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Song perception in communication networks

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SONG PERCEPTION IN COMMUNICATION NETWORKS

A Dissertation Presented

by

SARAH E. GOODWIN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

MAY 2016

Organismic and Evolutionary Biology

SONG PERCEPTION IN COMMUNICATION NETWORKS

A Dissertation Presented

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SARAH E. GOODWIN

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DEDICATION

To:

My mother, who would have been proud, to my husband, Mark Krause, for the endless support, and to little Lyle, the best experiment one could dream of.

FRONTISPIECE
ILLUSTRATION OF SELECTED QUOTATION I.

In long-standing tradition of the Podos Lab, the frontispiece of my dissertation includes the cartoon contest winner. Cartoons were submitted to illustrate the quotation below.

Inspired by SPY vs SPY

"The old chipping birds are very intelligent. The turn of the head and the quick glance from the eye show that their familiar bravery is due to no thoughtless confidence, but is based on keen observation and bird wit."

Quotation by Florence Merriam Bailey
"Birds Through an Opera Glass," 1889
Illustration by Theresa Murphy

ACKNOWLEDGMENTS

A few short sentences will not suffice to express my gratitude to and admiration for Jeff Podos, my advisor. Jeff is a shining example of what it means to train graduate students, and I will remain forever grateful for the opportunity to be a part of his lab. He taught me to think broadly and deeply, to confidently discuss science, and by example, how to be the best citizen of our field. Without Jeff's strong guidance and gentle critiques, it is difficult to imagine completing this degree, and furthermore, arriving here with my love of science intact. Thank you, Jeff Podos.

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Thank you to the Organismic and Evolutionary Biology community as well, including numerous graduate students, faculty, and staff. Special thanks go to Luke Remage-Healey, Craig Albertson, and Paige Warren for their graduate "review" and pep talks. I thank Kara Powder too for her friendship and treats. And of course, special thanks go to the heart of the Organismic and Evolutionary Biology program – Penny Jaques. Many, many thanks, Penny.

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Finally, I wish to thank my family – Mark Krause, my husband, and Lyle Krause, our son. Thank you for the support and laughter. Thanks also to my sister, Hannah, for our weekly lunches, and my brother, Adam, who followed a convergent research path via the US Navy. And of course, thank you to my lab family, both nestling and fledged: Amy Strauss, Jesse McClure, Dave Hof, Dana Moseley, and Ben Taft.

ABSTRACT

SONG PERCEPTION IN COMMUNICATION NETWORKS

MAY 2016

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Communication is a cornerstone of animal behavior and mediates myriad interactions pertaining to survival and reproduction. For animals that communicate acoustically, signals are carried to multiple receivers in what is described as communication networks. In my dissertation, I explore how songbirds and their songs are perceived and used in networks. First, I examine a dilemma many animals face when communicating in a network – how do animals contend with overlapping, conspecific noise? Using a playback experiment in the field, I document Black-capped Chickadees (*Poecile atricapillus*) shifting the frequency of their song in the presence of overlapping noise. Next, I examine song function in communication networks, and evidence for social eavesdropping. Using Chipping Sparrows (*Spizella passerina*), I first explored what song parameters territorial males find salient. I found residents are attentive to variation in trill rate or how quickly notes are repeated per unit time. In a parallel experiment, I found no evidence that males attended to a related song parameter – the total frequency range covered in a song, although I did find evidence these two parameters trade-off. In further work, I found males are attentive to the song performance of their neighbors, and occasionally cooperate to help expel intruders. My work reveals that males cooperate under specific circumstances; when the resident under attack has a relatively slow song, and the simulated intruder has a comparatively fast song. These field studies suggest neighbor-turned-allies are most likely to help nearby residents when the intruder is relatively threatening, and suggests males may eavesdrop on their neighbors. Finally, I surveyed Chipping Sparrow neighborhoods throughout Western Massachusetts and was unable to detect any effect of social factors on territory choice. Together, my work describes some disadvantages and advantages songbirds face in communicating in networks, and contributes to our understanding of the importance of networks in signal evolution.

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CHAPTER 1

SHIFT OF SONG FREQUENCIES IN RESPONSE TO MASKING TONES

Published in *Animal Behaviour* Nov. 2012

Abstract

Ambient noise can interfere with signal transmission and detection across many taxa and modalities. Evidence suggests that, over time, signals evolve to minimize interference from ambient noise and other signalling animals. Less well studied is the possibility of short-term behavioural responses to transient ambient noise, in which animals actively adjust signal parameters to recover signalling efficacy. Here we test animals' capacity to adjust vocal signal parameters in the face of transient acoustic interference. In field trials we monitored the songs of territorial male black-capped chickadees, *Poecile atricapillus*, determined the frequencies of their 'fee-bee' songs, and broadcast tones to closely mask subjects' 'bee' notes. We also presented control nonmasking tones of 5 kHz, well above birds' song frequencies. Our main finding was that males responded to masking tones by shifting song frequencies after an average of 66.4 s from tone onset, whereas frequency shifts in the presence of nonmasking tones occurred only after an average of 95.8 s. The quicker shift in frequencies in the face of masking noise provides new evidence for vocal behavioural plasticity, and further reveals how behavioural plasticity together with evolutionary adaptations can minimize the detrimental effects of ambient noise on communication.

Introduction

Animal communication signals enroute from sender to receiver are often subject to interference. For example, loud ambient noise for acoustic signals, or murky media for visual signals, can reduce the ability of receivers to detect those signals, a phenomenon known as 'masking' (Klump 1996). Signals that minimize masking in their respective habitats have generally been favoured over evolutionary time because of their greater efficacy (Ryan and Cummings 2005). In the acoustic realm, signal frequency and timing features evolve to minimize habitat-specific degradation (acoustic adaptation hypothesis; Morton 1975; Wiley 1991). Masking interference from other vocalizing animals provides another source of selection on vocal behaviour. In chorus settings, taxa as diverse as frogs, cicadas and birds reduce masking interference by partitioning their signals in time and structure among species (Garcia-Rutledge and Narins 2001; Sueur 2008; Luther 2009), and by accentuating signal differences when ranges overlap (character displacement, e.g. Schluter 2000).

While acoustic signals are typically adapted for transmission efficacy, they can still be masked when the sound environment is dynamic or unpredictable. Two such scenarios that have received particular attention in recent years are when signallers are masked by vocalizing conspecifics (Todt and Naguib 2000) or by anthropogenic noise (Brumm and Slabbekoorn 2005). Available evidence suggests that animals faced with either scenario are indeed able to adjust their vocal output, at least to some extent. Frogs (Grafe 1996) and birds (Wasserman 1977; Popp et al. 1985) may avoid masking by conspecifics by actively alternating the timing of their signals, by switching to other signal types (if they have a signal repertoire, Catchpole and Slater 2008), or by altering spectral characteristics of their signals (Mennill and Ratcliffe 2004a). Birds faced with anthropogenic noise, such as in urban environments, appear able to avoid acoustic masking by increasing frequency (Slabbekoorn and Peet 2003; Wood and Yezerinac 2006; Hu and Cardoso 2009), increasing amplitude (Brumm and Todt 2002; Brumm 2004; Nemeth and Brumm 2010), or by altering signal timing (Fuller et al. 2007).

Most prior studies on animals' responses to acoustic masking have been correlative. However, several recent studies on urban noise effects in birds have taken an experimental approach, presenting individuals with transient noise through loudspeakers and documenting subsequent vocal behaviour. This approach holds the promise of offering direct insights into how quickly and completely individuals may adjust to masking interference. Great tits, *Parus major,* played simulated city noise were found to switch to song types with more high-frequency elements, and when played an inverse high-frequency noise, they switched to song types with more low-frequency elements (Halfwerk and Slabbekoorn 2009). Reed buntings, *Emberiza schoeniclus,* responded to simulated traffic noise by singing with increased minimum frequencies, a pattern not found when the subjects were played heterospecific song (Gross et al. 2010). Chiffchaffs, *Phylloscopus collybita*, exposed to pre-recorded traffic noise in an otherwise quiet habitat sang at higher minimum frequencies, and returned to lower frequencies after cessation of playback (Verzijden et al. 2010). Finally, captive house finches, *Carpodacus mexicanus*, played urban noise also shifted the frequencies of their song upwards in response

(Bermudez-Cuamatzin et al. 2011). All of these species thus show some evidence of vocal plasticity in the face of transient masking noise, although much remains to be learned.

In the present study, we assessed vocal plasticity in response to masking noise in black-capped chickadees, *Poecile atricapillus*. This species is known to sing at higher frequencies in noisy environments (Proppe et al. 2012), to transpose the starting frequencies of their songs under natural conditions (Horn et al. 1992) and to match frequencies during social interactions (Horn et al. 1992; Mennill and Ratcliffe 2004a; Foote et al. 2008). These lines of evidence suggest that chickadees are especially attentive to the structure of conspecific vocalizations and other environmental sounds, and we hypothesized that chickadees would thus also be highly responsive to the presence of masking noise. In contrast to previous experimental studies on songbirds' responses to acoustic masking (cited above), which used broadband noise as experimental stimuli, here we present masking stimuli in the form of pure tones targeted to chickadees' song frequencies. Broadband masking stimuli might elicit different kinds of responses than narrow-frequency masking stimuli as they are structurally similar to a portion of the chickadee's song, a possibility that has yet to be tested. Moreover, the wealth of information already available on vocal communication and chickadee social behaviour (e.g. Smith 1991; Otter 2007) provides a useful context for interpreting data on the effects of masking. In our study, we compared birds' reactions to targeted pure-tones and to control pure-tones that did not overlap the singers' vocal frequencies. We predicted that, if chickadees respond to masking, then they should shift song frequencies more rapidly in the presence of masking pure-tones than in the presence of nonmasking control tones.

Methods

Black-capped chickadees are common resident birds across the central and northern extent of the U.S. and Canada. They are generalist foragers that thrive at woodland edges, and are common visitors at feeding stations (Foote et al. 2010). Both males and females produce a variety of vocalizations (Ficken et al. 1978; Smith 1991), but only males produce a two note 'fee-bee' song (Fig. 1), which functions in mate attraction and territory defence. Across most of their geographical range, the fee-bee song is highly stereotyped in relative note frequencies, exhibiting less than 2% variation in frequency ratios between the start and the end of the 'fee' note, and between the end of the 'fee' and the 'bee' note (Weisman et al. 1990). By contrast, individual males often vary considerably in the absolute frequencies of the fee-bee song, naturally transposing the entire song such that the bee note varies up and down a continuous range of about 2700–3600 Hz (Horn et al. 1992). Males typically shift their song frequency, under normal conditions, once every 30–40 songs (Horn et al. 1992; Christie et al. 2004).

We studied populations of chickadees in western Massachusetts in state and local parks across Hampshire and Franklin County (Quabbin Reservoir 42°17'45"N, 72°19'14"W; Mount Holyoke Range State Park 42°18'27"N, 72°30'55"W; Audubon Society's Arcadia Wildlife Sanctuary 42°17'30"N, 72°38'58"W; Mount Toby State Forest 42°29'35"N, 72°31'50"W; Amethyst Brook Conservation Area 42°22'42"N, 72°28’60”W; and Groff Park 42°21’30”N, 72°31’3”W). Focal males were separated by at least 500 m to minimize the risk of recording the same individual twice (Wilson and Mennill 2011). Our research was conducted between 28 April and 5 June 2010, and between 26 April and 30 May 2011. During these months, winter flocks disperse and males establish and defend territories with song (Smith 1991). Song output peaks during the dawn chorus, which begins about 30 min before sunrise and continues for about 30 min past sunrise. During this chorus, males sing at a nearly continuous rate and often from a single perch, facilitating the localization of individual males and our ability to conduct full experimental trials.

Experimental Trials

Prior to our study, we generated a library of ‘masking’ tones to be used for playback, using the tone generator function in Audacity 1.3.12 (http://audacity.sourceforge.net). We created nine pure tones at frequencies of 2900–3700 Hz in increments of 100 Hz, corresponding to the range of natural variation in the bee portion of chickadee song. We also generated a single control tone at 5000 Hz, a frequency well above observed frequencies in chickadee songs but presumably still within their capacity to hear (e.g. Dooling 1982; Henry and Lucas 2010).

For each trial, we first located a singing male within 1 h before dawn each morning, and positioned our playback equipment within 10 m. Each trial lasted 10 min and consisted of five sequential 2 min blocks (Fig. 2), which included both a 2 min masking tone and the 2 min control tone. Focal males were recorded for 2 min, then presented either a 2 min masking tone or control tone followed by 2 min of silence, then the other tone, again followed by 2 min of silence (Fig. 3). Presentation order of the control tone and masking tone were balanced across trials. While the bird was singing in the 2 min time block preceding the masking treatment, we inspected real-time spectrograms of the male's song using Syrinx (Burt 2001) and a Dell Inspiron 600m laptop computer receiving input from a second Sennheiser K6/ME66 shotgun microphone. From these real-time spectrograms we were able to measure the frequency of the bee note of the focal bird's songs and to select the masking tone (from the nine available) that best matched the focal bird's bee frequency. We verified the match between the tone selected and the birds own song in our trial recordings. In the masking treatment, tones closely matched the last bee note, with an average difference of 37.36 ± 6.18 Hz between the masking tone and the song. We played back tones using an iPod Nano connected to a portable speaker (Radio Shack, Cat. No. 40-1434). We standardized the amplitude of tones (either the control or the masking tone, depending on which was played first) to 80 db at 0.5 m as measured with a handheld sound level meter (Radio Shack, Cat. No. 33-2050). Other playback trials that did not use tones have used a greater playback amplitude (i.e. Mennill and Ratcliffe 2004a, 90 db at 1 m), but in this study the tones we used were perceived as sufficiently loud to require ear protection. If a focal male stopped singing for more than 3 min during the trial, or flew from his perch such that we could no longer be certain we were recording the same male, we terminated the trial. During the entire trial, the focal bird was recorded using a Marantz PMD 660 solid-state recorder and a Sennheiser K6/ME66 microphone.

Ethical Note

Tones were played to chickadees at amplitudes below their natural singing levels. While this may have interfered with chickadees' singing behaviour, the effect was likely transient and of no lasting consequence. Our methods were approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee (IACUC No. 2010-002).

Vocal Behaviour and Analyses

From recordings of each trial, we extracted measures of vocal behaviour across the control and masking tone playback (2 min), as well as from the 2 min pretrial recording. We measured latency (s) to the first song frequency shift, the number of songs sung before the first frequency shift, song rate (songs/s), pause length in song after initiating playback (measured from tone onset up to the first song), the birds last singing frequency before a frequency shifted song, the direction of the first frequency shift (up or down) and the magnitude of the shift in Hz. All song measurements were estimated in RavenPro 1.3, using an FFT size of 5000 for frequency measures, corresponding to a frequency resolution of 8.8 Hz with a sampling rate at 44.1 kHz (Charif et al. 2008). We measured the frequency of each song using power spectra to determine the frequency with the greatest amplitude on the second half of the bee note for each song. If a bird did not shift frequency during the tone playback or the following 2 min, we coded its latency measure with the maximum value possible, 120 s, and we coded the total number of songs before a shift as the total number of songs during the tone.

All data were analysed in R (R Development Core Team 2011). We first checked for correlations among our variables of central interest, latency (s) to shift frequency and the number of songs before a frequency shift. We identified strong correlations in these variables (Spearman rank correlation: $r^2 = 0.75$, $P < 0.0001$); therefore, we consider only latency to shift frequency in further analysis. We constructed a generalized linear model (GLM, family = quasi, link = identity) to evaluate how latency to shift song frequency varied in response to treatment group (control or masked tone), the order of presentation and the tone used. We then evaluated how other song behaviours varied by treatment type, using a MANOVA and the following response variables: the duration (s) of the pause after tone initiation, the bird's last singing frequency before a shift, the direction of the shift (up or down) and the magnitude of the shift. We then used Friedman tests and post hoc Wilcoxon signed-ranks tests to examine how latency and song rate varied by treatment type. All means are reported ± 1 SE.

Results

Although we initiated trials on 64 males, males often moved or stopped singing (as a result of the experiment or the end of the dawn chorus). Therefore, we only recorded 20 complete trials. Because we wished to restrict our results to those trials where a male received a complete treatment, we limit our data analyses to those 20 trials.

Before the onset of any playback, males shifted frequency every 26.6 ± 7.5 songs or every 90.62 ± 9.47 s, slightly below the range observed for other studies (30–40 songs; Horn et al. 1992; Christie et al. 2004). Eight males shifted song frequencies during control playback, whereas 14 males shifted song frequencies during masking playback. Five of the males did not shift across either treatment.

After controlling for the order of presentation and the tone used during playbacks, latency to shift song frequency varied only in response treatment type (GLM: $F_{1, 38} = 5.19$, $P = 0.029$). Other measures of song behaviour were invariant across control and masking tones. Pause duration after tone onset, the bird's own song frequency before the first frequency shift, shift direction and shift magnitude were all similar across control and masked treatments (MANOVA: Hotelling's trace = 0.42, $F_{1,4} = 1.78$, $P = 0.179$). Song rates across the 2 min ambient recording and the tone playback periods were also similar (Friedman test: $\chi^2 = 2.33$, $P = 0.314$). Latency to shift song frequency, however, did vary by treatment type (Friedman test: $\chi^2 = 7.43$, $P = 0.024$; Fig. 4). Birds shifted their song frequency more rapidly after the onset of masking tones (66.47 ± 10.48 s latency to shift) than after the onset of the control tone (95.78 ± 7.78 s; Wilcoxon signed-ranks test: T = 104, N = 20, $P = 0.013$). Conversely, chickadees shifted song frequencies at similar rates during pretrial and control tone treatments (90.62 ± 9.47 s; Wilcoxon signed-ranks test: T = 23, N = 20, $P = 0.398$), and shifted more slowly during the pretrial treatment than during the masking treatment (Wilcoxon signed-ranks test: T = 100, N = 20, $P = 0.025$).

