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Original Article

Natural and anthropogenic sounds reduce song performance: insights from two emberizid species

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Anthropogenic sounds influence animal vocal behaviour, species distributions, and community assemblages. Natural sounds also have the potential to affect the behaviour and ecology of animals, but it is currently unknown if the effects of natural sounds match those of anthropogenic sounds. Here, we quantified and compared the effects of natural and anthropogenic sounds on avian song performance by calculating trade-off frontiers based on trill rate and bandwidth of 2 emberizid species. Chipping sparrows (*Spizella passerina*) and white-crowned sparrows (*Zonotrichia luecophrys*) were recorded in areas with and without anthropogenic sound and along a natural sounds gradient generated from ocean surf, respectively. We analysed individuals' song performance relative to the trade-off frontier and found that both species vocalizing in environments with louder background sounds sang songs that were significantly further below the trade-off frontier than songs sung by birds in quiet settings. Chipping sparrows vocalizing in noisy areas sang almost twice as far below the trade-off frontier than individuals in quiet areas, and white-crowned sparrow song performance declined by ~25% with each 3 dB(A) increase in environmental sounds, or halving the size of a signaller's listening area. These results suggest that natural and anthropogenic sounds can have a significant effect on song performance, a trait known to influence the outcome of male-male contests and influence female mate choices. Considering that natural sounds are pervasive, quiet acoustic refuges may be far more important than previously thought, and anthropogenic development may be infringing on larger portions of prime habitat than we realize.

Key words: **anthropogenic sound, natural sound, signal trade-off, song performance, songbird, trade-off frontier.**

INTRODUCTION

Many animals, and birds in particular, rely heavily on the acoustic environment for behaviours critical to survival and reproductive success, including mate selection, intraspecific competition, predator detection, prey localization, group cohesion, and territory establishment (Bradbury and Vehrencamp 2011). New research focused on the influence of anthropogenic noise suggests that altered acoustics can influence vocal behaviours (reviewed in Patricelli and Blickley 2006, Slabbekoorn 2013) and change avian communities (Bayne et al. 2008, Francis et al. 2009) due to masking effects, where there is sufficient frequency and amplitude overlap of an acoustic signal. A well-documented response to noise is the upshifting of minimum frequencies of vocal signals in noisy areas, presumably to counter the masking effects of low-frequency anthropogenic noise (Slabbekoorn 2013). Despite this response being relatively widespread (reviewed in Roca et al. 2016), there is still a debate regarding the masking relief provided by small increases in vocal frequency (e.g. Nemeth and Brumm 2010, Halfwerk et al. 2011, Parris and McCarthy 2013), and if these adjustments compromise the acoustic signals when used in either natural or anthropogenic acoustic environments.

Intuitively, behavioural adjustments that might increase detection should help individuals dispatch signals in challenging signalling conditions, yet we still have little information on potential costs of signal changes in response to environmental sound levels. Low-frequency sounds are difficult to produce for small birds and thus may represent an honest signal of male body characteristics

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related to size or condition (Ten Cate et al. 2002, Podos and Nowicki 2004). Thus, behavioural adjustments that reduce the use of low-frequency song components to be heard in noisy conditions might lessen the attractiveness of the signal to females. However, evidence for a preference for low-frequency song is not clear-cut, as other work also supports a preference for high-frequency signals (reviewed in Cardoso 2012). Instead, a focus on song trill performance, which is a trade-off between a trilled syllable's frequency bandwidth and the rate at which the trilled elements are sung (e.g. Podos 1997), has the potential to shed new light on the potential costs of behavioural adjustments to cope with background sound levels. Importantly, song trill performance is a known target of sexual selection in many avian species (e.g. Ballentine et al. 2004, Janicke et al. 2008, Araya-Ajoy et al. 2009, Juola and Searcy 2011, Vehrencamp et al. 2013). Indeed, several studies have demonstrated the importance of song performance for both mate attraction or to repel competitors (e.g. Draganoiu et al. 2002, Illes et al. 2006, Cramer and Price 2007, Janicke et al. 2008, DuBois et al. 2011, Juola and Searcy 2011, Luther et al. 2015, Job et al. 2016), and thus, it has the potential to provide better insights on the possible costs associated with signalling in noisy environments.

Although effects of anthropogenic noise on wildlife has received considerable recent attention (reviewed in Patricelli and Blickley 2006, Slabbekoorn and Ripmeester 2008, Barber et al. 2010, Francis and Barber 2013, Swaddle et al. 2015), river and ocean surf noise can be at least as powerful as some forms of anthropogenic noise at frequencies relevant to many animals, including birds (Figures 1 and 2). However, the influence of sounds from these sources on free-living animals remains largely unexplored (reviewed in Brumm and Slabbekoorn 2005). Moreover, there are over 150 000 km of marine shoreline (NOAA 2014) and 5.6 million km of rivers and streams in the United States (US EPA 2014), exposing vast areas to the sounds of moving water in the United States alone. Limited evidence suggests that masking from sounds generated from moving water and other natural sources might be a long-standing evolutionary problem, for example: king penguins (*Apten odytes patagonicus*) increase their call rate in wind noise (Lengagne et al. 1999); chaffinches (*Fringilla coelebs*) sing longer songs near waterfalls (Brumm and Slater 2006); and tawny owls (*Strix aluco*) vocalize less in rain-generated noise (Lengagne and Slater 2002). Still, the body of literature investigating the effects of natural noise on avian populations and vocal behaviour is greatly underrepresented in contrast to the large number of publications investigating the effects of anthropogenic sounds (reviewed in Shannon et al. 2015). For example, it is unclear whether common song adjustments observed for many passerines in response to anthropogenic sounds also occur in response to natural sounds, or if there are any significant consequences to these adjustments.

