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RESEARCH ARTICLE

Vocal performance is a salient signal for male–male competition in White-crowned Sparrows

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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 trade-off 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 trade-off 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 2 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.

Keywords: birdsong, male–male competition, vocal performance, sexual selection, *Zonotrichia leucophrys nuttalli*

El desempeño vocal es una señal sobresaliente de competencia entre machos en *Zonotrichia leucophrys*

RESUMEN

La comunicación vocal en aves canoras es importante para la señalización agresiva porque una señal honesta permite que sus receptores evalúen las cualidades de sus competidores. Un aspecto del canto que los individuos coespecíficos pueden evaluar es el desempeño vocal. Un ejemplo de desempeño vocal es qué tan bueno es un individuo en el compromiso entre la tasa de trino y el ancho de banda en la producción de notas repetidas. Se cree que este tipo de desempeño vocal (desviación vocal) es una señal honesta porque la habilidad de un macho de maximizar el ancho de banda y la tasa de trino está limitada por restricciones motoras en la modificación del sonido. Además, qué tan bueno es un macho para repetir este compromiso puede brindar información a los receptores sobre el emisor y el nivel de desempeño vocal de un macho puede afectar la fuerza de su respuesta a cantos con alto desempeño. Pusimos a prueba si los machos se evalúan unos a otros basados en el desempeño vocal en una importante especie modelo, *Zonotrichia leucophrys*. Demostramos que los machos de *Z. leucophrys* responden más fuertemente a los cantos de desempeño alto que a los de desempeño bajo en dos localidades diferentes, lo que apoya la hipótesis de que los machos usan el desempeño vocal para evaluar a sus competidores. También presentamos evidencia inicial de que el desempeño vocal varía entre machos y es repetible en los individuos.

Palabras clave: cantos de aves, competencia entre machos, desempeño vocal, selección sexual, *Zonotrichia leucophrys nuttalli*

INTRODUCTION

In animal communication, 2 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 and 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 and 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 and Harper 2004).

Bird song is a commonly studied communication signal used in competition (Catchpole 1987, Catchpole and 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 and 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 and Suthers 1989). Similarly, other index signals maintained by breathing patterns or energy allocation may also affect the amount of time spent singing (Lambrechts and 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 trade-off 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 (Nowicki and Marler 1988, Westneat et al. 1993, Podos 1996, Riede et al. 2006). In birds with broadband trilled notes, there is a trade-off 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 trade-off, 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 trade-off 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 Island Canary (*Serinus canaria*; Drăgănoiu et al. 2002), Swamp Sparrow (*Melospiza georgiana*; Ballentine et al. 2004), and Lincoln's Sparrow (*Melospiza lincolni*; Caro et al. 2010).

Female preference for high performance is even found in a mammal species, singing mice (*Scotinomys teguina*; 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 Blackbird (*Agelaius phoeniceus*) respond less to high-performance songs (Cramer and Price 2007), whereas Swamp Sparrows (Dubois et al. 2011) and Nightingales (*Luscinia megarhynchos*; Schmidt et al. 2008) respond more to high-performance songs. Banded Wren (*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.

The White-crowned Sparrow (*Zonotrichia leucophrys*) is a well-studied species for understanding how birds learn song (Marler and Tamura 1964), form dialects (Baptista 1975, Petrinovich and Baptista 1984, Baker and Thompson 1985, Nelson et al. 2004), choose mates (Chilton et al. 1990, MacDougall-Shackleton et al. 2002), defend territories (Patterson and Petrinovich 1978, Nelson and Soha 2004, Poesel and 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 2 breeding populations of Nuttall's White-crowned Sparrow (*Z. l. nuttalli*) in Point Reyes, California, and San Francisco, California. 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, California ($n = 51$ males, 367 songs), and in Golden Gate Park, Lake Merced, and throughout the Presidio in San Francisco, California ($n = 109$, 780 songs), using a digital recorder (PMD 661, Marantz, Kanagawa, Japan), omnidirectional microphone (ME-62, Sennheiser, Wedemark, Germany), and parabola (SME-1000, Saul Mineroff Electronics, Elmont, New York, USA). Some of these males were also tested with playbacks (Point Reyes $n = 19$, San Francisco $n = 16$; see Playback design below). Point Reyes males that were 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 to 12 (mean \pm SD: Point Reyes 6.5 ± 2.8 songs; San Francisco 7.75 ± 3 ; see [Supplemental Material Appendix A](#) for individual data). 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, 10.2 ms 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 1,572 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 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 8 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). 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 4 McClure low-performance stimuli with slower trill rates (Table 1). Because stimulus pairs were reused in