Discussion

Our main finding was that male chickadees presented with masking tones shifted song frequencies more quickly than when presented with a nonmasking tone. The higher rate of frequency shifting in the masking treatment was not a correlated effect of differences in song output, as birds sang at similar rates across treatment types. Furthermore, birds did not vary in a suite of other song behaviours measured during control and masking playbacks. Thus, we can conclude that chickadees attend to and respond quickly to masking noise by shifting their song frequencies. Our findings accord with and build upon a growing body of literature illustrating individual vocal plasticity in response to acoustic interference (Halfwerk and Slabbekoorn 2009; Gross et al. 2010; Bermudez-Cuamatzin et al. 2011).

Prior studies of frequency shifting in chickadees have focused on this behaviour's potential role in social interactions. In particular, male chickadees engaged in song contests or bouts of countersinging have been observed to sometimes shift their songs to match the song frequencies of rivals, presumably as a signal of aggression (Horn et al. 1992; Mennill and Ratcliffe 2004a; Foote et al. 2008). Additionally, rival chickadees sometimes overlap each other such that one song begins before a rival's song ends, producing a temporarily highly masked sound environment, especially when song frequencies of rivals are matched. As with matching, overlapping might serve as a signal of a male's aggression: chickadees that are overlapped sometimes alter their own singing behaviour by shortening their songs (Mennill and Ratcliffe 2004a) and, in a two-speaker design, in which one speaker was timed to overlap the other, high-ranking males were more likely to approach the overlapping speaker (Mennill and Ratcliffe 2004b). However, the question of whether overlapping serves as a signal of aggression remains unresolved, especially because some responses to presumably aggressive, overlapping signals are behaviours that might also be expected to avoid signal jamming (Searcy and Beecher 2009, 2011; Naguib and Mennill 2010). Our study contributes to this discussion by confirming that frequency shifting can be driven not only by social context but also by attempts to maintain signal efficacy. In our experiment, the masking tone was a continuous narrow frequency band that overlapped and matched only one portion of the song (the bee), and thus did not approximate the structure of natural chickadee song. The masking tones did, however, simulate the same masking effect experienced in overlapping and matched contests, and thus frequency shifting documented here can be viewed as a mechanistic response to the sudden change in the sound environment. The extent to which frequency shifting during natural contexts can be attributed to social functions versus signalling efficacy remains to be determined.

One open question raised by our study is whether some chickadees show greater plasticity in their singing behaviour than others. In winter, chickadees form flocks with linear hierarchies with stable social ranks (Smith 1976, 1991), and social rank is positively correlated with a number of song parameters including song output at dawn (Otter et al. 1997), the ability to maintain consistent amplitude between fee and bee notes (Hoeschele et al. 2010), and the ability to maintain a consistent internote ratio between the fee and bee frequency (Christie et al. 2004). Might social dominance also correlate with frequency shifting behaviour? Available data argue against this possibility: both high- and low-ranking individuals shift frequencies at similar rates and with similar magnitudes (Christie et al. 2004), and rank is not correlated with the proportion of songs that are matched to the frequencies of neighbours (Fitzsimmons et al. 2008). However, matched bouts of disparately ranked individuals are shorter than those of closely ranked rivals (Foote et al. 2008), and contest-induced frequency shifting by subordinate males would provide a mechanism to explain this pattern. High-ranking males that lose singing contests face considerable loss of paternity (Mennill et al. 2002), and, therefore, may be particularly reluctant to shift frequency in social contexts. We were unable to collect dominance data on our study populations, but we suggest that the relation between plasticity in frequency-shifting behaviour and dominance status warrants further study.

Beyond conspecific interactions in chickadees, our results bear more generally on how vocalizing individuals may respond to transient masking interference. In urban environments, acoustic communication is disrupted by anthropogenic noise, a source of interference that will continue to compound as human infrastructure expands (Vitousek et al. 1997). Studies of urban birds have revealed that populations in areas with high-amplitude, low-frequency noise tend to sing at higher minimum frequencies, releasing them from masking (i.e. great tits: Slabbekoorn and Peet 2003; nightingales, Luscinia megarhynchos: Brumm and Todt 2002; Brumm 2004; song sparrows, Melospiza melodia: Wood and Yezerinac 2006; house finches: Fernández-Juricic et al. 2005). Several studies have also documented altered patterns of abundance in noisy areas (Reijnen and Foppen 1995; Reijnen et al. 1995, 1996, 1997; Forman et al. 2002), and two studies have linked these abundance patterns to song structures that may be differentially affected by masking noise (Rheindt 1995; Goodwin and Shriver 2011). That populations in noisy areas differ in their acoustic signals is well established, however, the timing of signal change remains understudied. With songbirds in particular, several hypotheses to explain vocal adaptations to urban noise are plausible and not mutually exclusive: habitat assortment, such that individuals that sing at higher frequencies selectively occupy louder habitats; learning bias, whereby individuals disproportionately hear and thus learn higher-frequency songs; adaptive evolution, whereby urban populations diverge genetically, and thus vocally, from quieter rural populations; or individual vocal plasticity, as described herein. Our results, and other similar recent results in other species, support the role for vocal plasticity in observed population differences in acoustic signals among urban and rural populations.

Yet we also note that individual vocal plasticity can be limited. One limitation is how quickly individuals can respond to acoustic interference. In our study, chickadees shifted song frequencies on average more than 1.5 min into the masking playback tone. During the lag time between the onset of the masking playback and the shift in frequency of the first song, signal efficacy was probably very low. Our results here echo those of Halfwerk and Slabbekoorn (2009), who measured spectral characteristics of the song types sung before and after presentation of broadband masking noise. While those birds shifted to song types that reduced masking, switches were not instantaneous: the more masked bouts continued between approximately 100 and 600 s before a switch to a different song type. This evidence, combined with our results herein, suggest the observed flexibility in shifting song frequencies may be constrained or limited, perhaps in relation to the length of the bout at a certain frequency. In support of this hypothesis, in some birds, song type switching is correlated with the length of the bout, rather than the number of songs delivered (Riebel and Slater 1999), which could lead to inflexibility in switching even if the signals are masked. Another limitation to vocal plasticity is the specific morphology of the species in question. Vocalizing animals are constrained to certain frequency ranges as a result of their size, structure and vocal apparatus (Fletcher and Tarnopolsky 1999; Podos and Nowicki 2004). Although noisy environments may favour the production of specific frequencies or frequency ranges as a release from masking, some species may be mechanistically unable to produce those frequencies. With such limitations and constraints in mind, we might expect noise-induced changes in signal design to be complemented by eventual geographical shifts away from habitats with masking noise, especially for those species most constrained in their ability to modify song structure in response to noise (Rheindt 2003; Goodwin and Shriver 2011).

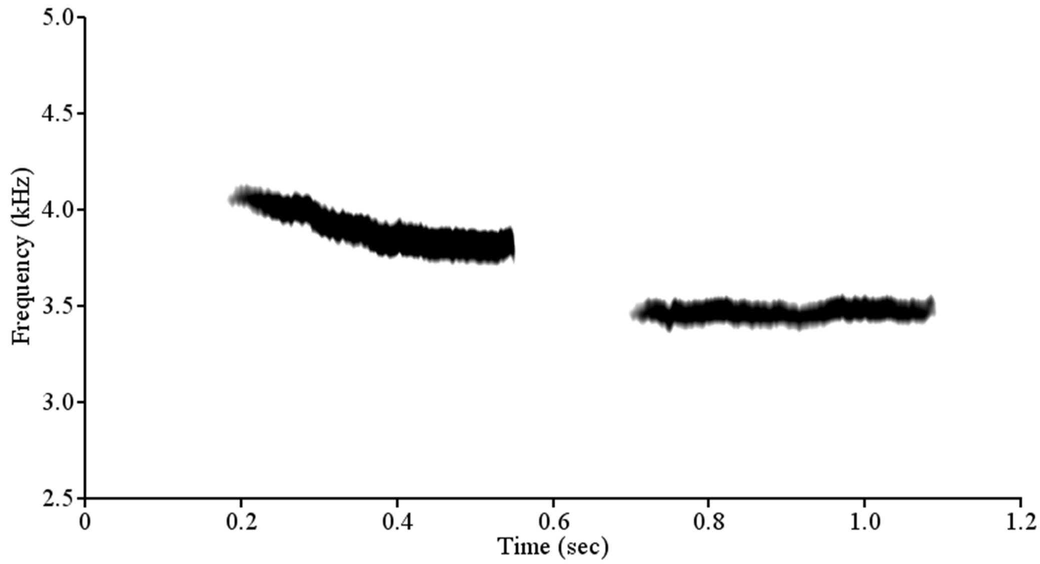


Figure 1. Spectrogram of typical black-capped chickadee “fee bee” song. FFT = 256

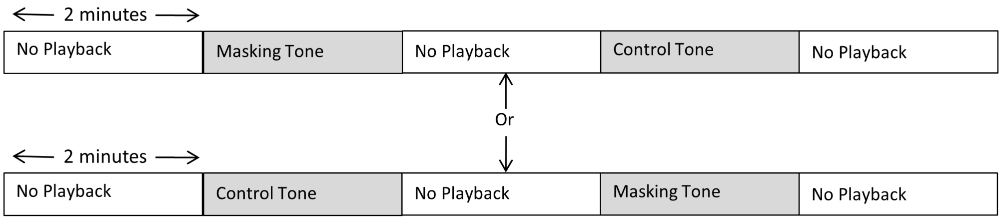
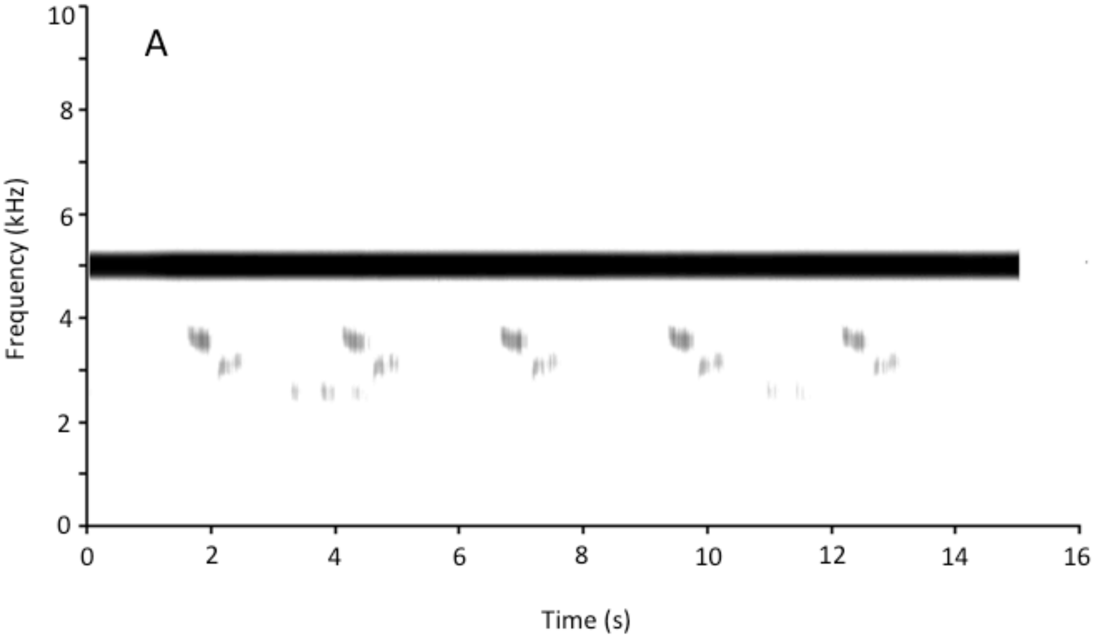


Figure 2. Timeline of experimental trial. Focal males were recorded for 2 min without playback and for 2 min following playback of a masking tone and then the control tone (upper panel), or vice versa (lower panel). Each playback tone was followed by 2 min of silence.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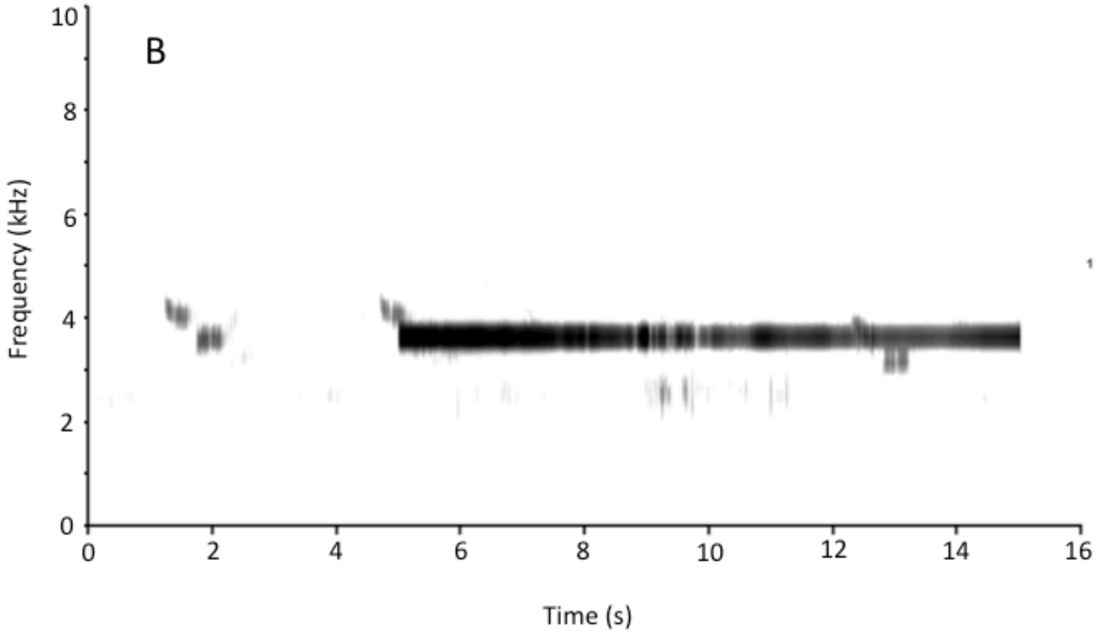
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Figure 3. Spectrograms depicting (a) the control treatment, where the playback tone was above the frequency range of the chickadee song (here an example of the male continuing to sing at the same frequency), and (b) the masking treatment, where the playback tone masked the bee portion of the last song (here an example of a rapid shift away from a masking tone approximately 8 seconds after the onset of tone playback). FFT = 256.

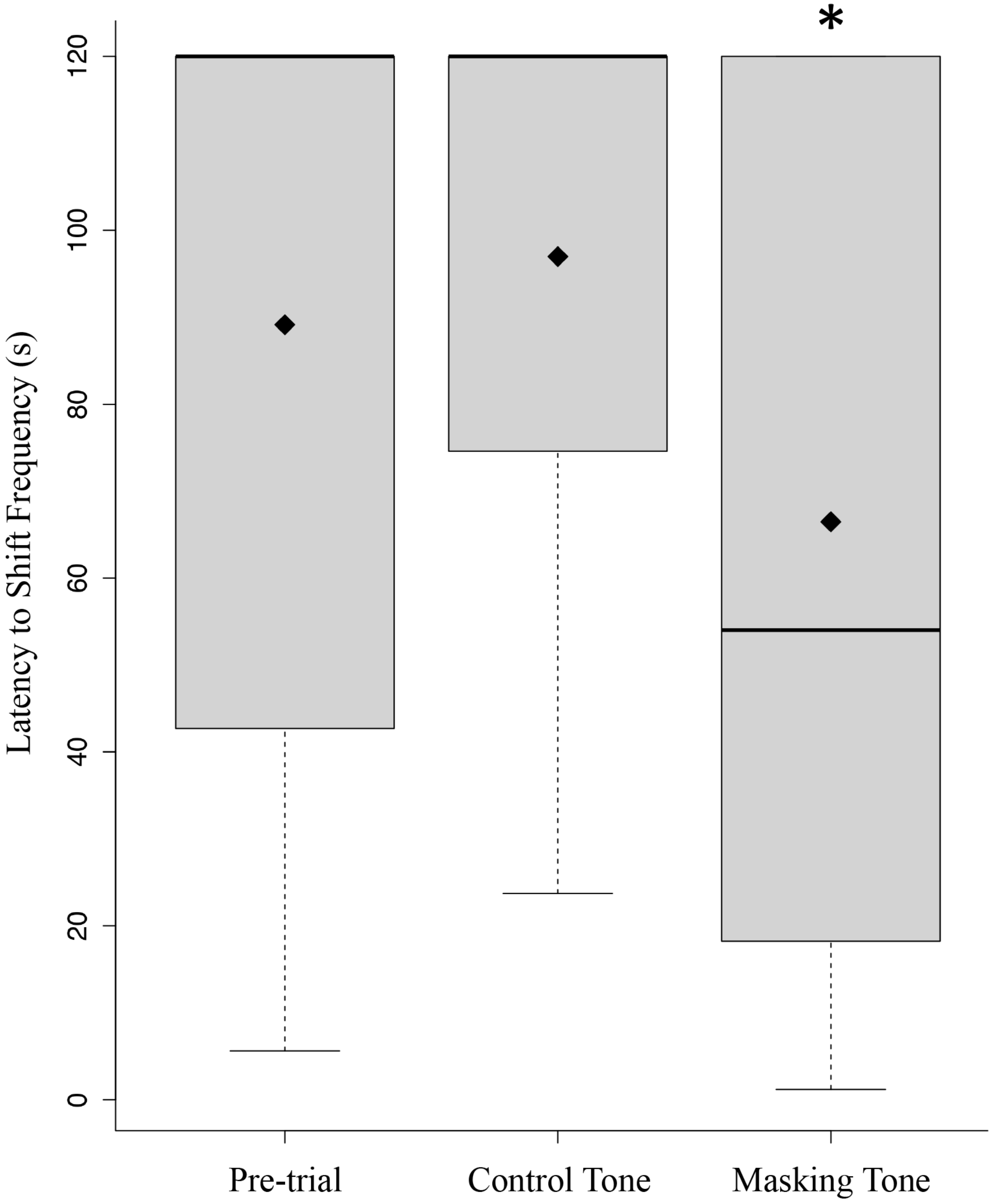


Figure 4. Box plot of latency to shift song frequency as a function of treatment (grey boxes are 25% quartiles, whiskers extend to the range of the data, dark lines indicate the medians, and black diamonds indicate the means). Maximum latency was capped at 120 s when birds did not shift frequency, making the upper bound of the quartiles and the range the same across treatments. *$P < 0.05$.

