NATURAL AND SEXUAL SELECTION SHAPE THE ACOUSTIC PHENOTYPE OF URBAN BIRDS

AN ABSTRACT

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OF

DOCTOR OF PHILOSOPHY

BY

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ABSTRACT

Anthropogenic noise is an evolutionarily recent phenomenon and many animals respond by changing the pitch and timing of their vocalizations to avoid masking. A benefit to modifying a vocal mating signal in the context of noise is increased transmission distance. This same modification may pose a fitness cost if that signal feature is also sexually selected. Bird song is a well-studied sexual signal used in territory defense and mate attraction. Physically difficult to produce components of song are thought to be honest signals of male quality. One such trait is a male's ability to maximize the rate of note production at a given frequency bandwidth; this tradeoff is known as vocal performance. Studies have shown modifications to song in the context of noise, specifically to trill rate and bandwidth. Costs of these modifications may include increased conflict with neighboring males, which could potentially lead to decreased body condition, loss of a territory, or less time spent attracting a female. Few studies have investigated this tradeoff between environmentally induced selection (i.e. natural selection) and social selection (i.e. sexual selection) on song in an urban landscape. Therefore, a gap remains in our knowledge of the consequences on fitness of urban song adaptation for signalers. Using the white-crowned sparrow (*Zonotrichia leucophrys*) in the San Francisco Bay Area of California, the objectives of my dissertation research include 1) testing if vocal performance is a salient signal for white-crowned sparrows, 2) testing if receivers are responding specifically to variation in trill rate or bandwidth, and 3) testing the effect of ambient noise level on receiver assessment of vocal performance.

Overall, my dissertation research suggests that both anthropogenic and natural soundscapes shape the evolution of song and receiver behavior. Modifications to song structure that increase signal detection come at the cost of decreased signal salience for male competitors. Additionally, anthropogenic noise appears to change how males utilize vocal performance. Therefore, species living in noisy areas may face consequences of decreased fitness over time due to masked honest signals and increased male-male conflict.

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A DISSERTATION

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INTRODUCTION

Many animals use acoustic signals – such as frog calls or meerkat alarms – to communicate. Signals specifically used to compete for or select a mate are under sexual selection. Selection therefore favors signaling traits that indicate competitive ability or mate quality. For example, performance of signaling traits that are costly to produce, such as those that are physically limited by the animal's size or coordination are more likely to convey honest information about the sender. Selection also favors signaling traits that maximize the transmission of this information in a given environment. For example, other sounds in the environment (the soundscape) can reduce the ability of individuals to detect or decode information in the signal. However, individuals may not always be able to maximize both performance and transmission of a signal. This leads to two critical questions – when faced with this trade-off which aspect of the signal do senders maximize and how does this decision affect communication? I address these questions using a well-studied sexual signal – bird song – in anthropogenic soundscapes, which are evolutionarily recent selective environments. No research to date has focused on whether physically limited signals lose potency in male-male competition or female mate choice in noisy soundscapes. Across many bird species, songs have decreased in frequency bandwidth, likely to avoid masking by the low frequency noise generated by machines such as cars. Decreasing bandwidth maximizes transmission distances in noisy

environments; however, increasing bandwidth maximizes performance of the coordination of vocal musculature and beak movements required to produce fast rates of note production (trill rate). This performance measure is referred to as ‘vocal performance’. Here, I tested whether vocal performance functions in male-male competition in White-crowned Sparrows (*Zonotrichia leucophrys*). I then asked how assessment of performance varies across different urban and rural soundscapes in San Francisco and Point Reyes, California. I played songs of varying performance levels on male's territories to simulate intrusion of a competitor and then measured the behavioral response of the territorial males. These behavioral experiments provided insight into how males assess trill rate, bandwidth, and overall vocal performance in the context of quiet areas and noisy areas. I found that males discriminate between high and low vocal performance songs in both urban and rural areas when the differences in performance are large between stimuli. However, when differences in vocal performance are small, urban and rural males differ in their response. Rural males respond similarly to songs of similar performance levels, and more to high performance songs whether they are maximized with trill rate or bandwidth. Urban males respond less to narrow bandwidth songs as compared to wide bandwidth songs, but do not seem to differentiate trill rates. In both urban and rural areas, males in noisier territories tend to approach more closely to stimuli, perhaps so that they can actually hear differences in song structure. These results indicate that noise affects assessment of a physically limited trait and affects response behaviors, and may have functional consequences in the form of increased territorial disputes and decreased fitness.

Chapter 1. Vocal Performance Is A Salient Signal For Male-Male Competition In White-Crowned Sparrows

ABSTRACT

Vocal communication in songbirds is important for aggressive signaling, such that an honest signal allows receivers to assess a competitor's qualities. One aspect of song that conspecifics may assess is vocal performance. An example of vocal performance is how well an individual performs the tradeoff between trill rate and bandwidth in production of repeated notes. This type of vocal performance (vocal deviation) is thought to be an honest signal because a male's ability to maximize both bandwidth and trill rate is limited by motor constraints on sound modification. Further, how well a male can repeat this tradeoff may provide receivers with information about the signaler, and a male's own level of vocal performance can affect the strength of response to high performance songs. We tested whether males assess each other based on vocal performance in an important model species, the White-crowned Sparrow (*Zonotrichia leucophrys*). We show that male White-crowned Sparrows respond more strongly to high performance songs than to lower performance songs in two different locations, supporting the hypothesis that males utilize vocal performance to assess competitors. We also provide initial evidence that vocal performance varies among males and is repeatable within individuals.

INTRODUCTION

In animal communication, two common functions of signals are mate choice and competition. In mate choice, receivers select for honest signals of mate quality to avoid low quality mates. In competition, receivers assess honest signals of competitive ability to avoid costly conflicts. A signal is considered honest if it reliably conveys information about the signaler, such that a receiver benefits by making an appropriate decision in response to the signal (Searcy & Nowicki 2005). However, the signaler does not always benefit from being honest. Therefore, understanding how signal honesty is ultimately maintained is of particular interest in behavioral ecology. Signal honesty can be maintained if falsely signaling leads to social, physical, or fitness costs for the signaler. Signals related to physical attributes are called index signals (Maynard Smith & Harper 2004). Index signals are difficult to "fake", because the energy or musculature needed to perform or create the signal are limited by the signaler's physical characteristics (Maynard Smith & Harper 2004).

Bird song is a commonly studied communication signal used in competition (Catchpole 1987; Catchpole & Slater 2008), and the honesty of song determines the usefulness to the receiver. One mechanism thought to maintain honesty in song is physical constraints on sound production and modification (Nowicki & Searcy 2005). There are multiple ways in which song traits can be physically constrained. For example, song quality may be constrained by the musculature involved with singing, which itself may be affected by early developmental conditions (Nowicki et al. 1998). An example of a physical limitation on song production is the ability to sing fast individual notes, where long notes require more time for respiratory recovery (Hartley & Suthers 1989). Similarly, other index signals maintained by breathing patterns or energy allocation may also affect the amount of time spent singing (Lambrechts & Dhondt 1987), song rate (Hofstad et al. 2002), amplitude changes during song broadcasting (Forstmeier et al. 2002; Cardoso et al. 2007), and/or sound to silence ratios (Poesel et al. 2001).

One limitation on song production thought to maintain signal honesty is the tradeoff between rate of note production and bandwidth (Podos 1997). Birds coordinate rapid vocal tract and beak movements to actively track fundamental frequencies and filter out harmonics, in part to produce pure tone signals (Westneat et al. 1993; Podos 1996; Nowicki & Marler 1988; Riede et al. 2006). In birds with broadband trilled notes, there is a tradeoff between the rate of note production (trill rate) and note bandwidth. At slow trill rates, males can produce wide or narrow frequency bandwidths, but as trill rate increases, bandwidth is constrained resulting in a triangular distribution of songs (Podos 1997). An upper bound regression line can be calculated from this triangular distribution (Podos 1997). Distance from the upper bound regression line is a measure of a male's ability to perform the tradeoff, which is often referred to as vocal deviation. Small vocal deviation is higher performance, and large vocal deviation is lower performance (Podos 2001). Because producing this tradeoff is physically challenging, vocal deviation may provide receivers accurate information about male quality. Hereafter, we refer to vocal deviation as vocal performance.

Both females and males in a number of species respond to variation in vocal performance, supporting the hypothesis that vocal performance functions in mate choice and male-male competition (Podos et al. 2009). Female songbirds prefer higher performance songs in Common Canaries (*Serinus canaria*; Drăgănoiu et al. 2002), Swamp Sparrows (*Melospiza georgiana;* Ballentine et al. 2004) and Lincoln Sparrows (*Melospiza lincolnii*: Caro et al. 2010). Female preference for high performance is even found in a mammal species, singing mice (Pasch et al. 2011). Indirect measures of mate choice also demonstrate a preference for higher performance songs, as vocal performance correlates with reproductive success in some species (Cramer et al. 2011; Sprau et al. 2013). In the context of competition, male birds also give differential response to high and lower performance songs, but the direction of this response is species specific. Red-winged Blackbirds (*Agelaius phoeniceus*) respond less to high performance songs (Cramer & Price 2007), whereas Swamp Sparrows (*M. georgiana;* Dubois et al. 2011), and Nightingales (*Luscinia megarhynchos*; Schmidt et al. 2008) respond more to high performance songs. Banded Wrens (*Thryophilus pleurostictus*) approach high performance songs first (Illes et al. 2006) but then spend more time near lower performance songs (Illes et al. 2006; De Kort et al. 2009). This variation in receiver response to vocal performance might be explained by something other than high versus low signal values. For example, in Swamp Sparrows, a male's own vocal performance is a factor in his response to simulated intruders (Moseley et al. 2013), where high performance males respond most strongly to high performance stimuli, and low performance males respond less strongly to high performance stimuli. Therefore, it is important to consider the vocal performance of the receiving male when assessing response to varying performance levels.

White-crowned Sparrows (*Zonotrichia leucophrys*) are a well-studied species for understanding how birds learn song (Marler & Tamura 1964), form dialects (Nelson et al.

2004; Petrinovich & Baptista 1984; Baker & Thompson 1985; Baptista 1975), choose mates (Chilton et al. 1990; MacDougall-Shackleton et al. 2002), defend territories (Patterson & Petrinovich 1978; Nelson & Soha 2004; Poesel & Nelson 2012), and for testing acoustic adaptation (Derryberry 2009; Derryberry et al. 2016). Although the song of white-crowned sparrows has long been studied, the function of vocal performance is unknown in the context of male-male competition and mate choice in this species. Luther et al. (2016) tested normal bandwidth vs. reduced bandwidth songs in a territorial playback experiment in an urban population of White-crowned Sparrows and found that males responded more strongly to normal bandwidth songs. These findings are consistent with the hypothesis that males respond to variation in vocal performance; however, the study tested only response to differences in bandwidth, not in trill rate and bandwidth, so males may have been responding only to variation in bandwidth, not vocal performance. Additionally, the vocal performance of each tested male was not considered. Here, we directly test the hypothesis that male White-crowned Sparrows respond to variation in vocal performance (both trill rate and bandwidth) using territorial playback experiments in two breeding populations of Nuttall's White-crowned Sparrow (NWCS; *Z. l. nuttalli*), Point Reyes, CA and San Francisco, CA. We predict that males will give a stronger response to higher performance songs, because higher performance songs probably indicate territorial intrusion by a high quality competitor. We take into consideration the effect of each male’s own performance on his response to high and low performance stimuli using mixed effects models. We also assess whether variation in vocal performance is repeatable within males during a song bout. We predict that within males, songs will be highly repeatable in vocal performance levels, because we expect males are maximizing their performance of this physically constrained song trait.

METHODS

Song Data

Between 2010 and 2016, we recorded songs of territorial males in Abbott's Lagoon area in Point Reyes National Seashore, Marin County, CA (*n* = 51 males, 367 songs) and in Golden Gate Park, Lake Merced, and throughout the Presidio in San Francisco, CA (*n* = 109, 780 songs) using a Marantz PMD 661 digital recorder, Sennheiser ME-62 omnidirectional microphone, and Saul Mineroff SME-1000 parabola. Some of these males were also tested with playbacks (Point Reyes *n* = 19, San Francisco *n* = 16; see Playback design below). Point Reyes males recorded and tested sang the McClure dialect as described by Baker and Thompson (1985), and San Francisco males recorded and tested sang the San Francisco dialect as described by Baptista (1975). The number of songs recorded per male ranged from 2-12 (mean ± SD; Point Reyes 6.5 ± 2.8 songs; San Francisco 7.75 ± 3). All songs for each male were sampled from the same song bout. We recorded songs with a sampling rate of 44.1 kHz and stored recordings as uncompressed .wav files. We then resampled songs at 25 kHz for analysis in SIGNAL 5 (Beeman 1998). Next, we high-pass filtered songs at 1500 Hz to remove noise below the range of White-crowned Sparrow songs. We took terminal trill minimum and maximum frequencies at -36 dB relative to the peak amplitude frequency from spectrograms (256 pt transform, frequency resolution: 97.7 Hz, 10.2ms time resolution) to capture variation in frequency bandwidth while excluding background noise (Podos 1997). To calculate trill bandwidth, we subtracted the minimum frequency from the maximum frequency. Terminal trill rate was calculated as the average number of notes produced per second (Hz). We calculated vocal performance as the orthogonal deviation of each song from an upper bound regression of trill bandwidth on trill rate (Podos 2001). We used the published equation for the upper bound regression on a set of 1572 Emberizidae songs, $y= -0.124x +7.55$ (Podos 1997). We did not use a published white-crowned sparrow equation (Derryberry 2009) because that dataset did not include songs from the McClure dialect. Nearly half of all our recorded songs fell above this upper-bound regression, making the published white-crowned sparrow equation not a suitable representation of an upper-bound limit. All of the recorded songs of both dialects fell below the published upper-bound regression for sparrows (Emberizidae; Podos 1997), and so we used this equation.

Repeatability of Vocal Performance

To test our prediction that vocal performance is a repeatable signal within males, we calculated repeatability using the ICC package (Wolak et al. 2012) in the R platform (R Development Core Team 2011). The ICC library uses one-way ANOVAs to calculate the intraclass correlation coefficient, which is a measure of variation within versus between individuals in vocal performance.

Song Stimuli

To create stimuli for song playback experiments, we used songs of known color-banded males holding territories the previous year who sang the McClure dialect in Point Reyes and the San Francisco dialect in San Francisco. Songs selected for stimuli had high signal to noise ratios. We drew pairs of songs that differed naturally by at least 500 Hz in trill bandwidth and then manipulated each song to create fast or slow trill versions that were amplitude normalized using SIGNAL 5 (Beeman 1998); thus, stimulus pairs were not from the same male. Although this approach does not control for possible familiarity, we limited the possibility of familiarity by drawing stimulus songs from a different breeding season than the one in which we ran playback analyses. We created specific trill rates by repeating the first trill note eight times to create a consistent bandwidth with the desired spacing between notes. Thus, we made a pair of stimuli: (1) wide bandwidth, fast trill rate, hereafter referred to as “high performance” and (2) narrow bandwidth, slow trill rate, hereafter referred to as “low performance” (McClure stimulus exemplars illustrated in Figure 1.1). We created 7 stimulus pairs in Point Reyes and 6 stimulus pairs in San Francisco. The average difference in deviation between high performance stimuli and low performance stimuli within pairs was 6.2 ± 1.3 for McClure stimuli and 13.9 ± 2 for San Francisco stimuli. All San Francisco stimuli and McClure stimuli fall within the natural range for their locations, except for four McClure low performance stimuli with slower trill rates (Table 1.1). Because stimulus pairs were reused in playback analyses, we include the effect of stimulus identity on response (see **Statistical Analyses** below).

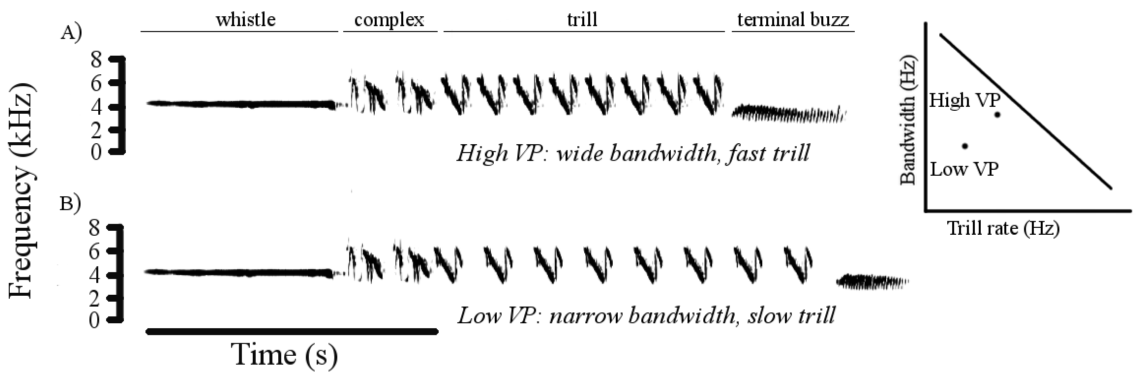


Figure 1.1. Examples of high performance and low performance stimuli used in male territorial playback experiments in McClure dialect, (A) wide bandwidth, fast trill rate exemplar, (B) narrow bandwidth, slow trill rate exemplar. Inset indicates relative placement of two stimuli to the performance limit of frequency bandwidth by trill rate, where VP stands for vocal performance.