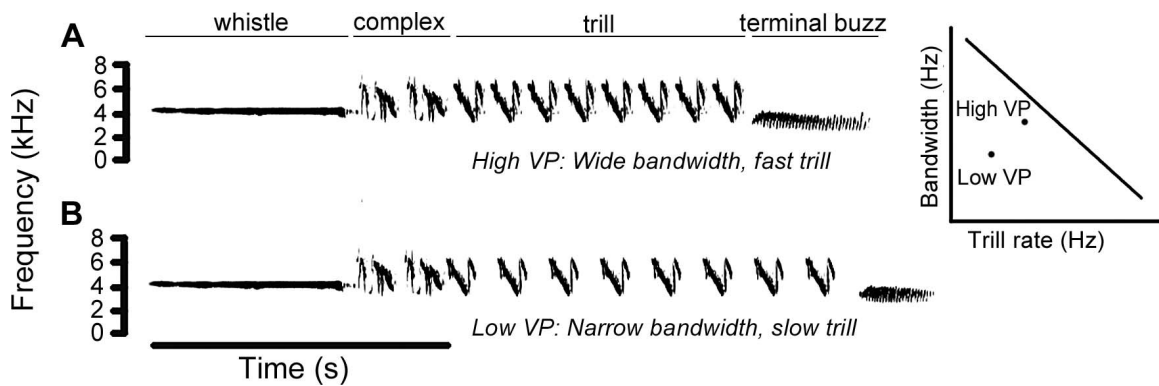


FIGURE 1. Examples of high-performance and low-performance stimuli used in male territorial playback experiments in McClure dialect: **(A)** wide bandwidth, fast trill rate exemplar, **(B)** narrow bandwidth, slow trill rate exemplar. Inset indicates relative placement of 2 stimuli to the performance limit of frequency bandwidth by trill rate, where VP stands for vocal performance.

playback analyses, we include the effect of stimulus identity on response (see Statistical Analyses below).

In creating our 2 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 2 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 (Drăgănoiu et al. 2002, Ballentine et al. 2004, Dubois et al. 2011, Moseley et al. 2013). We manipulated all stimuli, so male response is not due to playback of manipulated versus unmanipulated stimuli.

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 stages 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, a speaker (inMotion iMT320, Altec Lansing, New York, New York, USA) with a portable media player (6th generation iPod Nano; Apple, Cupertino, California, USA) was placed near the territory center on a platform 0.5 m 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 1 m from the speaker using a 7-range sound level meter (RadioShack, Fort Worth, Texas, USA) and the songs were broadcast at a song bout speed (6 songs min^{−1}) typical for this species.

We started playback when the focal male was in view and within 24 m of the speaker. Each trial consisted of a 3 min playback period and a 6 min post-playback period. In

TABLE 1. The range of vocal deviation, trill rates, and bandwidths of songs as compared to stimuli, showing range; mean ± SD. VP stands for vocal performance.

Type	No. of songs	Vocal deviation	Trill rate (Hz)	Bandwidth (Hz)	Repeatability
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	0.51
McClure High VP stimuli	7	17.7–21.8; 19.9 ± 1.5	8.4–9.9; 9.2 ± 0.5	3700.9–4127; 3939.2 ± 152.2	
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	0.74
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	

White-crowned Sparrows, responses to different simulated intrusions vary most after playback has stopped (Nelson and Soha 2004), so we used a longer post-playback period 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 s 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 >16 m. We used the median distance of each category and 24 m for the >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 2 measures of response. First, we analyzed response as measured by approach distance to the speaker, because in 2 closely related species, Song Sparrow (*M. melodia*) and Swamp Sparrow, 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 6 behavioral measures to yield a composite measure of response. We compared response to high- and lower-performance songs by fitting models using Akaike's Information Criterion (AIC_c). 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). 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 $3,594.2 \pm 385.4$ 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 $2,753.2 \pm 648.8$, and average vocal performance was 22.2 ± 5.2 . We report the range for trill rate, frequency bandwidth, and vocal performance in Table 1. Repeatability of vocal performance for Point Reyes was 0.51 (0.4–0.63 95% CI, $n = 51$, $F = 8.44$, $df = 50$ and 313, $P < 0.001$), and 0.74 for San Francisco (0.68–0.80 95% CI, $n = 109$, $F = 21.5$, $df = 108$ and 671, $P < 0.001$), 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 3 principal components with eigenvalues greater than 1 for Point Reyes, and 2 principal components in both Point Reyes subset and San Francisco (see Table 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_c . 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 variable and not a significant component of models, and thus we rejected these models as uninformative (Burnham and Anderson 2002, Arnold 2010). All AIC_c tables and importance values for model exploration are included in Appendix B.