CHAPTER 2

TEAM OF RIVALS: ALLIANCE FORMATION IN TERRITORIAL SONGBIRDS IS PREDICTED BY VOCAL SIGNAL STRUCTURE

Published in *Biology Letters* Feb. 2014

Abstract

Cooperation and conflict are regarded as diametric extremes of animal social behavior, yet the two may intersect under rare circumstances. We here report that territorial competitors in a common North American songbird species, the Chipping Sparrow (*Spizella passerina*), sometimes form temporary coalitions in the presence of simulated territorial intruders. Moreover, analysis of birds' vocal mating signals (songs) reveals that coalitions occur nearly exclusively under specific triadic relationships, in which vocal performances of allies and simulated intruders exceed those of residents. Our results provide the first evidence that animals like Chipping Sparrows rely on precise assessments of mating signal features, as well as relative comparisons of signal properties among multiple animals in communication networks, when deciding when and with whom to form temporary alliances against a backdrop of competition and rivalry.

Introduction

Social behavior in many animal species often features a fine balance between competition and cooperation. In particular, competitive rivals may rescind competition and form temporary alliances when their interests align. Coalitions have been documented in wide-ranging contexts including cooperative hunting, mate attraction, and predator deterrence (Dugatkin 1997). A fundamental open question about coalitions is how animals decide when and with whom they will cooperate (Getty 1987). We expect animals to be highly selective when choosing allies, as too strong an ally could compete for resources whereas too weak an ally could prove ineffective. One way animals evaluate one another when seeking or competing for mates is by assessing sexual signals, stereotyped displays that provide reliable information about signaler attributes (Andersson 1994). It follows that animals may likewise assess sexual signals when forming alliances, although this possibility remains unexplored.

In our work investigating territorial dynamics and signaling behavior in Chipping Sparrows (*Spizella passerina*), we made the unexpected discovery that neighboring rival males sometimes form temporary defense coalitions in response to simulated territorial intrusion (see (Elfstrom 1997) for a natural observation of coalition forming in Rock Pipits, *Anthus petrosus*). More specifically, in experiments in which we simulate territorial intrusion via song playback, we have observed neighbors foraying into focal male territories, with the two birds then maintaining close proximity and performing simultaneous, parallel defensive responses directed at the simulated intruder (singing, flying, displaying). Might Chipping Sparrows forming coalitions use song to guide strategic decisions about when and with whom they will cooperate?

The most prominent feature of Chipping Sparrow song is its trilled organization, in which notes are repeated in rapid succession (e.g., Fig. 5a and b). Trilled songs are limited in their structure by vocal performance constraints, i.e., biomechanical limits in how birds can activate and coordinate the multiple vocal motor systems involved in song production [Podos 1996; Podos 1997; Suthers et al. 2012). Males that can best execute challenging motor displays tend to be treated as superior rivals (Byers et al. 2010), and in songbirds accumulating evidence suggests that high-performance trills, e.g. fast trills, are especially threatening (Illes et al. 2006; Moseley et al. 2013).

Here we test the hypothesis that males eavesdrop on and assess relative song performance of rivals and would-be allies, particularly trill rate, as a guide to territorial coalition-formation. To test this hypothesis we quantified salient aspects of song variation, tested residents' responses to variation in trill rate using a playback experiment, and examined the circumstances under which coalitions formed.

Methods

Quantifying Song Variation and Vocal Performance

We recorded songs of Chipping Sparrows in Hampshire and Franklin counties, MA, USA between May 2010 and July 2012 using Sennheiser ME66/K6 shotgun microphones and Marantz PMD660 solid state recorders, and supplemented field recordings (n = 70) with recordings from Cornell University's Macaulay Library of Natural Sounds (n = 90). We used SIGNAL 4.0 to measure trill rate and frequency bandwidth from amplitude spectra. We regressed maximum frequency bandwidth from 5 Hz trill rate bins onto trill rate to define the upper bound regression, the putative performance boundary (Podos 1997).

Playback Experiment

We located singing males across western MA, USA between May 15 and July 20 2012. We mapped the territories of singing males for four hours per day over two days (~0500-0700). Males (n = 24) then received two song playbacks simulating an intruder at the center of their territories (SME amplified field speaker) between 0700 and 1000 over two consecutive days with either a fast or slow trill rate, with presentation order alternated by trial. We created stimuli by increasing or decreasing trill rate while ensuring the song was within the observed population range. Playbacks consisted of four minutes of song delivered at 6.5 songs per minute, followed by two minutes of silence. After two minutes of silence, a taxidermic mount of a Chipping Sparrow was revealed to allow residents an opportunity to attack and the playback resumed for another four minutes, followed again by two minutes of silence, totaling 12 minutes for each playback. All behaviors were recorded with a Sennheiser K6/ME66 shotgun microphone and Marantz PMD660 solid state recorder and analyzed by an observer blind to treatment type.

We focused first on playbacks in which no coalitions formed. We used a repeated measures design and Wilcoxon signed-ranks tests to compare receiver response to fast versus slow trill rate, for univariate responses as well as combined behavioral responses (Principal Component Analysis scores). We also asked whether subjects' responses to playback co-varied with the degree to which their own trill rates differed from stimulus trill rates (Moseley et al. 2013). Finally, for trials in which coalitions formed, we compared trill rates of residents and allies, and asked whether particular triadic relationships were more conducive to coalition formation than others.

Results

Our analysis of song structure revealed an acoustic signature of constraints on trill production: a triangularly-distributed biplot of trill rate by frequency bandwidth, circumscribed by a significantly negatively-sloped upper performance boundary (upper bound linear regression, $R^2 = 0.89$, $P = 0.002$, Fig. 5c). In playback trials in which coalitions did not form, males responded more vigorously to stimuli with fast trill rates. A PCA reduced responses into one principal component that explained 34% of total response variation, with the most aggressive behaviors loading positively (e.g. time spent within 2 m of the speaker, number of attacks). PC scores were significantly greater in response to fast trill rates (Wilcoxon signed-ranks: $P = 0.003$). Similarly, univariate analyses indicate that males responding to faster trill rates approached the speaker more closely (Wilcoxon signed-ranks: $P = 0.031$), spent more time within 2 m of the speaker ($P = 0.006$), and attacked the mount more often ($p = 0.018$). The aggressive responses of focal males also varied in accordance with the degree to which stimulus trill rates exceeded their own trill rates. Specifically, males responded more aggressively when intruders sang relatively faster trills (linear regression, $R^2 = 0.152$, $P = 0.027$), providing further evidence that trill rates are a salient vocal feature in the assessment of territorial rivals.

In our 48 playback trials we observed the formation of 9 coalitions. In each case, neighboring males left their territories, trespassed on their neighbors', and directed defensive responses towards the simulated intruder. Analysis of trill rates of resident males, simulated intruders, and neighboring coalition-formers reveals two clear patterns concerning when and with whom neighbors form defense coalitions. First, birds formed coalitions exclusively when their own trill rates exceeded those of the residents they were assisting (9 of 9 coalitions observed, binomial test: $P = 0.004$). Second, in 8 of 9 coalitions observed, trill rates of simulated intruders exceeded resident trill rates ($p = 0.039$). As a further test of the statistical significance of these patterns, we tallied the relative rankings of trill rate of all three parties involved in each coalition (ally, resident, simulated intruder) and tested observed rankings against rankings that would be generated by chance. While there were six possible rankings, coalitions formed only in three triadic relationships: intruder > ally > resident, 6 cases; ally > intruder > resident, 2 cases; and ally > resident > intruder, 1 case (multinomial exact test: $P = 0.004$, Fig. 6).

Discussion

Chipping Sparrow songs show evidence of a vocal performance constraint, consistent with patterns now shown in diverse vocalizing species (Podos et al. 2009). Our playback trials revealed that territorial Chipping Sparrows attend to variation in one prominent performance variable, trill rate. More specifically, the birds responded more vigorously when simulated intruders sang the more difficult to produce, faster songs, and also when there was a stronger disparity between intruder trill rates and their own.

More significantly, our results suggest that males eavesdrop on vocal interactions in neighboring territories, assess relative trill rates of songs involved in these interactions, and initiate coalitions most often when the intruder represents a comparatively elevated threat. This finding aligns with the hypothesis that cooperative defense coalitions should be initiated only when the benefits of the coalition outweigh the associated costs (Getty 1987). In particular, to the extent that trill rate serves as a reliable indicator of territorial threat (Illes et al. 2006; Moseley et al. 2013; Podos et al. 2009), Chipping Sparrows with a low trill rate neighbor should benefit by retaining that neighbor as a 'dear enemy' (Fisher 1954) in favor of a new neighbor with a higher trill rate. By contrast, Chipping Sparrows should have little incentive to assist neighbors who themselves have a faster trill rate, and especially not when that neighbor is challenged with an even faster intruder: indeed we never observed coalitions under such circumstances.

Prior studies on cues guiding coalition formation have focused on size disparities and their visual assessment. For example, empirical work on fiddler crabs (Backwell and Jennions 2004; Booksmythe et al. 2010) reports coalitions forming most often when territorial allies are larger than intruders, and when intruders in turn are larger than residents. This pattern is predicted because allies should expend less energy evicting an intruder than in re-establishing territory boundaries with a new, larger neighbor. In these species, intruders may even target territory holders that have neighbors too small or weak to assist in their eviction

(Milner et al. 2011). Both lines of evidence suggest that would-be allies and intruders assess size disparities when deciding to attack or retreat. Our work with Chipping Sparrows takes the additional step of showing that animals can base decisions about coalition formation not just on incidental visual size cues but also on stereotyped communication signals that evolve under pressures of sexual selection. Acoustic communication networks offer animals opportunities to detect and compare signals of multiple individuals both rapidly and concurrently. Female songbirds in communication networks sample songs to guide comparative mate choice (McGregor 2005) and may cuckold their mates perceived as being on the losing end of song contests (Mennill et al. 2002). The facility with which male signals in communication networks can be compared by females elevates selective pressures on signal value, structure, and strength (Logue and Forstmeier 2008). Males, likewise, attend to songs within their local neighborhoods, for example treating established neighbors with reduced aggression at territorial boundaries (Fisher 1954), retaliating against defecting neighbors that intrude (Akcay et al. 2009), or expanding into neighboring territories when those neighbors fail to vigorously defend their territories against other intruders (Freeman 1987). Our finding here, that males forming coalitions strategically compare vocal attributes between themselves, neighbors, and simulated intruders, further highlights the complexities of the social environment in territorial dynamics, and for the first time demonstrates the use of a stereotyped, specialized signal in establishing brief periods of cooperation among otherwise combative rivals.

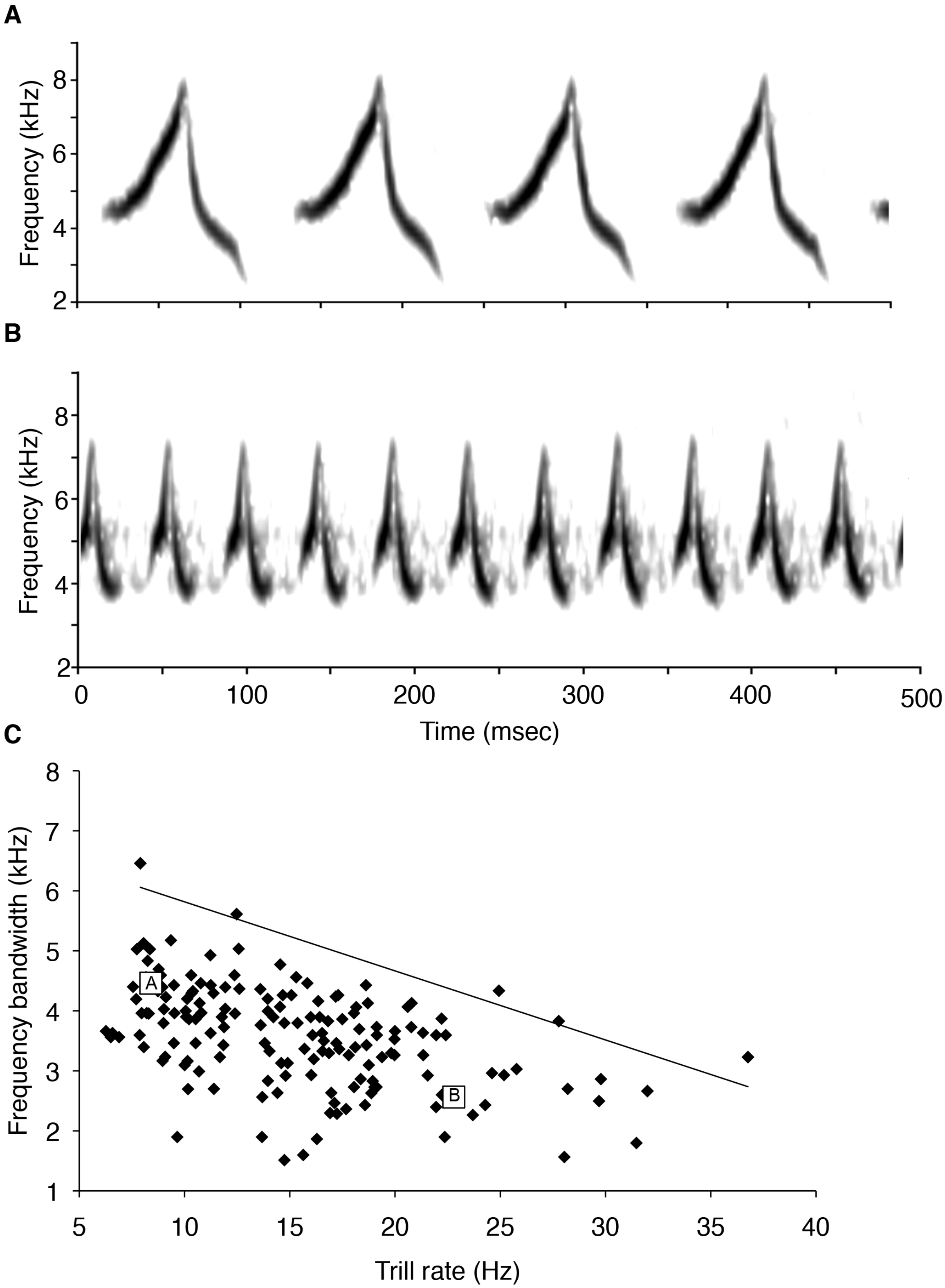

A
Frequency (kHz)
8
6
4
2
B
Frequency (kHz)
8
6
4
2
0
100
200
300
400
500
Time (msec)
C
Frequency bandwidth (kHz)
8
7
6
5
4
3
2
1
5
10
15
20
25
30
35
40
Trill rate (Hz)
A
B

Figure 5. Chipping Sparrow songs show evidence of a vocal constraint. Chipping Sparrow songs (two examples shown in A and B), comprised of rapidly repeated notes, show broad population level variation trill rate and frequency bandwidth. A bi-plot of trill rate and frequency bandwidth (n = 160 males) reveals a performance trade-off in vocal production (upper bound regression, $R^2 = 0.89$, $P = 0.002$, C).

