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The Adaptive Significance of Vocal Performance in Songbird Communication

Adrienne L. DuBois
University of Miami, adriennedubois@gmail.com

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UNIVERSITY OF MIAMI

THE ADAPTIVE SIGNIFICANCE OF VOCAL PERFORMANCE IN SONGBIRD COMMUNICATION

By

Adrienne L. DuBois

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of the University of Miami
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Doctor of Philosophy

THE ADAPTIVE SIGNIFICANCE OF VOCAL PERFORMANCE IN SONGBIRD COMMUNICATION

Adrienne L. DuBois

Approved:

William A. Searcy, Ph.D.
Professor of Biology

Terri A. Scandura, Ph.D.
Dean of the Graduate School

Michael S. Gaines, Ph.D.
Professor of Biology

Keith D. Waddington, Ph.D.
Professor of Biology

Jeff Podos, Ph.D.
Professor of Biology
University of Massachusetts, Amherst

Richard R. Tokarz, Ph.D.
Associate Professor of Biology

DUBOIS, ADRIENNE L. (Ph.D., Biology)
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The question of how honesty is maintained in animal communication is a perplexing one, especially in the context of aggressive communication, in which the interests of signalers and receivers are opposed. Relevant information for receivers in aggressive interactions includes the fighting ability of the signaler and its likelihood of attack. Signalers may, however, benefit from manipulation of signals to exaggerate this information. To address questions of signal honesty, this dissertation investigates the use of a performance signal in the song of swamp sparrows (*Melospiza georgiana*). Performance signals are ones that are physically demanding to perform and that therefore reveal the signaler's physical ability. The particular measure of vocal performance examined here is vocal deviation, which refers to the ability of birds to produce trilled songs approaching a performance boundary defined by the tradeoff between song trill rate (the rate at which elements of a song are repeated) and frequency bandwidth (the range of frequencies encompassed in a song). Three questions regarding the adaptive significance of vocal performance were investigated in the swamp sparrow 1) whether vocal performance is used as a signal in male-male communication, 2) whether vocal performance should be classified as an index signal of male quality, and 3) whether vocal deviation serves as a signal of aggressive intent. Results from four studies indicate that vocal performance plays a role in male-male signaling. Signalers appear to use vocal performance as a signal and receivers attend to differences in vocal performance.

Evidence also indicates that vocal performance can be classified as an index signal, because males are constrained in their ability to produce high performance song and high vocal performance is correlated with aspects of male quality, such as age and size. Finally, this dissertation does not support classification of vocal performance as a signal of aggressive intent, because vocal performance fails to predict aggressive escalation.

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Chapter 1

Introduction

A crucial question in animal communication is whether signals are “honest.” Signals are said to be honest if “some characteristic of the signal… is consistently correlated with some attribute of the signaler or its environment and receivers benefit from having information about this attribute” (Searcy and Nowicki 2005). Receivers should respond to signals only if they are honest in this sense, but selection may often act on signalers to exaggerate their signals, thus diminishing honesty. How then is signal honesty maintained? This dissertation addresses the question of honest communication with respect to a vocal performance trait, “vocal deviation,” used in male aggressive signaling in a songbird.

When the interests of signalers and receivers are in line, such as when close genetic relatives signal to each other, there is an obvious benefit to maintaining an honest signaling system, as both players will benefit from the exchange. The benefits of honest signaling are less obvious when the interests of signalers and receivers are in direct opposition, as is true in aggressive contexts (Searcy and Nowicki 2005). Still, mechanisms to maintain honesty in such contexts do exist. One such mechanism is performance constraints. In aggressive signaling, receivers benefit from information about opponents’ aggressiveness and fighting ability. While aggressiveness may be encoded in “strategic signals,” which all signalers are able to produce, fighting ability may be conveyed by “index signals,” signals whose performance is constrained by physical ability, and thus can only be performed by a capable subset of the population (Maynard Smith and Harper 2003, Hurd and Enquist 2005).

Bird song is often used as a model for questions about the evolution of communication, including how honesty is maintained in aggressive communication. In the temperate zone, song is typically a male trait, used both in intersexual communication, to attract and stimulate females, as well as in intrasexual aggressive communication, to establish and defend breeding territories. Song is thus generally regarded as a "dual function" signal (Catchpole and Slater 1995, Searcy and Nowicki 2000). Bird song can be considered to contain many different signals related to traits such as song performance, timing, structure, and output. These traits vary individually and interspecifically and all can be influenced by both inter-and intra-sexual selection (Gil and Gahr 2002).