For approach distance, the model with stimulus type significantly predicts male response as compared to a null model (Point Reyes: $\chi^2 = 7.25$, $P = 0.007$; Point Reyes subset: $\chi^2 = 7.65$, $P = 0.005$; San Francisco: $\chi^2 = 4.73$, $P = 0.02$). We found that males gave a significantly different

TABLE 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.

Response variables	Loadings			Raw response (mean \pm SD)	
	PC1	PC2	PC3	High performance	Low performance
Point Reyes					
Latency to sing (s)	0.036	0.903	−0.119	11 \pm 10.5	43.1 \pm 70.6
No. songs during playback	0.18	−0.861	−0.258	20.1 \pm 5.2	14.7 \pm 8.3
Distance during post-playback (m)	−0.455	0.555	0.309	6 \pm 3.2	11.9 \pm 7.8
No. wing waves	0.898	0.003	0.131	3 \pm 4	1 \pm 2
No. flyovers	0.831	−0.054	−0.27	7.4 \pm 4.6	3.4 \pm 4.1
No. songs during post-playback	0.664	−0.318	−0.381	31.9 \pm 14.9	23.5 \pm 14.6
Latency to approach (s)	−0.183	−0.057	0.877	33.7 \pm 68	39 \pm 41.7
Distance during playback (m)	−0.027	0.484	0.659	3.6 \pm 2.6	6.5 \pm 4.5
Eigenvalues	3.4	1.58	1.05		
Percentage of variation	42.55	19.73	13.13		
Point Reyes subset					
Latency to sing (s)	0.786	−0.058		11.4 \pm 9	90 \pm 95.4
No. songs during playback	−0.869	0.255		20.1 \pm 5.4	9.9 \pm 9.5
Distance during post-playback (m)	0.504	−0.537		6.1 \pm 3	13.6 \pm 8.2
No. wing waves	0.212	0.842		3.1 \pm 3.3	1.3 \pm 2.2
No. flyovers	−0.313	0.807		6.6 \pm 4.3	4.7 \pm 3.9
No. songs during post-playback	−0.203	0.842		30.3 \pm 18.4	22.3 \pm 17.7
Latency to approach (s)	0.746	−0.288		47.1 \pm 107.4	32.9 \pm 25
Distance during playback (m)	0.9	0.097		3 \pm 2.1	6.3 \pm 4.4
Eigenvalues	3.82	1.88			
Percentage of variation	47.7	23.5			
San Francisco					
Latency to sing (s)	−0.05	0.873		36.3 \pm 40.1	59.4 \pm 97.3
No. songs during playback	−0.271	−0.87		14.7 \pm 7.2	11.6 \pm 6.7
Distance during post-playback (m)	0.774	−0.148		7.9 \pm 6.1	12.9 \pm 5.2
No. wing waves	−0.575	0.363		2.1 \pm 4.1	0.38 \pm 0.8
No. flyovers	−0.587	−0.17		3 \pm 3.5	1.5 \pm 2.3
No. songs during post-playback	−0.664	−0.224		27.9 \pm 18.9	14.7 \pm 10.8
Latency to approach (s)	0.726	0.02		43.8 \pm 47.9	86.9 \pm 130.1
Distance during playback (m)	0.818	0.219		5.3 \pm 3.6	7.9 \pm 3.8
Eigenvalues	3.06	1.72			
Percentage of variation	38.27	21.53			

response to playback of high-performance versus lower-performance songs for PC1 (Point Reyes PC1: $\chi^2 = 6.26$, $P = 0.01$; San Francisco PC1 $\chi^2 = 5.86$, $P = 0.01$) and PC2 (Point Reyes PC2: $\chi^2 = 4.76$, $P = 0.03$). 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 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 B); the null model and the stimulus type model were significantly different ($\chi^2 = 3.93$, $P = 0.04$). 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: $\chi^2 = 0.27$, $P = 0.6$; Point Reyes subset PC2: $\chi^2 = 2.42$, $P = 0.12$). San Francisco PC2 had Male VP as the top model, within 0.44 AIC of the null, which also was not significantly different ($\chi^2 = 0.66$, $P = 0.42$).