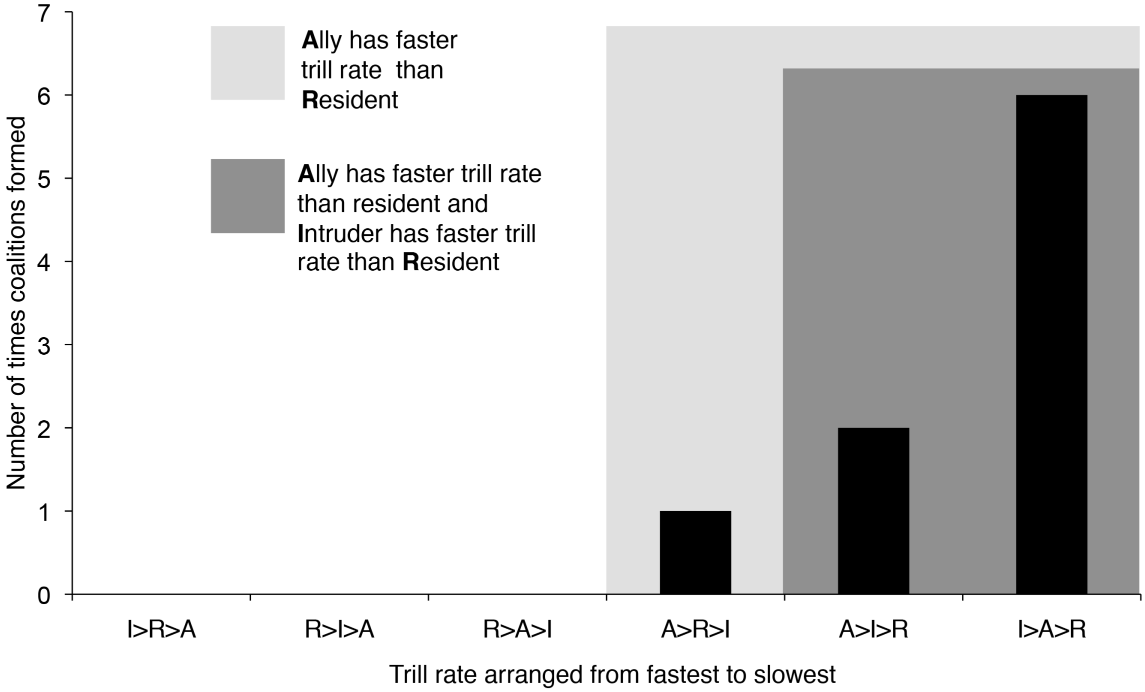


Figure 6. Defense coalitions form under specific triadic relationships. Coalitions (n = 9) form only when the ally's trill rate exceeds that of the resident he is assisting (light gray box, binomial exact test, $p = 0.004$). Moreover, given an ally with a faster trill rate, coalitions form most often when trill rates of simulated intruders exceeds both the resident and the ally, or is intermediate to the two (dark gray box). We observed no coalitions in other circumstances, in contrast to what we would expect by chance (multinomial exact test, $P = 0.004$).

CHAPTER 3

TERRITORIAL RESPONSE TO VARIATION IN FREQUENCY BANDWIDTH IN CHIPPING SPARROWS

Introduction

Sexually selected traits provide information to animals seeking or competing for mates, and evolve in response to those selective pressures (Andersson 1994). Common targets of sexual selection are male motor traits that reveal signalers' quality (Byers et al. 2010), such as acrobatic displays (Barske et al. 2011), or the production of complex bird song (Searcy and Nowicki 2005). Trilled songs, a rapid repetition of similar notes, appear to be especially relevant in both inter and intra sexual contexts in part because of the mechanical difficulty associated with singing quickly and with consistency both structurally and temporally (Sakata and Vehrencamp 2012), and singing quickly and across wide frequency ranges (Podos 1997). Males that meet these vocal challenges are sometimes regarded as superior rivals and preferred mates (Ballentine et al. 2004, Illes et al. 2006, Moseley et al. 2013). An important question remains: are all signal components influenced by mechanical constraints salient (or equivalently salient) in signal perception and function?

Male traits that entail repeated demonstrations of vigor or ability are found in diverse animals. Examples include leg waving in wolf spiders (Hebets and Uetz 1999) and fiddler crabs (Matsumasa and Murai 2005), firefly light flashing (Lewis and Cratsley 2008; Demary et al., 2006), circle chasing in pronghorn (Byers 1997), display flights in bats (Voigt et al. 2001), and long bouts of rapid chirping in crickets (Wagner and Hoback 1999), to name just a few. These examples are likely targets of sexual selection because lower quality males are eventually revealed via inferior performances, and therefore the displays may serve as reliable indicators of condition (Grafen 1990, Andersson 1994).

Repeated renditions of songs or elements within songs have also been well studied among birds. Birds that have high song output tend to be better competitors (i.e. Alatalo et al. 1990, Houtman 1992). Within song, males that sing more consistently, hitting the same frequency, structure, and amplitude song after song or note after note, are sometimes rewarded with greater extra-pair paternity (Byers 2007). Species that trill their songs – rapidly repeating syllables to form their songs – may also be evaluated for the rate of note repetition (trill rate) and how far their frequency range traverses (frequency bandwidth). Individuals that maximize these performance traits may be regarded as superior prospective mates or rivals (Ballentine et al. 2004, Illes et al. 2006, Mosely et al. 2013). However, little research has focused on male response to variation in frequency bandwidth, specifically. One study has used artificially manipulated songs, and found males responded most aggressively at intermediate performance levels (de Kort et al. 2009). The reduced aggression at high bandwidth was taken as evidence for a retreat from an especially threatening intruder (see also Moseley et al. 2013).

Chipping Sparrows, the study species of much of my dissertation work, defend their territories and attract mates using trilled songs (Liu 2004). In previous work, I determined that song in this species, as with many other species, appears to be constrained in that songs with a wider frequency bandwidth tend to be sung with reduced trill rate (Goodwin and Podos 2014, Chapter 2). Furthermore, I found that territorial males attend to variation in trill rate; residents respond more vigorously when presented with fast trilling simulated intruders. Here, I ask if natural variation in frequency bandwidth evokes a similar, elevated response. Using a playback design, I measured how territorial males respond to trills with varied frequency bandwidth but constant trill rate. I predict that residents presented with intruders with wide frequency bandwidths, a greater physical challenge to produce, will respond more vigorously as they perceive a greater threat.

Methods

Estimation of trade-off

In previous work I described a trade-off between frequency bandwidth and trill rate in Chipping Sparrows (Goodwin and Podos 2014). In brief, I created a library of Chipping Sparrow songs by recording singing males throughout Hampshire and Franklin counties in Massachusetts during the breeding seasons (May-July) of 2009-2012, and supplemented those recordings with recordings from the Macaulay Library of Natural Sounds. Those recordings were made using a Marantz PMD 660 digital recorder with a Sennheiser K6/ME66 directional microphone. The song library comprised 160 males, 90 of my own recordings and 70 from the Macaulay Library. From each recording, I selected three songs without overlapping background noise and measured two parameters using the acoustic program Signal 4.0 (Beeman 2002): trill rate between subsequent notes (Hz) as measured and averaged between five consecutive notes, and frequency bandwidth or the total frequency range covered by each note (KHz). Frequency bandwidth was calculated for each song from power spectra as the difference between the minimum and maximum frequency -18dB from peak frequency (Zollinger et al. 2012). I averaged the three measurements of both parameters within male. I then plotted average trill rate against frequency bandwidth, producing a graph with a roughly triangular distribution of points.

Here, I use a revised performance boundary calculation that takes into account the possibility that data are skewed towards lower trill rates, which can generate spurious correlations (Wilson et al. 2014). Rather than grouping trill rate data by bins of equal size, here I define seven trill rate bins in which equal numbers of data points are included. From those bins I selected the maximum frequency bandwidth measured and the associated trill rate per bin, and used linear regression on those values to generate a line approximating a performance boundary (Fig. 7). As a further test of the statistical significance of the performance boundary observed, I also used quantile regression on the entire trill rate and frequency bandwidth data set (Wilson et al. 2014).

Playback Study

Stimulus Preparation:

I created a set of stimuli with paired high (wide frequency bandwidth) and low performance (narrow frequency bandwidth) versions, with trill rate held constant. I derived stimuli from the library of Chipping Sparrow songs, taking care to select recordings distant from where any playbacks would be conducted. To create stimuli, I selected two exemplar songs from each of 19 song types; selecting one song with a wide frequency bandwidth, and one with a reduced bandwidth. From each song, I isolated a single note using Signal 4.0 (Beeman 2002) and concatenated the note to produce a 2.5 s song of standardized amplitude. This procedure created one high performance, wide bandwidth song, and one low performance, narrow bandwidth song. I also measured the vocal deviation of each stimuli as the orthogonal distance to the regression line from all Emberizid sparrows (from Podos 1997). I used the Emberizid line rather than the Chipping Sparrow line to ensure that most points fell below the family wide performance boundary, and to allow comparison with other studies.

Experimental Design:

I used playbacks to simulate intruders on the territories of fifteen breeding males during the breeding season (May 1 – July 1) of 2013. Before each playback trial I mapped territories of focal males during the dawn chorus by following singing males and noting their location on an aerial map for approximately two hours as the males traversed their territories. This technique allowed me to definitively place the speaker within the residents' territory, although a more thorough sampling would be necessary to more finely demarcate the edges. Resident males then received playback trials of each performance level on consecutive days between 0600 and 1000. The order of presentation for performance level was balanced across playbacks.

To set up the playbacks, I placed a speaker on the ground at the center of the territories of focal males, and connected it to an mp3 player (iPod Nano) with a 10 m cable. I placed flagging at intervals of 2, 4, and 8 m from the speaker as a distance aid for dictating proximity. Next to the speaker I placed a covered taxidermic mount of a Chipping Sparrow attached to a pole to provide residents an opportunity to attack. Playbacks consisted of 4 minutes of song delivered at a rate of six songs/minute, followed by two minutes of silence, then another 4 minutes of song delivered at the same rate with the mount uncovered, followed by another two minutes of silence. Revealing the mount part-way through the trial gives residents a chance to attack the perceived intruder after they have located the source of the singing (Searcy et al. 2006). During playbacks, an observer recorded singing behavior of residents with a Marantz PMD 660 digital recorder and a Sennheiser K6/ME66 directional microphone, and dictated behavioral responses such as flights, attacks, and the distance from the speaker.

I extracted behavioral measurements from notes and field recordings using RavenPro Version 1.5 (Bioacoustic Research Program 2014). I summarized songs, flights, and attacks as the total number of each that occurred over the 12 minute playback. I summarized distance measurements as the total amount of time spent within each distance category (i.e. 2, 4, 8 and >8 meters).

Statistical Analyses:

I evaluated residents' responses to playback within stimuli sets, to test if males responded differently to low and high bandwidth stimuli. To do so, I first used a Principal Components Analysis (PCA) to reduce response variables. I then compared resultant PCA scores, as well as raw (univariate) response variables using Wilcoxon signed-ranks tests. PC scores provide a composite picture of male response behaviors, while the univariate responses reveal variation in each type of response. All statistical tests were conducted using R (R Core Team 2016).

Results

Trade-off Between Trill Rate and Frequency Bandwidth

Chipping Sparrow songs have been described previously as trading-off, such that songs sung with a faster trill rate tend to be sung with a lower frequency bandwidths (Goodwin and Podos 2014). I here further describe this relationship in two ways, both of which account for the potentially problematic issue of reduced samples at higher trill rates (Wilson et al. 2014). First, a linear regression of the maximum frequency bandwidth and associated trill rates derived from bins with equal numbers of data points reveals a significantly negative relationship, albeit a more gradual slope than found previously -0.115 (slope = -0.067, $R^2 = 0.59$, $P = 0.044$, Fig. 7). Furthermore, a quantile regression of the entire data set confirms the statistical validity of this negative relationship (90th percentile, slope = -.057, $P < 0.0001$).

Playback Response

A PCA of the bandwidth data from the 15 pairs of playbacks reduced the response to one variable, PC1, that explained 40.6% of the variation. Raw response behaviors loaded both positively and negatively (i.e. closest approach and latency loaded negatively, while time spent within 2 meters loaded positively, Table 1). I found no significant difference in responses by performance level, both according to PC scores (Wilcoxon signed-rank test: $P = 0.28$) and to all univariate response variables

(Fig. 8, Wilcoxon signed-rank tests: all $P > 0.05$). The statistical power observed here was quite low (for PC scores, power = 0.26, delta = 0.39), indicating that a near doubling of sample sizes would be required to detect any difference between response behaviors by stimuli. I compared this power to that observed in the trill rate study (Goodwin and Podos 2014), and found much higher power in that study (for PC scores, power = 0.98, delta = 1.51).

Discussion

Territorial Chipping Sparrows did not appear to attend to variation in frequency bandwidth. When presented with playbacks of wide and narrow bandwidth, their response behaviors were similar across a suite of measures. This lack of response to the more difficult to produce, wider bandwidth, appears to occur in spite of their attention to a related parameter, trill rate (Goodwin and Podos 2014).

As with any negative data, these results should be interpreted with caution. While it is possible that Chipping Sparrows do not attend to variation in frequency bandwidth, it is also possible that they do but my study design and sample size did not allow their detection. Although I previously found Chipping Sparrows attend to trill rate, this current study on frequency bandwidth was performed on a different set of individuals in a different year, which could introduce noise in the data. Another difference between the study that investigated this one and the trill rate study is how the stimuli were constructed. The trill rate stimuli were constructed by adding and removing space between the same isolated note (Goodwin and Podos

2014). Here, to create narrow and wide frequency bandwidth songs, I isolated two notes; one narrow bandwidth and one wide bandwidth, from different songs. The only alternative to this technique would be to artificially stretch and narrow the same note (de Kort et al. 2009), although such a manipulation could introduce other sources of perceptual error. It is possible then that Chipping Sparrows perceived the frequency bandwidth stimuli in a manner different than the trill rate stimuli (i.e. identifying two different individuals that varied in ways other than the variation in the frequency bandwidth).

Furthermore, if Chipping Sparrows do attend to frequency bandwidth, perhaps they do so only when the variation is greater than that which I tested. I examined this limitation more fully by exploring the range of variation in both stimulus sets (the present study, and Goodwin and Podos 2014). I detected no difference among stimuli sets in the range of the parameters covered, and the degree to which they varied in vocal deviation. From the song library, I found Chipping Sparrow trill rates to range from 6.27 – 36.76 Hz, and frequency bandwidth to range from 1.512 – 6.458 KHz. Stimuli sets spanned on average 30.3 percent of the trill rate range and 25.9 percent of the frequency bandwidth range, and these did not statistically differ (T-test, t = 0.967, d.f. = 35, $P = 0.34$, Fig. 9). I also examined vocal deviation in high and low performance versions of each stimuli set to see if there were any systematic bias in the trill rate or bandwidth set. Average difference in vocal deviation between high and low performance stimuli did not differ by set (trill rate average 1.14, frequency bandwidth average 1.19: T-test, t = 0.27, d.f. = 35, $P = 0.79$). This confirms that I had presented Chipping Sparrows with stimuli with a similar level of variation as I had presented in a previous trill rate experiment. Overall, the statistical power was relatively low though, especially as compared to the previously conducted trill rate experiment, perhaps because of an overall reduced response by resident birds.

A second finding was further evidence that trill rate and frequency bandwidth in Chipping Sparrows trade off with one another, such that as one parameter increases, the other necessarily decreases. This result is echoed in several other trilling species (Illes et al. 2006; DuBois et al. 2011; Moseley et al. 2013), and leads to the prediction that composite parameters that take into account how well animals maximize both parameters (i.e. vocal deviation) will often be targets of sexual selection. This prediction arises from an evolutionary perspective, where animals reliably signaling high performance must optimize both parameters, or signals would converge on simple fast trills or simple wide bandwidth songs. In other words, the trade-off itself helps to maintains honesty in the system.

Yet, if male Chipping Sparrows do indeed fail to attend to variation in frequency bandwidth, a natural question is why trill rate alone remains salient. First, evidence of a performance tradeoff between two parameters perhaps need not guarantee that both parameters serve a signaling function. At the outset, I had predicted that trill rate and frequency bandwidth would be parameters of interest because of the above recent evidence from closely related species. However, trill rate can trade-off with other song parameters, such as relative amplitude, consistency in amplitude, consistency in structure, and note complexity. If those parameters also trade off with one another, those constraints could maintain the honesty of the system. Trill rate could then still be constrained by other parameters, like frequency bandwidth, but functional evidence might only support trill rate as being salient.

Moreover, the salience of trill rate may not be tied to the vocal trade-off, and could rather be a stand-alone index of quality. In this case, the trade-off would be incidental to the signaling system, and the signal (trill rate) would still be salient, with highest quality males capable of singing the fastest possible songs. Of course, if trill rate is the only salient song parameter, I would expect males to converge on the fastest possible song irrespective of note structure or other complications. While Chipping Sparrow song is perhaps simple in structure, as compared to other Emberizid sparrows (at most a few notes), we still find variation in note structure, and most importantly, a wide variation in trill rate. This would seem unusual if males were converging on the fastest possible trills.

Trill rate may also function as an index signal, with female choice maintaining the observed diversity in song structure. While territorial dynamics can be a strong selective force in shaping signal structure, so too is female choice (Andersson 1994). Specifically, if females are choosy, and are selecting for male song parameters, the adaptive landscape becomes more complex. For example, if females exclusively attend to trill rate in the absence of other male song parameters, I would expect directional selection on trill rate, and again, convergence on the fastest possible rate. This seems unlikely given what we observe of natural singing behavior. Alternatively, females may attend to (either instead of, or in addition to trill rate) other song parameters such as consistency, frequency bandwidth, or even note complexity. Theory suggests that females may be more likely to attend to signals of complexity, although evidence along this front remains scant (Catchpole 1980, Searcy et al. 1992). My own experiments investigating female choice in the lab have so far proven inconclusive (Goodwin, unpublished data).