In creating our two stimulus types, we could have standardized either trill length or the number of notes in the trill, but not both. If we standardized trill length for the two stimulus types, then the type with a slow trill would have had fewer trill notes. If we standardized the number of trill notes, then the type with a slow trill would have been longer. We standardized the number of trill notes rather than trill length to avoid truncating individual trill notes. Thus, the lower performance song is longer in duration.

Our manipulations of song stimuli used in these experiments were necessary and consistent with manipulations of trill rate in previous studies (Moseley et al. 2013; Ballentine et al. 2004; Dubois et al. 2011; Drăgănoiu et al. 2002). We manipulated all stimuli, so male response is not due to playback of manipulated versus unmanipulated stimuli.

Table 1.1. The range of vocal deviation, trill rates, and bandwidths of songs as compared to stimuli, showing range; mean ± SD.

Type	No. songs	Vocal deviation	Trill rate (Hz)	Bandwidth (Hz)
McClure dialect	367	14.2—36.7; 23.2 ± 3.2	6.8—10.2; 8.7 ± 0.5	1944.4—4724; 3594.2 ± 385.4
McClure Low VP stimuli	7	21.9—28.2; 26.1 ± 1.6	6.25—7.4; 6.7 ± 0.4	3193.3—3595.2; 3442.2 ± 148.5
San Francisco dialect	780	5.3—37.4; 22.2 ± 5.2	6.1—13.3; 9.2 ± 1.3	1690.4—5735.4; 2753.2 ± 648.8
SF High VP stimuli	6	12.3—17.4; 15.6 ± 1.9	11.3—12.1; 11.8 ± 0.4	3877.6—4553.3; 4144.6 ± 254.7
SF Low VP stimuli	6	26.5—33.9; 29.4 ± 2.8	6.1—6.9; 6.3 ± 0.3	2559.7—3472; 3104.8 ± 350.8

Playback Design

We used territorial playback experiments to test whether free-living adult males respond to variation in vocal performance. Territorial playback is a standard experimental design that simulates territorial intrusion by playing songs on subjects' territories and measuring their behavioral response (McGregor et al. 1992). No male heard his own song or that of a neighbor. Playbacks were conducted between sunrise and noon during the chick and fledgling parts of the breeding cycle in 2015. Each male was tested twice, with 48 hours between trials to minimize habituation. Order of presentation was randomized across males and neighbors were never tested on the same day. We tested 19 males in Point Reyes and 16 males in San Francisco.

For each focal male, we observed song perches and determined the approximate location of the territory center before trials. Before each trial, an inMotion iMT320 speaker (Altec Lansing) with an Apple iPod Nano (6th generation) was placed near the territory center on a platform 0.5m above the ground. The same location was used each time the male was tested. The amplitude of each stimulus was standardized at 81 dB SPL measured at 1m from the speaker using a Radioshack 7-range Sound Level Meter, and the songs were broadcast at a song bout speed (6 songs/min) typical for this species.

We started playback when the focal male was in view and within 24m of the speaker. Each trial consisted of a three-minute playback period and a six-minute post-playback period. In White-crowned Sparrows, responses to different simulated intrusions vary most after playback has stopped (Nelson & Soha 2004), so we used a longer post-playback to ensure that relevant behavior was recorded. During each trial, we recorded male distance from the speaker, flyovers, wing waves, and number of songs at 10-sec intervals. We also calculated latency to approach and latency to sing. To estimate distance, we placed a string radiating out from the speaker with distance categories marked with flagging tape. The distance categories used were 0–2 m, 2–4 m, 4–8 m, 8–16 m, and greater than 16 m. We used the median distance of each category and 24 m for the "greater than 16 m" category to calculate the male's average distance from the speaker during the combined playback and post-playback periods (Peters et al. 1980).

Statistical Analyses

To assess male response to playbacks, we used two measures of response. First, we analyzed response as measured by approach distance to the speaker, because in two closely related species, song sparrows (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*), distance to the playback speaker is a significant predictor of the likelihood of the focal male to attack an intruder (Peters et al. 1980; Searcy et al. 2006). Thus, significant differences in approach distance have interpretable, functional consequences. Second, we used a principal components analysis to reduce variation in all six behavioral measures to yield a composite measure of response. We compared response to high and lower performance songs using Akaike's Information Criterion (AIC_c) to explore linear mixed models. We assessed response both as approach distance and with our composite measures. We tested combinations of stimulus type ("high performance" and "low performance"), male vocal performance, and Julian date as fixed effects and bird identity and song exemplar as random effects. AIC_c values within 2 units of the top model were examined for pretender variables, in which a model differs by one fixed effect but does not increase the model fit (Arnold 2010), and thus is uninformative. Furthermore, we examined parameter importance in model averaged models using MuMin (Barton 2011) to examine pretender variables. We used likelihood ratio tests to obtain P-values of the top model against a null model without the effect (Bolker et al. 2009). We performed statistical analyses using R (R Development Core Team 2011) package *lme4* (Bates et al. 2015) and library *AICcmodavg* to assess models (Mazerolle 2016). We also used post-hoc Welch's t-tests to assess directionality of responses and corrected P-values using false discovery rate. We analyzed the Point Reyes and San Francisco locations separately, and then ran a subset of the males within the Point Reyes dataset that were tested only with songs that fell within the natural range of McClure dialect trill rates, as 4 of our 7 McClure low performance stimuli had slower trill rates than our sampling of the population (see Table 1.1). Hereafter, we refer to this subset as the Point Reyes subset (*n* = 7) when reporting results.

RESULTS

Vocal Performance Varies Between Males And Is Repeatable Within Males

Across Point Reyes birds (367 songs), the average trill rate was 8.7 ± 0.5 Hz, average trill bandwidth was 3594.2 ± 385.4 Hz, and average vocal performance was 23.2 ± 3.2. For San Francisco birds (780 songs), the average trill rate was 9.2 ± 1.3, average bandwidth was 2753.2 ± 648.8, and average vocal performance was 22.2 ± 5.2. We report the range for trill rate, frequency bandwidth and vocal performance in Table 1.1. Repeatability of vocal performance for Point Reyes was 0.51 (0.4–0.63 95% CI, $n = 51$, $F_{50, 313} = 8.44$, $P < 0.001$), and 0.74 for San Francisco (0.68–0.80 95% CI, $n = 109$, $F_{108, 671} = 21.5$, $P < 0.001$) indicating that differences between males in vocal performance were greater than differences among songs within a male, particularly for males singing the San Francisco dialect.

Males Approach More Closely To High-Performance Songs

Variation in all behavioral measures of response to playback was reduced to three principal components with eigenvalues greater than 1 for Point Reyes, and two principal components in both Point Reyes subset and San Francisco (see Table 1.2 for loadings for PC1 and PC2). For both locations and Point Reyes subset, the model that best predicted approach distance was a model with stimulus type as the fixed effect. Point Reyes PC1, Point Reyes PC2, and San Francisco PC1 also had a top model of stimulus type. For Point Reyes approach distance, Point Reyes PC2, Point Reyes subset approach distance, San Francisco approach distance, and San Francisco PC1 a model including stimulus type and male vocal performance was the second best model, within 2 AIC. However, the model fit was not improved upon inspection of log-likelihood values and importance in model averages. Therefore, male vocal performance is a pretender variables and not a significant component of models, and thus we rejected these models as uninformative (Arnold 2010; Burnham & Anderson 2002). All AIC_c tables and importance values for model exploration are included in Appendix 1.

For approach distance, the model with stimulus type significantly predicts male response as compared to a null model (Point Reyes: $\chi^2(1) = 7.25$, $P = 0.007$; Point Reyes subset: $\chi^2(1) = 7.65$, $P = 0.005$; San Francisco: $\chi^2(1) = 4.73$, $P = 0.02$). We found that males gave a significantly different response to playback of high performance versus lower performance songs for PC1 (Point Reyes PC1: $\chi^2(1) = 6.26$, $P = 0.01$; San Francisco PC1 $\chi^2(1) = 5.86$, $P = 0.01$) and PC2 (Point Reyes PC2: $\chi^2(1) = 4.76$, $P = 0.03$). Based on loadings, males approached more closely, gave more wing waves, flew over more, and sang more songs in response to playback of higher performance songs consistently across analyses (see Table 1.2). Point Reyes subset PC1 had the null as the top model, but a model with stimulus type as the fixed effect was within 2 AIC_c (Appendix 1); the null model and the stimulus type model were significantly different ($\chi^2(1) = 3.93$, $P =0.04$). Point Reyes PC3 and Point Reyes subset PC2 also had the null as the top model which was not significantly different from the second best stimulus type model (Point Reyes PC3: $\chi^2(1) = 0.27$, $P = 0.6$; Point Reyes subset PC2: $\chi^2(1) = 2.42$, $P = 0.12$). San Francisco PC2 had Male VP as the top model, within 0.44 AIC of the null, which also was not significantly different ($\chi^2(1) = 0.66$, $P = 0.42$).

Post-hoc Tests

Males approached the speaker more closely during playback of high performance songs than during playback of lower performance songs (Point Reyes: high performance: 5 ± 2 [m; mean ± SE], low performance: 10 ± 6, Figure 1.2A; Point Reyes subset: high performance: 5.1 ± 2, low performance: 11.1 ± 5.9, Figure 1.2B; San Francisco: high performance: 7.1 ± 4.9, low performance: 10.6 ± 4.4; Figure 1.2C). A closer approach to a simulated intruder on a male's territory can be interpreted as a stronger response to a specific stimulus; thus, males responded significantly more strongly to high performance songs than to lower performance songs (Point Reyes: $t = -4.3$, d.f. = 18, $P = 0.003$; Point Reyes subset: $t = -3.6$, d.f = 6, $P = 0.009$; San Francisco: $t = -2.32$, d.f. = 15, P=0.04).

For composite response variables, we found that males gave a significantly different response to playback of high performance versus lower performance songs for PC1 (Point Reyes: $t = -3.24$, d.f. = 18, $P = 0.009$; Point Reyes subset: $t = -3.06$, d.f. = 6, $P = 0.02$; San Francisco, $t = -2.63$, d.f. = 15, $P = 0.04$) and Point Reyes PC2 ($t = 3.43$, d.f. = 18, $P = 0.03$); but not PC2 for Point Reyes subset and San Francisco (Point Reyes subset: $t = 2$, d.f. = 6, $P = 0.1$; San Francisco, $t = -0.83$, d.f. = 15, $P = 0.42$). Point Reyes PC3 also was not significantly predicted by stimulus type ($t = -0.49$, d.f. = 18, $P = 0.63$). Because a male’s own vocal performance did not have strong predictive power in our models, we additionally examined the differences between a male’s own vocal performance and that of the high and low stimuli he heard. Focal male vocal performance was typically as different from high performance stimuli as from low performance stimuli in Point Reyes (difference in focal male VP and high performance stimulus heard: 3.6 ± 3.8, difference in focal and low performance stimulus: 4.4 ± 2.8; mean ± SD deviation units) and in San Francisco (difference in focal male VP and high performance: 8.1 ± 3.7; difference in focal male VP and low performance: 6.1 ± 5.6). Paired t-tests reveal that in both locations, there is no significant difference in the performance difference between a male's own vocal performance and that of the high and low performance stimuli (Point Reyes: $t = 1.15$, d.f. = 15, $P = 0.26$; San Francisco: $t = -0.73$, d.f. = 18, $P = 0.5$), which might explain why a male's own vocal performance value does not explain variation in response to these two stimuli.

Table 1.2. Varimax rotated matrices show variable loadings onto PC1, PC2, and PC3 and responses to playback. Distance measures are in meters and latency measures are in seconds. Latency to sing and latency to approach are measured in seconds, distance during playback and post-playback is measured in meters, wing waves, flyovers, and songs are the total number performed.

Point Reyes

	Loadings			Raw Response (mean ± SD)	
Response variables	*PC1*	*PC2*	*PC3*	*High VP*	*Low VP*
Latency to sing (s)	0.036	**0.90**	-0.12	11 ± 10.5	43.1 ± 70.6
No. Songs during playback	0.18	**-0.86**	-0.26	20.1 ± 5.2	14.7 ± 8.3
Distance during post-playback (m)	-0.45	**0.55**	0.31	6 ± 3.2	11.9 ± 7.8
No. Wing waves	**0.90**	0.003	0.13	3 ± 4	1 ± 2
No. Flyovers	**0.83**	-0.05	-0.27	7.4 ± 4.6	3.4 ± 4.1
No. Songs during post-playback	**0.66**	-0.32	-0.38	31.9 ± 14.9	23.5 ± 14.6
Latency to approach (s)	-0.18	-0.06	**0.87**	33.7 ± 68	39 ± 41.7
Distance during playback (m)	-0.03	0.48	**0.66**	3.6 ± 2.6	6.5 ± 4.5
Eigenvalues	3.4	1.58	1.05		
% of variation	42.6	19.7	13.1		
Point Reyes subset					
Latency to sing (s)	**0.79**	-0.06		11.4 ± 9	90 ± 95.4
No. Songs during playback	**-0.87**	0.26		20.1 ± 5.4	9.9 ± 9.5
Distance during post-playback (m)	0.50	**-0.54**		6.1 ± 3	13.6 ± 8.2
No. Wing waves	0.21	**0.84**		3.1 ± 3.3	1.3 ± 2.2
No. Flyovers	-0.31	**0.81**		6.6 ± 4.3	4.7 ± 3.9
No. Songs during post-playback	-0.20	**0.84**		30.3 ± 18.4	22.3 ± 17.7
Latency to approach (s)	**0.75**	-0.29		47.1 ± 107.4	32.9 ± 25
Distance during playback (m)	**0.9**	0.10		3 ± 2.1	6.3 ± 4.4
Eigenvalues	3.82	1.88			
% of variation	47.7	23.5			
San Francisco					
Latency to sing (s)	-0.05	**0.87**		36.3 ± 40.1	59.4 ± 97.3
No. Songs during playback	-0.27	**-0.87**		14.7 ± 7.2	11.6 ± 6.7
Distance during post-playback (m)	**0.77**	-0.15		7.9 ± 6.1	12.9 ± 5.2
No. Wing waves	**-0.57**	0.363		2.1 ± 4.1	0.38 ± 0.8
No. Flyovers	**-0.59**	-0.17		3 ± 3.5	1.5 ± 2.3
No. Songs during post-playback	**-0.66**	-0.22		27.9 ± 18.9	14.7 ± 10.8
Latency to approach (s)	**0.73**	0.02		43.8 ± 47.9	86.9 ± 130.1
Distance during playback (m)	**0.82**	0.22		5.3 ± 3.6	7.9 ± 3.8
Eigenvalues	3.06	1.72			
% of variation	38.3	21.5			

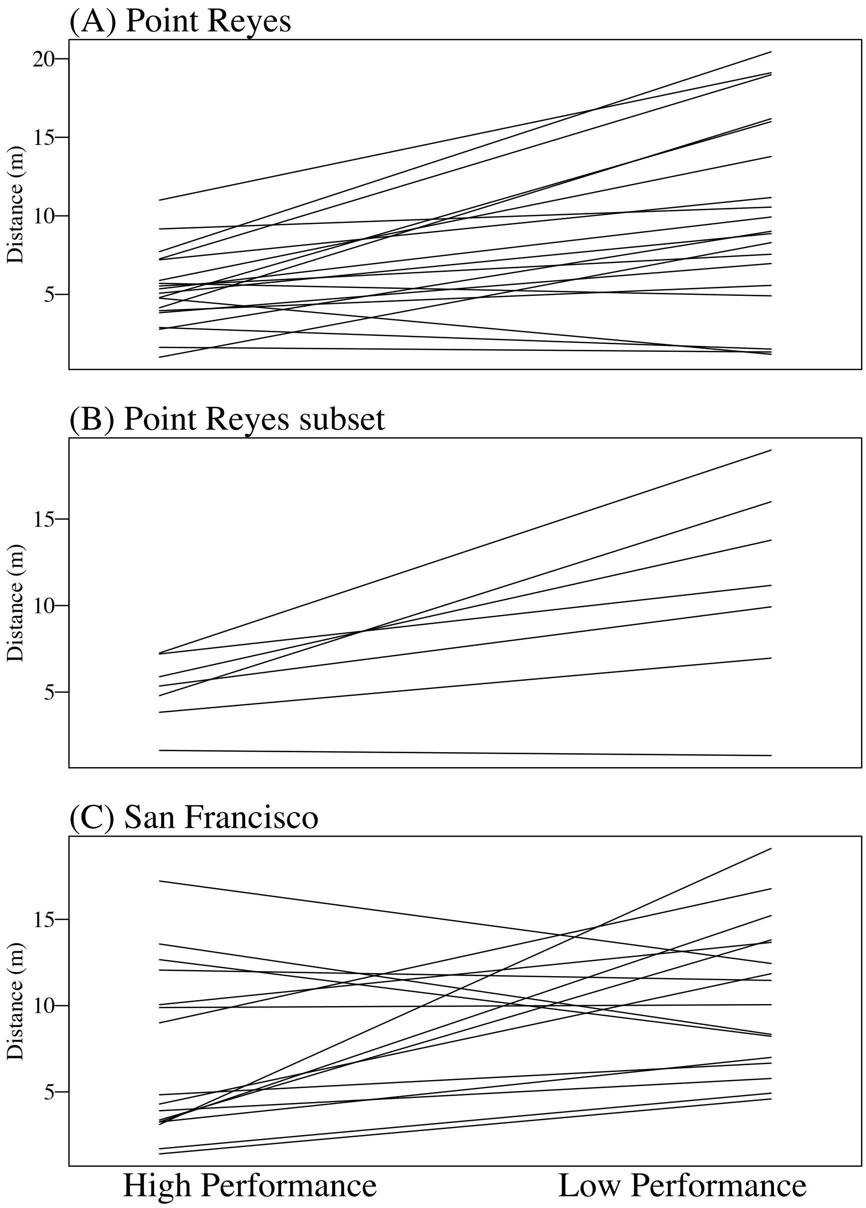


Figure 1.2. Birds approach high performance songs more closely than low performance songs in A) Point Reyes, B) a subset of Point Reyes birds that heard stimuli within the McClure natural range, and C) San Francisco. Each line connects an individual bird's approach distance to high performance stimuli on the left to low performance stimuli on the right. Greater slope indicates stronger discrimination between stimuli. Each line represents an individual's paired response.