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 \pm SE], low performance: 10 ± 6 , Figure 2A; Point Reyes subset: high performance: 5.1 ± 2 , low performance: 11.1 ± 5.9 , Figure 2B; San Francisco: high performance: 7.1 ± 4.9 , low performance: 10.6 ± 4.4 ; Figure 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: $t = -4.3$, $df = 18$, $P = 0.003$; Point Reyes subset: $t = -3.6$, $df = 6$, $P = 0.009$; San Francisco: $t = -2.32$, $df = 15$, $P = 0.04$).

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: $t = -3.24$, $df = 18$, $P = 0.009$; Point Reyes

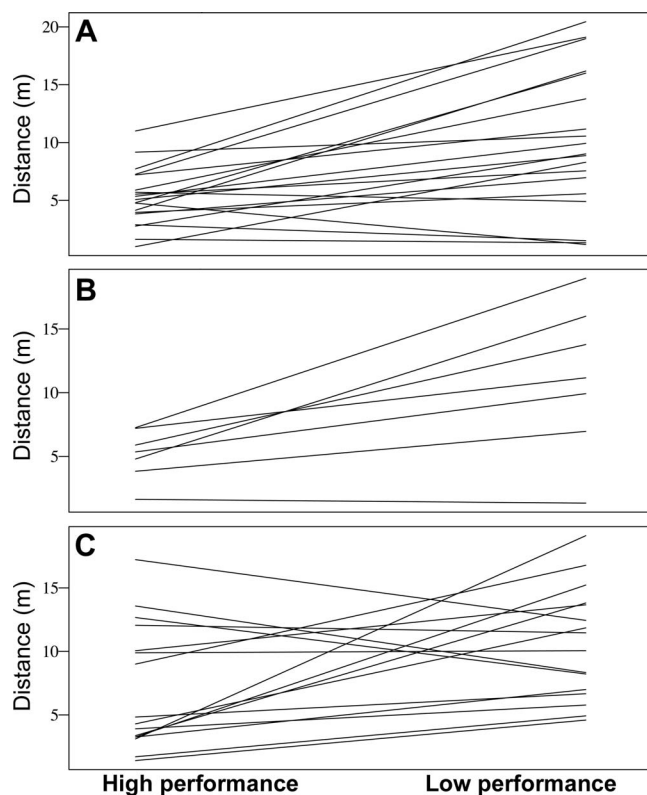


FIGURE 2. Birds approach high-performance songs more closely than low-performance songs in (A) Point Reyes, (B) a subset of Point Reyes birds that heard stimuli within the McClure natural range, and (C) San Francisco. Each line connects an individual bird's approach distance to high-performance stimuli 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.

subset: $t = -3.06$, $df = 6$, $P = 0.02$; San Francisco, $t = -2.63$, $df = 15$, $P = 0.04$) and Point Reyes PC2 ($t = 3.43$, $df = 18$, $P = 0.03$) but not PC2 for Point Reyes subset and San Francisco (Point Reyes subset: $t = 2$, $df = 6$, $P = 0.1$; San Francisco, $t = -0.83$, $df = 15$, $P = 0.42$). Point Reyes PC3 also was not significantly predicted by stimulus type ($t = -0.49$, $df = 18$, $P = 0.63$).

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 \pm 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: $t = 1.15$, $df = 15$, $P = 0.26$; San Francisco: $t = -0.73$, $df = 18$, $P = 0.5$), which might explain why a male's own vocal performance value does not explain variation in response to these 2 stimuli.

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 for song parts). The whistle is an alerting mechanism and important for song development and acquisition in young birds (Marler 1970, Soha and Marler 2001, Soha and Whaling 2002). The note complex is thought to allow recognition of individuals (Nelson and Poesel 2007), and often varies within a dialect (Dewolfe et al. 1974, Baptista 1975). Nelson and Poesel (2010) suggested 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 and 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 et al. 2016). Luther et al. (2016) suggested 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 and 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 2 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 (Ballentine et al. 2004, Dubois et al. 2011). Banded Wrens also have high repeatability (0.82–0.86) within 2 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 (Cramer 2013b). In playback experiments, male House Wrens do not respond to differences in vocal performance (Cramer 2013a). 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.