Finally, while an evolutionary perspective can help explain current song diversity and signaling systems, a proximate explanation might help us understand why trill rate in particular remains a common intrasexual territorial signal. Territorial signals, by their nature, must be capable of transmitting information beyond the boundaries of residents' territories. Across song parameters, different components of song achieve that goal to varying degrees. Frequency components, for example, tend to degrade quickly, with faster attenuation of higher frequency sound. Timing features, by contrast, are well perceived at greater distances (Naguib et al. 2008). Males distant to the sound source might more reliably extract information from timing features such as trill rate, than the rapidly attenuated frequency parameters. This propensity to be discerned at great distance could be one reason why trill rate remains an important signal in many territorial systems.

Here, I have presented evidence that Chipping Sparrow songs trade-off trill rate and frequency bandwidth, but that males do not seem to attend to frequency bandwidth (current study) in the same degree to which they attend to trill rate (Goodwin and Podos 2014). Future work is needed to parse out whether trill rate could be trading off with other parameters as a performance signal, or whether other forces such as female choice may be maintaining diversity.

Table 1. Structure correlations (loadings) for PC1 of response behaviors for territorial Chipping Sparrows challenged with wide and narrow frequency bandwidth stimuli. Values reflect simple correlations between factors and original variables.

Factor	**Structure Correlation**
Number of Attacks	0.561
Number of Flights	0.805
Time Spent w/in 2 m	0.604
Time Spent w/in 4 m	.
Time Spent w/in 8 m	0.51
Number of Songs	.
Closest Approach	-0.848
Latency to Approach	-0.842

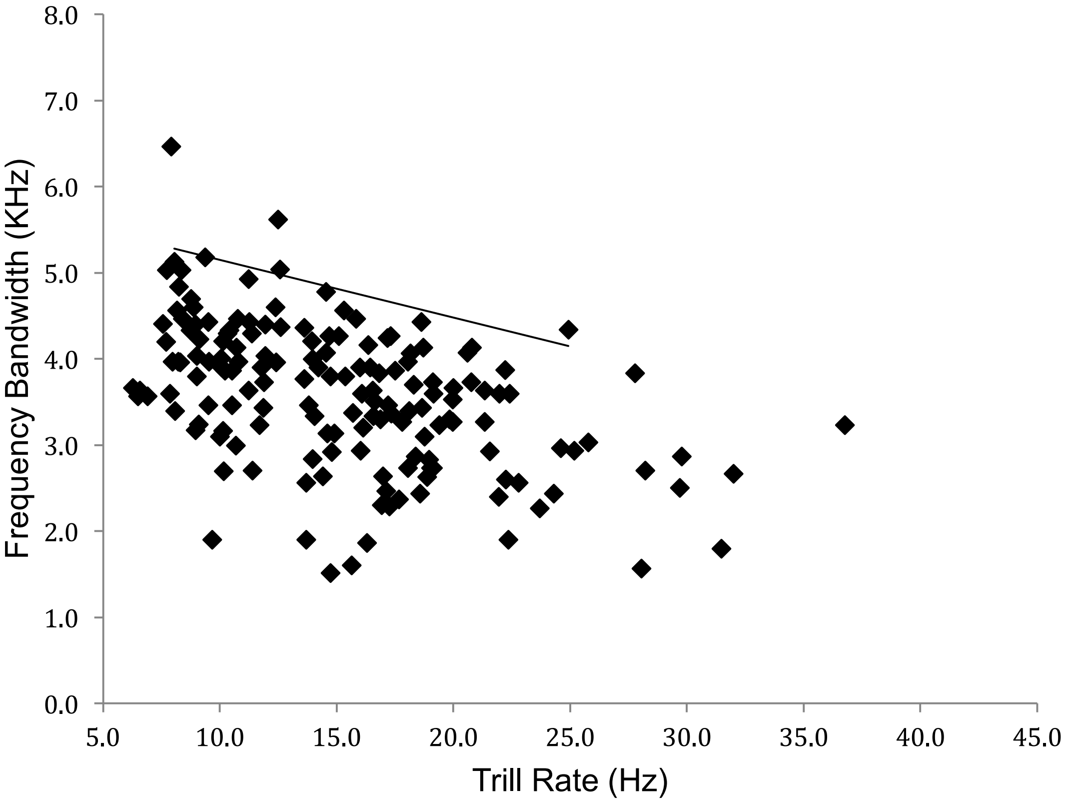


Figure 7. Chipping Sparrow songs appear to trade-off trill rate and frequency bandwidth such that the fastest trilled songs tend to have the most narrow frequency bandwidth. The solid line represents the linear regression of maximum bandwidth data from trill rate binned by equal data sizes, a more robust measure of performance boundaries (Wilson et al. 2014). Reproduced with permission from Goodwin and Podos (2014), with new performance line.

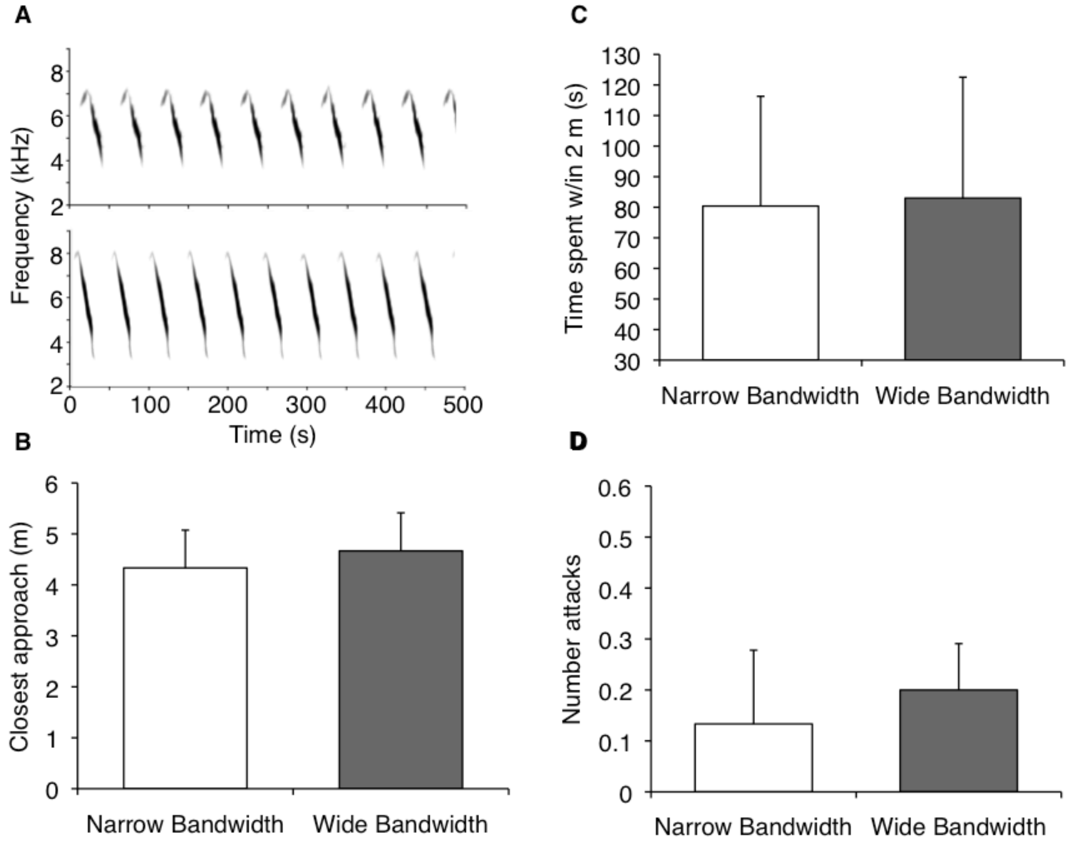


Figure 8. Resident Chipping Sparrows (n=15) did not respond more vigorously to stimuli that varied in frequency bandwidth (Wilcoxon signed-rank tests: all *P* > 0.05). Panel A represents an example set of stimuli, and panels B-D depict select univariate response behaviors that were shown to be significantly different in response to varied trill rate (Goodwin and Podos 2014).

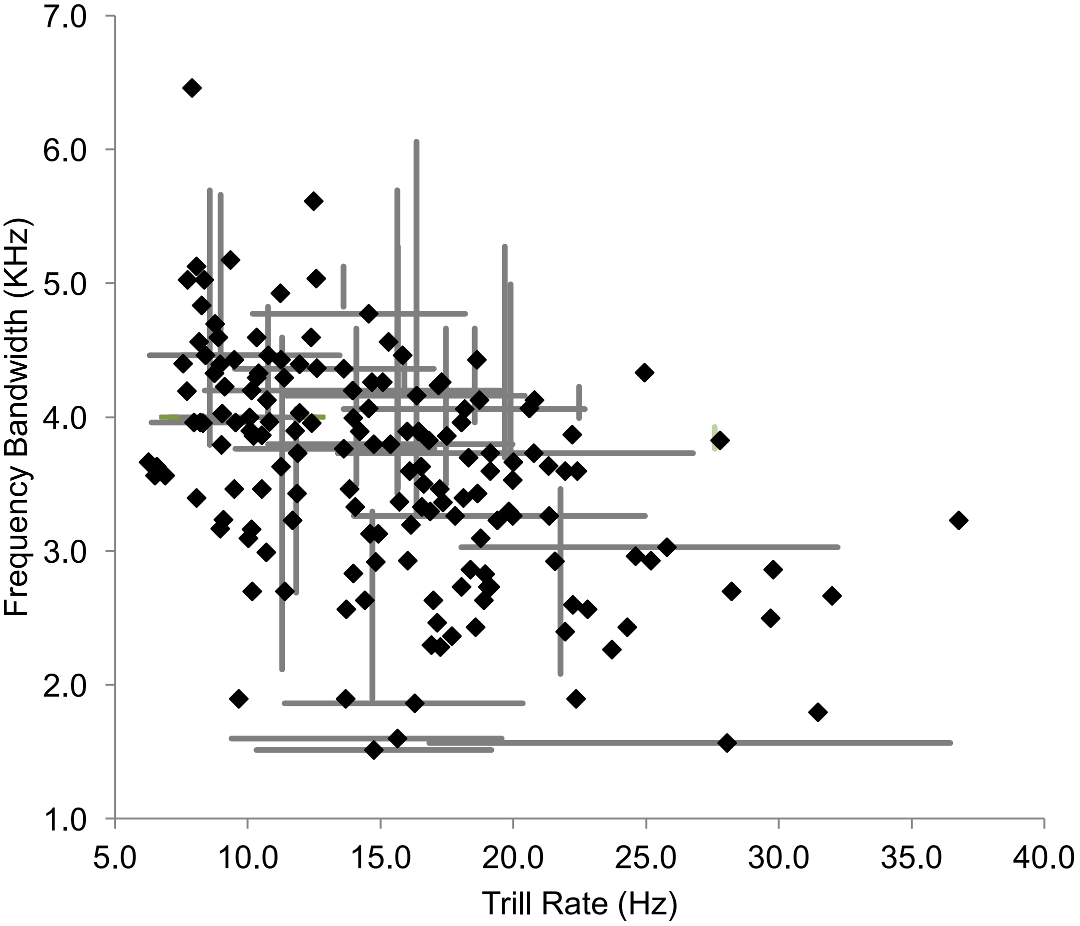


Figure 9. Chipping Sparrows were presented with stimuli that covered a similar range of variation in trill rate (horizontal lines) and frequency bandwidth (vertical lines). End points of each line represent the low and high performance version of each stimulus pair. Stimuli sets covered on average 30.3 percent of the trill rate range and 25.9 percent of the frequency bandwidth range, and these were not statistically different (T-test, t = 0.967, d.f. = 35, *P* = 0.34).

CHAPTER 4

SONG VARIATION IN CHIPPING SPARROW NEIGHBORHOODS

Introduction

Territorial animals defend their resources, especially their territories, against conspecific competitors (Noble 1939, Nice 1941). Animals are not distributed at random, rather they carefully select territories after some evaluation. Therefore, the decision to defend a particular area represents the confluence of multiple factors, including habitat quality, food availability, timing during the breeding season, and the potential territory holder's resource holding potential (Hinde 1956, Brown and Orians 1970). Additionally, social factors such as the presence of conspecific neighbors may also play a role in territory decisions. Neighbors can interact in both positive and negative ways with territory holders, and likely affect ultimate decisions on territory location (reviewed in Stamps 1992). In this chapter, I examine neighborhoods and the territorial signals residents use to defend their resources.

The classic approach in studying animal territoriality applies an economic perspective to habitat evaluation and territory choice. During the 1970s, ecologists modeled habitat selection as a function of the intrinsic quality of different sites, with better quality locales theoretically resulting in greater fitness for the occupant (Brown 1969; Brown and Orians 1970). One of the principal assumptions of these models was that as the density of conspecifics increases, the fitness of territory holders would concurrently decrease (Fretwell and Lucas 1970). Conspecifics were treated solely as competitors, with only negative effects on neighboring territory holders.

In reality, the relationships among neighbors are complex, and living alongside competitors can on occasion yield positive consequences. Conspecifics can provide information about habitat quality for prospecting, unsettled males (Stamps 1987), and in some species, high settlement rates encourage the settlement of further individuals up until the point of saturation (Stamps 1991). As another example, aggregations of males can serve as attractants to prospecting females, and empirical work has demonstrated that clusters of high quality males present an especially potent attraction (Beehler and Foster 1988, Svensson and Petersson 1992). Densely packed neighborhoods can also serve as early warning systems for predators. For instance, animals may give alarm calls and alert nearby neighbors to potential threats, giving animals a chance to take cover (Leavesley and Magrath 2005). Rival neighbors in some species do also occasionally cooperate, in some cases helping expel intruders (Healey 1967; Elfstrom 1997; Goodwin and Podos 2014). Rivals-turned-allies may benefit from helping to eject intruders, as they avoid having to renegotiate territorial boundaries with a new, potentially stronger neighbor (Detto et al. 2010; Goodwin and Podos 2014).

Animals may also benefit from the presence of territorial neighbors using information gleaned from social eavesdropping (McGregor 2005). As a result of information gathered via eavesdropping, animals may expand their territories (Beeman 1987), seek extra-pair paternity (Mennill et al. 2002), or fight off intruders with greater vigor (Peake et al. 2001). Furthermore, animals may use eavesdropped signals to compare rival males or prospective mates. Signals that are more similar should be easier to compare ("alignable," Logue and Forstmeier 2008), whereas signals that are proportionally different should be easier to discriminate (Webers Law, see Akre and Johnsen 2014). These perceptual limitations could influence *who* a neighbor wants nearby, or alternatively, not nearby.

For the purposes of this chapter, I have identified four social factors that may affect territory choice, and made predictions of how neighborhood dynamics should proceed in light of each factor (Table 2). If animals aggregate by quality, then I expect some neighborhoods to host higher than average quality males. Next, if cooperative defense is important, I expect to find low quality males seeking high quality neighbors, producing a patchwork of high and low quality neighbors. The third factor, comparative evaluation, yields the same prediction. Here, I predict that high quality males will tolerate low quality neighbors to encourage easy discrimination among prospective mates, once more resulting in a non-random neighborhood. Finally, if animals find discrimination easier when signals are more similar, the degree to which signals are "alignable" can generate varied dynamics. I predict that high quality males will prefer lower performance signals nearby, to facilitate favorable comparisons, and conversely, I expect low quality males to prefer dissimilar signals nearby to discourage accurate comparison.

My study of territory choice and spatial variation focused on male songbirds. Males use song to defend their territories and attract mates, and song can be relatively easily recorded and analyzed (Catchpole and Slater 2008). Furthermore, in some species, certain song parameters are related to individual quality (Searcy and Nowicki 2005). Additionally, songs lend themselves well to measures of similarity (Marler and Pickert 1984, Lachlan et al. 2010), and those measures can also be mapped onto territories and scrutinized for patterns.

My chapter focuses on Chipping Sparrows (*Spizella passerina*). Chipping Sparrows sing a single, simple trilled song that they crystallize using a neighbor tutor (Liu 2001). Although males sing one song type, songs vary across individuals. My previous work indicates that Chipping Sparrows are attentive to variation in how quickly songs are trilled in territorial interactions, and also reveals that Chipping Sparrows are attentive to neighbors and neighborhood dynamics (Goodwin and Podos 2014). Here, I describe how song parameters and measures of song similarity are distributed in various Chipping Sparrow neighborhoods, and investigate to what extent male aggregations, cooperative defense, comparative evaluation, and signal alignability influence neighborhood composition.

Methods

Study Species

Chipping Sparrows are territorial, migratory songbirds found across much of North America during the breeding season. Juveniles disperse from the natal area, with less than four percent of banded individuals returning to within 2 km of their natal site (Liu 2001). Males most often defend one territory, and frequently shift territory locations throughout the breeding season (Liu 2001). During the dawn chorus, male territory holders rapidly traverse the edges of their territories, delivering short bursts of song, directed at their neighbors (Liu 2004).

Study Sites

Between May and July of 2012 -2014, I sampled sixteen song neighborhoods in Hampshire, Franklin, and Hampden County in Massachusetts. Neighborhoods were a mix of private (primarily tree nurseries) and state-owned locations, and I secured permission to record birds at all sites. I selected sites that were fairly homogenous in habitat (i.e. Christmas tree farms and cemeteries), to reduce the effect variation in habitat quality may have on territory choice. In each neighborhood, I systematically recorded all singing individuals with Marantz PMD 660 solid-state recorder and a Sennheiser K6/ME66 microphone (79 total males sampled).