Here, we sought to answer 2 main questions: how is environmental sound level related to song performance, and do natural sources and anthropogenic sources of ambient sounds appear to have the same influence on song performance, when compared across 2 emberizid species exposed to either natural or anthropogenic sounds? To answer these questions we focused on chipping sparrows (*Spizella passerina*) defending territories in quiet areas and areas exposed to anthropogenic noise and white-crowned sparrows (*Zonotrichia leucophrys*) defending territories along a gradient of exposure to background sounds generated from ocean surf. Both species persist in loud and quiet habitats and are common species in their respective environments (Francis et al. 2009, Luther et al. 2015). Nevertheless, we hypothesized that because the song frequency range of both species makes them susceptible to masking by ambient sounds generated from human activities or moving water (Figures 1 and 2), changes to vocalizations in noisy environments has the potential to decrease song performance if changes to the trill bandwidth are not matched with changes to the trill rate (Figure 2a). If, for example, increases in repetition rate compensate for decreases in bandwidth, an individual's song could effectively maintain the same level of performance (i.e. distance from trade-off frontier; Figure 2a). However, if vocalizing in noisy environments reduces the trill bandwidth or rate without a compensatory change in the other song trait, song performance could decline (Figure 2b and c). Thus, we investigated these possible outcomes in the context of ambient sounds generated from natural and anthropogenic

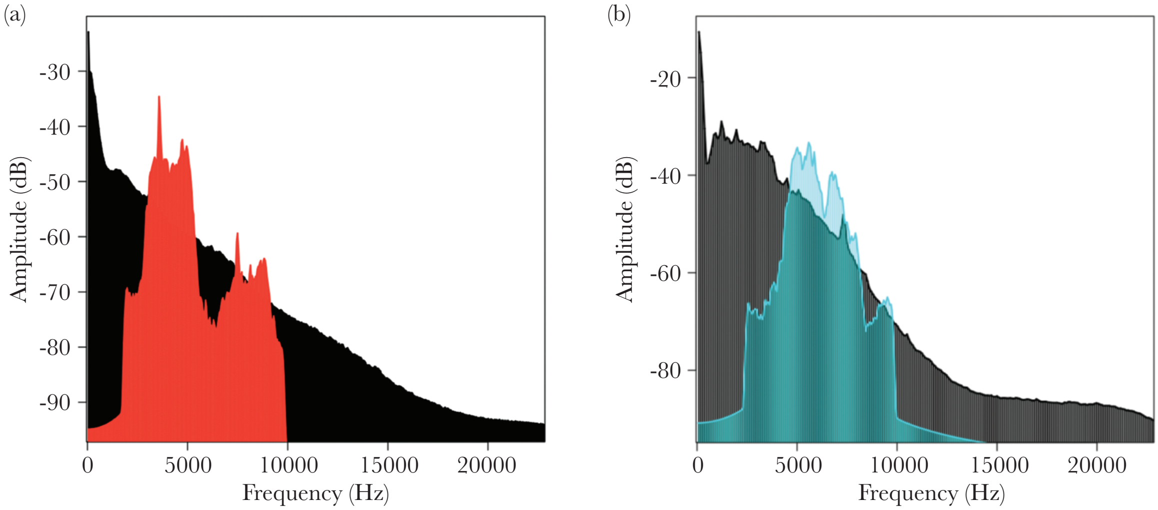

Figure 1

Power spectra of (a) white-crowned sparrow song (red) and ocean surf noise (black) and (b) chipping sparrow song (blue) and natural gas compressor noise (grey). The spectral bandwidth of both chipping sparrow and white-crowned sparrow songs and ambient noise overlap substantially and create acoustic conditions with a high probability of acoustic masking by noise.