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LITERATURE CITED

- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Baker, M. C., and D. B. Thompson (1985). Song dialects of White-crowned Sparrows: Historical processes inferred from patterns of geographic variation. *The Condor* 87:127–141.
- Ballentine, B., J. Hyman, and S. Nowicki (2004). Vocal performance influences female response to male bird song: An experimental test. *Behavioral Ecology* 15:163–168.
- Baptista, L. F. (1975). Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). University of California Publications in Zoology 105.
- Barton, K. (2011). MuMIn: Multi-model inference. R package version 1.0.0. R Foundation for Statistical Computing, Vienna, Austria.
- Bates, D., M. Maechler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Beeman, K. (1998). Digital signal analysis, editing, and synthesis. In *Animal Acoustic Communication: Sound Analysis and Research Methods* (S. L. Hopp, M. J. Owren, and C. S. Evans, Editors). Springer-Verlag, Berlin, Germany. pp. 59–104.
- Boake, C. R. B. (1989). Repeatability: Its role in evolutionary studies of mating behavior. *Evolutionary Ecology* 3:173–182.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Botero, C. A., R. J. Rossman, L. M. Caro, L. M. Stenzler, I. J. Lovette, S. R. de Kort, and S. L. Vehrencamp (2009). Syllable type consistency is related to age, social status and reproductive success in the Tropical Mockingbird. *Animal Behaviour* 77: 701–706.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference*. Springer-Verlag, New York, NY, USA.
- Cardoso, G. C., J. W. Atwell, E. D. Ketterson, and T. D. Price (2007). Inferring performance in the songs of Dark-eyed Juncos (*Junco hyemalis*). *Behavioral Ecology* 18:1051–1057.
- Caro, S. P., K. B. Sewall, K. G. Salvante, and K. W. Sockman (2010). Female Lincoln's Sparrows modulate their behavior in response to variation in male song quality. *Behavioral Ecology* 21:562–569.
- Catchpole, C. K. (1987). Bird song, sexual selection and female choice. *Trends in Ecology & Evolution* 2:94–97.
- Catchpole, C. K., and P. J. B. Slater (2008). *Bird Song: Biological Themes and Variations*, 2nd edition. Cambridge University Press, Cambridge, UK.
- Chilton, G., M. R. Lein, and L. Baptista (1990). Mate choice by female White-crowned Sparrows in a mixed-dialect population. *Behavioral Ecology and Sociobiology* 27:223–227.
- Cramer, E. R. A. (2013a). Vocal deviation and trill consistency do not affect male response to playback in House Wrens. *Behavioral Ecology* 24:412–420.
- Cramer, E. R. A. (2013b). Physically challenging song traits, male quality, and reproductive success in House Wrens. *PLOS One* 8:e59208. doi:10.1371/journal.pone.0059208
- Cramer, E. R. A., M. L. Hall, S. R. de Kort, I. J. Lovette, and S. L. Vehrencamp (2011). Infrequent extra-pair paternity in the Banded Wren, a synchronously breeding tropical passerine. *The Condor* 113:637–645.
- Cramer, E. R. A., and J. J. Price (2007). Red-winged Blackbirds *Agelaius phoeniceus* respond differently to song types with different performance levels. *Journal of Avian Biology* 38: 122–127.
- de Kort, S. R., E. R. B. Eldermire, E. R. A. Cramer, and S. L. Vehrencamp (2009). The deterrent effect of bird song in territory defense. *Behavioral Ecology* 20:200–206.
- Derryberry, E. P. (2009). Ecology shapes birdsong evolution: Variation in morphology and habitat explains variation in White-crowned Sparrow song. *The American Naturalist* 174: 24–33.
- Derryberry, E. P., R. M. Danner, J. E. Danner, G. E. Derryberry, J. N. Phillips, S. E. Lipshutz, K. Gentry, and D. A. Luther (2016).