I sampled neighborhoods twice, beginning recordings at the dawn chorus (approximately forty-five minutes before sunrise) and remaining until all singing birds were recorded and their locations noted. I used aerial photographs from the 2001 MassGIS 1:5,000 color orthophotographs to note the approximate territory locations of singing individuals. Because males often move rapidly about the edges of their territories and sing during this time, rough territory boundaries are readily drawn by following singing males.

Song Measurements

From the recordings, I used Raven Pro (Version 1.4) to select three high quality exemplars of song from each male. I applied a bandpass filter to remove extraneous noise below 1500 Hz and above 9500 Hz. I then extracted two measurements related to vocal performance: trill rate and frequency bandwidth. From these two measures I calculated the composite performance measure of vocal deviation (Podos 1997). Next, I calculated similarity measures across song pairings using two methods, spectrogram cross correlation and dynamic time warping (details below). The performance traits were measured for each song, while similarity measures were extracted from every possible pairwise comparison (both within and outside neighborhoods).

I calculated trill rate as the reciprocal of the average time between successive notes as measured across three notes per song, and frequency bandwidth as the difference between the minimum and maximum frequency relative to -24 dB peak frequency in the power spectra using Signal 4.0 (Zollinger et al. 2012). I then averaged those values across the three song exemplars to arrive at final measures of trill rate and frequency bandwidth for each individual. I calculated vocal deviation by calculating the orthogonal distance between the Emberizid-wide performance maximum line and trill rate by frequency bandwidth coordinates (Podos 1997).

To calculate similarity measures, I applied two techniques; spectrogram cross correlation (using RavenPro 1.4) and dynamic time warping (using Luscinia sound analysis program, http://rflachlan.github.io/Luscinia/ under the GPL license). For both analyses, I used three-note subsets of one example song from each male. Spectrogram cross correlation uses a sliding window technique to line up and measure degree of overlap in spectrograms. In RavenPro, I used the batch correlation tool, set normalize, and selected spectrogram cross correlation, generating a matrix of peak correlation values (the greater the value, the more similar the comparison). Dynamic time warping, a more robust method for generating similarity measures, uses an algorithm to search for the best alignment of two songs based on the distance between acoustic features outline below (Lachlan et al. 2010). In Luscinia, I checked the following features for alignment: time, fundamental frequency, fundamental frequency change, vibrato amplitude (0.5), 0.001 compression factor, 1 SD ratio, 5 maximum element length, 0.2 cost for alignment error, weight by relative amplitude and a log transformation of frequencies. The output from this analysis was a matrix of Euclidean distance between every possible song comparison in my data set. Greater values (distance) indicate a comparison of more dissimilar songs. Finally, I assigned categorical song types to the songs of each male in the study using Borror's (1959) classification, with amendments as needed for song types not described (Table 3).

Statistical Analysis

To determine if neighborhoods featured aggregations of males with songs of similar performance levels, I compared average vocal performance variables across neighborhoods using one-way ANOVAs with performance variables (trill rate, frequency bandwidth, and vocal deviation) grouped by neighborhood. To determine if neighborhoods were home to pair-wise high and low performance males, as predicted both from the interests of cooperative defense and comparative evaluation, I used an ANOSIM (999 permutations, Euclidean distance) to determine if neighborhoods were any different in performance traits than what would be expected from a random assemblages of the population. Finally, to determine if song similarity ("alignability") corresponded to neighbor composition, I performed three analyses. First, I examined whether neighborhoods supported males with songs that were more (or less) similar to each other than to the sampled population at large. I used a t-test to compare within-neighborhood similarity (using both values from the spectrogram cross correlation and the dynamic time warping) to pair-wise values from outside of neighborhoods. Next, I examined whether song types were more or less likely to be clumped in neighborhoods. I estimated the likelihood of each song type in the population sampled as a proportion of total songs observed, and then used multinomial exact tests in each neighborhood with more than five singing males (n = 8) to determine if song types were found more or less often than expected by chance. Finally, to determine if male quality is related to song similarity – i.e. do higher quality males have neighbors with more similar songs? – I calculated a multiple linear regression between the average within neighborhood performance traits (trill rate, frequency bandwidth, and vocal deviation) and pair-wise song similarity using the more robust dynamic time warping values. All analyses were performed in R (R Development Core Team 2016).

Results

I sampled seventy-nine singing males across sixteen neighborhoods. Neighborhoods ranged in size from a single bird at the smallest (excluded from analysis) to 10 birds at the largest.

To determine whether some neighborhoods had higher or lower average song performance traits, I used one-way ANOVAs to compare sample means of trill rate, frequency bandwidth, and vocal deviation among the song neighborhoods. None of the variables showed significant heterogeneity among neighborhoods (all *P*

< 0.05, Table 4), although there was a trend toward heterogeneity with frequency bandwidth (ANOVA $F_{14,64} = 1.089$, $P = 0.057$).

Next, to determine if neighborhoods held non-random clusters of performance traits as predicted from comparative evaluation and cooperative defense, I used an ANOSIM permutation procedure with groupings by neighborhood. Here, I found neighborhoods to be no different than what would be expected by chance (ANOSIM 999 permutations, R = 0.040, $P = 0.176$).

To examine song similarity and the relationship between similarity and performance, I first compared average within-neighborhood spectrogram cross correlation and dynamic time warping values to outside-neighborhood values using t-tests. Neither spectrogram cross correlation (T-test, t = 1.244, D.F.= 214.7, $P = 0.215$) nor dynamic time warping (T-test, t = 0.450, D.F. = 222.4, $P = 0.652$) differed significantly within versus outside neighborhoods. Furthermore, in the eight neighborhoods with more than five singing males, I detected no pattern in how song types were distributed (multinomial exact tests, all $P > 0.05$, Table 5). That is, songs were distributed at random within neighborhoods with respect to how often they were found in the population at large. One neighborhood, however, trended toward having an overrepresentation of rare song types, with five males each singing a distinct and uncommon song type (Fig. 10). Finally, a multiple linear regression between pair-wise dynamic time warping values averaged within neighborhoods and associated performance traits revealed no relationship between song similarity and performance (multiple linear regression, $R^2 = 0.046$, F=0.112, $P = 0.95$).

Discussion

Chipping Sparrow neighborhoods appear to be arranged without obvious patterning with respect to performance traits (trill rate, frequency bandwidth, and vocal deviation), and with no clear patterning in song similarity. I did find a trend toward heterogeneity in frequency bandwidth, which could suggest the formation of performance aggregations, but concurrent work indicates males do not in fact attend to variation in that parameter (see Chapter 3). These data represent a small portion of available song neighborhoods, and like all negative data, must be interpreted cautiously. Furthermore, these data are restricted to only a handful of performance traits and measures of song similarity, and could be missing parameters crucial to Chipping Sparrow communication and territoriality.

With those caveats, it remains somewhat surprising that no statistically supported patterns emerged. Social animals are likely under selection for improved social cognition, particularly in the form of ordered social knowledge, and for those animals that form triadic coalitions, transitivity in social relationships (Seyfarth and Cheney 2015). From a handful of other systems, fascinating arrangements have been observed and described. Work on fiddler crabs show males are more likely to attract females if they court alongside a smaller male (Callendar et al. 2013), generating a non-random assemblage of neighborhoods with paired large and small males (Callendar et al. 2013). Like Chipping Sparrows, some species of fiddler crabs do also form defense coalitions under specific circumstances (Backwell and Jennions 2004; Detto et al. 2010). In songbirds, work on Lazuli buntings (*Passerina amoena*) finds males are more tolerant of low quality neighbors as signaled in plumage, resulting in a patchwork pattern of high and low quality individuals (Greene et al. 2000). Despite the high attention Chipping Sparrows give to their neighbors, I found no evidence that song influenced territory choice.

I was also unable to address whether songs were more similar within neighborhoods than between neighborhoods. Chipping Sparrows learn their song types from immediate neighbors during their second spring (Liu 2001), so some amount of song type sharing was expected. Another reason to expect some song type sharing within neighborhoods comes from the observation that more similar songs are easier to compare (more “alignable”, see Logue and Forstmeier 2008). This greater ease of comparison could lead to high performance males treating a young, lower performance singer of the same song type less aggressively, as the young bird could quickly be evaluated as low quality. Yet, I detected no pockets of song types or song similarity in any of the neighborhoods sampled, and in fact, found a trend towards the opposite pattern – an over-dispersion of song types in one neighborhood. One possible explanation for this observation concerns the propensity of Chipping Sparrows to shift their territories during the breeding season. Unlike many other songbirds, Chipping Sparrows abandon their territories at a high rate, and seemingly with little provocation (Liu 2001). It is possible that a drive to avoid unfavorable comparisons could keep lower quality males from settling near similar song types, but many more data are needed.

It is also useful to note that this study took place well after territories had been established, which may have affected my findings. Early returning males begin to arrive in the study area the first week of April, and those early territorial encounters and arrangements may have differed from what I observed later in the season. Indeed, work on lizards demonstrates the behaviors and outcomes of first encounters between territory holders differs from later encounters (Stamps and Krishnan 1994). Thus, the "snapshot" approach I took here of examining the more stable, later-season territorial arrangements may have obscured more detailed patterning.

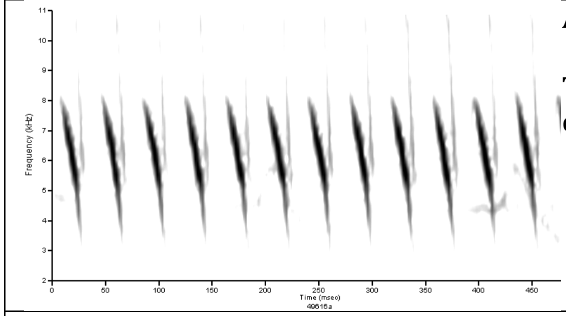
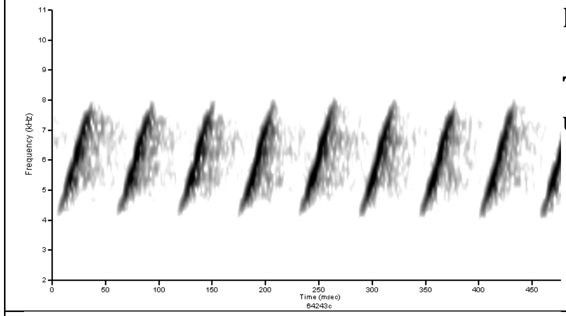
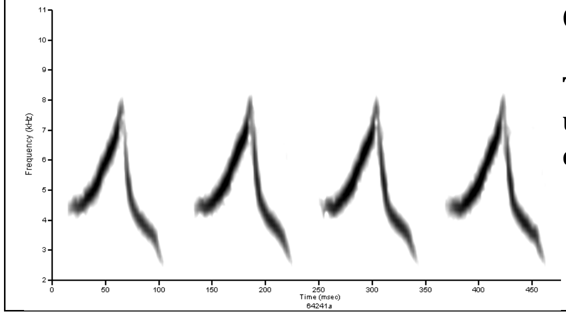
Finally, it is possible that the lack of patterning found represents an outcome of conflicting forces – a desire for favorable evaluations coupled with frequent territorial challenges. To elaborate, males should tend to be evaluated more favorably when they are compared against lower quality males. Low quality males might then avoid settling near high quality males. However, Chipping Sparrows form defensive coalitions to eject intruders, and are most likely to form when the neighbor sings at a higher performance level than the resident. By contrast then, a high quality neighbor is desirable for low quality males who wish to maintain their territories. Taken together, the push and pull of both factors could lead to a neighborhood that is apparently organized at random with respect to social factors, whereas in fact it is shaped by a tangle of social factors that are all important.

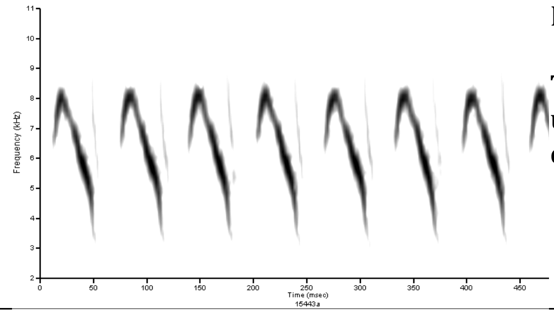
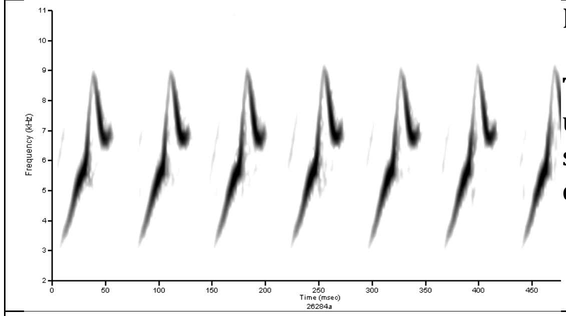
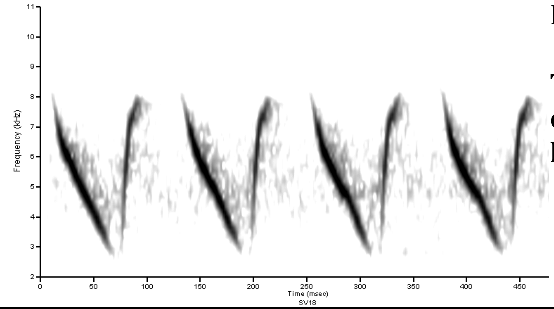
A more thorough examination of these conflicting expectations while require more than descriptive work. To wit, if the outcome of divergent social forces is an apparent "average" neighborhood, no collection of observed data could discern that result. Rather, an experimental approach should be the next step. Future work should include manipulations where males of similar and dissimilar song types of varied performance levels are simulated (or removed) from neighborhoods, and movement types and the formation or lack of formation of coalitions monitored. Additionally, long-term monitoring of neighborhoods, especially during critical settlement periods, may help parse out the factors involved with territory choice. Such data, coupled with the observational data contained herein, would give a more complete picture of the social factors involved in Chipping Sparrow territorial arrangement.

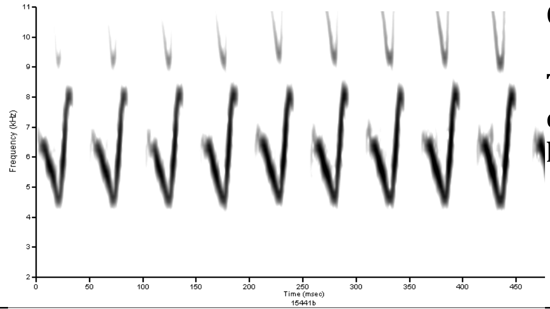
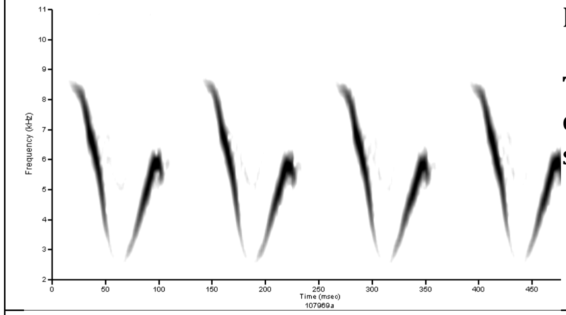
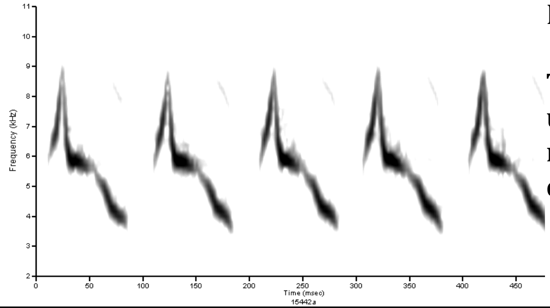
Table 2. Social factors that may affect territorial arrangements of Chipping Sparrows, along with expected behaviors and predicted outcomes.