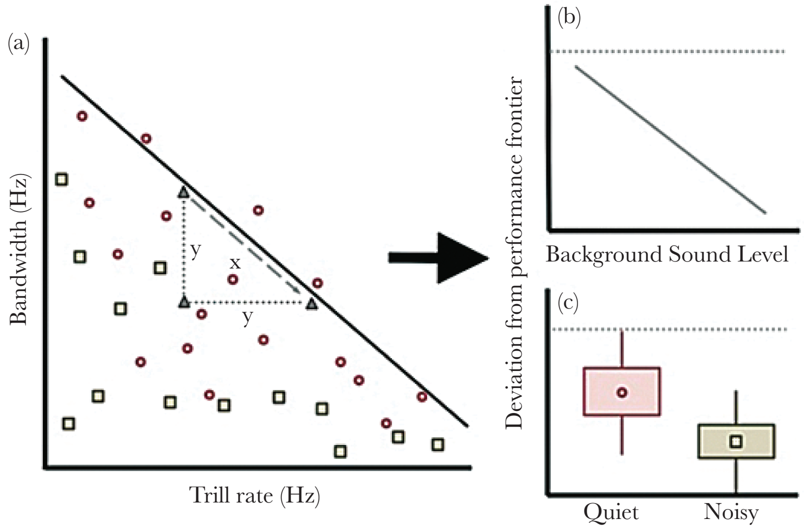

Figure 2
(a) Graphical model of a predicted song trade-off frontier; an approximate representation of a physical limitation and an attractive song performance to females of a species. As an individual reduces the bandwidth of its songs, it needs to compensate by increasing the trill rate in order to maintain a similar song performance, as illustrated by the triangle shifting along the dashed arrow denoted as "x". If an individual reduces either trill rate or bandwidth of its song without compensating with the other variable, it would result in reduced song performance (dotted lines denoted as "y"), and could result in either (b) or (c). (b) illustrates hypothetical reduction in song performance measured as greater deviation from the trade-off frontier with increasing background sound levels, and (c) illustrates hypothetical songs of birds in noisier habitats fall further below the trade-off frontier than songs from quieter habitats. Horizontal dotted line in (b) and (c) denote the trade-off frontier.

sources, as well as changes to several behavioural song adjustments that have been explored in recent studies involving anthropogenic noise (reviewed in Slabbekoorn 2013).

METHODS

Song recordings

Chipping sparrow songs were recorded between 11 May 2009 and 2 July 2009 in the San Juan Basin in northern New Mexico within Rattlesnake Canyon Habitat Management Area (RCHMA). RCHMA is managed by the Bureau of Land Management (BLM) and is a heavily developed natural gas extraction field (Francis et al. 2011b), with over 18 000 natural gas wells (BLM 2003). Many of these gas wells are coupled with gas-well compressors, which generate high volumes of noise ranging above 5 kHz in frequency (Francis et al. 2009; Figure 1).

White-crowned sparrows were recorded in Montaña de Oro State Park (MDO), on the Central Coast of California from 9 June 2015 to 13 July 2015. MDO includes a coastline that has not been altered by the development of major roadways (i.e. Highway 1 or 101), making ocean surf the main source of ambient noise, which is also primarily low frequency (Figure 1). Fifteen individuals were recorded 20–940 m from the ocean, providing a wide range of background sound levels.

For both species, we only recorded individuals that were ≥200 m from one another to ensure independence of samples. Several (>3) successive songs were recorded with a Marantz PMD 660 digital recorder using a directional shotgun microphone (Audio-technica AT-815) pointed directly at the vocalizing individual. Recordings were taken as close as possible to the singing bird; an average of 20.67 m (SD = 6.66) for the white-crowned sparrows and 17.13 m (SD = 7.19) for the chipping sparrows. After recording a white-crowned sparrow song bout, we measured background sound levels (A-weighted L_{eq}, fast sampling, re. 20 μPa) with a Larson-Davis 824 or 831 sound level meter for 2 min as close to the singing perch as possible. We used the A-weighted decibel scale because it's most relevant for bird vocalizations (Dooling and Popper 2007). All measurements and recordings were made when wind speed was less than category 3 on the Beaufort Wind Scale (e.g. Francis et al. 2011b).

Song analysis

For each recording for both species, we typically analysed 5 songs in RAVEN PRO 1.4 (Charif et al. 2010) that were randomly selected. Prior to analyses, all recordings were standardized to the same peak amplitude, which in all cases was the song of the target individual in the recording. All 55 chipping sparrow recordings were originally analysed for Francis et al. (2011b) to obtain species-level mean song features and 23 recordings had fewer than 5 songs per recording. In these cases, all songs were used in analysis. Similarly for white-crowned sparrows 8 individuals had fewer than 5 songs, and we analysed on average 4 songs per individual. Song peak frequency (the frequency of the song with the most acoustic energy) was measured automatically following placement of a selection box around the entire song. Minimum frequency (lowest frequency of the entire song) was measured manually using a selection box at the margin of notes on the spectrogram while refining box placement using the selection bars on the power spectrum views and maximum frequency (highest frequency of the entire song) was measured in the same manner (Sampling rate = 48 kHz, Hamming window, FFT length = 1024). Frequency range or "bandwidth" was measured as the difference between the maximum frequency and the minimum frequency. There is an ongoing debate as to whether minimum and maximum frequency should be measured visually from spectrograms or using a fixed change in amplitude from peak frequency (e.g. Zollinger et al. 2012, Cardoso and Atwell 2011, Cardoso and Atwell 2012). Therefore, for 38 randomly selected chipping sparrow songs from 8 randomly selected chipping sparrow recordings, we compared the minimum and maximum frequency measurements made from spectrograms that had been completed for a previous study (i.e., Francis et al. 2011b), to measurements made using a threshold of −30 dB relative to peak frequency (e.g., Francis 2015). There was no difference in minimum (paired Wilcoxon tests, $V = 434$, $P = 0.216$) or maximum frequency ($V = 487.5$, $P = 0.091$) between methods, thus we maintained our original data set for further analyses. We quantified all white-crowned sparrow songs using both the spectrogram approach and the −30 dB threshold method. Because there was no significant difference between the 2 methods for either minimum or maximum frequency (Wilcoxon rank sum tests: $V = 124$, $P = 0.65$; $V = 118$, $P = 0.84$), we used the spectrogram measurements for subsequent analyses to maintain consistency with the chipping sparrow analyses.

