal components. This decrease in bandwidth is caused by both lower maximum frequency and higher minimum frequency (Table 1). The buzz and trill are wide-band notes by definition (Fig. 2), and the bandwidth of trills are often assessed by females and competitors as a part of vocal performance (Ballentine, Hyman, and Nowicki 2004; Illes, Hall, and Vehrencamp 2006; Dubois, Nowicki, and Searcy 2011; Moseley, Lahti, and Podos 2013; Phillips and Derryberry 2017a,b). Laboratory bioacoustic experiments have shown that highly modulated sounds with large bandwidths are the most difficult for a receiver to hear through noise (Lohr, Wright, and Dooling 2003). Furthermore, when a note has a small bandwidth, energy is spread into fewer frequencies, and those tones penetrate noise more effectively than a wide bandwidth with power spread throughout the frequency range (Lohr, Wright, and Dooling 2003). A smaller bandwidth allows more power to fewer tones, and increases the active space of a sound. Thus, it appears that white-crowned sparrows in noisy areas have narrow bandwidth buzzes and trills with more energy in a smaller range of tones. This reduced bandwidth may occur because a practicing bird cannot hear itself or other singing birds at masked frequencies (Marler et al. 1973).

Interestingly, we did find that whistle length, buzz length and overall song length tends to decrease with increasing noise in urban but not non-urban territories (Fig. 5), similar to results in urban great tits (*P. major*) (Slabbekoorn and den Boer-Visser 2006; Mockford and Marshall 2009; but see Hamao, Watanabe, and Mori 2011), European blackbirds (*Turdus merulus*) (Nemeth and Brumm 2009) and plumbeous vireo (*Vireo plumbeus*) (Francis, Ortega, and Cruz 2011). This may be due to males singing shorter, faster songs when faced with noise more repetitively in cities. If the effect of noise is different depending on what habitat a bird is in, this may be another indication of habitat type leading to population level differences. A larger sample size may help elucidate this pattern in future studies.

While most examples of acoustic adaptation focus on the breeding season (Slabbekoorn 2013; Derryberry et al. 2016), little research has addressed the period of learning and practice that

Table 2: Multiple regression model: PC3 ∼1 + noise + habitat + noise*habitat

Coefficients	Estimate (β)	SE	T	P
(Intercept)	−0.62	1.14	−0.54	0.59
Noise	0.01	0.03	0.49	0.62
Habitat	−3.70	1.96	−1.89	0.07
Noise*habitat	0.07	0.04	1.78	0.08

Table 3: Multiple regression model: buzz length ∼1 + noise + habitat + noise*habitat

Coefficients	Estimate (β)	SE	T	P
(Intercept)	0.66	0.13	4.87	>0.0001
Noise	0.001	0.003	0.06	0.95
Habitat	0.42	0.22	1.88	0.06
Noise*habitat	−0.008	0.004	−1.73	0.09