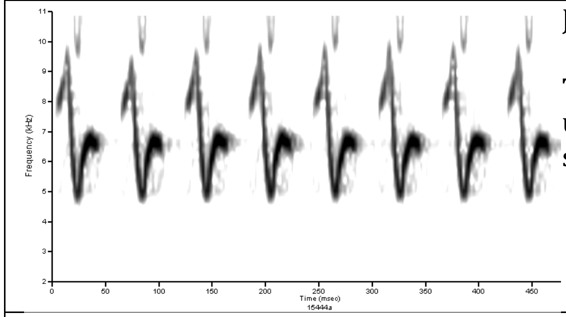
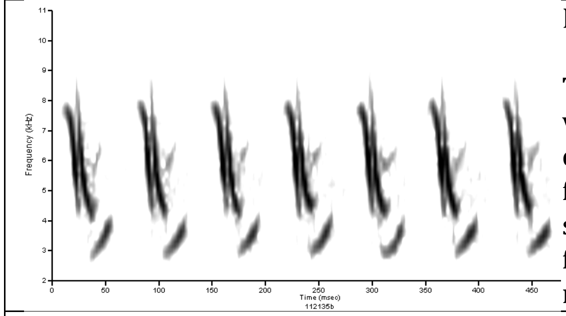
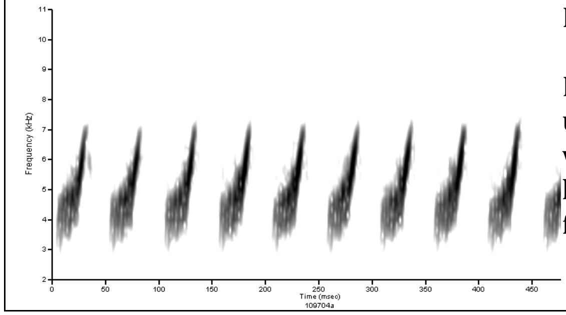
Factor	**Perspective**	**Expectation**	**Predicted Outcome**
male aggregation	all males	clumping of high quality males	heterogenity among neighborhoods with some neighborhoods having higher than expected average performance traits
cooperative defense	all males	low quality males will seek high quality neighbors to help defend territory, high quality males tolerant of low quality neighbors to avoid contending with stronger usurpers	within neighborhood, males will be observed in high and low performance "pairs," or high contrast in performance traits
comparative evaluation	high quality males	high quality males will seek low quality neighbors to increase chance of favorable evaluation by females	within neighborhood, males will be observed in high and low performance "pairs," or high contrast in performance traits
alignable signals	high quality males	high quality males will seek low quality neighbors with similar song types to encourage easy and favorable comparison	neighborhoods with more high performance males will have greater song similarity
	low quality males	low quality males will seek neighbors will disimilar song types to make unfavorable comparisions more difficult to assess	neighborhoods with more low quality males will have greater song disimilarity

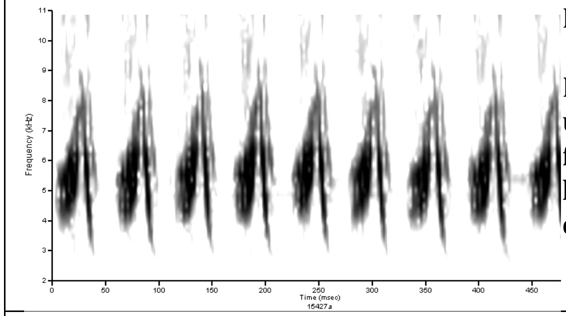
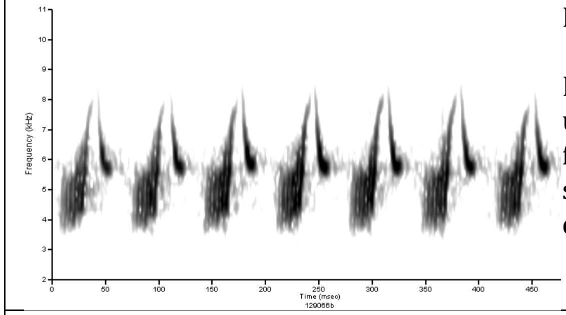
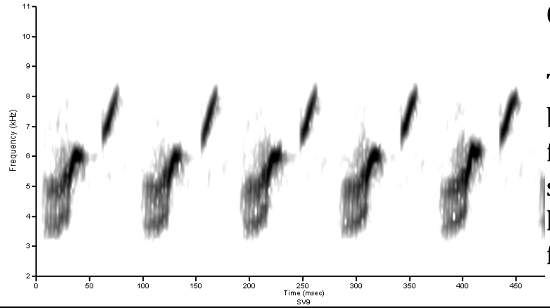
Table 3. Chipping Sparrow song types, with examples, type and descriptions, and observed occurrence in this study as a proportion of observed songs.

Example Song	Type, Description	Borror (1959) Description	Observed
	A, Tonal downsweep	Pattern 4, 5, 6: The phrases not buzzy in quality, each phrase a down-slurred note	0.038
	B, Tonal upsweep	Not described	0.0125
	C, Tonal, long upsweep, long downweep	Not described	0.1625

 D, Tonal, short upsweep, long downsweep	Pattern 19, 21, 22, 23, 24, 25: Phrases not buzzy in quality, each phrase beginning with an up-slur, the rest of the phrase down-slurred to a pitch lower than the lowest pitch in the original up slur	0.25
 E, Tonal, long upsweep, short downseep	Pattern 26, 27: Phrases not buzzy in quality, each phrase an up-slur over an octave or more, then a down-slur over about half an octave	0.0375
 F, Tonal, long downsweep, long upsweep	Pattern 7-14: The phrases not buzzy in quality, each phrase a down-slur followed by an up-slur	0.0625

	G, Tonal, short downsweep, long upsweep	Pattern 7-14: The phrases not buzzy in quality, each phrase a down-slur followed by an up-slur	0.0625
	H, Tonal, long downweeep, short upsweep	Pattern 7-14: The phrases not buzzy in quality, each phrase a down-slur followed by an up-slur	0.025
	I, Tonal, Short upsweep, modulated downsweep	Pattern 16 - 18, 20: Phrases not buzzy in quality, each phrase beginning with an up-slur, the rest of the phrase down-slurred to a pitch lower than the lowest pitch in the original up slur	0.0825

	J, Tonal, short up, long down, short up	Pattern 15: The phrases not buzzy in quality, each phrase a single note consisting of an up-slur, a down-slur, and an upslur	0.0375
	K, Tonal two voice downsweep, followed by short low frequency note	Not described	0.0125
	L, Buzzy upsweep, wider buzz at lower frequency	Pattern 1: song is a simple trill, phrases buzzy in quality, 1 noted phrase	0.0375

	M, Buzzy upsweep followed by long tonal downsweep	Not described	Not found in these neighborhoods, but found at other sites.
	N, Buzzy upsweep followed by short tonal downsweep	Not described	Not found in these neighborhoods, but found at other sites.
	O, Two-note, buzzy low frequency and short, tonal higher frequency	Pattern 3: song is a simple trill, phrases are buzzy in quality, 2 noted phrase	0.0875

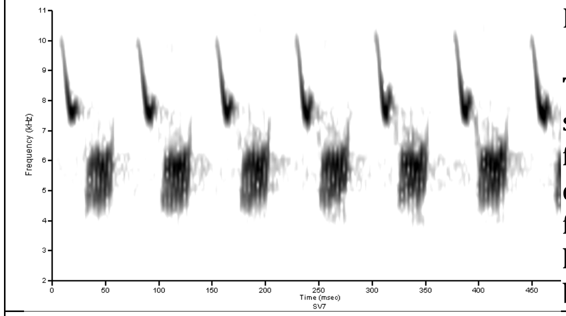
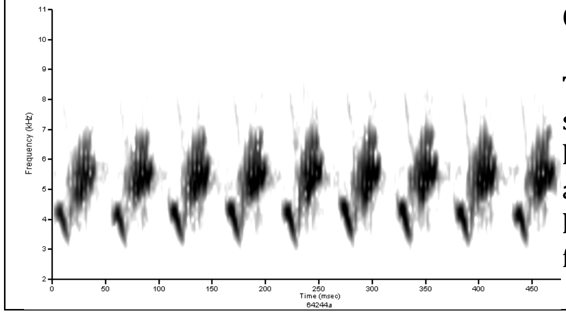
 P, Two note, short high frequency downslur, followed by low frequency buzz	Pattern 2: song is a simple trill, phrases are buzzy in quality, 2 noted phrase	0.075
 Q, Two note, short tonal low frequency and buzzy higher frequency	Not described	0.0125

Table 4. Chipping Sparrow song neighborhoods display no heterogeneity in song performance variables as measured across eighty males in 16 song neighborhoods (one-way ANOVAS, all P > 0.05)

Variable	**F**	**DF**	***P***
Trill Rate	1.424	14, 64	0.168
Frequency Bandwidth	1.809	14, 64	0.057
Vocal Deviation	1.484	14, 64	0.143

Table 5. Chipping Sparrow song neighborhoods have song types proportionate to their representation in the population at large (multinomial exact tests, all P > 0.05).

Song Neighborhood	**Number of males**	**Number of song types**	***P***
Aspen Grove	6	5	0.98
Brookside Easthampton	10	6	0.48
Brookside Sunderland	6	3	0.94
Pine Hill	8	5	0.55
South Cemetery	8	6	0.73
Spring Grove	5	5	0.47
St. Stanislaus	5	5	0.09
West Shutesbury	6	5	0.23

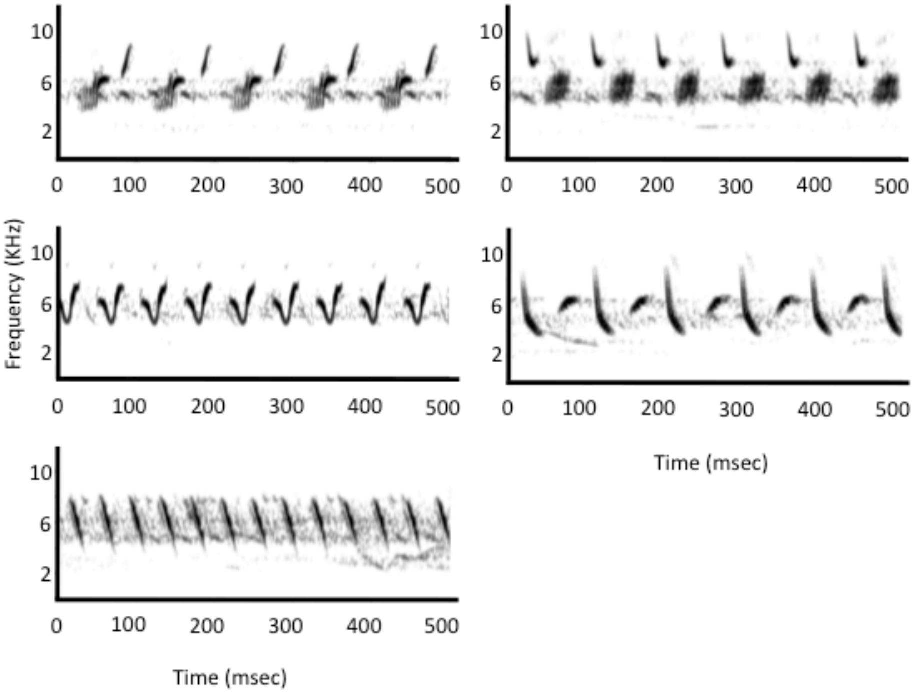
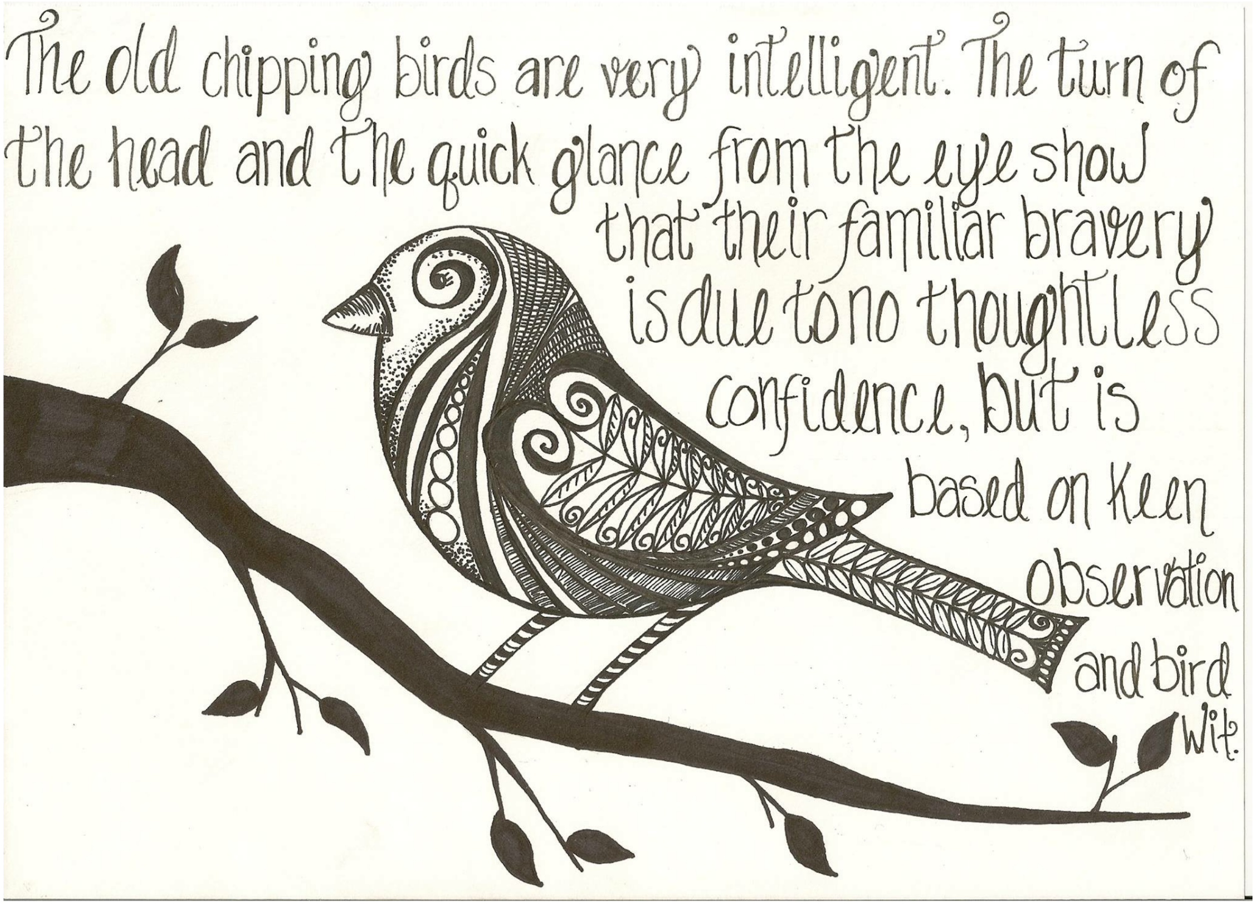


Figure 10. Songs found at St. Stanislaus song neighborhood, where each of five singing males sang a different and uncommon song type (multinomial exact test, *P* = 0.09).

APPENDIX

ILLUSTRATION OF SELECTED QUOTATION II



"The old chipping birds are very intelligent. The turn of the head and the quick glance from the eye show that their familiar bravery is due to no thoughtless confidence, but is based on keen observation and bird wit."

Quotation by Florence Merriam Bailey
"Birds Through an Opera Glass," 1889
Illustration by Hannah Sarat

BIBLIOGRAPHY

Akre, K. L. and Johnsen, S. Psychophysics and the evolution of behavior. *Trends in Ecology and Evolution.* 29(5): 291-300.

Akçay, Ç., Wood, W. E., Searcy, W. A., Templeton, C. N., Campbell, S. E. and Beecher, M. D. 2009. Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. *Animal Behaviour.* 78: 97-102.

Alatalo, R. V., Glynn, C., and Lundberg, A. 1990. Singing rate and female attraction in the pied flycatcher: an experiment. *Animal Behaviour*, 39(3): 601-603.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey. 624 pp.

Backwell, P. R. Y. and Jennions, M. D. 2004 Coalition among male fiddler crabs. *Nature* 430(6998): 417.

Ballentine, B., Hyman, J., and Nowicki, S. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology,* 15(1): 163-168.

Barske, J., Schlinger, B. A., Wikelski, M., and Fusani, L. 2011. Female choice for male motor skills. *Proceedings of the Royal Society of London B: Biological Sciences*: rspb20110382.

Beehler, B. M. and Foster, M. S. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. *American Naturalist,* 131(2): 203-219.

Beeman, S. F. 1987. Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests. *Behavioral Ecology and Sociobiology,* 20: 43-52.

Beeman, K. 2002. SIGNAL 4.0: Engineering Design, Belmont, Massachusetts.

Bermudez-Cuamatzin, E., Rios-Chelen, A. A., Gil, D. and Garcia, C. M. 2011. Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, 7: 36–38.

Booksmythe, I., Jennions, M. D., and Backwell, P. R. Y. 2010 Interspecific assistance: fiddler crabs help heterospecific neighbours in territory defence. *Biology Letters,* 6:748-750.

Borror, D. J. 1959. Songs of the Chipping Sparrow. *Ohio Journal of Science,* 59(6): 347-356.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. *Wilson Bulletin,* 81:293-329.

Brown, J. L. and Orians, G. H. 1970. Spacing patterns in mobile animals. *Annual Review of Ecological Systematics,* 1:239-262.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology,* 73: 434-440.

Brumm, H. and Slabbekoorn, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior*, 35: 151–209.

Brumm, H. and Todt, D. 2002. Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour*, 63: 891–897.

Burt, J. 2001. *SYRINX-PCA: A Windows Program for Spectral Analysis, Editing, and Playback of Acoustic Signals.* http://syrinxpc.com/index.html.

Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press.

Byers, B. E. 2007. Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behavioral Ecology*, 18(1): 130-136.

Byers, J., Hebets, E., and Podos, J. 2010. Female mate choice based upon male motor performance. *Animal Behaviour*, 79(4): 771-778.

Callander, S., Hayes, C. L., Jennions, M. D., and Backwell, P. R. Y. 2013. Experimental evidence that immediate neighbors affect male attractiveness. *Behavioral Ecology,* 24(3): 730-733.

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among european warblers of the genus Acrocephalus. *Behaviour*, 74(1): 149-165.

Catchpole, C. K. and Slater, P. J. B. 2008. *Bird Song: Biological Themes and Variations*. 2nd edn. Cambridge: Cambridge University Press.