We measured song length from the start of the first note to the end of the final note. Number of syllables and notes in each song were counted. Syllables were identified as 2 or more notes grouped to form a single coherent unit and trills were defined as a syllable repeated at least 2 times consecutively (Pieplow and Francis 2011). Thus, a chipping sparrow song is a single trill of between 15 and 60 syllables and the typical song from white-crowned sparrows in our study population ended with a trill consisting of approximately 4 syllables. We calculated the trill repetition rate for chipping sparrows by dividing the number of syllables per song by song length (Podos 1997). For white-crowned sparrows, we measured trill rate by dividing the number of trill syllables by the duration of the trill in each song. Finally, we calculated mean values for all song features per recorded individual (i.e. per recording).

Because small datasets may be insufficient to accurately calculate trade-off frontiers involving frequency bandwidth and trill rate (Wilson et al. 2014), we supplemented each dataset with additional trill rate and bandwidth data from the literature exclusively for calculating the trade-off frontiers. However, we excluded these data from subsequent analyses (e.g. deviation from the trade-off frontier, trill bandwidth, trill rate, etc.) because context regarding the acoustic environment when these recordings were made was unavailable. For chipping sparrows, we obtained 8 additional measurements from Wilson et al. (2014) and 8 other individuals from songs available through Xeno-Canto.com, which were analysed in RAVEN PRO 1.4 as described above. This increased the sample size for the chipping sparrow trade-off analysis by 31%. For white-crowned sparrows, we used a large dataset representing 375 additional white-crowned sparrows originally published by Derryberry (2009) and available from Wilson et al. (2014).

Statistical analysis

To define trade-off frontiers for both species, we used quantile regression ($\tau = 0.9$) within the *quantreg* package (Koenker 2013) in program R to explain the relationship between bandwidth and trill rate (Wilson et al. 2014). The quantile regression method was chosen as it can effectively calculate the trade-off frontier without arbitrarily binning data sets, and can accommodate both normal and non-normal distributions (Wilson et al. 2014; Cade and Noon 2003). Significance of all quantile regressions were determined using the Hall–Sheather bandwidth analysis, except for the quantile regression sub-analysis for white-crowned sparrows songs recorded in MDO, in which case we used bootstrapping method available in the "quantreg" package because the Hall–Sheather method failed to converge (Koenker 2013). One outlier was eliminated from the chipping sparrow dataset based on the criteria that the bandwidth was greater than 1.5 times the interquartile range plus the third quartile (e.g. Sokal and Rohlf 1995; Asner et al. 2003). No outliers were removed from the white-crowned sparrow dataset. Once trade-off frontiers were defined, we calculated the vocal deviation from the trade-off frontier for each individual we recorded by subtracting values estimated from the quantile regression slope and intercept from the observed values. As such, more negative values reflect greater deviation from the trade-off frontier and worse song performance.

We used 2-sample *t*-tests to compare chipping sparrow song performance in quiet (~30–45 dB(A)) versus noisy areas (~45–70 dB(A); Francis et al. 2012) and linear regression to determine whether white-crowned sparrow song performance was related to the amplitude of ocean surf noise. Because song performance has not been widely evaluated in the context of background acoustics, it is also important to identify whether other chipping sparrow and white-crowned sparrow song features vary with ambient sound levels in ways similar to those documented for other species in response to anthropogenic noise (reviewed in Slabbekoorn 2013). For chipping sparrows, we tested for differences in bandwidth, highest frequency, lowest frequency, peak frequency, trill rate, and song length in quiet versus noisy environments using *t*-tests for parametric data and Wilcoxon rank-sum tests for non-parametric data. For white-crowned sparrows, we analysed the same features, but using linear regression across the sound level gradient. Where appropriate, we used the natural logarithm or Box-Cox transformation to normalize response variables prior to analysis. Variance tests were performed prior to all parametric tests to ensure no significant differences in variances existed. All analyses were completed in program R.

RESULTS

We recorded 37 chipping sparrows singing in noisy areas and 18 singing in quiet areas. Previous work in this system documented that sound levels for vocalizing birds were approximately 20 dB(A) higher on noisy sites relative to quiet sites (e.g. Francis et al. 2011b, Francis et al. 2012). We sampled 15 white-crowned sparrows singing in a gradient of ocean noise spanning 29.60–58.70 dB(A). In both cases, the range of background acoustic conditions represent a large reduction in the active space for a signaller (Lohr et al. 2003) or listening area for a receiver (Barber et al. 2010, Kleist et al. 2016).

Performance trade-off in noise

We found a significant trade-off between the bandwidth of the songs and the repetition rate of the songs for both chipping sparrows (Quantile regression (tau = 0.9), $t = -2.53$, $P = 0.04$; Figure 3a) and white-crowned sparrows (Quantile regression (tau = 0.9), $t = -19.89$, $P < 0.001$; Figure 3b). The trade-off between bandwidth and repetition rate was also present in sub-analyses restricted to only those individuals recorded at our study sites (Supplementary Material, Supplementary Figures S1 and S2); however, for the subsequent analyses we used the intercept and slopes from the quantile regressions (tau = 0.9) reported above. In the analysis of differences in vocal deviation from the trade-off frontier, chipping sparrows singing in areas influenced by anthropogenic sounds sang songs that were almost twice as far below the trade-off frontier than those in quiet areas ($t = 2.649$, df = 52, $P = 0.011$; Figure 3c). For white-crowned sparrows, song performance declined by almost 25% with