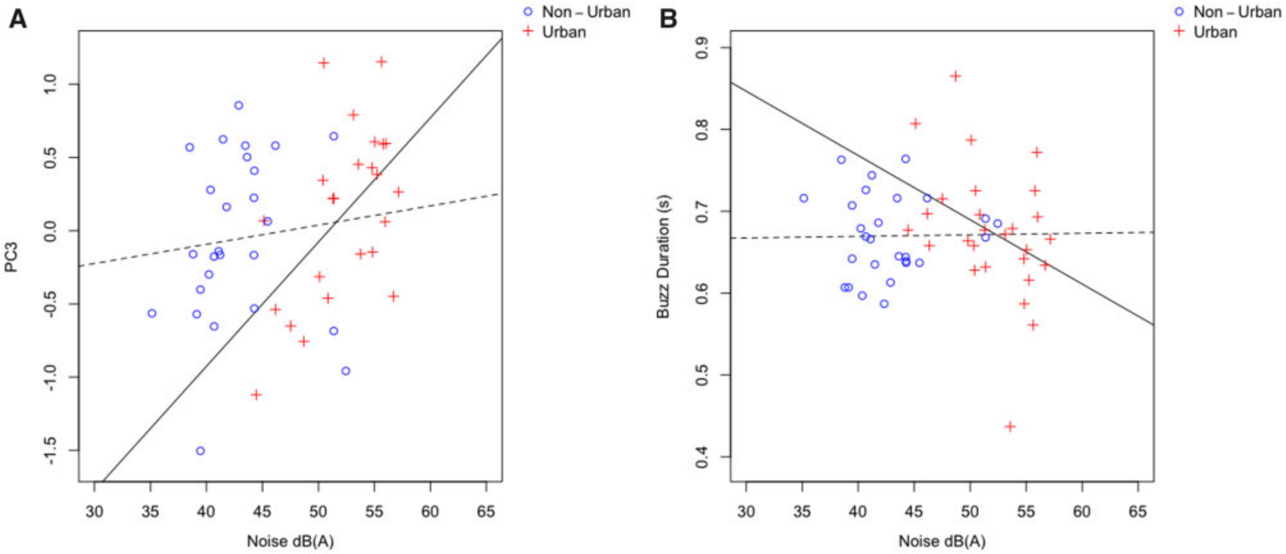

Figure 5: (**A**) Within urban locations (solid line), there is a stronger positive correlation between noise and PC3, which is loaded positively with buzz minimum frequency and negatively with buzz bandwidth. (**B**) Within urban locations (solid line), there is a stronger negative correlation between noise and buzz duration, where buzz notes tend to be shorter as noise increases. Solid lines denote urban linear slopes and dashed lines denote non-urban linear slopes

occurs on wintering grounds (Sorensen, Jenni-Eiermann, and Spottiswoode 2016). Juvenile songbirds in their critical learning period will learn from those singing around them in their first year, so urban noise during the wintering period may have a significant impact on the crystallization of a juvenile's song. Even if the most sensitive phase of learning is done on the breeding ground, wintering grounds provide important practice time for juveniles that rely on auditory feedback from themselves and other birds singing around them (Konishi 1965; Leonardo and Konishi 1999; Sorensen, Jenni-Eiermann, and Spottiswoode 2016). If the juvenile learns a song that transmits successfully in a noisy environment, his fitness may be increased in similar environments. Alternatively, if an urban wintering bird returns to a quiet non-urban breeding ground where females can hear and prefer low frequencies and wide bandwidth, that bird's success may decrease. One study shows that canaries raised in noise were partially deafened, with a loss of hearing in higher frequencies and fewer song syllables (Marler et al. 1973), supporting that noise in the winter affects song development. However, after noise was removed, some birds gained additional syllables to their repertoire, suggesting that certain aspects of song can recover after deafening by noise. Although natural noise levels on the wintering ground are less likely to reach artificial levels used in deafening experiments, high noise levels during song practice may have residual effects on song type and hearing ability, and these effects remain to be explored. Our results indicate that winter noise may be affecting auditory feedback of white-crowned sparrows, leading to a loss of higher frequency in winter song.

White-crowned sparrows overproduce songs while in a plastic phase before typically crystallizing one song type (Dewolfe, Baptista, and Petrinovich 1989; Nelson, Marler, and Morton 1996). Therefore, for the white-crowned sparrow to adapt its song to noise, it is likely the lowest note (the trill), would be affected by low frequency urban noise. If a migratory white-crowned sparrow is practicing and crystallizing a song in a noisy environment, his song may be permanently adjusted to transmit in noise. Recent studies in *Z. l. nuttalli* show males adjust their amplitude plastically in noise but not their frequency (Derryberry et al. 2017), or trill performance (Gentry and Luther 2019) suggesting crystallization and physical ability limit the frequency characteristics of song. Furthermore, *Z. l. nuttalli* raised in captivity with a noise treatment played at the same time as both low- and high-pitched tutor songs crystallized the higher pitch tutor song, while control males crystallized either song randomly (Moseley et al. 2018). However, winter song can be more plastic, or de-crystallized (Nelson, Marler, and Morton 1996). Thus, it will be important to differentiate between individual plasticity in response to noise or permanent song change between the breeding season and winter. Future studies recording the same individuals multiple times throughout the year can test whether their songs are always at a certain frequency or shifted only during loud background noise on wintering grounds.