- Patterns of song across natural and anthropogenic soundscapes suggest that White-crowned Sparrows minimize acoustic masking and maximize signal content. *PLOS One* 11(4):e0154456. doi:10.1371/journal.pone.0154456
- Dewolfe, B. B., D. D. Kaska, and L. J. Peyton (1974). Prominent variations in the songs of Gambel's White-crowned Sparrows. *Bird-Banding* 45:224–252.
- Drăgănoiu, T. I., L. Nagle, and M. Kreutzer (2002). Directional female preference for an exaggerated male trait in Canary (*Serinus canaria*) song. *Proceedings of the Royal Society B: Biological Sciences* 269:2525–2531.
- Dubois, A. L., S. Nowicki, and W. A. Searcy (2011). Discrimination of vocal performance by male Swamp Sparrows. *Behavioral Ecology and Sociobiology* 65:717–726.
- DuBois, A. L., S. Nowicki, and W. A. Searcy (2009). Swamp Sparrows modulate vocal performance in an aggressive context. *Biology Letters* 5:163–165.
- Forstmeier, W., B. Kempenaers, A. Meyer, and B. Leisler (2002). A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal Society B: Biological Sciences* 269:1479–1485.
- Hartley, R. S., and R. A. Suthers (1989). Airflow and pressure during Canary song: Direct evidence for mini-breaths. *Journal of Comparative Physiology A* 165:15–26.
- Hofstad, E., Y. Espmark, A. Moksnes, T. Haugan, and M. Ingebrigtsen (2002). The relationship between song performance and male quality in Snow Buntings (*Plectrophenax nivalis*). *Canadian Journal of Zoology* 80:524–531.
- Illes, A. E., M. L. Hall, and S. L. Vehrencamp (2006). Vocal performance influences male receiver response in the Banded Wren. *Proceedings of the Royal Society B: Biological Sciences* 273:1907–1912.
- Lambrechts, M., and A. A. Dhondt (1987). Differences in singing performance between male Great Tits. *Ardea* 75:43–52.
- Luther, D. A., J. Phillips, and E. P. Derryberry (2016). Not so sexy in the city: Urban birds adjust songs to noise but compromise vocal performance. *Behavioral Ecology* 27:332–340.
- MacDougall-Shackleton, E. A., E. P. Derryberry, and T. P. Hahn (2002). Nonlocal male Mountain White-crowned Sparrows have lower paternity and higher parasite loads than males singing local dialect. *Behavioral Ecology* 13:682–689.
- MacDougall-Shackleton, S. A. (1997). Sexual selection and the evolution of song repertoires. In *Current Ornithology*, 14th edition (V. Nolan, E. D. Ketterson, and C. Thompson, Editors). Plenum, New York, NY, USA. pp. 81–124.
- Marler, P. (1970). A comparative approach to vocal learning: Song development in White-crowned Sparrows. *Journal of Comparative and Physiological Psychology* 71:1–25.
- Marler, P., and M. Tamura (1964). Culturally transmitted patterns of vocal behavior in sparrows. *Science* 146:1483–1486.
- Maynard Smith, J., and D. Harper (2004). *Animal Signals*. Oxford University Press, Oxford, UK.
- Mazerolle, M. J. (2016). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-4. <https://cran.r-project.org/package=AICcmodavg>
- McGregor, P. K., C. Catchpole, T. Dabelsteen, J. Falls, L. Fusani, H. Gerhardt, F. Gilbert, A. Horn, G. M. Klump, D. Kroodsmä, et al. (1992). Design of playback experiments: The Thornbridge Hall NATO ARW consensus. In *Playback and Studies of Animal Communication* (P. K. McGregor, Editor). Plenum Press, New York, NY, USA. pp. 1–9.
- Moseley, D. L., D. C. Lahti, and J. Podos (2013). Responses to song playback vary with the vocal performance of both signal senders and receivers. *Proceedings of the Royal Society B: Biological Sciences* 280:20131401.
- Nelson, D. A., K. I. Hallberg, and J. A. Soha (2004). Cultural evolution of Puget Sound White-crowned Sparrow song dialects. *Ethology* 110:879–908.
- Nelson, D. A., and A. Poesel (2007). Segregation of information in a complex acoustic signal: Individual and dialect identity in White-crowned Sparrow song. *Animal Behaviour* 74:1073–1084.
- Nelson, D. A., and A. Poesel (2010). Song length variation serves multiple functions in the White-crowned Sparrow. *Behavioral Ecology and Sociobiology* 65:1103–1111.