DISCUSSION

Overall, we found that males respond differently to high and low performance songs. Within males, vocal performance tends to be repeatable, suggesting that this feature of song could be used as a source of information for receivers at the time of sampling. Together, our findings suggest that male White-crowned Sparrows are using vocal performance to assess competitors.

We found that male White-crowned Sparrows distinguished between songs based on vocal performance levels of the terminal trill. Focal males gave stronger responses to higher performance trills. Playback stimuli differed in trill performance levels, and playback simulated an intruding male, so we interpret the difference in response by our focal males to reflect a difference in their perception of a potential intruder's motivation and/or abilities as a competitor. An intruding male that has the motivation and/or ability to sing a high performance song may pose more of a threat as an opponent than an intruder producing a lower performance song. A higher quality competitor may pose a stronger threat in terms of competition for mates or ability to gain and hold resources, such as a territory. We did not find support for a male’s own vocal performance influencing response strength. This may be due to the fact that there was not much variation among the males tested in the difference between their own vocal performance level and that of the stimuli they heard. Our findings support the hypothesis that male White-crowned Sparrows can use performance level of their terminal trill to assess competitors.

Previous studies show that White-crowned Sparrow males use various parts of their songs for different functions (see Figure 1.1 for song parts). The whistle is an alerting mechanism and important for song development and acquisition in young birds (Marler 1970; Soha & Marler 2001; Soha & Whaling 2002). The note complex is thought to allow recognition of individuals (Nelson & Poesel 2007), and often varies within a dialect (Baptista 1975; Dewolfe et al. 1974). Nelson and Poesel (2010) suggest that females use the note complex to recognize their male when they return to the nest. Trill variation seems to hold the most information for sexual selection. Soha and Whaling (2002) found that males respond more strongly to playback of trills alone than of the whistle or note complex alone, suggesting that trills carry important information for male-male competition and female mate choice. Males sing songs with shorter trills (fewer trill notes) when receivers are close, and longer trills (more trill notes) when receivers are distant (Nelson & Poesel 2010), and thus trill length as determined by the number of notes may indicate a male's aggressive intentions. We find stronger response to high performance songs, which are also shorter in trill length. Thus, males may be also responding to variation in trill length in our study. Further, males respond more to normal bandwidth songs than to reduced bandwidth songs with the same length terminal trill (Luther, Phillips, et al. 2016). Luther et al. (2016) suggest this may be because a change in bandwidth changes vocal performance. Our results support these findings, and demonstrate that males attend to variation in vocal performance.

Finding that males respond less to lower performance songs suggests that males producing lower performance songs are advertising a reduced competitive ability. Swamp sparrows also show more aggression toward high performance songs (Dubois et al. 2011), or at least to performance levels that match their own (Moseley et al. 2013). Thus, our results are consistent with studies of a closely related species suggesting vocal performance indicates male competitive ability. It is important to keep in mind that not all species react with higher aggression levels toward high performance songs. In a two-speaker experiment that manipulated trill rate, Banded Wrens approached fast trill songs first but spent more time near slower trill songs. Each male's own performance level affected their response to playback such that males with higher performance were more likely to approach high performance stimuli (Illes et al. 2006). In a second study that manipulated bandwidth, Banded Wren males were found to approach less closely to medium and high performance songs, likely because these stimuli were assessed as more aggressive (De Kort et al. 2009). Red-winged Blackbirds also respond less to higher performance songs than to lower performance songs, as the high performance stimuli may have been perceived as intruders of higher quality than the males holding territories (Cramer & Price 2007). Our results are different from these previous studies in that we do not find an effect of a male's own performance level on how they respond to variation in song performance. Males with relatively high versus lower performance songs both respond more strongly to playback of high performance songs.

Few studies have assessed repeatability of vocal performance. We found natural, repeatable variation in performance of terminal trills within a song bout among male White-crowned Sparrows holding territories in two separate locations. Males producing the same song type varied in vocal performance, such that some males produced high performance renditions and others produced lower performance renditions. We also found that individual males were repeatable in their performance of terminal trills during a song bout, similar to the range found in closely related species (Ballentine et al. 2004). In one survey of repeatability of male signal production in different taxa, repeatability ranged between 0.21 and 0.85 (Boake 1989). Our measures of vocal performance repeatability (0.51 and 0.74) occur on the high end of this range, indicating consistent variation in the ability of males to perform the trade-off between trill rate and bandwidth, at least within a given song bout.

Repeatability of vocal performance may affect how it is used in male-male competition and female mate choice. Swamp Sparrow males tend to produce a given song type at the same level of vocal performance (repeatability 0.53—0.84; Ballentine et al. 2004), although they can increase performance to a certain extent within a song type in aggressive encounters (DuBois et al. 2009). However, a test of this intra-male variation showed males did not discriminate between intra-male songs, but both male and female Swamp Sparrows respond to inter-male variation in vocal performance (Dubois et al. 2011; Ballentine et al. 2004). Banded Wrens also have high repeatability (0.82—0.86) within two trill types and discriminate between vocal performance levels (Illes et al. 2006), but trill rate differs with aggressive context and vocal performance improves with the age of the male (Vehrencamp et al. 2013). In contrast, House Wrens (*Troglodytes aedon*) have highly variable songs and do not sing the pitch of their trills consistently (Emily R. A. Cramer 2013). In playback experiments, male House Wrens do not respond to differences in vocal performance (E. R. A. Cramer 2013). Thus, in the few species for which we have information about both response and repeatability (*n* = 4), when vocal performance functions in male-male competition, it is also repeatable (Ballentine et al. 2004, Illes et al. 2006, and this study). Future studies should consider the repeatability of vocal performance when assessing its function in male-male competition and female mate choice. Furthermore, future studies on White-crowned Sparrows should investigate repeatability across song bouts to test whether males are able to change performance of their song across motivational states and with more experience across years. These types of studies would provide additional evidence to whether vocal performance is a useful signal for receivers to assess males in multiple contexts.

Furthermore, there may also be an association between repertoire size and use of vocal performance. Cardoso et al. (2007) suggest that for birds with a repertoire of song types, the vocal performance value of an individual song type may not be informative about a male's singing ability, as different song types may have different performance values. Indeed, in some species with large repertoires, other measures of performance, such as song consistency or complexity may be more informative for receivers (Botero et al. 2009). Because White-crowned Sparrow males produce only one song type and have a high repeatability of performance when producing that song, the vocal performance value of a song should be informative of a male's singing ability.

Conclusions

Our study highlights vocal performance of trills as a salient, repeatable feature of song for male-male competition in White-crowned Sparrows. Our findings are informative in a model species and for future studies of birds that have limited, single song repertoires, which represents about 25% of avian species (MacDougall-Shackleton 1997). Future research is needed to examine if vocal performance is assessed for female mate choice in White-crowned Sparrows.

Chapter 2. Equivalent Function Of Bandwidth And Trill Rate: Support For A Performance Constraint As A Competitive Signal

ABSTRACT

Sexual signals that are physically limited can be reliable indicators of quality or motivation in male-male competition and female mate choice. One such example of a motor constraint in birds is the production of repeated notes, which are limited in the frequency bandwidth and trill rate at which notes can be produced. How well a bird maximizes frequency bandwidth and trill rate is one measure of vocal performance, commonly referred to as 'vocal deviation'. In theory, fast songs with narrow bandwidths and slow songs with wide bandwidths should have similar values of vocal deviation. In many species, both males and females respond to variation in vocal deviation, supporting that it is a sexually selected signal. However, most studies manipulate only one of these components, either trill rate or bandwidth, rather than both individually when testing receiver response to vocal deviation. Therefore, a critical question remains as to whether songs with purported equal values of vocal deviation – fast songs with narrow bandwidths and slow songs with wide bandwidths – elicit similar levels of response from receivers. We tested whether receivers respond specifically to the tradeoff between trill rate and bandwidth (i.e., vocal deviation) or only to variation in one of the component parts. Using territorial playback experiments with wild male white-crowned sparrows (*Zonotrichia leucophrys*), we found that males approached more closely to high

performance songs (fast trill, wide bandwidth) than to lower performance songs (fast trillslow bandwidth, and slow trill, wide bandwidth) and did so regardless of whether performance varied because of differences in trill rate or in bandwidth. Furthermore, we found there was no significant difference in male response to fast songs with narrow bandwidths as compared to slow songs with wide bandwidths. Our data empirically support the hypothesis that receivers are responding specifically to the physical limitation on the production of repeated notes.

INTRODUCTION

Sexual signals are used to defend territories and attract mates, and it is generally thought that receivers should pay attention to sexual signals that accurately convey the quality or motivation of the signaler (Andersson 1994; Searcy & Nowicki 2005). Signal honesty can be maintained if there are constraints to producing the sexual signal (Zahavi 1975; Maynard Smith & Harper 2004). Well-studied examples of costs include developmental costs and performance limits. For instance, nutritional condition during signal development can affect signal expression, such as carotenoid based coloration (Fish: Frischknecht 1993; Birds: Hill & Montegomerie 1994), UV coloration (Birds: Delhey et al. 2006; Insects: Lim & Li 2007) , and repertoire size of vocal signals (Birds: Nowicki et al. 1998, 2002). Another example of production constraints is mechanical limits on ability to execute motor patterns, which can limit performance of a signal. Physically limited sexual signals, or index signals, are abundant across taxa (Bradbury & Vehrencamp 2011; Maynard Smith & Harper 2004; Maynard Smith & Harper 1995). For example, female frilled lizards choose to mate with males that run the fastest (Husak et al. 2006). Visual signals of weaponry, like antlers in Roe deer (Vanpé et al. 2007) or horns in rhinoceros beetles (Emlen et al. 2012) are signals of overall body size, age, and can indicate fighting ability. Low pitch acoustic signals can also indicate body size, and therefore competitive ability (Linhart & Fuchs 2015; Hall et al. 2013). Sexual selection is expected to favor signalers that maximize signal expression or signaling skill for any of these costly to produce signals.

Performance limits on sound production are an example of index signals in animals that use acoustic communication (Podos 1997; Cardoso & Mota 2009; Nemeth et al. 2013). For example, in songbirds, there are multiple performance limits on vocalizations that contain rapidly repeated notes, or trills (Sockman 2009; Sprau et al. 2013; Podos et al. 2009). One performance limit is a motor constraint on the production of trills. In birds, the speed at which the beak, syringeal and oropharyngeal musculature can move constrains the rate at which an individual filters out harmonics and tracks fundamental frequencies (Nowicki et al. 1998; Riede et al. 2006; Westneat et al. 1993; Nowicki & Marler 1988), which limits the frequency bandwidth and rate at which notes can be produced (Podos 1997). Maximizing one component of this performance limit necessarily means reducing the other component; thus, either the rate of production or the frequency bandwidth can be maximized, but not both. When examining individuals in a population or across related taxa, an upper-bound regression line can be calculated from a plot of trill rate and bandwidth (Podos 1997). The orthogonal distance of a song, or vocal deviation, from this upper-bound regression line is an estimate of how well an individual performs on the tradeoff between trill rate and bandwidth. From the calculated vocal deviation we can infer that a small deviation is higher vocal performance and a large deviation is lower vocal performance (Podos 2001). Because of a triangular distribution, fast songs with narrow bandwidths and slow songs with wide bandwidths can have similar values of vocal performance as measured by vocal deviation. Hereafter, any reference to vocal performance refers to specifically to vocal deviation, where a smaller deviation is 'high performance', and a larger deviation is 'low performance'.

Numerous studies have investigated the function of vocal performance in sexual selection. These empirical studies provide evidence that females prefer high vocal performance songs over low vocal performance songs (canaries: Drăgănoiu et al. 2002; swamp sparrows: Ballentine 2004; Lincoln's sparrows: Caro et al. 2010; banded wrens: Cramer et al. 2011; singing mice: Pasch et al. 2011). Additionally, males seem to assess vocal performance during competition (Dubois et al. 2011; Illes et al. 2006; Cramer & Price 2007; Moseley et al. 2013; De Kort et al. 2009), at least in some species (but see Cramer 2013a, 2013b). Vocal performance is also shown to correlate to quality or motivation in some species. For example, in banded wrens, vocal performance increased with age, suggesting it is a reliable signal of male quality or motivation (Vehrencamp et al. 2013). Another study with a limited sample size also found evidence for males with high vocal performance attaining more extra-pair copulations (Cramer et al. 2011). While there is support for the function of performance as measured by vocal deviation in sexual selection (Vehrencamp et al. 2017; Cardoso 2017; Podos 2017), there are differences in the methodological approaches used to test the function of vocal deviation.

Most experimental tests of the salience of vocal performance in male-male competition and female choice maximize one component – either the rate of note production or the bandwidth of the notes. The majority of these studies find support for a stronger response by receivers to either faster production of notes or to wider bandwidth notes (reviewed in Podos et al. 2009). In studies manipulating trill rate, males respond with more soft songs or an initial approach to high performance trills (Moseley et al. 2013; Illes et al. 2006) and females prefer fast trills (Pasch et al. 2011). In studies manipulating bandwidth, male white-crowned sparrows respond more to wide bandwidth songs (Luther, Phillips, et al. 2016), and male banded wrens sing more but approach less to wide bandwidth songs (De Kort et al. 2009). In studies that manipulate both bandwidth and trill rate simultaneously, males respond more strongly to high performance songs (Dubois et al. 2011) and females prefer high performance males (Ballentine et al. 2004). In Draganoui et al. (2002), female canaries were presented with three types of trilled songs with varying bandwidth and trill rates. Females performed more copulation solicitation displays to a super stimulus, a fast trill and wide bandwidth beyond the natural range, but generally equally to lower performance songs, suggesting that females give equal responses to songs of equal performance, although this was not explicitly tested (Drăgănoiu et al. 2002). Therefore, an empirical question remains as to whether receivers, and specifically male receivers, are responding to the tradeoff between trill rate and bandwidth (i.e., vocal performance) or only to variation in one of the component parts.

Here, we test the hypothesis that trill rate and bandwidth are both important components in the assessment of vocal performance in male-male competition in white-crowned sparrows (*Zonotrichia leucophrys*). We predict that songs of equal vocal deviation will elicit similar responses from territorial males, whether performance varies due to trill rate or to frequency bandwidth. Previous work indicates that male white-crowned sparrows respond more strongly to wide bandwidth songs compared to narrower bandwidth songs (Luther, Phillips, et al. 2016) and to higher performance songs than to lower performance songs when both trill rate and frequency bandwidth are manipulated concurrently (Phillips & Derryberry 2017). Using a repeated measures design, we test response to fast trill, wide bandwidth songs (high performance); fast trill, narrow bandwidth songs (mid-performance); and slow trill, wide bandwidth songs (mid-performance). This set of experiments allows us to compare response to high and mid-performance songs when performance is manipulated by changing trill rate and then again bandwidth, thus allowing us to assess male response to songs of similar vocal deviation.

METHODS

Location and Subjects

We tested territorial males at the Abbott's Lagoon and Kehoe Beach region in Point Reyes National Seashore, California, USA, during mid-breeding season, June, of 2015 and 2016. The habitat is coastal scrub, which consists of low laying shrubs, dominated by coyote bush (*Baccharis pilularis*), various lupines (*Lupinus spp.*), and poison oak (*Toxicodendron diversilobum*). In this species, males in the same location tend to produce the same song type, known as a dialect (Marler & Tamura 1964; Marler & Tamura 1962). All males sang one song type, which was the McLure dialect as described in Baker and Thompson (1985).

Recording bird songs in the wild

In 2014 and 2015, we recorded songs from the McLure dialect in Point Reyes with a digital Marantz PMD 661, Sennheiser ME-62 omnidirectional microphone with windscreen mounted onto a Saul Mineroff SME-100 Parabola. Songs were recorded at 44.1 kHz and stored in uncompressed Wave format. We drew from these recordings to create stimuli for playbacks.