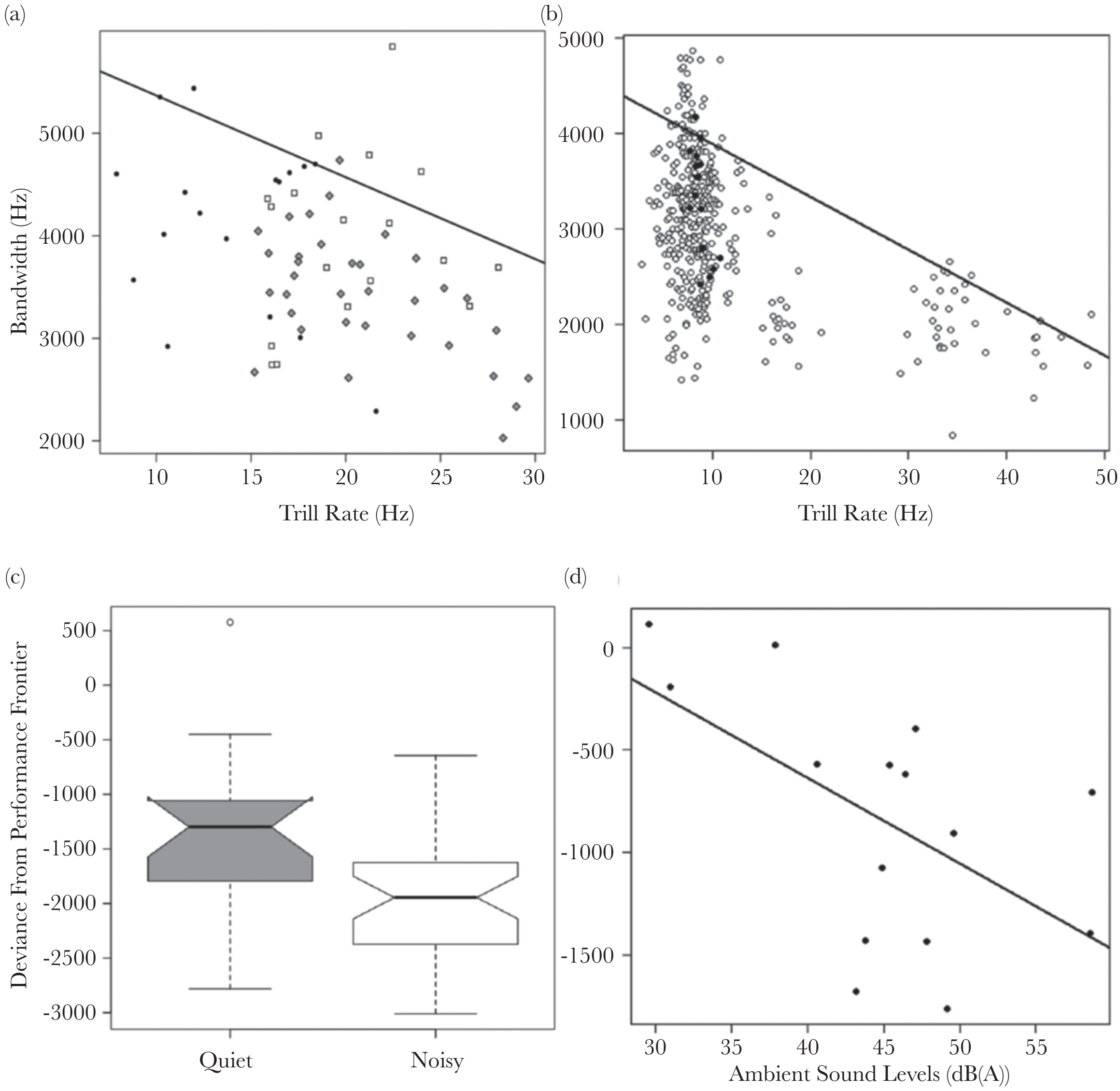

Figure 3

Trade-off frontiers of chipping sparrows (a) and white-crowned sparrows (b). Both species showed significant trade-offs between bandwidth and trill repetition rate ($P = 0.04$ and $P < 0.0001$, respectively). (c) Box-plot of the deviations from the trade-off frontier for chipping sparrows recorded in both quiet and noisy habitats. Individuals in noisy habitats sang significantly further below the trade-off frontier than individuals in quiet habitats ($P = 0.011$). (d) Regression plot of deviation from the trade-off frontier for white-crowned sparrows. There was a significant reduction in song performance with increases in background sound levels ($P = 0.028$).

each 3 dB(A) increase in ocean sound amplitude ($F_{1,13} = 6.096$, $R^2 = 0.319$, $P = 0.028$; Figure 3d).