Charif, R. A., Waack, A. M. and Strickman, L. M. 2008. *Raven Pro 1.3 User's Manual*. Ithaca, New York: Cornell Laboratory of Ornithology.

Christie, P. J., Mennill, D. J. and Ratcliffe, L. M. 2004. Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behavioral Ecology and Sociobiology*, 55: 341–348.

Demary, K., Michaelidis, C. I., and Lewis, S. M. 2006. Firefly courtship: behavioral and morphological predictors of male mating success in *Photinus greeni*. *Ethology*, 112(5): 485-492.

Detto, T., Jennions, M. D., and Backwell, P. R. Y. 2010. When and why do territorial coalitions occur? Experimental evidence from a fiddler crab. *American Naturalist,* 175(5): 119-125.

Dooling, R. J. 1982. Auditory perception in birds. In: *Acoustic Communication in Birds. Vol. 1* pp. 95–130. New York: Academic Press.

DuBois, A. L., Nowicki, S., and Searcy, W. A. 2011. Discrimination of vocal performance by male swamp sparrows. *Behavioral ecology and sociobiology*, 65(4): 717-726.

Dugatkin, L. A. 1997 *Cooperation Among Animals: an Evolutionary Perspective.* Oxford: Oxford University Press.

Elfström, S. T. 1997 Fighting behaviour and strategy of rock pipit, *Anthus petrosus*, neighbours: cooperative defence. *Animal Behaviour,* 54: 535–542.

Fernández-Juricic, E., Poston, R., De Collibus, K., Morgan, T., Bastan, B., Martin, C., Jones, K. and Tremino, R. 2005. Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. *Urban Habitats,* 3: 49–69.

Ficken, M. S., Ficken, R. W. and Witkin, S. R. 1978. Vocal repertoire of black-capped chickadee. *Auk*, 95: 34–48.

Fisher, J. 1954 Evolution and bird sociality, in *Evolution as a Process*, Huxley, J., Hardy, A. C. and Ford, E. B. (Eds). London: Allen and Unwin.

Fitzsimmons, L. P., Foote, J. R., Ratcliffe, L. M. and Mennill, D. J. 2008. Frequency matching, overlapping, and movement behaviour in diurnal countersinging interactions of black-capped chickadees. *Animal Behaviour*, 75: 1913–1920.

Fletcher, N. H. and Tarnopolsky, A. 1999. Acoustics of the avian vocal tract. *Journal of the Acoustic Society of America*, 105: 35–49.

Foote, J. R., Fitzsimmons, L. P., Mennill, D. J. and Ratcliffe, L. M. 2008. Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. *Behavioral Ecology*, 19: 1192–1199.

Foote, J. R., Mennill, D. J, Ratcliffe, L. M. and Smith, S. M. 2010. Black-capped chickadee (*Poecile atricapillus*). In: *The Birds of North America Online* (Ed. by A. Poole). Ithaca, New York: Cornell Lab of Ornithology.

Forman, R. T. T., Reineking, B. and Hersperger, A. M. 2002. Road traffic and nearby grassland bird patterns in a suburbanizing landscape. *Environmental Management,* 29: 782–800.

Freeman, S. 1987 Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests. *Behavioral Ecology and Sociobiology,* 21: 307-311.

Fretwell, S. D., and Lucas, H. L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, 19: 16-44.

Fuller, R. A., Warren, P. H. and Gaston, K. J. 2007. Daytime noise predicts nocturnal singing in urban robins. *Biology Letters*, 3: 368–370.

Garcia-Rutledge, E. J. and Narins, P. M. 2001. Shared acoustic resources in an old world frog community. *Herpetologica,* 57: 104–116.

Getty, T. 1987 Dear enemies and the prisoner's dilemma: why should territorial neighbors form defensive coalitions? *American Zoologist,* 27: 327–336.

Goodwin, S. E. and Shriver, W. G. 2011. Traffic noise influences occupancy rate of forest birds. *Conservation Biology*, 25: 406–411.

Goodwin, S. E. and Podos, J. 2014. Team of rivals: alliance formation in territorial songbirds is predicted by vocal signal structure. *Biology Letters,* 10(2): 20131083.

Grafe, T. U. 1996. The function of call alternation in the African reed frog (*Hyperolius marmoratus*): precise call timing prevents auditory masking. *Behavioral Ecology and Sociobiology,* 38,:149–158.

Grafen, A. 1990. Sexual selection unhandicapped by the Fisher process. *Journal of theoretical biology*, 144(4): 473-516.

Greene, E., Lyone, B. E., Muehter, V. R., Ratcliffe, L., Oliver, S. J., and Boag, P. T. 2000. Disruptive sexual selection for plumage coloration in a passerine bird. *Nature*, 407(6807): 1000-1003.

Gross, K., Pasinelli, G. and Kunc, H. P. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *American Naturalist*, 176: 456–464.

Halfwerk, W. and Slabbekoorn, H. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Animal Behaviour,* 78: 1301–1307.

Healey, M. C. 1967. Aggression and self-regulation of population size in deermice. *Ecology*, 48(3): 377-392.

Hebets, E. A., and Uetz, G. W. 1999. Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus Schizocosa (Araneae: Lycosidae). *Animal Behaviour*, 57(4): 865-872.

Henry, K. S. and Lucas, J. R. 2010. Auditory sensitivity and the frequency selectivity of auditory filters in the Carolina chickadee, *Poecile carolinensis*. *Animal Behaviour*, 80: 497–507.

Hinde, R. A. 1956. The biological significance of territories of birds. *Ibis*, 98:340-369.

Hoeschele, M., Moscicki, M. K., Otter, K. A., van Oort, H., Fort, K. T., Farrell, T. M., Lee, H., Robson, S. W. J. and Sturdy, C. B. 2010. Dominance signaled in an acoustic ornament. *Animal Behaviour*, 79: 657–664.

Horn, A. G., Leonard, M. L., Ratcliffe, L., Shackleton, S. A. and Weisman, R. G. 1992. Frequency variation in songs of black-capped chickadees (*Parus atricapillus*). *Auk*, 109: 847–852.

Houtman, A. M. 1992. Female zebra finches choose extra-pair copulations with genetically attractive males. *Proceedings of the Royal Society of London B: Biological Sciences*, 249(1324): 3-6.

Hu, Y. and Cardoso, G. C. 2009. Which birds adjust the frequency of vocalizations in urban noise? *Animal Behaviour*, 79: 863–867.

Illes, A. E., Hall, M. L., and Vehrencamp, S. L. 2006. Vocal performance influences male receiver response in the banded wren. *Proceedings of the Royal Society B,* 273(1596): 1907-1912.

Klump, G. A. 1996. Bird communication in the noisy world. In: *Ecology and Evolution of Acoustic Communication in Birds*, pp. 321–338. Ithaca, New York: Cornell University Press.

de Kort, S. R., Eldermire, E. R., Cramer, E. R., and Vehrencamp, S. L. 2009. The deterrent effect of bird song in territory defense. *Behavioral Ecology*, 20(1): 200-206.

Lachlan, R. F., Verhagen, L., Peters, S., and Cate, C. T. 2010. Are there species-universal categories in bird song phonology and syntax? A comparative study of Chaffinches (*Fringilla coelebs*), Zebra Finches (*Taenopygia guttata*), and Swamp Sparrows (*Melospiza georgiana*). *Journal of Comparative Psychology*, 124(1): 92-108.

Leavesley, A. J., and Magrath, R. D. 2005. Communicating about danger: urgency alarm calling in a bird. *Animal behaviour*, 70(2): 365-373.

Lewis, S. M., and Cratsley, C. K. 2008. Flash signal evolution, mate choice, and predation in fireflies. *Annual Review of Entomology*, 53: 293-321.

Liu, W. C. 2001. Song development and singing behavior of the Chipping Sparrow (Spizella passerina) in western Massachusetts. Doctoral dissertation, University of Massachusetts, Amherst.

Liu, W. C. 2004. The effect of neighbours and females on dawn and daytime singing behaviours by male Chipping Sparrows. *Animal Behaviour*, 68(1): 39-44.

Logue, D. M. and Forstmeier, W. 2008 Constrained performance in a communication network: implications for the function of song-type matching and for the evolution of multiple ornaments. *American Naturalist,* 172: 34-42.

Luther, D. 2009. The influence of acoustic community on songs of birds in a Neotropical rain forest. *Behavioral Ecology*, 20: 846–871.

Marler, P., and Pickert, R. 1984. Species-universal microstructure in the learned song of the swamp sparrow (*Melospiza georgiana*). *Animal Behaviour*, 32(3): 673-689.

Matsumasa, M., and Murai, M. 2005. Changes in blood glucose and lactate levels of male fiddler crabs: effects of aggression and claw waving. *Animal Behaviour*, 69(3): 569-577.

McGregor, P. K. 2005 *Animal Communication Networks.* Cambridge: Cambridge University Press.

Mennill, D. J. and Ratcliffe, L. M. 2004a. Overlapping and matching in the song contests of black-capped chickadees. *Animal Behaviour*, 67: 441–450.

Mennill, D. J. and Ratcliffe, L. M. 2004b. Do male black-capped chickadees eavesdrop on song contests? A multi-speaker playback experiment. *Behaviour*, 141: 125–139.

Mennill, D. J., Ratcliffe, L. M. and Boag, P. T. 2002. Female eavesdropping on male song contests in songbirds. *Science*, 296: 873.

Milner, R. N. C., Jennions, M. D. and Backwell, P. R. Y. 2011 Know thine enemy's neighbor: neighbor size affects floater's choice of whom to fight. *Behavioral Ecology,* 22: 947-950.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. *American Naturalist,* 109: 17–34.

Moseley, D. L., Lahti, D. C., and Podos, J. 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(1768): 20131401

Naguib, M., Schmidt, R., Sprau, P., Roth, T., Flörcke, C., and Amrhein, V. 2008. The ecology of vocal signaling: male spacing and communication distance of different song traits in nightingales. *Behavioral Ecology*, 19(5): 1034-1040.

Naguib, M. and Mennill, D. J. 2010. The signal value of birdsong: empirical evidence suggests song overlapping is a signal. *Animal Behaviour,* 80: e11–e15.

Nemeth, E. and Brumm, H. 2010. Bird songs and anthropogenic noise: are urban songs adaptive? *American Naturalist*, 176: 465–475.

Nice, M. M. 1941. The role of territory in bird life. *The American Midland Naturalist,* 25(3): 441-487.

Noble, G. K. 1939. The role of dominance in the social life of birds. *The Auk*, 263-273.

Otter, K. 2007. *Ecology and Behavior of Chickadees and Titmice: an Integrated Approach*. Oxford: Oxford University Press.

Otter, K., Chruszcz, B. and Ratcliffe, L. M. 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology,* 8: 167–173.

Peake, T. M., Terry, A. M. R., McGregor, P. K., and Dabelsteen, T. 2001 Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proceedings of the Royal Society B: Biological Sciences*, 268: 1183–1187

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(2): 537-551.

Podos, J. and Nowicki, S. 2004. Performance limits on birdsong production. In: *Nature's Music: the Science of Birdsong* (Ed. by P. Marler and H. Slabbekoorn), pp. 318–341. New York: Elsevier/Academic Press.

Podos J, Lahti, D. C., and Moseley, D. L. 2009 Vocal performance and sensorimotor learning in songbirds. *Advances in the Study of Behavior*, 40: 159–195.

Popp, J. W., Ficken, R. W. and Reinartz, J. A. 1985. Short-term temporal avoidance of interspecific acoustic interference among forest birds. *Auk*, 102: 744–748.

Proppe, D. S., Avey, M. T., Hoeschele, M., Moscicki, M. K., Farrell, T., St Clair, C. C. and Sturdy, C. B. 2012. Black-capped chickadees *Poecile atricapillus* sing at higher pitches with elevated anthropogenic noise, but not with decreasing canopy cover. *Journal of Avian Biology*, 43: 325–332.

R Development Core Team 2016*. R: a Language and Environment for Statistical Computing*.Vienna: R Foundation for Statistical Computing.

Reijnen, R. and Foppen, R. 1995. The effects of car traffic on breeding bird populations in woodland. 4. Influence of population-size on the reduction of density close to a highway. *Journal of Applied Ecology*, 32: 481-491.

Reijnen, R., Foppen, R., Terbraak, C. and Thissen, J. 1995. The effects of car traffic on breeding bird populations in woodland. 3. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology*, 32: 187–202.

Reijnen, R., Foppen, R. and Meeuwsen, H. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation*, 75: 255–260.

Reijnen, R., Foppen, R. and Veenbaas, G. 1997. Disturbance by traffic of breeding birds: evaluation of the effect and considerations in planning and managing road corridors. *Biodiversity and Conservation,* 6: 567–581.

Rheindt, F. E. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? *Journal für Ornithologie*, 144: 295–306.

Riebel, K. and Slater, J. B. 1999. Song type switching in the chaffinch, *Fringilla coelebs*: timing or counting? *Animal Behaviour,* 57: 655–661.

Ryan, M. J. and Cummings, M. E. 2005. Animal signals and the overlooked costs of efficacy. *Evolution,* 59: 1160–1161.

Sakata, J. T. and Vehrencamp, S. L. 2012. Integrating perspectives on vocal performance and consistency. *Journal of Experimental Biology,* 215:201-209.

Schluter, D. 2000. Ecological character displacement in adaptive radiation. *American Naturalist, Supplement,* 156: S4–S16.

Searcy, W. A. and Nowicki, S. 2005. The Evolution of Animal Communication: Reliability and Deception in Signalling Systems. Princeton University Press, Princeton, New Jersey.

Searcy, W. A., Anderson, R. C., and Nowicki, S. 2006. Bird song as a signal of aggressive intent. *Behavioral Ecology and Sociobiology*, 60(2): 234-241.

Searcy, W. A. and Beecher, M. D. 2009. Song as an aggressive signal in songbirds. *Animal Behaviour,* 78: 1281–1292.

Searcy, W. A. and Beecher, M. D. 2011. Continued scepticism that song overlapping is a signal. *Animal Behaviour,* 81: e1–e4.

Seyfarth, R. M, and Cheney, D. L. 2015. Social cognition. *Animal Behaviour*, 103: 191-202.

Slabbekoorn, H. and Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature*, 424: 267.

Smith, S. M. 1976. Ecological aspects of dominance hierarchies in black-capped chickadees. *Auk,* 93: 95–107.

Smith, S. M. 1991. *The Black-capped Chickadee: Behavioral Ecology and Natural History*. Ithaca, New York: Cornell University Press.

Stamps, J. 1987. Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. *American Naturalist* 129(5): 629-642.

Stamps, J. 1991. The effect of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology*, 28(1): 29-36.

Stamps, J. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior*, 23: 173-232.

Stamps, J. and Krishnan, V. V. 1994. Territory acquisition in lizards: I. first encounters. *Animal Behaviour,* 47(6): 1375-1385.

Sueur, J. 2008. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biological Journal of the Linnean Society,* 75: 379–394.

Suthers, R. A., Vallet, E. and Kreutzer, M. 2012 Bilateral coordination and the motor basis of female preference for sexual signals in canary song. *Journal of Experimental Biology,* 215: 2950-2959.

Svensson, B. G. and Petersson, E. 1992. Why insects swarm: testing the models for lek mating systems on swarming *Empis borealis* females. *Behavioral Ecology and Sociobiology*, 31(4): 253-261.

Todt, D. and Naguib, M. 2000. Vocal interactions in birds: the use of song as a model in communication. In: *Advances in the Study of Behavior* (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon and T. J. Roper), pp. 247–296. New York: Academic Press.

Verzijden, M. N., Ripmeester, E. A. P., Ohms, V. R., Snelderwaard, P. and Slabbekoorn , H. 2010. Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise*. Journal of Experimental Biology,* 213: 2575–2581.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. and Melillo, J. M. 1997. Human domination of Earth's ecosystems. *Science,* 277: 494–499.

Voigt, C. C., von Helversen, O., Michener, R., and Kunz, T. H. 2001. The economics of harem maintenance in the sac-winged bat, Saccopteryx bilineata (Emballonuridae). *Behavioral Ecology and Sociobiology*, 50(1): 31-36.

Wagner, W. E., and Hoback, W. W. 1999. Nutritional effects on male calling behaviour in the variable field cricket. *Animal Behaviour*, 57(1): 89-95.

Wasserman, F. E. 1977. Intraspecific acoustical interference in white-throated sparrow (*Zonotrichia albicollis*). *Animal Behaviour*, 25: 949–952.

Weisman, R., Ratcliffe, L., Johnsrude, I. and Hurly, T. A. 1990. Absolute and relative pitch production in the song of the black-capped chickadee. *Condor,* 92: 118–124.

Wiley, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist,* 138: 973–993.

Wilson, D. R. and Mennill, D. J. 2011. Duty cycle, not signal structure, explains conspecific and heterospecific responses to the calls of black-capped chickadees. *Behavioral Ecology,* 22: 784–790.

Wilson, D. R., Bitton, P. P., Podos, J., and Mennill, D. J. 2014. Uneven sampling and the analysis of vocal performance constraints. *The American Naturalist*, 183(2): 214-228.

Wood, W. E. and Yezerinac, S. M. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk*, 123: 650–659.

Zollinger, S. A., Podos, J., Nemeth, E., Goller, F., and Brumm, H. 2012. On the relationship between, and measurement of, amplitude and frequency in birdsong. *Animal Behaviour*, 84(4): e1-e9.