Measuring vocal performance of recordings

We calculated vocal performance using the published equation for the upper bound regression on a set of 1572 Emberzidae songs, $y= -0.124x +7.55$ (Podos 1997). We did not use the white-crowned sparrow performance limit as calculated in Derryberry (2009), as that dataset did not include birds from this region, whose songs occurred above that upper-bound regression line in the bandwidth plane. The Emberizid performance limit is not confounded by sampling limitations (Wilson et al. 2014) and encompasses the range of our samples; therefore it seemed a better estimation of performance limits.

Creating vocal stimuli

We created three stimulus types from McLure dialect songs: (A) fast trill rate, wide bandwidth, B) fast trill rate, narrow bandwidth, and C) slow trill rate, wide bandwidth (see Fig. 2.1).

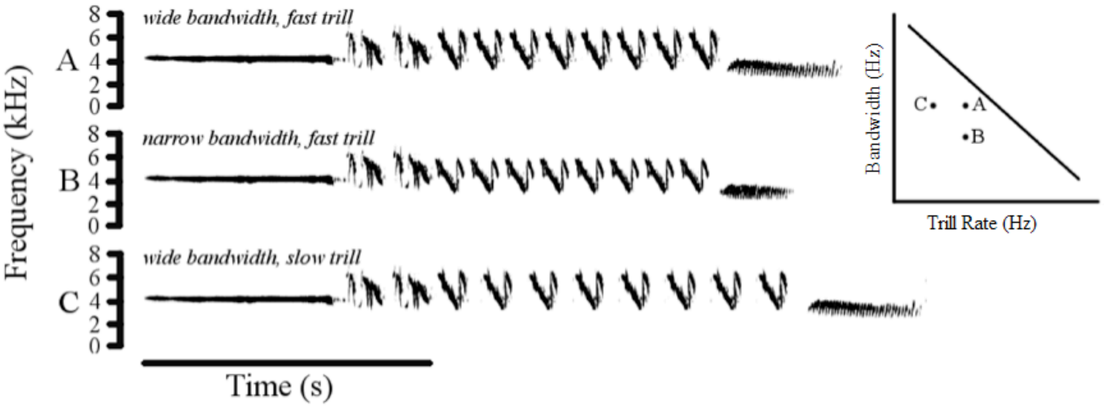


Figure 2.1. Examples of three stimuli used, A) wide bandwidth, fast trill (high-performance), B) narrow bandwidth, fast trill (mid-performance), and C) wide bandwidth, slow trill (mid-performance). Inset denotes relative deviation of each stimulus type from the upperbound regression line. Wide bandwidth, fast trill songs (A) are closer to the upperbound regression line than (B) and (C), which are equidistant from the upperbound regression line.

We created stimulus sets based on naturally occurring variation in bandwidth, such that 'wide bandwidth' songs were at least 500 Hz greater in bandwidth than 'narrow bandwidth' songs. We then manipulated trill rate to create 'fast' versus 'slow' trills by concatenating the first trill note from each exemplar song with the desired amount of silence, such that each song had 8 trill syllables. It is not possible to standardize both trill length and the number of trill notes. Standardizing trill length would have necessitated truncating trill syllables. Therefore, we chose to standardize the number of trill notes. Wide bandwidth, fast trill stimuli were the highest performance (*n* = 18; mean ± SE; 20.9 ± 2 vocal deviation), and within the natural range for this population (deviation: 14.2—36.7; trill rate: 6.8—10.2 Hz; bandwidth: 1944.4—4724 Hz; Phillips & Derryberry 2017). Fast trill, narrow bandwidth stimuli deviation was closer to average performance in this population (*n* = 18; stimulus mean ± SE; 24.6 ± 1.8; population 22.7 ± 2.9, Phillips &

Derryberry 2017) than the high performance stimuli. Slow trill, wide bandwidth stimuli averaged 23.5 ± 1.8 vocal deviation, which does not statistically differ from the 18 fast trill, narrow bandwidth stimuli (two sample t-test, t_{34}=1.78, $P = 0.08$). Slow trill rate stimuli ranged from just below the population range of trill rate, in order to make slow trill, wide bandwidth stimuli equal in performance level to fast trill, narrow bandwidth stimuli (stimulus trill range 6.25—7.4 Hz, population range 6.8—10.2 Hz). Six out of 18 slow trill, wide bandwidth stimuli fell outside the natural trill rate range for this dialect but not for the species range (Derryberry 2009), and ranged from 6.25 to 6.66 trill notes per second.

We normalized the amplitude of stimuli using SIGNAL 5 (Beeman 1998) and standardized playback amplitude to 81 dB (A) SPL at one meter using a Larson Davis 831 Sound Level Meter (PCB Piezotronics).

Experimental playback design

To test whether equivalent vocal deviation elicits similar responses from territorial males, we conducted three standard territorial playback experiments (McGregor et al. 1992), two in 2015 and one in 2016. All experiments were run between 0600 and 1200, when birds were actively singing. In 2015, we used a repeated measures design with two stimuli, one experiment testing response to changes in bandwidth ($n = 16$) and the other testing response to changes in trill rate ($n = 14$). For these experiments, we used 7 stimulus sets per experiment. In 2016, we used a repeated measures design with all three stimuli ($n = 20$). We used 18 stimulus sets (54 songs) for this experiment, reusing 2 stimulus sets. Altogether, we tested 50 individual males.

Prior to playback, we observed each male's movement and song perches for at least 20 minutes and then estimated the center of the territory. In all experiments, we randomized presentation order across males. We did not test neighboring males on the same day, or present stimuli from males who were recorded in the same area who could have been neighbors. Males received stimulus types with at least 24 hours between trials. We placed an inMotion iMT320 speaker (Altec Lansing) with an Apple iPod Nano (6th generation) near the territory center at a height of 0.5 m. To estimate distance to the speaker of male movements, we marked distance in categories of 0-2, 2-4, 4-8, and 8-16 from the speaker location. When the male was within 16 m, we began the trial. We presented 6 songs per minute for 3 minutes of playback, which is a natural song rate for this species. We continued to observe males for 6 minutes after playback, for a total of 9 minutes of observation per male. We recorded male distance from the speaker every 10 seconds during playback and postplayback. Because approach distance to the speaker is an interpretable, aggressive signal of motivation to attack, we focus on this as our response variable (Searcy et al. 2006; Ballentine et al. 2008; McGregor et al. 1992; Catchpole & Slater 2008). All playbacks adhered to Institutional Animal Care and Use Committee protocols (Tulane IACUC 0427-R, Federal IACUC PWR_GOGA.PORE_Derryberry_Songbird_2014.A2), and Point Reyes Scientific Research and Collecting Permit (PORE-00014).

Statistical Analyses

We analyzed data from the three experiments combined. To meet the assumptions of normality for parametric tests, we log transformed the response variable, average approach distance. We then used $\mathrm{AIC_c}$ for small sample size to compare models that predict average distance, which include combinations of stimulus type and breeding status as fixed effects. To account for the effects of year-to-year variation, stimulus reuse, and individual identity, we included year, stimulus exemplar, and bird as random effects. We used R (R Development Core Team 2011) packages AICmodavg (Mazerolle 2016) and lme4 (Bates et al. 2015) to examine models. We then used post-hoc Tukey's t-test using package multcomp (Hothorn et al. 2008) to test the directionality of response. We also ran models and tests as described above for a subset of data, which excluded trials where slow trill, wide bandwidth stimuli were outside the population range. Lastly, to assess the effects of stimuli outside the natural trill rate range, we ran a t-test between 'below population range stimuli' versus 'stimuli within the natural range' for slow trill, wide bandwidth songs.

RESULTS

Stimulus type predicts approach distance

The top model included stimulus type as the fixed effect, with an evidence ratio of 419.3 over the null model and 75% model weight (Table 2.1). The random effect of bird explained more variance than stimulus exemplar or year of testing (Table 2.2). Stimulus type significantly predicted average approach distance (Table 2.2). Males approached significantly closer to wide bandwidth songs than they did to narrower bandwidth songs (wide bandwidth, fast trill: 7.1 ± 4.8 m, narrow bandwidth, fast trill: 10.8 ± 6.8 m; Tukey test: $n = 36$, $z = 3.22$, $P = 0.003$; Figure 2). Males approached closer to fast trills than to slower trills (fast trill, wide bandwidth: 6.6 ± 5 m, slow trill, wide bandwidth: 12 ± 7 m;

Tukey test: $n = 34$, $z = 4.16$, $P < 0.001$; Figure 2.2). Responses to the two stimuli of similar vocal deviation were not significantly different (fast trill, narrow bandwidth: 11.4 ± 7.1 m; slow trill, wide bandwidth: 13.8 ± 7.4 m; Tukey test: $n = 20$; $z = 0.91$, $P = 0.63$; Figure 2.2).

Table 2.1. Model ranks for average approach distance using AIC_c, for all playback data ($n = 50$).

Model	K	AIC_c	ΔAIC_c	w_i	Cum. w_i
Stimulus Type	7	286.1	0	0.75	0.75
Stimulus Type + Breeding Status	9	288.37	2.27	0.24	0.99
Intercept only (Null)	5	298.16	12.07	0.001	0.99
Breeding Status	7	299.69	13.6	0.001	1

Table 2.2. Variance estimates of random factors and statistical analyses of linear mixed model results.

Random Effects		
Parameter	*Variance*	*Std.Dev.*
Stimulus Exemplar	0	0
Bird	0.13	0.36
Year	0	0
Residual	0.45	0.67

Fixed effects					
Parameter	*Estimate*	*SE*	*df*	*t-value*	*P*
(Intercept)	1.62	0.11	112.23	15.03	< 2e-16
Type B	0.48	0.15	80.16	3.218	0.00186
Type C	0.63	0.15	81.33	4.162	7.79E-05

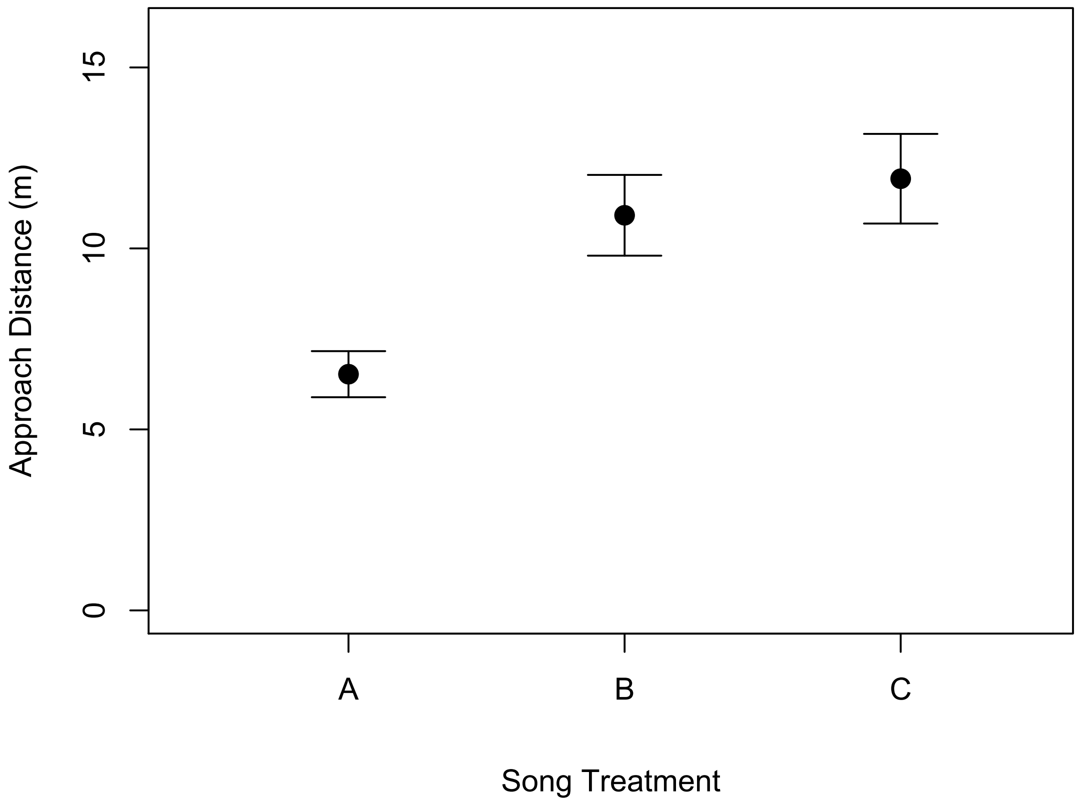


Figure 2.2. Mean and standard error of approach distance for three stimulus types: A) high performance song with a wide bandwidth and fast trill, B) a mid-performance song with a narrow bandwidth and fast trill rate, and C) a mid-performance song with wide bandwidth and slow trill rate.

Because six of our slow trill, wide bandwidth stimuli had trill rates below the natural rate of 6.8, we also re-ran the above analysis with males tested with these stimuli dropped (total *n* = 41). This subset of data also resulted in a top model of stimulus type as a fixed effect, with an evidence ratio of 48.2 and 88% model weight. Males approached significantly closer to wide bandwidth songs than they did to narrower bandwidth songs (wide bandwidth, fast trill: 7.1 ± 4.8 m, narrow bandwidth, fast trill: 10.5 ± 6.6 m;

Tukey's t-test: $n = 30$, $z = 2.9$, $P = 0.009$). Males approached closer to fast trills than to slower trills (fast trill, wide bandwidth: 8 ± 4.8 m, slow trill, wide bandwidth: 12.1 ± 6.8 m; Tukey's t-test: $n = 19$, $z = 3.16$, $P = 0.004$). Responses to the two stimuli of similar vocal deviation were not significantly different (fast trill, narrow bandwidth: 11 ± 6.8 m, slow trill, wide bandwidth: 13.7 ± 7.1 m; Tukey's t-test: $n = 14$, $z = 0.81$, $P = 0.7$). Average approach distance does not significantly differ for stimuli above 6.8 trill rate and below 6.8 trill rate (Welch's t-test, $t_{67.2} = -0.6$, $P = 0.55$).

DISCUSSION

Overall, our data support that white-crowned sparrow males respond more strongly to high performance (small deviation) songs than to lower performance (large deviation) songs, and that songs of similar vocal deviation elicit similar responses, as measured by average approach distance. Approach distance in emberizids is known to predict likelihood to attack (Searcy et al. 2006; Peters et al. 1980), and thus is a meaningful, interpretable measurement for male-male competition (McGregor et al. 1992; Catchpole & Slater 2008). These results support the hypothesis that males assess the signals of competitors based on a physical motor constraint, and not based solely on variation in one component of the constraint.

To our knowledge, our results are the first to show that two songs of similar vocal deviation, a fast trill, narrow bandwidth song, and a slow trill, wide bandwidth song, elicit similar approach responses from territorial males. Podos (1997) first proposed that during song production, males are limited in their capacities to sing wide bandwidth songs at a fast rate, because the bill gape and muscle movements needed to produce these types of notes dictate this capacity. Thus, researchers hypothesize that the better a male can perform this difficult tradeoff, the better competitor or mate he might be. Another possibility is that maximizing this tradeoff indicates motivation as trill rate increases (Vehrencamp et al. 2013; DuBois et al. 2009). Either way, vocal performance as measured by vocal deviation may be a reliable signal for receivers in contexts of male-male competition. Previously, we showed that males respond significantly different to high performance and low performance songs in two locations, with high performance songs receiving a stronger response, likely because males perceive these stimuli as high-quality intruders (Phillips and Derryberry 2017). Our experimental design presented here tested both differences in trill rate and bandwidth, as well as songs of similar vocal deviation against each other within a male, such that we provide initial evidence for both trill rate and bandwidth playing an important role in male-male competition. Specifically, our results suggest that songs of similar deviation from an upperbound regression line elicit similar responses from receivers, suggesting that birds are using the actual performance tradeoff, and not just a single component of the tradeoff, to assess competitors.

Few studies take this repeated measures approach within a species. In banded wrens, males have been tested with just trill rate (Illes et al. 2006) and just bandwidth (De Kort et al. 2009), but not across the same individuals. These experiments found that males approach less closely to wide bandwidth but sang more to high performance than median or low performance songs (De Kort et al. 2009), and approach fast trills first but spend more time near slow trills (Illes et al. 2006). The only other study that tests trill rate and bandwidth salience for sexual selection in a similar way is Drăgănoiu et al. (2002), which tests female preference in canaries. This experiment altered bandwidth and trill rate independently and found an equal response to manipulated songs with similar performance values in a triangular distribution (Drăgănoiu et al. 2002). Our results in addition to the results of Drăgănoiu et al. (2002) support that both trill rate and bandwidth can increase performance, and that when trill rate and bandwidth are both increased, it elicits a stronger response in male-male competition and female choice than when one component is decreased. Interestingly, even though some of our slow trill, wide bandwidth stimuli were slower than the natural rate, they did not elicit less of a response than the fast trill, narrow bandwidth songs that are within the natural range. Therefore, our findings indicate that males give a similar level of response to songs that have equivalent vocal deviation, whether that vocal deviation is achieved due to a fast trill rate or to a wide bandwidth, and whether or not one modification may be supernormal.