Changes in song features

Differences in deviation from the trade-off frontier among chipping sparrows in noisy and quiet areas were due to a 13.4% reduction in bandwidth among birds singing in noisy areas relative to quiet areas ($t = 2.670$, df = 52, $P = 0.010$; Figure 4a). The smaller bandwidth is explained by a higher minimum frequency ($t = -3.536$, df = 52, $P = 0.002$; Figure 4b), but the maximum frequency and peak frequency for birds in noisy areas were unchanged relative to those in quiet areas (both, $P > 0.35$). Chipping sparrows did not appear to sing at a different trill rate in noisy compared to quiet areas ($W = 282$, $P = 0.78$); however, songs in noisy areas were more than 25% longer in noisy areas relative to quiet areas ($W = 134$, $P < 0.001$; Figure 4c) and had 37.5% more notes ($W = 174.5$, $P = 0.005$). Based on this unexpected result, we conducted a post hoc analysis regressing the natural logarithm of song bandwidth on the natural logarithm of song length. We found a strong negative relationship between song length and song bandwidth ($F_{1,59} = 10.11$, $R^2 = 0.14$, $P = 0.002$), perhaps reflecting another song performance trade-off that warrants additional investigation.

The presence of ocean sound appears to influence several white-crowned sparrow trill features. Increases in ocean sound amplitude corresponded with a 47% reduction in the bandwidth of the trill across the range of observed sound levels ($F_{1,13} = 5.86$, $R^2 = 0.31$, $P = 0.049$; Figure 5a). Similar to the chipping sparrow, this reduction appears to be driven by a 20% increase in trill minimum frequency ($F_{1,13} = 13.21$, $R^2 = 0.50$, $P = 0.003$; Figure 5b). However,

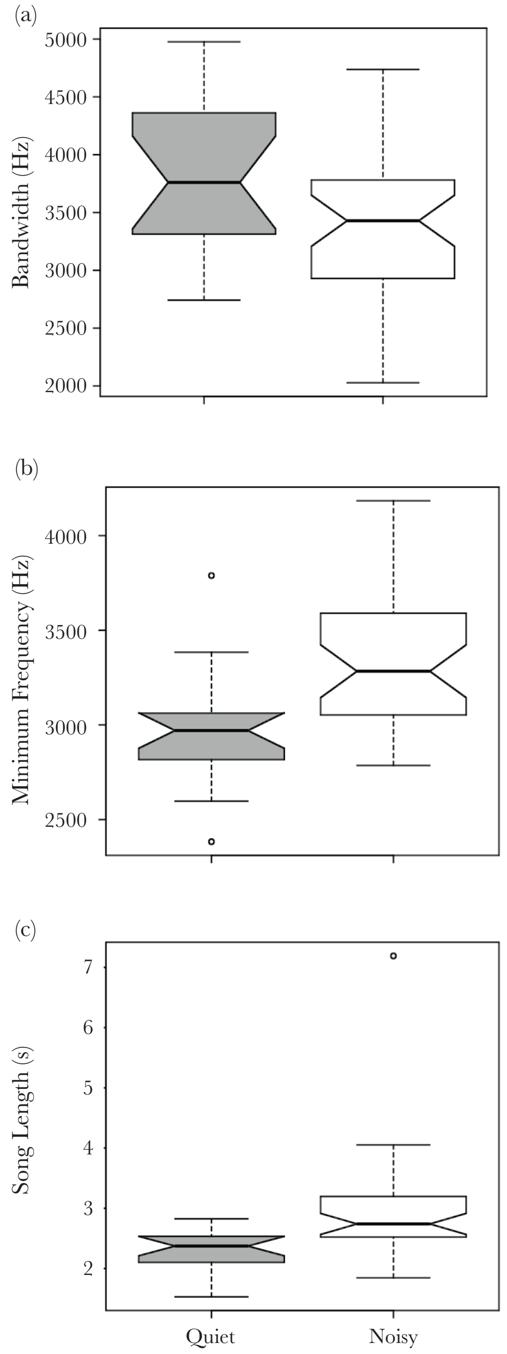

Figure 4

(a) Box-plot of chipping sparrow song bandwidth in the presence of natural gas-well-compressor noise in NW New Mexico. Songs recorded in noisy habitats had significantly smaller bandwidths than songs recorded in quiet habitats ($P = 0.01$). (b) Box-plot of chipping sparrow song minimum frequencies. Songs in noisy sites had significantly higher minimum frequencies than songs in quiet sites ($P = 0.002$). (c) Box-plot of chipping sparrow song length in noisy and quiet sites. Songs were significantly longer in noisy sites than quiet sites ($P < 0.001$).