Previous research on bird song has identified many components of song that function in intersexual interactions, intrasexual interactions, or both (Searcy and Nowicki 2005). Much research effort has focused on the effect of intersexual selection on three categories of song attributes: measures of song complexity such as song type repertoire size and syllable repertoire size, measures of song output such as singing rate and song length, and song characteristics that vary geographically to produce dialects (see reviews in Catchpole and Slater 1995, Collins 2004, Searcy and Nowicki 2005). Although there is good evidence for the function of many of these components in intersexual interactions, it is somewhat less clear how intrasexual selection has affected song and singing behavior (Searcy and Nowicki 2000). Singing behaviors that have been suggested to signal quality or aggressive intent in male-male interactions include song type matching, song type switching, song overlapping, and the production of low amplitude "soft song" (Krebs et al. 1981, Kramer and Lemon 1983, Vehrencamp 2000, 2001, Burt et al. 2001, Searcy et al. 2006, Kunc et al. 2006). Evidence supporting an aggressive function for these behaviors, however, is mixed (Searcy and Beecher 2009).

Vocal performance is another aspect of song likely to be important in intrasexual interactions. Vocal performance is the ability to produce physically or physiologically demanding songs (Podos 2001, Forstmeier et al. 2002, Ballentine et al. 2004, Cardoso et al. 2009), and refers broadly to a number of song characteristics, including use of “special syllables” (Vallet and Kreutzer 1995, Vallet et al. 1998), percentage peak performance (Forstmeier et al. 2002), acoustic density (Leadbeater et al. 2005, Holveck and Riebel 2007, Cardoso et al. 2009), residual intervals (Cardoso et al. 2007, Cardoso et al. 2009), predicted amplitude (Cardoso et al. 2007, Cardoso et al. 2009), and vocal deviation (Podos 2001).

In this dissertation, I focus on one of these vocal performance characteristics, vocal deviation, for two main reasons. First, the different measures of performance listed above differ broadly in the mechanism proposed to constrain singers. For example, males may be constrained in their ability to maintain high sound amplitude during song, because of tradeoffs between producing high amplitude sounds while singing songs that change in frequency (Forstmeier et al. 2002). Respiratory limits may constrain males in their ability to sing songs with short intervals of respiratory recovery (Cardoso et al. 2009). Constraints on vocal deviation, however, are explained by what is perhaps the best-resolved biomechanical model (described below). Although vocal deviation is specific to species that sing a trilled song, it can be broadly applied to any taxon meeting this requirement. A second reason for focusing on vocal deviation is that this performance measure has been well-studied in the model species used in this dissertation research, the swamp sparrow, *Melospiza georgiana*. Swamp sparrows were used to investigate the biomechanics of changing acoustic frequency during singing (Westneat et al. 1993, Hoese et al. 2000) and constraints on song production (Podos 1996). Vocal deviation in swamp sparrows has also been investigated regarding associations with male quality (Ballentine 2009) and female preference (Ballentine et al. 2004).

Vocal deviation is defined with reference to the tradeoff between a song's frequency bandwidth (the range of frequencies encompassed by a song) and trill rate (the rate at which song elements are repeated; Podos 2001). Singers are limited in their ability to produce songs with simultaneously broad bandwidths and rapid trill rates, owing to morphological constraints (Westneat et al. 1993, Hoese et al. 2000). Songs that approach a population-level maximum of performance capability are said to have small vocal deviations, and are considered higher vocal performance songs. Songs that fall well short of the maximum are low performance songs (Podos 2001).

Understanding why there is a tradeoff between bandwidth and trill rate requires an understanding of vocal tract morphology and mechanics in songbirds. The vocal organ of birds is the syrinx, located at the base of the trachea. Songbirds have the most developed syrinx among avian taxa (Suthers and Zollinger 2004, Catchpole and Slater 1995). Air flows through the syrinx, vibrating membranes to produce sound. Syringeal muscles alter the tension and positioning of these membranes to modulate the acoustic characteristics of the sound. Other elements in the avian vocal tract, however, appear to act as a filter and modify sounds after they leave the syrinx (Nowicki 1987). For example, Westneat et al. (1993) found correlations between the beak gape of individuals and the frequency of notes produced in two species of Emberizid sparrows. Opening the beak shortens the vocal tract, resulting in a high-frequency sound, while closing the beak accomplishes the opposite. Therefore, to produce a large change in frequency, a bird must greatly change the angle of the beak to alter the vocal tract (see also Goller et al. 2004). The ability of birds to use and coordinate beak movements appears to increase during the course of song development, and this increase corresponds with an improvement in tonal quality of songs (Podos et al. 1995). Furthermore, disrupting the natural ability of birds to modify beak position alters the acoustic properties of songs (Hoese et al. 2000). Additional constraints on song production include limitations on movement of parts of the vocal tract other than the beak to alter the vocal tract's resonance properties and the necessity to coordinate respiratory and syringeal musculature (reviewed by Nowicki et al. 1992). Because of these constraints on song production, birds are limited in their ability to make the alterations of vocal tract configuration needed to manipulate note frequencies while doing so rapidly to increase trill rate. This limitation results in a trade-off between the magnitude of the changes in frequency that a bird can produce and the rate at which these changes in frequency can occur. Individuals differ in their physical ability to maximize simultaneously both the trill rate and the frequency bandwidth of songs, and these differences in physical ability produce differences in vocal performance.