This study supports numerous other works on the salience of vocal deviation in sexual selection, particularly male-male competition. Although previous studies tested male response to variation in vocal performance as measured using vocal deviation, this variation was created either by manipulating only trill rate (swamp sparrows: Moseley et al. 2013), only bandwidth (banded wrens: De Kort et al. 2009; white-crowned sparrows: Luther et al. 2016), testing different songs types (red-winged blackbirds: Cramer & Price 2007) or by simultaneously changing both trill rate and bandwidth (swamp sparrows: Dubois et al. 2011; house wrens: Cramer 2013b; white-crowned sparrows: Phillips & Derryberry 2017). The results of these studies are consistent with the hypothesis that males judge the abilities or the threat of competitors based on vocal performance; however, males may differ in the direction of response to high vocal performance. While studies in most emberizids have typically found a stronger response to high performance songs (Phillips & Derryberry, *in press*; Dubois et al. 2011), high performance songs in other species have elicited avoidance behaviors, perhaps because a high performer is perceived to be too threatening (Illes et al. 2006; De Kort et al. 2009; Cramer & Price 2007), and avoidance has been shown to depend on the degree vocal performance was increased and the receiver's vocal performance (Moseley et al. 2013). Whether a male receiver's response is approaching or retreating, a differentiated response to varying performance levels supports that males are assessing their competitor, and thus the signal is functional and potentially under sexual selection, especially if song performance is not phenotypically plastic.

There are limits on the degree to which we can interpret how similar levels of vocal performance affect male response. Our slow trill, wide bandwidth stimuli were longer than our fast trill, narrow bandwidth stimuli (of similar deviation), and had longer gaps of silence between trilled notes. If song length were more important for communication than vocal deviation, we would have expected males to respond more to longer songs; instead, male response was not explained by variation in song length. Because we used natural variation in bandwidth, so as to avoid altering note morphology, inter-note silence gaps also differed between fast trill, narrow bandwidth stimuli and slow trill, wide bandwidth stimuli. Inter-note silence can affect other performance measures of song, including acoustic density (Cardoso et al. 2009), percentage peak performance (Forstmeier et al. 2002), and frequency excursion (Podos et al. 2016). It may be that our stimulus songs of similar vocal deviation are not equivalent in these other measures of performance. Thus, we conclude only that songs of similar vocal deviation elicit similar levels of response. Finally, we test response to three relative points in the trill rate bandwidth tradeoff plane, when there are many other comparisons that could be made. Future studies should test different configurations of trill rate and bandwidth, perhaps comparing songs of similar deviation to a lower performance stimulus. A need to test the effect of each of these factors – song length, internote silence, and more points on the vocal deviation plane – on response indicates the breadth of work remaining in the study of vocal performance.

Sexually selected vocalizations may convey physical traits or motivational states of the sender, but other factors can also shape the evolution of these signals, potentially creating a conflict of selective pressures. The acoustic properties of different sounds are well known to be influenced by environmental factors, such that low, slow pure tones are less attenuated in dense habitat than modulated, fast notes, thus maintaining long distance communication (Endler 1992; Wiley & Richards 1978; Wiley & Richards 1982; Morton 1975). Beyond effects of the physical landscape, the soundscape may also influence song evolution, such that birds in low frequency, noisy habitats often have high pitched, and/or narrow bandwidth songs to avoid masking (Martens & Geldudig 1990; Patricelli & Blickley 2006; Luther & Gentry 2013; Derryberry et al. 2016). One might predict that songs will evolve to best propagate in a given environment and still convey sender quality or motivation. Our results support equal salience for wide bandwidth and fast trills, which means that animals may be able to maintain high performance values and long communication distances if they maintain or compensate with one component of vocal deviation (e.g., either trill rate or frequency bandwidth). In species where this balance is constrained by other factors, one might predict that vocal performance, at least as measured by vocal deviation, becomes less important to receivers. Thus, in some environments, we might predict that either trill rate or frequency bandwidth may become the more salient trait or even a different performance trait (e.g., song complexity or consistency) may be more likely to indicate quality (Sakata & Vehrencamp 2012; Cardoso et al. 2007; Cardoso et al. 2012). The idea that different types of performance may be favored depending on the type of environment provides an interesting path for future vocal performance research.

Conclusions

Vocal performance, as measured by performance of the tradeoff between trill rate and bandwidth in the production of trilled notes, is a salient signal for male white-crowned sparrows. We provide evidence for songs of similar performance level eliciting a similar approach response from male competitors, which supports vocal performance, trill rate, and bandwidth as sexually selected traits. The majority of previous studies manipulated only trill rate or bandwidth, leaving open the question of whether selection is acting on the tradeoff or only on either trill rate or bandwidth. Thus, our results in this system are an important stepping-stone to better understanding the performance tradeoff between trill rate and bandwidth, and provides evidence that manipulating trill rate or bandwidth are equally effective ways of testing vocal performance salience for sexual selection. There are many future opportunities to explore vocal performance function across diverse taxa and habitats, and additional studies will help expand our current knowledge of the evolution of physical tradeoffs as meaningful communication signals.

Chapter 3. Effects Of Anthropogenic Noise On Function Of A Sexually Selected Trait

ABSTRACT

Many animal species modify their communication signals in response to noise pollution, but we do not fully understand the functional consequences of these modifications. Birdsong is a long distance communication signal, affected by the soundscape between sender and receiver. Birds are known to modify their song with background noise levels – for example, slowing the rate of note delivery, raising the peak frequency, and/or narrowing song bandwidth – likely to avoid masking. However, these same song traits are under sexual selection in many bird species, with preferences often for song characteristics that are difficult to produce, leading to potential conflict between songs that transmit further and songs that indicate male quality. One such trait that can be affected by acoustic adaptation to anthropogenic soundscapes is 'vocal performance', which is a performance constraint on the production of fast trilled vocalizations at relatively wide bandwidth. Vocal performance is under sexual selection in many animals, including the well-studied Nuttall's white-crowned sparrow (*Zonotrichia leucophrys nuttalli*) in which males respond more strongly to high performance songs. Using this species, we measure male response to high performance songs and lower performance

songs along a gradient of ambient noise levels with repeated measures playback experiments in the city of San Francisco, CA. We predict that males in noisier areas will not discriminate between high and lower performance songs when performance varies because of bandwidth due to masking of wide bandwidth songs but that males will discriminate between high and lower performance songs when performance varies because of trill rate. Further, we predict that males will respond more strongly to song playback in noisier areas but that discrimination between stimuli will decrease. We find support for our hypothesis that noise affects response to song performance although our findings are opposite of our predictions; urban male white-crowned sparrows give the same response to fast and slow trills but discriminate between wide and narrow bandwidth songs. We also find that territory noise levels predict male response; males respond more strongly to stimulus songs in noisier conditions, however the strength of discrimination between stimulus treatments does not change. Our results suggest that anthropogenic noise can indirectly affect song function in the context of male-male competition, possibly favoring the evolution of vocal performance through maximizing bandwidth and not trill rate in urban areas. This finding supports that aggressive signal content in the form of bandwidth may be lost in areas of high noise, where songs tend to have narrow bandwidths to increase transmission distance. Further, anthropogenic noise can also directly affect male responsiveness to song, possibly leading to more territorial conflict in urban areas.

INTRODUCTION

The acoustic adaptation (or sensory drive) hypothesis states that organisms will adapt their vocalizations to transmit best in their respective environments (Morton 1975; Endler 1992). There are many studies supporting this hypothesis in natural soundscapes, with organisms changing the timing, amplitude, or frequency of vocalizations to maximize sound transmission to receivers (Luther & Gentry 2013). More recently, research has shown that animals also adjust their signals to evolutionarily unprecedented anthropogenic soundscapes (Swaddle et al. 2015). This phenomena occurs across a variety of taxa, including mammals (Rabin et al. 2003), amphibians (Parris et al. 2009), fish (Radford et al. 2014; Slabbekoorn et al. 2010), invertebrates (Morley et al. 2014), and birds (Slabbekoorn 2013). Bird song has the most accumulated evidence for an effect of anthropogenic noise on communication, with many species singing higher pitched songs in urban areas (Slabbekoorn 2013).

Generated by machines – such as boats, cars, and industrial equipment – anthropogenic noise is typically loudest at low frequencies (< 2 kHz), and often overlaps (i.e. masks) the lower frequency range of animal signals (Shannon et al. 2016). Masking can decrease the ability of receivers to detect or discriminate the information content of a signal (Lohr et al. 2003) and thus alter the behavioral response of the receiver. For example, masking noise decreases the ability of budgerigars (*Melopsittacus undulates*) and zebra finches (*Taeniopygia guttata*) to discriminate between different calls (Lohr et al. 2003). Furthermore, great-tits (*Parus major*) are less efficient at discriminating low frequency songs in urban noise (Pohl et al. 2012). Another study shows that female grey treefrogs (*Hyla chrysoscelis*) took longer to orient and approach male signals in masking noise, and their detection thresholds increased (Bee & Swanson 2007). Therefore, masking noise can even lead to 'evolutionarily inappropriate responses' by receivers (Wiley 1994), resulting in fitness costs to the signaler, the receiver, or both.

As songs in birds are often used for mate attraction and territory defense, environmentally induced modifications to signals may pose fitness costs and benefits (Catchpole & Slater 2008). In the context of mate choice, fertile females typically prefer low pitch songs when they can hear them, suggesting sexual selection on lower song frequencies via mate choice; however, in noisy conditions, females respond more to high pitch songs, suggesting a benefit to males of being heard by a receiver (Halfwerk et al. 2011; Pohl et al. 2012). In the context of male-male competition, territorial males of several species respond less to urban associated increases in song minimum frequency (Luther & Derryberry 2012; Ripmeester et al. 2010; Mockford & Marshall 2009). These findings suggest that males that produce songs with higher minimum frequencies are less competitive, at least in areas with lower noise levels (Dowling et al. 2011). Therefore, noise can affect how signals are perceived, and acoustic adaptation may sometimes work in opposition to preference or the competitive function of the signal.

Birds adjust not only pitch but also many other features of song to urban noise levels, but the functional consequences of these changes remains poorly resolved. A loss of bandwidth due to changes in minimum but not maximum frequency in noisy areas has been reported in song sparrows (*Melospiza melodia*; Wood & Yezerinac 2006), dark-eyed juncos (*Junco hyemalis*; Slabbekoorn et al. 2007), great tits (*Parus major*; Hamao et al. 2011), European robins (*Erithacus rubecula*; Montague et al. 2012), and chipping sparrows (*Spizella passerina*, Job et al. 2016). Cardinals (*Cardinalis cardinalis*) and catbirds (*Dumetella carolinensis*) show a reduced bandwidth from changes in both minimum and maximum frequencies with increasing levels of noise (Dowling et al. 2011). City birds also change the rate or number of notes in noise, with some birds singing fewer notes (Nemeth & Brumm 2010; Wood & Yezerinac 2006; Cartwright et al. 2014), or more of certain notes, like the twitter phase of European blackbirds (Slabbekoorn & den Boer-Visser 2006). These adjustments to bandwidth and trill rate may be adaptations to transmit better in urban soundscapes, as slow trills and narrower bandwidths are less likely to degrade in 'urban canyons' (Warren et al. 2006; Wiley & Richards 1978; Gall et al. 2012), and narrow bandwidths require lower signal-to-noise ratios to be detectable (Lohr et al. 2003). However, variation in trill rate and bandwidth is also under sexual selection in the contexts of female mate choice and male-male competition (Pasch et al. 2011; Drăgănoiu et al. 2002; Phillips & Derryberry 2017; Luther, Phillips, et al. 2016; Moseley et al. 2013; Dubois et al. 2011; Podos et al. 2009). Therefore, adjustments to trill rate and bandwidth via acoustic adaptation or masking of sexually selected features may interfere with a signaler's ability to convey information to a receiver.

Broadband vocalizations of repeated notes (trills) are difficult to produce because many songbirds coordinate rapid vocal tract and beak movements to track dominant frequencies and filter out harmonics (Westneat et al. 1993; Podos 1996) . In birds with broadband trilled notes, there is a tradeoff between the rate of note production (trill rate) and note bandwidth. To sing slow trill notes, males can produce wide or narrow frequency bandwidths, because the timing between notes allows for mechanical movements of the bill, laryngeal muscles, and syrinx (Hoese et al. 2000; Riede et al.

2006; Nowicki et al. 2002). As a male increases his trill rate, timing between notes is decreased, and bandwidth is limited by mechanical constraints. A review across a family of songbirds, Emberizidae, found that this performance tradeoff forms a triangular distribution (Podos 1997), which has since been described in many other taxonomic groups (reviewed in Podos et al. 2009; Derryberry 2009; Pasch et al. 2011). How well a male can perform this tradeoff is called vocal deviation, and can be measured as the orthogonal deviation from an upper bound regression on this triangular distribution; a larger deviation score indicates lower performance, and a small deviation indicates high performance (Podos 2001; see Appendix 3 for relationships between beak size and vocal deviation).

We lack an understanding of the communication function of vocal performance as measured by vocal deviation (hereafter, vocal performance) for sexual selection in the context of urban soundscapes. Therefore, it remains unknown whether this measure of vocal performance remains a viable signal in areas of high anthropogenic noise, such as cities. Female birds and mammals prefer higher performance songs, including canaries (*Serinus canaria*; Drăgănoiu et al. 2002), swamp sparrows (*Melospiza georgiana;* Ballentine et al. 2004), Lincoln's sparrows (*Melospiza lincolnii*; Caro et al. 2010), and female singing mice (*Scotinomys spp.*; Pasch et al. 2011). Males are also able to discriminate between high and low performance songs in red-winged blackbirds (*Agelaius phoeniceus*; Cramer & Price 2007), banded wrens (*Thryophilus pleurostictus;* Illes et al. 2006), swamp sparrows (*Melospiza georgiana;* Dubois et al. 2011), nightingales (*Luscinia megarhynchos*; Schmidt et al. 2008), and white-crowned sparrows (*Zonotrichia leucophrys;* Phillips & Derryberry 2017). However, no studies have considered transmission selective pressures on vocal performance in conjunction with selective pressure for signals that inform receivers of signaler of quality, and many species that do attend to vocal performance occur in urban areas.

Some studies have begun to look at whether response to song playback changes across different soundscapes. A recent study showed that territory noise level affected male chipping sparrow (*Spizella passerina*) and spotted towhee (*Pipulo maculatus*) response to playback of population average songs. Males took longer to approach stimulus songs in noise (Kleist et al. 2016), suggesting that soundscapes may interfere with receiver detection and discrimination of sexually selected vocal signals. Other studies found that males defending urban territories are more aggressive than their rural counterparts (Scales et al. 2011; Evans et al. 2010; Scales et al. 2013; Foltz et al. 2015; Davies & Sewall 2016), but do not test if anthropogenic noise is a factor in this elevated aggression, or 'urban anger'. One study found male cardinals tend to sing more in response to songs with high minimum frequency in noisy conditions, and that discrimination strength is reduced in noise between stimulus treatments (Luther & Magnotti 2014). However, it remains to be tested whether noise levels affect receiver response to variation in vocal performance for male-male competition and/or female mate choice.

The Nuttall's white-crowned sparrow (*Zonotrichia leucophrys nuttalli*; NWCS) is a good system in which to address this question because of previous work both on the function of vocal performance in male-male competition and on correlations between anthropogenic noise levels and variation in trill rate, bandwidth and vocal performance of their songs. In previous studies, we found that male NWCS in both urban and rural areas respond more strongly to high performance than to much lower performance songs (Phillips & Derryberry 2017). Further, males in rural areas respond equally to songs of similar vocal deviation, whether that vocal deviation is close to population average performance through increasing bandwidth or through increasing trill rate. We do not know if this pattern of response holds in anthropogenic noise. In urban areas, NWCS adjust both trill rate and bandwidth in response to anthropogenic noise levels: males defending territories with higher noise levels on average (hereafter, noisier territories) produce songs with faster trill rates but narrower bandwidths than males on quieter territories and have lower performance songs (Luther, Phillips, et al. 2016). A previous playback experiment showed that urban males respond less to songs with narrower bandwidths (Luther, Phillips, et al. 2016; Phillips & Derryberry 2017) yielding the hypothesis that noise-dependent adjustments of bandwidth and trill rate might have functional consequences, and that these consequences could vary with ambient noise levels.

Here, we test this hypothesis by measuring male response to variation in vocal performance as measured by vocal deviation across an urban gradient of noise, using NWCS breeding in San Francisco, CA. We measure response to three stimulus treatments: 1) a high performance song with fast trill, wide bandwidth, 2) a lower performance song with fast trill, narrow bandwidth (typically found in noisier territories), and 3) a lower performance song with slow trill, wide bandwidth (typically found in quieter territories). We make several predictions about the importance and directional responses of males to vocal performance across noise conditions. First, we predict that males in noisier areas will not respond differently to wide bandwidth (high performance) and narrow bandwidth (low performance) songs, because noise masks low frequencies in the song potentially making it difficult for males to detect differences in bandwidth. We predict that even in noisy conditions males will respond more to fast trill (high performance) than to slow trill (low performance) songs, as our urban birds are not found in 'urban canyons' where reverberation can mask fast trills. Based on studies finding stronger response to playback in cities (Scales et al. 2011; Evans et al. 2010; Scales et al. 2013; Foltz et al. 2015; Davies & Sewall 2016), we also predict that males will respond more strongly to song playback in noisier areas. Finally, we predict that discrimination between song types is reduced, consistent with studies on other avian species (Luther & Magnotti 2014).