Although Nelson (1999) suggested that Gambel's white-crowned sparrow had the shortest sensitive phase for song learning based on the reduced time on breeding grounds, the practicing of multiple song types by juvenile males may allow for the wintering environment to affect which song will be crystallized. Males from noisy wintering grounds may still crystallize a wider bandwidth song on the breeding ground through selective attrition (Nelson and Marler 1994), and it is an open line of inquiry as the technology to follow long-distant migrants from wintering ground to breeding ground becomes available. If the frequency shift in trill and bandwidth is a permanent adaptation evolving culturally through social learning, note bandwidth should decrease, become less modulated, and possibly shorten for birds that winter in noisy urban locations as seen in our results. Recent studies (Luther and Derryberry 2012; Derryberry et al. 2016) with *Z. l. nuttalli* showed that minimum frequencies have increased alongside traffic noise over time and space, and that males respond more to current songs than to low frequency historical songs. Furthermore, *Z. l. nuttalli* males also respond more strongly to wide bandwidth songs than narrow bandwidth songs, in both urban and non-urban areas and across noise gradients, indicating that bandwidth is an important sexually selected signal for male–male competition (Phillips and Derryberry 2017a,b, 2018). A preliminary experiment conducted in the FCMA in winter 2008 found that white-crowned sparrows' response to playback was delayed in noisy areas, suggesting urban noise is disrupting normal flock communication (unpublished data), which has also been found in other species (Kleist et al. 2016).

Even with these findings, there is a lot of unexplained variation in the PCA and linear models. Increased information about 3D physical features and surface types present at each recording location may improve the explanatory power of our models for song frequency and duration (Francis, Ortega, and Cruz 2011). We were unable to measure amplitude differences between urban and non-urban birds given the difficulty of accurately capturing this type of data. While it has been suggested that frequency shifts may be associated with a primary amplitude difference (Nemeth and Brumm 2010), recent work shows that minimum frequencies do not plastically shift with increases in amplitude in this species (Derryberry et al. 2017). Therefore, frequency shift, especially a loss of bandwidth and vocal performance (Luther, Phillips, and Derryberry 2016), may have consequences for male–male competition and female choice.

Ultimately, to understand the evolutionary consequences of wintering ground noise on song learning, future research and technology will be required to follow these wintering birds to their breeding grounds to assess differential reproduction rates between wintering first year males from noisy areas and quiet areas. Females of many species prefer low frequency, high performance songs (Ballentine, Hyman, and Nowicki 2004; Slabbekoorn and Ripmeester 2008; Halfwerk et al. 2011; Huet des Aunay et al. 2014), while males often assess frequency and performance for male–male competition, including in white-crowned sparrows (Phillips and Derryberry 2017a,b). Therefore, birds that winter in noisy areas may be less successful once on a breeding territory in attracting mates and defending territories if that territory is relatively quiet. Alternatively, females who winter in noisy areas may prefer songs similar to those of the males heard during winter, and there will be no reproductive loss, but perhaps reduced gene flow between populations wintering in urban versus non-urban areas. To fully understand the implications of these results, more research must be done on the dispersal patterns of long-distance migrants. Once it is known exactly where birds wintering in urban areas breed, we can compare how songs transmit between the two environments. For white-crowned sparrows that winter in highly developed California, it seems likely they would breed in more non-urban undeveloped parts of Canada and Alaska, but whether this soundscape and landscape mismatch occurs remain to be discovered.

Conclusions

Urban development has a wide range of effects on community structure, breeding success and social interactions for many species (Francis, Ortega, and Cruz 2011). We are just beginning to recognize the subtle impacts of anthropogenic noise on communication systems, and research must continue to gain insights into which species can successfully adapt to noisy soundscapes across life cycles and migratory pathways. This study provides initial evidence that winter song frequencies may be affected by urban noise for migratory birds. Our results provide a first step into understanding how urban noise affects communication in a long-distance migratory species, and provides a framework for a multitude of future research. *Zonotrichia leucophrys gambelii* can be used as a model species for migratory birds' ability to cope with anthropogenic alterations to habitats and soundscapes. As many common winter backyard birds are drawn to cities by a readily available food supply, the social dynamics of wintering flocks may change over time, creating population level differences in behavior and communication systems.

Supplementary data

Supplementary data are available at *JUECOL* online.

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