- Nelson, D. A., and J. A. Soha (2004). Perception of geographical variation in song by male Puget Sound White-crowned Sparrows, *Zonotrichia leucophrys pugetensis*. *Animal Behaviour* 68:395–405.
- Nowicki, S., and P. Marler (1988). How do birds sing? *Music Perception* 5:391–426.
- Nowicki, S., S. Peters, and J. Podos (1998). Song learning, early nutrition and sexual selection in songbirds. *American Zoologist* 190:179–190.
- Nowicki, S., and W. A. Searcy (2005). Song and mate choice in birds: How the development of behavior helps us understand function. *The Auk* 122:1–14.
- Pasch, B., A. S. George, P. Campbell, and S. M. Phelps (2011). Androgen-dependent male vocal performance influences female preference in Neotropical singing mice. *Animal Behaviour* 82:177–183.
- Patterson, T. L., and L. Petrino (1978). Territory size in the White-crowned Sparrow (*Zonotrichia leucophrys*): Measurement and stability. *The Condor* 80:97–98.
- Peters, S. S., W. A. Searcy, and P. Marler (1980). Species song discrimination in choice experiments with territorial male Swamp and Song sparrows. *Animal Behaviour* 28:393–404.
- Petrino, L., and L. F. Baptista (1984). Song dialects, mate selection, and breeding success in White-crowned Sparrows. *Animal Behaviour* 32:1078–1088.
- Podos, J. (1996). Motor constraints on vocal development in a songbird. *Animal Behaviour* 51:1061–1070.
- Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51:537–551.
- Podos, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* 409:185–188.
- Podos, J., D. C. Lahti, and D. L. Moseley (2009). Vocal performance and sensorimotor learning in songbirds. In *Advances in the Study of Behavior*, Volume 40 (M. Naguib, K. Zuberbühler, N. S. Clayton, and V. M. Janik, Editors). Academic Press, London, UK. pp. 159–195.
- Poesel, A., K. Foerster, and B. Kempenaers (2001). The dawn song of the Blue Tit *Parus caeruleus* and its role in sexual selection. *Ethology* 107:521–531.
- Poesel, A., and D. A. Nelson (2012). Delayed song maturation and territorial aggression in a songbird. *Biology Letters* 8:369–371.
- R Development Core Team (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Riede, T., R. A. Suthers, N. H. Fletcher, and W. E. Blevins (2006). Songbirds tune their vocal tract to the fundamental frequency of their song. *Proceedings of the National Academy of Sciences USA* 103:5543–5548.
- Schmidt, R., H. P. Kunc, V. Amrhein, and M. Naguib (2008). Aggressive responses to broadband trills are related to subsequent pairing success in Nightingales. *Behavioral Ecology* 19:635–641.
- Searcy, W. A., R. C. Anderson, and S. Nowicki (2006). Bird song as a signal of aggressive intent. *Behavioral Ecology and Sociobiology* 60:234–241.
- Searcy, W. A., and S. Nowicki (2005). *The Evolution of Animal Communication*. Princeton University Press, Princeton, NJ, USA.
- Soha, J. A., and P. Marler (2001). Vocal syntax development in the White-crowned Sparrow (*Zonotrichia leucophrys*). *Journal of Comparative Psychology* 115:172–180.
- Soha, J. A., and C. Whaling (2002). Responses of adult White-crowned Sparrows to playback of song phrases: Implications for the ontogeny of song recognition. *The Condor* 104:848–854.
- Sprau, P., T. Roth, V. Amrhein, and M. Naguib (2013). The predictive value of trill performance in a large repertoire songbird, the Nightingale *Luscinia megarhynchos*. *Journal of Avian Biology* 44:567–574.
- Vehrencamp, S. L., J. Yantachka, M. L. Hall, and S. R. de Kort (2013). Trill performance components vary with age, season, and motivation in the Banded Wren. *Behavioral Ecology and Sociobiology* 67:409–419.
- Westneat, M. W., J. H. Long, Jr., W. Hoese, and S. Nowicki (1993). Kinematics of birdsong: Functional correlation of cranial movements and acoustic features in sparrows. *The Journal of Experimental Biology* 182:147–171.
- Wolak, M. E., D. J. Fairbairn, and Y. R. Paulsen (2012). Guidelines for estimating repeatability. *Methods in Ecology and Evolution* 3:129–137.