METHODS

Song recordings and stimuli

We recorded songs using a Marantz PMD 661 digital recorder, Sennheiser omnidirectional microphone, and Saul Mineroff SME-1000 parabola from males 2-3 years prior to conducting playbacks. The songs were recorded at 44.1 kHz sampling rate and stored as .wav files. To measure trill rate and bandwidth, we first resampled songs at 25 kHz and high pass filtered songs at 1500 Hz to remove noise below the range of NWCS songs. We then took trill minimum and maximum frequencies at -36 dB relative to the peak amplitude frequency from spectrograms (256 pt transform, frequency resolution: 97.7 Hz, 10.2ms time resolution); this method captured variation in frequency bandwidth while excluding background noise (Podos 1997). We calculated frequency bandwidth as the difference between the maximum and minimum frequencies, and trill rate as the average number of trill notes produced per second. We collected all song data in Signal 5 (Beeman 1998). To calculate vocal performance, we used the published equation for the upper bound regression on a set of 1572 Emberzidae songs, $y = -0.124x + 7.55$ (Podos 1997). We calculated vocal performance as the orthogonal deviation of each song from this upper bound regression.

We drew from the measured recordings described above to create stimuli for song playback experiments. Songs selected for stimuli had high signal to noise ratios. All stimuli were from the San Francisco dialect (Baptista 1975). From the recordings, we drew pairs of songs that differed naturally by at least 500 Hz in trill bandwidth and then manipulated each song to create a slow and a fast trill version. To create specific trill rates, we repeated the first trill note eight times with the desired spacing between notes. We made stimulus sets that consisted of three song treatments: (A) wide bandwidth, fast trill rate, (B) narrow bandwidth, fast trill rate, and (C) wide bandwidth, slow trill rate (Figure 1). We calculated the necessary slow and fast trill rate for each stimulus set such that stimuli 'wide bandwidth, slow trill rate' and 'narrow bandwidth, fast trill rate' would have roughly the same vocal performance value (t-test, $t = 1.3$, d.f. = 32, $P = 0.2$; Table 3.1). Amplitude is known to affect male response to playback in this species (Luther, Danner, et al. 2016), thus we normalized stimuli amplitude in SIGNAL 5 (Beeman 1998) and calibrated amplitude from the speaker at 1 meter to 81 dB with a Larson Davis 831 Sound Level Meter (PCB Piezotronics). All features of manipulated songs were within the normal range of songs for the San Francisco dialect (Phillips & Derryberry 2017) (Table 3.1). We created 17 stimulus sets for trials based on the availability of high quality recordings with 500 Hz differences in bandwidth.

Table 3.1. The range of vocal deviation, trill rates, and bandwidths of San Francisco songs as compared to stimuli. Ranges for SF dialect are from Phillips & Derryberry (2017).

Song Type	**No. of songs**	**Vocal deviation**	**Trill rate (Hz)**	**Bandwidth (Hz)**
SF dialect	780	5.3—37.4; 22.2 ± 5.2	6.1—13.3; 9.2 ± 1.2	1690.4—5735.4; 2753.2 ± 648.8
SF narrow bandwidth, fast trill stimuli	17	12.2—33; 23.9 ± 4.2	9.3—12.5; 11.4 ± 0.9	1975.7—4699.8; 3194.1 ± 563.8
SF wide bandwidth, slow trill stimuli	17	10.9—32.3; 22 ± 4.2	6.1—6.67; 6.3 ± 0.2	2768.7—5424.1; 4034.6 ± 515.8
SF wide bandwidth, fast trill stimuli	17	6.4—26.6; 16.7 ± 4	9.3—12.5; 11.4 ± 0.9	2768.7—5424.1; 4034.6 ± 515.8

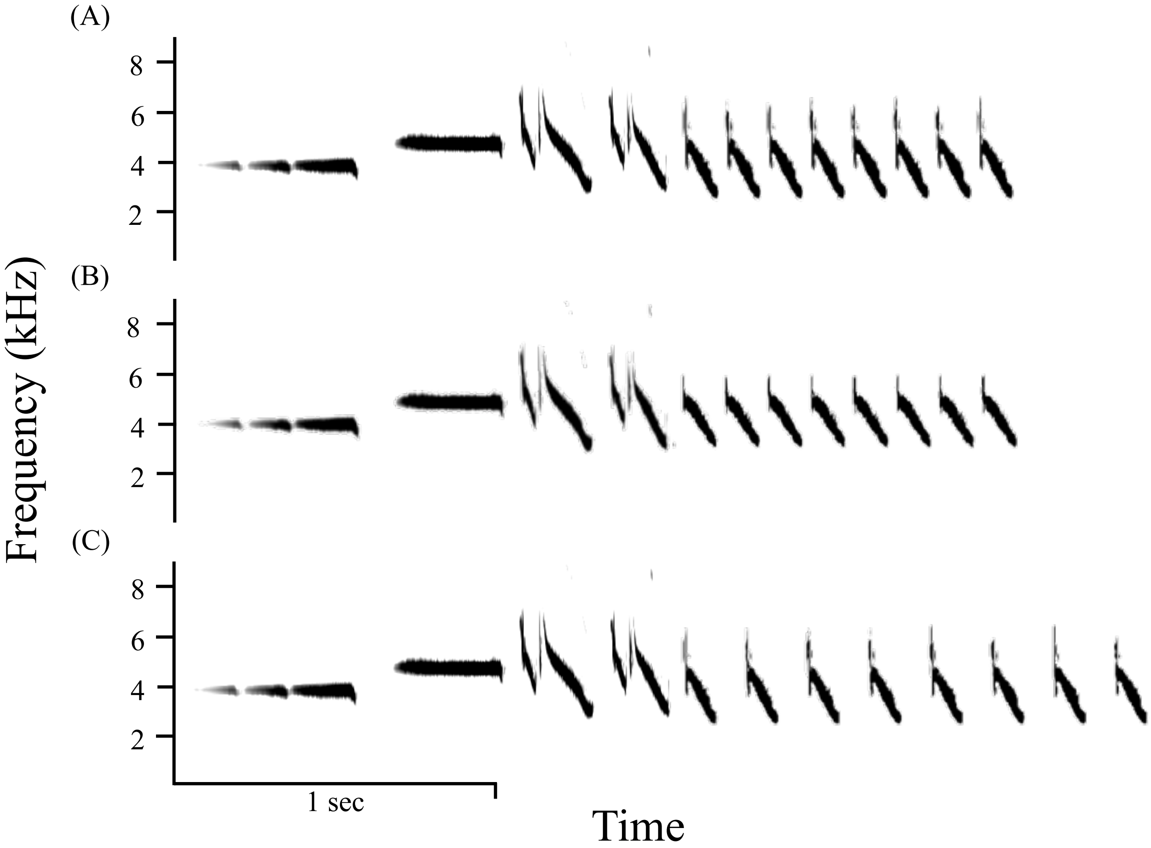


Figure 3.1. Example stimulus set of A) fast trill, wide bandwidth song, B) fast trill, narrow bandwidth song, and C) slow trill, wide bandwidth song.

Playback experiment design

We used repeated measures territorial playback experiments to test whether free-living adult males (n = 22) in urban environments responded differently to songs that varied in vocal performance and its component parts, trill rate and bandwidth. Territorial playback is a standard experimental design that simulates territorial intrusion by playing songs on subjects' territories and measuring their behavioral response (McGregor et al. 1992). Subjects held territories in the Presidio of San Francisco (Golden Gate National Recreation Area) in the May 2016 breeding season. Playbacks were conducted between sunrise and noon during the breeding season. We tested each male three times, once for each stimulus treatment; trials were conducted with at least 48 hours between trials to minimize habituation. Order of presentation was randomized across males. Neighbors were never tested on the same day, and we did not use songs from neighboring males as stimuli.

For each focal male, we observed song perches and determined the approximate location of the territory center. Before each trial, an inMotion iMT320 speaker (Altec Lansing) with an Apple iPod Nano (6th generation) was placed near the territory center on a platform 0.5m above the ground. The same location was used each time the male was tested. We started the playback when the focal male was in view within 24m of the speaker to ensure he was on his territory. Once a trial began, songs were broadcast at a typical song bout speed (6 songs/min).

During each trial, we recorded the male's movement behaviors at 10-sec intervals. We recorded responses during a three-minute playback period and a six-minute post-playback period. The response variables therefore are approach distance from the speaker

(m) during both playback and post-playback. We examine these two responses because they are interpretable as likelihood to attack (McGregor et al. 1992; Searcy et al. 2006; Peters et al. 1980). To approximate distance measures, we placed a string radiating out from the speaker with distance categories marked with flagging tape. The distance categories used were 0–2 m, 2–4 m, 4–8 m, 8–16 m, and greater than 16 m. We used the median distance of each category and 24 m for the 'greater than 16 m' category to calculate the male's average distance from the speaker during the combined playback and post-playback periods (Peters et al. 1980).

Playback procedures adhered to guidelines set by Tulane University Institutional Animal Care and Use Committee (protocol 0427-R), California State Collecting Permit (6799), Golden Gate Recreation Area Scientific Research and Collecting Permit (GOGA-00079), and San Francisco Parks and Recreation Permit (032014).

Ambient noise level measurements

We measured ambient noise levels within five minutes of playback experiments using a Larson Davis 831 Class 1 Sound level meter (PCB Piezotronics). We took readings for one minute in each cardinal direction for a total of 4 minutes, following published methods (Brumm 2004). Our values were recorded in LAeq, which accounts for noise fluctuations over time and adjusts for the range of audible noise for humans, which overlaps with that of songbirds (Rossing 2007).

Statistical analyses

To assess the overall effects of noise, stimulus treatment, and the interactions between noise and stimulus treatment on approach distance during playback and post-playback, we explored all combinations of the fixed effects of stimulus treatments and territory noise using linear mixed-effect models implemented in lme4 (Bates et al. 2015) and Akaike's Information Criterion for small sample sizes, AICc (Mazerolle 2016). We examined the interaction between noise and stimulus treatment because of our prediction that discrimination strength between stimuli would change with noise levels, which would result in different slopes for the relationship between noise and response for each stimulus treatment. We re-used 5 stimulus sets (stimulus sets: n = 17, focal males: n = 22); thus, we included stimulus exemplar as a random effect in all models. Because males were tested with multiple stimuli in a repeated measures design, bird identity was also included as a random effect in all models. To examine relative variable importance, we averaged models within the 95% confidence interval using MuMIn (Barton 2011), as suggested by Burnham & Anderson (2002). Response variables were log-transformed to meet normality assumptions. To examine directionality of response to fixed effects, we used post hoc Tukey t-tests for stimulus treatment and linear regression for territory noise. To account for multiple comparisons in post-hoc tests, we use Bonferonni correction, with $\alpha = 0.017$. We performed all statistical analyses in R (R Development Core Team 2011).

RESULTS

Stimulus treatment and territory noise level affect playback approach distance

AIC_c model selection supports that stimulus treatment + territory noise best predicts playback distance ($AIC_c = 164.4$, weight = 0.46, ER = 39.56, Table 3.2). The next best model, within 2 AIC_c includes stimulus treatment (Table 3.2). A model average of the three models within the 95% confidence interval (CI) shows stimulus treatment with a relative importance of 100%, territory noise with a relative importance of 65%, and the interaction between the two has a relative importance of 16%. Post-hoc tests show playback approach distance is significantly closer to fast trill, wide bandwidth songs than to fast trill, narrow bandwidth songs (Tukey's t-test: $z = 3.47$, $P < 0.001$) but not to slow trill, wide bandwidth songs (Tukey's t-test: $z = 1.78$, $P = 0.17$; Figure 3.2A). Males did not differ in their response to songs of equal vocal performance (i.e., fast trill, narrow bandwidth and slow trill, wide bandwidth songs; Tukey's t-test: $z = -1.67$, $P = 0.21$; Figure 2A). Post-hoc analysis also showed that males approached the playback speaker more closely as territory noise increased across treatments ($R^2 = 0.09$, $F_{1,64} = 6.24$, $P = 0.015$; Figure 2B), but discrimination strength between high and low performance songs did not change with noise ($R^2 = 0.03$, $F_{1,42} = 6.24$, $P = 0.2$).

Table 3.2. AIC_c table for playback distance

Models	K	AIC_c	ΔAIC_c	w_i	Cumulative w_i
Treatment + Territory Noise	7	164.40	0	0.47	0.47
Treatment	6	165.03	0.63	0.34	0.81
Treatment + Territory Noise + Type*Noise	9	166.634	2.23	0.15	0.96
Territory Noise	5	170.05	5.64	0.03	0.99
Null	4	171.76	7.36	0.01	1

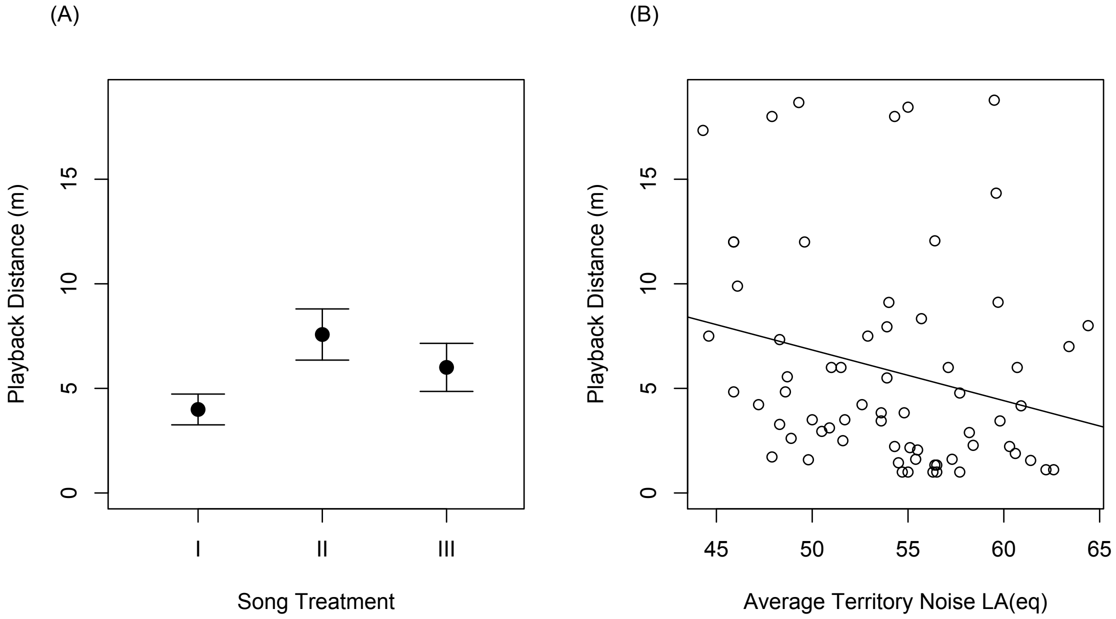


Figure 3.2. (A) Mean ± SE playback distance (m) response to three song treatments I) fast trill, wide bandwidth (4 ± 0.74 m), II) fast trill, narrow bandwidth (7.6 ± 1.22 m), and III) slow trill, wide bandwidth (6 ± 1.14 m). I is significantly different than II ($p < 0.001$), but I & III and II & III are statistically equal ($p > 0.05$). (B) Linear regression of male approach distance during playback and territory noise showing males approach more closely during playback when it is noisy ($p = 0.015$).

Noise affects post-playback approach distance

The top model for post-playback approach distance had a fixed effect of territory noise ($AIC_c = 165.49$, weight = 0.71, ER = 6.45, Table 3.3). Model averaging within the 95% CI shows the relative importance of territory noise across models was 88%, and stimulus treatment had a relative importance of 15%. Tukey's post-hoc comparison of stimulus treatments showed no significant differences between all three treatments (Figure 3.3A; all $p > 0.05$). A post-hoc linear regression shows territory noise to be a significant predictor of male response, with males approaching more closely as noise increases ($R^2 = 0.095$, $F_{1, 64} = 6.17$, $P = 0.012$; Figure 3.3B).