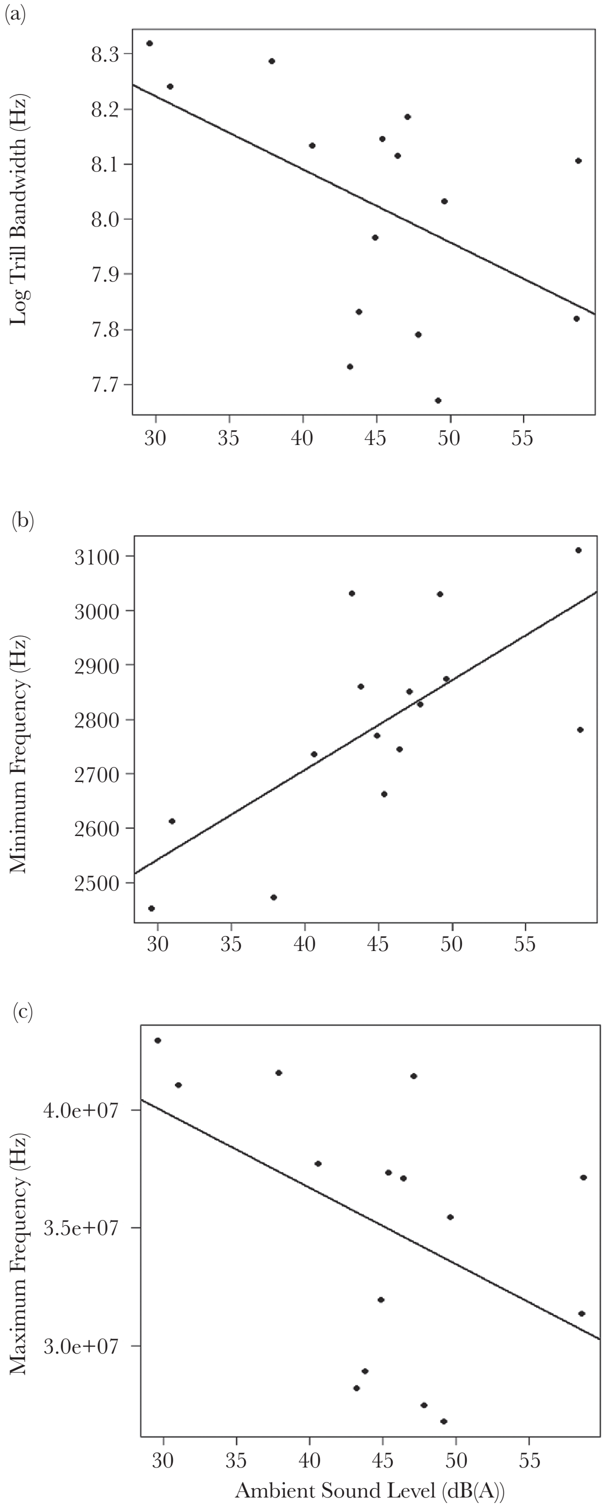

Figure 5

(a) Bandwidth of trilled notes of white-crowned sparrow songs along the ocean surf noise gradient. There was a significant decrease in bandwidth with increases in ocean surf noise ($P = 0.031$). (b) Minimum frequency of trilled notes in white-crowned sparrow songs along the ocean surf noise gradient. There was a significant increase in minimum frequencies with increasing background noise levels ($P = 0.003$). (c) Maximum frequency of trilled notes in white-crowned sparrow songs along the ocean surf noise gradient. There was a trend for reducing maximum frequencies with increasing background noise levels ($P = 0.074$).

in contrast to the chipping sparrow there was also a marginally non-significant trend of reduced maximum frequency of the trill with increases in ocean sound amplitude ($F_{1,13} = 3.76$, $R^2 = 0.22$, $P = 0.074$; Figure 5c). We found no influence of ambient ocean sound on trill rate or duration of the entire song (both, $P > 0.4$).

DISCUSSION

Here, we have shown that natural and anthropogenic sounds impact song performance of white-crowned and chipping sparrows respectively via decreases in song trill bandwidth. We found no evidence that chipping sparrows or white-crowned sparrows compensate for changes in trill bandwidth with changes in trill rate to maintain song performance. Thus, birds exposed to either ocean surf or anthropogenic sounds had significantly reduced song trill performance compared to those in less noisy environments. This consistency across sound types indicates that compromised song performance due to adjustments to ambient sounds is not unique among urban birds or those along noisy roadways, but affects individuals across both developed and undeveloped landscapes and from different sources of sound. We found that song adjustments were similar to those adjustments reported for other species (see below), such as increases in minimum frequency and reduced song or trill bandwidths. Chipping sparrows also sing longer songs in noisy environments, suggesting that they are increasing signal redundancy as well as adjusting the minimum frequency to overcome acoustic masking. For white-crowned sparrows, there was a marginally significant trend for decreasing trill maximum frequency with ambient sound levels, a pattern unreported in other songbirds, but one that may exemplify the physiological limit on bandwidth of a trill given a high repetition rate.

Many of the structural changes responsible for declines in performance are in line with previously documented changes in song features in response to anthropogenic sounds in other species (reviewed in Slabbekoorn 2013). For example, both species exhibited reduced bandwidth and increased minimum frequency of their trills. These changes have been documented previously in many species of songbirds (reviewed in Patricelli and Blickley 2006, Slabbekoorn 2013, Roca et al. 2016). Similar to chipping sparrows in this study, gray vireos (*Vireo vicinior*) and chaffinches (*Fringilla coelebs)* sing longer songs in areas with high levels of anthropogenic and natural environmental sounds respectively (Francis et al. 2011a, Brumm and Slater 2006). However, Job et al. (2016) found no influence of anthropogenic sound on chipping sparrow song length in Michigan, USA, suggesting different populations of the same species may respond to masking noise through different mechanisms theorized to improve communication in noisy conditions (i.e. increasing signal-to-noise ratio, increased signal redundancy; Wiley 2006, Bradbury and Vahrencamp 2011). Finally, similar to both species in this study, great tits (*Parus major*), spotted towhees (*Pipilo maculatus*), and European robins (*Erithacus rubecula*) increase minimum frequency and decrease song bandwidth in the presence of anthropogenic sounds (e.g. Slabbekoorn and Peet 2003, Halfwerk and Slabbekoorn 2009, Francis et al. 2012, McLaughlin and Kunc 2013, Montague et al. 2013).