Table 3.3. AICc model selection for post-playback approach distance

Model	K	AICc	ΔAICc	w_i	Cumulative w_i
Territory Noise	5	165.49	0	0.71	0.71
Stimulus Treatment + Territory Noise	7	168.74	3.24	0.14	0.85
Intercept only model	4	169.19	3.69	0.11	0.96
Stimulus Treatment	6	172.08	6.58	0.03	0.99
Treatment + Territory Noise + Type*Noise	9	173.60	8.11	0.01	1

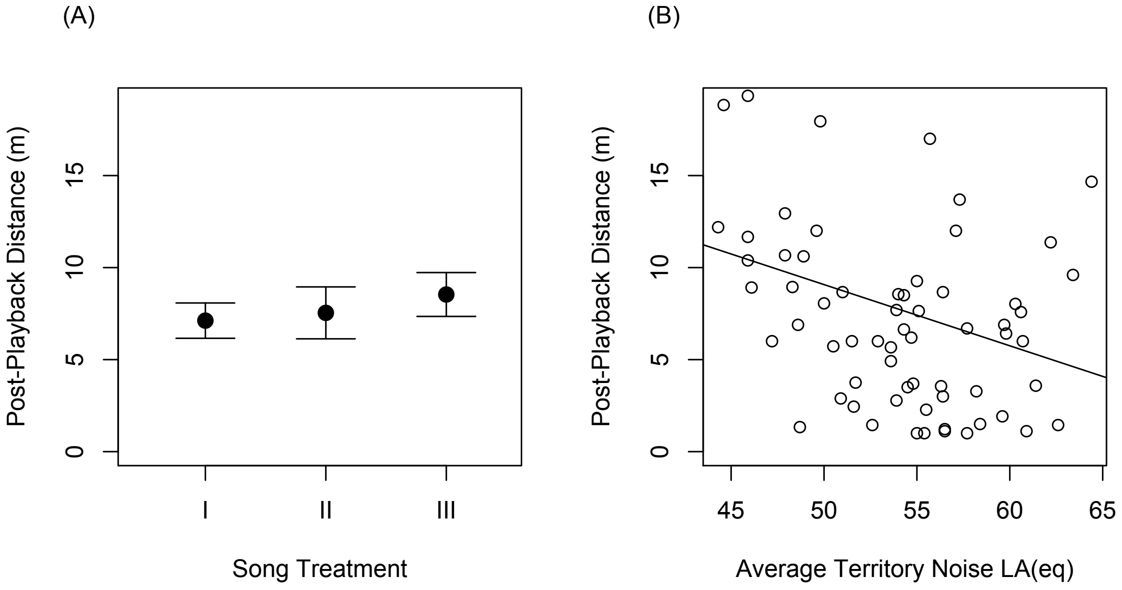


Figure 3.3. (A) Mean + SE of approach distance for post-postplayback for three stimulus treatments: I. fast trill, wide bandwidth (7.11 ± 0.96 m), II. fast trill, narrow bandwidth (7.54 ± 1.41 m), and III. slow trill, wide bandwidth (8.54 ± 1.19 m). All post-hoc comparisons between treatments *P* > 0.05. (B) Linear regression of male approach distance during post-playback and territory noise (*P* < 0.02).

DISCUSSION

Overall, we find that urban male white-crowned sparrows approach more closely to wide bandwidth than to narrow bandwidth songs, but they do not respond differently to fast and slow trills. These results are opposite of our predictions. Additionally, territory noise level affects response distance. As noise increases, males approach more closely to stimulus songs. This result aligns with our predictions of a more aggressive response in noise, yet introduces the possibility that aggression as measured by approach distance in urban areas may be because animals must approach more closely to be able to hear the signal. We found weak support for a predicted interaction between stimulus treatment and territory noise levels during the playback period, and no support for an interaction during the post-playback period. This result suggests no decrease in discrimination strength between stimulus types in noisy conditions. Together, our findings indicate that urban males assess variation in bandwidth but not in trill rate, and that males defending noisier territories may be more likely to face costly fights, because a closer approach to an intruding male increases the probability of attack (Searcy et al. 2006).

We find partial support for our hypothesis that noise-dependent adjustments of bandwidth and trill rate in urban populations have functional consequences. Specifically, males approached more closely to wide bandwidth songs than to narrow bandwidth songs during playback. A closer approach to a speaker in a male's territory is interpreted as a stronger response to that stimulus; thus, males respond more strongly to wide bandwidth songs. This finding is consistent with previous studies testing response to variation in song bandwidth (Luther et al. 2016b; Phillips and Derryberry in review), and supports the hypothesis that males producing narrower bandwidth songs have less potent signals in the context of male-male competition. Male NWCS that defend noisier territories produce songs with significantly narrower bandwidth than males that defend quieter territories (Luther et al. 2016b). This trend is found in many urban species, such as song sparrows (*Melospiza melodia*; Wood & Yezerinac 2006), dark-eyed juncos (*Junco hyemalis*; Slabbekoorn et al. 2007), great tits (*Parus major*; Hamao et al. 2011), European robins (*Erithacus rubecula*; Montague et al. 2012), chipping sparrows (*Spizella passerina*, Job et al. 2016), cardinals (*Cardinalis cardinalis*) and catbirds (*Dumetella carolinensis*) (Dowling et al. 2011). Thus, noise-dependent shifts in bandwidth have consequences for white-crowned sparrows and potentially for other songbird species, at least in the context of territory acquisition and maintenance.

We did not find support for adjustments to trill rate affecting male response. Male NWCS defending noisier territories produce songs with faster trill rates than males on quieter territories (Luther, Phillips, et al. 2016). Our experimental results here indicate that males respond similarly to fast trill and slow trill songs. Thus, the increase in trill rate alone on noisier territories in San Francisco does not appear to have a strong effect on male-male competition in this location. In contrast, in a previous study we found that males in nearby areas outside of the city limits of San Francisco (in Marin County) do respond to variation in trill rate (Phillips & Derryberry 2017), such that males respond less to slow trills than to fast trills when bandwidth is consistent. Furthermore, studies in other species, like swamp sparrows (*Melospiza georgiana*) and banded wrens (*Thryothorus pleurostictus*) find that males typically increase trill rate to indicate aggressive motivation (Botero et al. 2009; DuBois et al. 2009), and males assess differences in trill rate (Moseley et al. 2013; Illes et al. 2006). One reason for the lack of responsiveness to variation in trill rate in the city may be that slow trills transmit better in the city, even in areas that are not obvious 'urban canyons', like the Presidio of San Francisco. If this is the case, then males may be responding less to fast trills in urban areas because the fast trills do not transmit as far, much as female great tits respond less to typically potent low frequency songs during noisy times of day because low frequency songs do not transmit as well (Halfwerk et al. 2011). Although our previous work indicates that songs with higher minimum frequency and narrower bandwidth transmit over greater communication distances in urban areas (Derryberry et al. 2016), we do not know if trill rate affects transmission in city noise in this species. Further studies would need to test how trill rate affects communication distance in these areas.

We also found no difference in response to songs of similar vocal deviation. These stimuli approximated songs found on quiet versus noisier territories in the city (Table 3.1). Thus, finding an equal response to these two types of stimuli would seem to suggest no functional difference among the songs produced by males holding territories with different ambient noise levels. However, it is important to note that despite the increase in trill rate on noisier territories, urban males still produce songs of lower performance (Luther, Phillips, et al. 2016). Because our playback experiment indicates that male receivers respond less to songs of lower performance due to a narrower bandwidth, our results support that songs more typical of NWCS defending noisier territories are less potent than those of males defending quieter territories, on average.

We also find partial support for our hypothesis that the functional consequences of noise-dependent song adjustments vary with ambient noise levels. We predicted that the strength of response to variation in vocal performance would decrease with increasing levels of ambient noise and that overall level of response to stimulus playback would increase. This can also be described as a ceiling effect such that as response increases to all stimuli, the difference in response to different stimuli will decrease. Although we did find a significant increase in the level of response to all stimuli with increasing levels of noise, we did not find support for an interaction between song treatment and ambient noise levels, indicating that response slopes did not vary among the song treatments. In other words, males are responding less to narrow bandwidth songs on both quiet and noisier territories, not just less on noisier territories.

We found that males come closer to all stimulus song types in noise. A previous study found no effects of territory noise on male response, but did not examine approach distance during playback or post-playback, only latency measures (Luther, Phillips, et al. 2016). Another study in cardinals found that males sing more in response to playback in noise, perhaps to increase the chance of a response signal being detected by an intruder (Luther & Magnotti 2014). Our results suggest that to assess song performance, males may have to approach more closely to enter the active space or listening distance of the signal bandwidth (Kleist et al. 2016). If a male cannot assess an intruding male without getting closer, both are more likely to incur a physical cost. This is because closeness to approach is a significant predictor of likelihood to attack (Searcy et al. 2006). Another interpretation of our findings is that the urban environment, particularly high levels of noise, may lead to overall higher aggression levels in cities, or so-called 'urban anger'. Increased aggression has been observed in urban birds (Evans et al. 2010; Foltz et al. 2015; Scales et al. 2011), typically as measured by approach distance. However, the cause of urban anger has been elusive – studies have not found support for higher population density, available nesting habitat, or testosterone levels as predictors of aggression levels in urban males (Davies & Sewall 2016; Foltz et al. 2015), although one study finds some support for food availability as a driver of urban aggression (Foltz et al. 2015). We find that males on noisier territories approach more closely to simulated territory intrusions, and so this finding suggests that territory noise levels may also be a factor in increased levels of aggression in urban areas. It may be that males on noisy territories have a decreased response threshold, and increased detection threshold caused by acoustic masking, which leads to unnecessary or inappropriately strong responses (Wiley 2006; Leonard et al. 2005). Future experimental studies could test the effects of chronic noise on aggression levels, and if detection threshold patterns are similar in NWCS as in species previously tested (Lohr et al. 2003; Pohl et al. 2009; Pohl et al. 2012).

Despite the potential costs of signaling in noise, some animals may be able to adapt their songs to the acoustic environment but still maintain signal content for up close encounters like mate choice or territorial intrusions via plasticity, or tactical allocation. Selection should favor males to be flexible within their performance range, such that they sing at their performance limit only when a female or intruder is nearby (thus reducing the communication distance and associated effects of sensory drive). When territorial males are not contending with nearby intruders or potential mates, producing a song with a lower performance value that transmits further may be beneficial, as increasing communication distance may outweigh any performance costs (Nemeth et al. 2013). This type of tactical allocation falls under the 'Maximizing Received Signal Hypothesis' (Patricelli et al. 2016). Although white-crowned sparrows show immediate flexibility in song production by varying number of trill notes based on motivation levels (Nelson & Poesel 2012), a recent study shows males do not change song pitch in real time in response to changing levels of noise (Derryberry et al. 2017). If males in this species also do not exhibit immediate flexibility in vocal deviation, then tactical allocation is not a solution to conflicting selection pressures from urban noise and male-male competition.

Although we have demonstrated that males holding territories with high ambient noise levels may bear a cost in singing lower performance songs in the context of male-male competition, we do not know what costs they may face in the context of female mate choice. Females in other songbirds prefer high performance songs (Ballentine et al. 2004; Drăgănoiu et al. 2002), so urbanization of song may also affect female mate choice. It remains to be seen if female choice is affected by noise in white-crowned sparrows. One study suggests that great tit females may respond less to high-pitched songs that have narrower bandwidth, which in turn decreases performance (Halfwerk et al. 2011). Even if environmentally induced selection is not changing song performance, masking of songs could alter female preference for a pair-bonded mate (Swaddle & Page 2007). Additionally, males seem to enhance their performance via bandwidth when females are most fertile (Halfwerk et al. 2011). Given the functional importance of female mate choice in signal evolution, future studies examining whether preferences for song change in noisy anthropogenic conditions are essential.

Conclusions

Our study highlights a functional consequence of song modification in urban landscapes, particularly for birds with trilled vocalizations. Additionally, our study is the first to show that assessment of vocal performance, a known sexually selected trait, is at least partially affected by ambient noise levels. We found that males approach simulated intruders more closely in noisier conditions, suggesting an increase in the chance for territorial disputes as males assess sexual signals. Closer approach in noise may indicate increased aggression or the need for receivers to enter the active space of the signal to discriminate song characteristics—disentangling these two interpretations is an open field of inquiry. Future research is needed to examine these consequences in the context of other performance measures of song (song rate, repertoire size, amplitude) in additional species and across a wider range of soundscapes. As anthropogenic soundscapes become more the norm than the exception, understanding the impacts humans have on animal communication is critical.

APPENDIX 1

Point Reyes Subset

AICc for Approach distance

	K	*AICc*	*ΔAICc*	*w_i*	*Cum. w_i*	*LL*	*Evidence Ratio*
Type	5	94.53	0.00	0.71	0.71	-38.51	3.66
Null	4	97.12	2.59	0.19	0.90	-42.34	
Type + Male VP	6	100.92	6.40	0.03	0.93	-38.46	
Julian Date + Type	6	101.00	6.48	0.03	0.96	-38.50	
Julian Date	5	101.47	6.94	0.02	0.98	-41.98	
Male VP	5	101.95	7.42	0.02	1.00	-42.23	
Male VP + Julian Date	6	107.42	12.89	0.00	1.00	-41.71	
Type + Julian Date + Male VP	7	109.54	15.01	0.00	1.00	-38.43	

AICc for PC1

	K	*AICc*	*ΔAICc*	*w_i*	*Cum. w_i*	*LL*	*Evidence Ratio*
Null	4	46.50	0.00	0.56	0.56	-17.03	1.75
Type	5	47.63	1.12	0.32	0.88	-15.06	0.57
Male VP	5	51.49	4.99	0.05	0.93	-17.00	
Julian Date	5	51.52	5.02	0.05	0.97	-17.01	
Type + Male VP	6	53.78	7.28	0.01	0.99	-14.89	
Julian Date + Type	6	54.11	7.61	0.01	1.00	-15.06	
Male VP + Julian Date	6	57.97	11.47	0.00	1.00	-16.98	
Type + Julian Date + Male VP	7	62.40	15.90	0.00	1.00	-14.87	

AICc for PC2

	K	*AICc*	*ΔAICc*	*w_i*	*Cum. w_i*	*LL*	*Evidence Ratio*
Null	4	40.76	0.00	0.68	0.68	-14.16	3.74
Type	5	43.40	2.64	0.18	0.86	-12.95	0.27
Julian Date	5	45.51	4.75	0.06	0.93	-14.01	
Male VP	5	45.80	5.03	0.06	0.98	-14.15	

Julian Date + Type	6	49.64	8.87	0.01	0.99	-12.82	
Type + Male VP	6	49.90	9.13	0.01	1.00	-12.95	
Male VP + Julian Date	6	52.00	11.23	0.00	1.00	-14.00	
Type + Julian Date + Male VP	7	58.30	17.54	0.00	1.00	-12.82	

Point Reyes

AICc for Approach distance

	K	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*Evidence Ratio*
Type	5	27.42	0.00	0.51	0.51	-7.77	9.92
Type + Male VP	6	29.35	1.93	0.20	0.71	-7.32	
Julian Date + Type	6	30.05	2.63	0.14	0.85	-7.67	
Null	4	32.01	4.59	0.05	0.90	-11.40	
Type + Julian Date + Male VP	7	32.24	4.81	0.05	0.95	-7.25	
Julian Date	5	33.57	6.15	0.02	0.97	-10.85	
Male VP	5	33.78	6.36	0.02	0.99	-10.95	
Male VP + Julian Date	6	35.69	8.27	0.01	1.00	-10.49	

AICc for PC1

	K	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*Evidence Ratio*
Type	5	104.24	0.00	0.52	0.52	-46.18	6.04
Julian Date + Type	6	106.60	2.35	0.16	0.69	-45.94	
Type + Male VP	6	107.07	2.83	0.13	0.81	-46.18	
Null	4	107.84	3.60	0.09	0.90	-49.31	
Type + Julian Date + Male VP	7	109.62	5.38	0.04	0.94	-45.94	
Julian Date	5	109.78	5.54	0.03	0.97	-48.95	
Male VP	5	110.48	6.23	0.02	0.99	-49.30	
Male VP + Julian Date	6	112.61	8.37	0.01	1.00	-48.95	

AICc for PC2

	K	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*Evidence Ratio*
Type	5	109.17	0.00	0.42	0.42	-48.65	2.86
Type + Male VP	6	110.76	1.59	0.19	0.61	-48.03	
Null	4	111.27	2.10	0.15	0.75	-51.03	

Julian Date + Trial	6	111.98	2.81	0.10	0.86	-48.64	
Male VP	5	113.36	4.19	0.05	0.91	-50.74	
Trial + Julian Date + Male VP	7	113.75	4.57	0.04	0.95	-48.01	
Julian Date	5	113.94	4.76	0.04	0.99	-51.03	
Male VP + Julian Date	6	116.19	7.02	0.01	1.00	-50.74	

AICc for PC3

	K	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*Evidence Ratio*
Null	4	116.04	0.00	0.43	0.43	-53.41	2.71
Julian Date	5	118.04	2.00	0.16	0.59	-53.08	
Male VP	5	118.23	2.20	0.14	0.73	-53.18	
Type	5	118.43	2.39	0.13	0.86	-53.28	
Male VP + Julian Date	6	120.54	4.50	0.05	0.91	-52.91	
Julian Date + Trial	6	120.75	4.72	0.04	0.95	-53.02	
Type + Male VP	6	120.80	4.76	0.04	0.99	-53.04	
Type + Julian Date + Male VP	7	123.43	7.39	0.01	1.00	-52.85	

San Francisco

AICc for Approach distance

	K	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*Evidence Ratio*
Type	5	199.22	0.00	0.36	0.36	-93.46	2.60
Type + Male VP	6	200.25	1.03	0.21	0.57	-92.45	
Null	4	201.13	1.91	0.14	0.71	-95.83	
Julian Date + Type	6	201.69	2.47	0.10	0.82	-93.17	
Male VP	5	202.16	2.94	0.08	0.90	-94.93	
Type + Male VP + Julian Date	7	203.25	4.02	0.05	0.95	-92.29	
Julian Date	5	203.88	4.65	0.04	0.98	-95.78	
Male VP + Julian Date	6	205.21	5.99	0.02	1.00	-94.93	

AICc for PC1

	K	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*Evidence Ratio*
Type	5	95.80	0.00	0.34	0.34	-41.75	4.57

Type + Male VP	6	96.15	0.35	0.28	0.62	-40.39	
Julian Date + Type	6	97.74	1.94	0.13	0.75	-41.19	
Julian Date + Type + Male VP	7	98.82	3.02	0.08	0.83	-40.08	
Null	4	98.83	3.04	0.07	0.90	-44.68	
Male VP	5	99.19	3.39	0.06	0.97	-43.44	
Julian Date	5	101.39	5.59	0.02	0.99	-44.54	
Male VP + Julian Date	6	102.15	6.35	0.01	1.00	-43.39	

AICc for PC2

	K	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*Evidence Ratio*
Male VP	5	96.45	0.00	0.30	0.30	-42.07	1.25
Null	4	96.89	0.44	0.24	0.53	-43.70	
Male VP + Julian Date	6	97.88	1.43	0.14	0.68	-41.26	
Julian Date	5	98.78	2.33	0.09	0.77	-43.23	
Type + Male VP	6	98.82	2.37	0.09	0.86	-41.73	
Type	5	99.05	2.60	0.08	0.94	-43.37	
Julian Date + Type + Male VP	7	100.75	4.30	0.03	0.97	-41.04	
Julian Date + Type	6	101.33	4.89	0.03	1.00	-42.99	

APPENDIX 2.

Full model selection for playback and post-playback approach distance for birds tested with three stimuli in rural Abbott's Lagoon, California (Chapter 2). Included in models are territory noise level (LAeq) such that they are comparable to playback results in urban San Francisco (Chapter 3).

PLAYBACK APPROACH DISTANCE

AICc Model Selection

Models	*K*	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*	*ER*
Type+LAeq+Type*LAeq	10	298.5	0	0.54	0.54	-138.2	>543100
Type + LAeq	8	299.7	1.2	0.29	0.83	-141.2	
Type	7	300.92	2.4	0.16	0.99	-142.9	
LAeq	6	318.1	19.5	0	1	-152.6	
null	5	318.84	20.3	0	1	-154.1	

Full Model Averaged Coefficients

	Estimate	*SE*	*Adj. SE*	*z-value*	*P*	
(Intercept)	1.24E+00	3.17E-01	3.18E-01	3.89	0.0001	***
Type B	5.67E-01	1.53E-01	1.54E-01	3.677	0.0002	***
Type C	7.49E-01	1.68E-01	1.70E-01	4.414	1.02E-05	***
LAeq	-1.35E-03	6.43E-03	6.45E-03	0.209	0.83	
LAeq:Type B	-1.64E-05	9.49E-04	9.52E-04	0.017	0.98	
LAeq:Type C	-3.39E-05	1.72E-03	1.73E-03	0.02	0.98	

Conditional Average Coefficients

	Estimate	*SE*	*Adj. SE*	*z-value*	*P*	
(Intercept)	1.23756	0.31695	0.32	3.89	0.0001	***
Type B	0.56709	0.15265	0.15	3.677	0.0002	***
Type C	0.74922	0.16824	0.17	4.414	1.02E-05	***
LAeq	-0.02458	0.01354	0.01	1.796	0.07	.
LAeq:Type B	-0.03541	0.02627	0.03	1.333	0.18	
LAeq:Type C	-0.07325	0.03227	0.03	2.245	0.02	*

Model Averaged Relative variable importance (95% CI)

	Type	*LAeq*	*LAeq*Type*
Importance	1	0.05	<0.01
N containing models	3	2	1

Tukey Test

Hypotheses	*Estimate*	*SE*	*z-value*	*P*	
B - A == 0	0.56	0.14	3.89	0.0002	***
C - A == 0	0.71	0.15	4.839	< 1e-04	***
C - B == 0	0.16	0.16	0.947	0.61	

Linear Model

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	3.27	0.65	5.004	1.98E-06	***
LAeq	-0.03779	0.01	-2.618	0.01	*

Residual standard error: 0.8996 on 118 degrees of freedom
Multiple R-squared: 0.055   Adjusted R-squared: 0.046
F-statistic: 6.85 on 1 and 118 DF, p-value: 0.01

POST-PLAYBACK APPROACH DISTANCE

AICc Model Selection

Models	*K*	*AICc*	*ΔAICc*	w_i	*Cum.* w_i	*LL*
Type + LAeq	8	312.04	0	0.64	0.65	-147.37
Type+LAeq + Type*LAeq	10	313.37	1.33	0.33	0.97	-145.67
LAeq	6	318.58	6.55	0.02	0.99	-152.92
Type	7	322.87	10.82	0.003	0.99	-153.93
null	5	330.37	18.33	0.0001	1	-159.92

Full Model Averaged Coefficients

	Estimate	*SE*	*Adj. SE*	*z-value*	*P*	
(Intercept)	4.31E+00	6.20E-01	6.27E-01	6.879	< 2e-16	***
Type B	-3.36E-01	1.15E-01	1.16E-01	2.886	0.004	**
Type C	9.16E-02	1.15E-01	1.16E-01	0.789	0.43	
LAeq	-5.08E-02	1.37E-02	1.39E-02	3.664	0.0003	***
LAeq:Type B	3.57E-05	1.23E-03	1.24E-03	0.029	0.98	
LAeq:Type C	-1.04E-05	7.47E-04	7.54E-04	0.014	0.99	

Conditional Average Coefficients

	Estimate	*SE*	*Adj. SE*	*z-value*	*P*	
(Intercept)	4.31327	0.62	0.62703	6.879	< 2e-16	***
Type B	-0.335894	0.11	0.116378	2.886	0.003	**
Type C	0.091608	0.11	0.116108	0.789	0.43	
LAeq	-0.050796	0.01	0.013865	3.664	0.0002	***
LAeq:Type B	0.032742	0.02	0.018263	1.793	0.07	.
LAeq:Type C	-0.009555	0.02	0.020758	0.46	0.64	

Model-averaged importance

	LAeq	*Type*	*LAeq*Type*
Importance	1	1	<0.01
N containing models	2	2	1

Tukey Test

Hypotheses	*Estimate*	*SE*	*z-value*	*P*	
B - A == 0	0.42	0.17	2.42	0.04	*
C - A == 0	0.58	0.18	3.22	0.003	**
C - B == 0	0.15	0.19	0.78	0.71	

Linear Model

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	4.53	0.63	7.146	7.98E-11	***
LAeq	-0.06	0.01	-4.03	9.90E-05	***

Residual standard error: 0.8728 on 118 degrees of freedom
Multiple R-squared: 0.121, Adjusted R-squared: 0.1136
F-statistic: 16.24 on 1 and 118 DF, p-value: 9.904e-05

APPENDIX 3

Exploratory data on relationships between morphological measures, vocal deviation, and territory noise level (LAeq) across 3 urban and 3 rural locations in the Bay Area of California.
All significant or close to significant models are shown per location, including the top model from AICc model selection.

Principal Component Analysis Summary for all locations: PC1 is loaded with bill size measures and negatively with fat score. PC2 loads with weight, culmen length, and tarsus. PC3 loads with age and wing chord. Rotation Method: Varimax with Kaiser Normalization.

Rotated Component Matrix

Variable	*PC1*	*PC2*	*PC3*
Bill Width (mm)	**0.848**	-0.041	-0.08
Bill Depth (mm)	**0.818**	0.212	0.032
Length to Nares (mm)	**0.593**	0.483	0.089
Fat Score	**-0.406**	0.066	-0.146
Weight (g)	-0.053	**0.775**	0.114
Culmen Length (mm)	0.084	**0.748**	0.04
Tarsus (mm)	0.072	**0.682**	-0.092
Age	0.112	-0.033	**0.887**
Wing Chord (mm)	0.036	0.097	**0.877**

San Francisco (Urban)

Summary: Males with lower vocal performance have larger bills, have less fat reserves, and live in noisier territories.

AICc Top Model: Deviation~PC1+LAeq + PC1*LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	25.9043	5.7024	4.543	3.87E-05	***
PC1	11.9681	6.3789	1.876	0.0668	.
Laeq	0.1207	0.1069	1.13	0.2644	
PC1*Laeq	-0.2177	0.1276	-1.706	0.0946	.

Multiple R-squared: 0.1714, Adjusted R-squared: 0.1185
F-statistic: 3.241 on 3 and 47 DF, p-value: 0.03024

Deviation~ PC1

Coefficients	*Estimate*	*SE*	*t-value*	*P*

(Intercept)	31.533	0.6168	51.122	< 2e-16	***
PC1	1.5689	0.5831	2.691	0.00956	**

Residual standard error: 4.504 on 52 degrees of freedom
Multiple R-squared: 0.1222, Adjusted R-squared: 0.1053
F-statistic: 7.24 on 1 and 52 DF, p-value: 0.009564

Deviation~LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	21.46939	5.10779	4.203	0.000111	***
LAeq	0.18955	0.09536	1.988	0.052437	.

Residual standard error: 4.691 on 49 degrees of freedom
Multiple R-squared: 0.07462, Adjusted R-squared: 0.05574
F-statistic: 3.951 on 1 and 49 DF, p-value: 0.05244

Bandwidth~LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	3863.58	663.54	5.823	4.39E-07	***
Laeq	-26.78	12.39	-2.162	0.0355	*

Residual standard error: 609.4 on 49 degrees of freedom
Multiple R-squared: 0.08709, Adjusted R-squared: 0.06846
F-statistic: 4.674 on 1 and 49 DF, p-value: 0.03553

Richmond (Urban)

Summary: Noise and Beak Size/Fat Score (PC1) interact and affect vocal deviation.

AICc Top Model: Deviation~PC1 + LAeq + PC1*LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	204.2747	45.1666	4.523	0.0011	**
PC1	-153.1233	41.3308	-3.705	0.00408	**
LAeq	-3.4612	0.8665	-3.995	0.00254	**
PC1:LAeq	3.023	0.8072	3.745	0.00381	**

Residual standard error: 4.085 on 10 degrees of freedom
Multiple R-squared: 0.6362, Adjusted R-squared: 0.527
F-statistic: 5.828 on 3 and 10 DF, p-value: 0.0144

Fort Funston-Lake Merced (Urban)

Summary: Males with lower vocal performance have larger bills, have less fat reserves, and live in noisier territories.

AICc Top Model: Deviation ~ PC1 + LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	29.4674	6.5304	4.512	8.64E-05	***
PC1	4.3088	0.6125	7.035	6.72E-08	***
LAeq	-0.0107	0.1195	-0.09	0.929	

Residual standard error: 3.94 on 31 degrees of freedom

Multiple R-squared: 0.6158,   Adjusted R-squared: 0.591
F-statistic: 24.84 on 2 and 31 DF, p-value: 3.642e-07

Second best model: Deviation~PC1 + PC2 + LAeq

:

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	27.32572	6.95114	3.931	0.000461	***
PC1	4.17717	0.63056	6.625	2.47E-07	***
PC2	0.73094	0.79692	0.917	0.366352	
LAeq	0.03464	0.12961	0.267	0.791103	

Residual standard error: 3.951 on 30 degrees of freedom
Multiple R-squared: 0.6262,   Adjusted R-squared: 0.5889
F-statistic: 16.76 on 3 and 30 DF, p-value: 1.4e-06

PC2~LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	2.91184	1.39737	2.084	0.0445	*
LAeq	-0.06302	0.02561	-2.461	0.0189	*

Residual standard error: 0.8974 on 35 degrees of freedom
Multiple R-squared: 0.1475,   Adjusted R-squared: 0.1231
F-statistic: 6.055 on 1 and 35 DF, p-value: 0.01895

Commonweal (Rural)

Summary: Males with lower vocal performance tend to have larger bills, less fat reserves, and live in noisier territories.

AICc Top Model: Deviation~PC1

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	27.6054	0.8635	31.97	9.98E-10	***
PC1	-2.4597	1.236	-1.99	0.0818	.

Residual standard error: 2.72 on 8 degrees of freedom
Multiple R-squared: 0.3311,   Adjusted R-squared: 0.2475
F-statistic: 3.961 on 1 and 8 DF, p-value: 0.08176

Trill Rate ~ LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	2.92836	1.42173	2.06	0.0664	.
LAeq	0.09903	0.03228	3.067	0.0119	*

Residual standard error: 0.5355 on 10 degrees of freedom
Multiple R-squared: 0.4848,   Adjusted R-squared: 0.4332
F-statistic: 9.408 on 1 and 10 DF, p-value: 0.0119

PC1 ~ LAeq

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	-3.79648	1.09596	-3.464	0.0021	**
LAeq	0.08596	0.02352	3.655	0.00132	**

Residual standard error: 0.6594 on 23 degrees of freedom

Multiple R-squared: 0.3675, Adjusted R-squared: 0.34
F-statistic: 13.36 on 1 and 23 DF, p-value: 0.001318

Limantour (Rural)

Summary: Males with lower vocal performance tend to have larger bills and lower fat scores. Noise does not trend with performance or body measures.

AICc Top Model: Deviation~PC1

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	23.3986	0.8501	27.526	1.70E-11	***
PC1	2.5118	1.3164	1.908	0.0828	.

Residual standard error: 2.934 on 11 degrees of freedom
Multiple R-squared: 0.2487, Adjusted R-squared: 0.1804
F-statistic: 3.641 on 1 and 11 DF, p-value: 0.0828

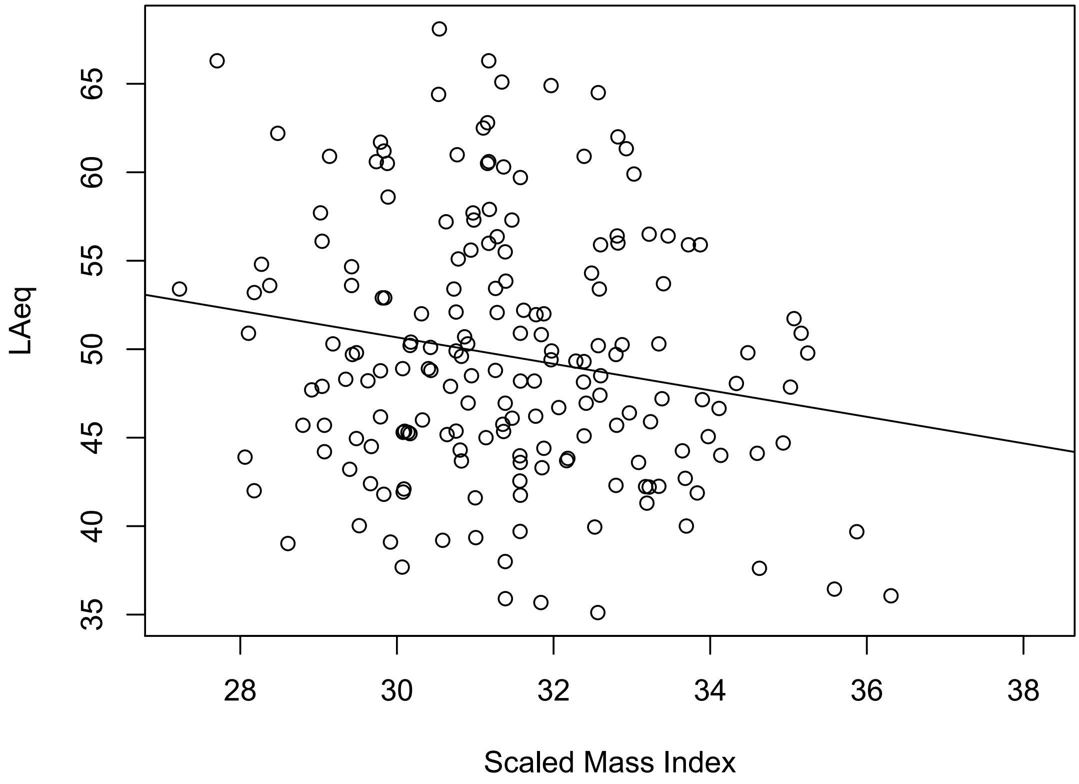
Abbott's Lagoon (Rural)

Summary: AICc top model is PC3, where older birds tend to be higher performance. Noise doesn't affect performance.

AICc Top Model: Deviation~PC3

Coefficients	*Estimate*	*SE*	*t-value*	*P*	
(Intercept)	22.8654	0.4801	47.63	5.62E-16	***
PC3	-1.2642	0.6448	-1.961	0.0717	.

Residual standard error: 1.81 on 13 degrees of freedom
Multiple R-squared: 0.2282, Adjusted R-squared: 0.1689
F-statistic: 3.845 on 1 and 13 DF, p-value: 0.07169



Appendix 3 Figure. Across 6 locations, males tend to be smaller on noisier territories ($R^2 = 0.03$, $F_{1,182} = 6.37$, $P = 0.01$). Scaled mass index calculated following Peig & Green (2009).

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