Although this study is the first to assess how song performance changes in response to anthropogenic and natural sounds, we were unable to evaluate both species' responses to ocean and anthropogenic noise because white-crowned sparrows only occur at our Coastal California sites and chipping sparrows only occur at our New Mexico sites. However, 2 recent studies support the notion that these different sources of background noise affect song performance in similar ways. Luther et al. (2015) found a similar effect of anthropogenic noise on white-crowned sparrow song performance, suggesting that this species does respond to natural and anthropogenic noise in a similar fashion. Although there are no published accounts of changes in chipping sparrow song features in response to natural sounds, Job and colleagues (2016) found that chipping sparrow song performance decreased significantly both with increasing anthropogenic noise and urban structure. Thus, collectively, there is strong support for a negative influence of background sound levels, regardless of source (i.e., natural or anthropogenic), on song performance. However, notwithstanding this and similar studies, explicit examination of these changes in terms of song performance has not been widely studied, despite having significant implications for avian reproductive success (e.g. Jamicke et al. 2008, Juola and Searcy 2011).

Reductions in song performance may have substantial effects on social interactions between songbirds. Birds rely heavily on vocalizations for mate selection and male-male competition (Gil and Gahr 2002). Both males and females cue into male song performance to determine the quality of rivals and mates, and elicit varied responses based on this key factor (Nowicki et al. 1998, Draganoiu et al. 2002, Ballentine et al. 2004, Illes et al. 2006, Cramer and Price 2007, DuBois et al. 2011). For instance, playback experiments using experimentally reduced song performance decreases the intensity of territorial response among another coastal white-crowned sparrow population (Luther et al. 2015). Although our approach was correlational and did not document single birds engaging in short-term behavioural adjustments to background sound conditions, it is probable that song shifts, and the subsequent reduction in song performance, are an outcome of these short-term adjustments. Such adjustments have been documented for other species singing in noisy conditions (e.g. Halfwerk and Slabbekoorn 2009, Gross et al. 2010, Goodwin and Podos 2013). Because females are known to discriminate among males based on song trill performance (Draganoiu et al. 2002, Ballentine et al. 2004, Caro et al. 2010), short-term behavioural shifts in response to ambient noise levels could result in fewer mating opportunities and could be considered a behavioural evolutionary trap (Schlaepfer et al. 2002). Reductions in song performance could also result in more physical altercations with male competitors. Future research should prioritize investigating the potential consequences of declines in song performance due to ambient sounds.

Importantly, as mentioned above, we cannot determine from this study whether reductions in song performance are a direct result of short-term behavioural adjustments, or if the presence and intensity of environmental sounds filter individuals with different song attributes. It is well documented that human-made noise can filter bird communities based on song frequency (e.g. Rheindt 2003, Goodwin and Shriver 2011, Francis et al. 2011b, Proppe et al. 2013, Francis 2015). In these studies, species with low frequency vocalizations avoid areas dominated by anthropogenic sounds more so than those with higher frequency vocalizations. It is possible that intraspecific filtering of individuals also occurs and that higher quality males, which have songs that are closer to the trade-off frontier, occupy higher quality acoustic habitats that have low ambient noise levels and lower quality males are allocated to noisy areas. Whether or not the observed relationship between song features and ambient sounds are generated from behavioural shifts or sorting among individuals, it is also possible that males that maintain territories in noisy areas obtain benefits from noisy environments and thus could explain use of noisy areas even though there appear to be costs. For example, at our New Mexico sites chipping sparrow nest success increases with anthropogenic noise exposure due to reduced nest predation (Francis et al. 2009), thus there are clear benefits to occupying some noisy areas, but this will likely depend on species-specific responses of predators. Whether decreased predation risk also occurs for white-crowned sparrows and other species that occupy natural noisy areas is unknown. Clearly, more research is necessary to understand potential trade-offs for occupying noisy area and to clarify whether intraspecific self-sorting could explain song patterns with respect to sound levels.

Regardless of whether altered song performance is a consequence of self-sorting or short-term behavioural adjustments, lower performance could have substantial effects on songbird reproductive success and behaviours, independent of potential benefits due to reduced nest predation risk as mentioned above. Trade-off frontiers between trill rate and bandwidth are known to be present in other birds with trilled songs, including many members of the large Emberizidae family (e.g. Ballentine et al. 2004, Podos 1997), but also wrens (Tryglodytidae; Illes et al. 2006, Cramer 2013), canaries (Fringillidae; Draganoiu et al. 2002), blackbirds (Icteridae; Cramer and Price 2007), and wood warblers (Parulidae; Cardoso and Hu 2011). This suggests that reduced performance due to ambient sounds may not be limited to the 2 species studied here, or even emberizids, and may be present across many passerine. Thus, this possibility should be investigated further to determine if other songbirds experience similar reductions in song performance with increased ambient sound levels, either natural or anthropogenic, given the similarities in behavioural adjustments to songs across species. This seems especially true when viewed in the context that ambient sounds from moving water are quite widespread—over 150 000 km of coastline and 5.6 million km of rivers and streams in the United States alone (NOAA 2014 and US EPA 2014) and that anthropogenic noise sources are growing 3 times faster than the human population (Barber et al. 2010). This spatial extent provides countless opportunities for us to better understand how and to what degree sounds shape various aspects of avian ecology and behaviour, including those behaviours closely tied to fitness studied here.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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