When songs (or mean performance values of individuals) are graphed by trill rate against frequency bandwidth, they tend to fall out in a triangular distribution, with few or no points in the upper right quadrant representing the combination of rapid trill rate and high frequency bandwidth (Figure 1.1). Podos (1997) first demonstrated this relationship for the Emberizidae, and calculated an upper-bound regression line that represented a performance limit for the family—above which songs cannot be produced. A song's vocal deviation is its orthogonal distance from that upper-boundary line (Podos 2001). Since Podos's description of trilled songs in the Emberizidae, a trade-off between trill rate and frequency bandwidth has been demonstrated in several species of songbirds across passerine families (domesticated canary, *Serinus canaria*, Draganoiu et al. 2002; yellow warbler, *Dendroica petechia*, Beebee 2004; Darwin's small tree finch, *Camarhynchus parvulus*, Christensen et al. 2006; banded wren, *Thryothorus pleurostictus*, Illes et al. 2006; dark-eyed junco, *Junco hyemalis*, Cardoso et al. 2007; red-winged blackbird, *Agaeliaus phoeniceus*, Cramer and Price 2007), as well as in nonpasserines (brown skua, *Catharacta antarctica lonnbergi*, Janicke et al. 2008, great frigatebird, *Frigata minor*, Juola 2010).

Evidence from a learning experiment supports the idea that motor constraints affect vocal production. Podos (1996) artificially increased the trill rates of tutor songs played to young male swamp sparrows. The male sparrows were subsequently unable to imitate the songs of their tutors, and compensated by reducing trill rates, reducing the numbers of notes within syllables, or producing songs with pauses interspersed between syllable segments. The close association between vocal mechanics and song attributes thus may impose a physical constraint that maintains honesty in the signal (Vehrencamp 2000, Searcy and Nowicki 2005).

Evidence supports the classification of vocal performance as an index signal of male quality. In swamp sparrows (*M. georgiana*), males' maximum vocal performance is positively correlated with age and size—two aspects of quality (Ballentine 2009). Variation in performance ability may translate into differential mating opportunities, as female swamp sparrows prefer higher performance songs (Ballentine et al. 2004).

Presumably, females show this preference because males with higher vocal performance make higher quality mates, in terms of ability to provide direct or indirect benefits. Signals of size and age are likely to be important also in male-male signaling, because older, larger males tend to win encounters with smaller, younger males (Searcy 1979, Richner 1989, Sandell and Smith 1991, Koivula et al. 1993, Yamaguchi and Kawano 2001). Therefore, vocal performance may be used as an assessment signal in male-male aggressive communication.

In this dissertation, I investigate the adaptive significance of vocal performance in male-male aggressive signaling in swamp sparrows (*M. georgiana*). Swamp sparrows are an ideal model system for vocal performance research for several reasons. Males hold territories throughout the breeding season and territory boundaries can be delineated clearly by singing posts used by the territory owner (Mowbray 1997). Males sing a relatively simple song, a 2-3 second trilled series of syllables, with each syllable composed of 2-5 notes (Marler and Pickert 1984). The simplicity of the song minimizes the possible effect of other song components on signaling. Repertoires are small relative to other species, with males in the study population singing an average of 3.1 song types (range 1-4) (Ballentine et al. 2004, $n = 91$). A wild population of swamp sparrows in Conneaut Marsh, Crawford County, Pennsylvania was used to conduct all dissertation research.

To investigate the adaptive significance of vocal performance, I addressed three questions regarding the use of vocal deviation as a signal. First, does vocal deviation function in male-male signaling in swamp sparrows? Vocal performance (measured in terms of vocal deviation) appears to function in male-female signaling in swamp sparrows. Female swamp sparrows prefer higher performance songs (Ballentine et al. 2004), presumably because high performance song indicates a high quality male (Ballentine 2009). Studies investigating performance in two other songbird species demonstrate male receivers respond to vocal performance as a signal, discriminating between high and low vocal performance levels (Illes et al. 2006, Cramer and Price 2007). In this dissertation I will examine the male-male signal function of vocal deviation by testing for receiver response to vocal deviation in swamp sparrows, as well as patterns of signaler behavior predicted by a male-male signal function of vocal deviation.

The second question I will address in this dissertation is whether vocal deviation should be classified as an index signal. Index signals are a class of performance signals that are honest because the quality being signaled is causally tied to both the intensity of the signal and the mechanism of signal production. Index signals are reliable because they physically cannot be faked (Maynard Smith and Harper 2003). Examples include the dominant frequency of calls in frogs and toads (Davies and Halliday 1978, Ryan 1985, Wagner 1989*a*, 1989*b*) and the formant dispersion of roars in red deer (*Cervus elaphus*, Reby and McComb 2003, Reby et al. 2005). Both of these signals are mechanistically tied to signaler body size and are thus honest signals of quality, in terms of male size. Constraints acting on index signals must prevent modulation sufficient to cause a decoupling of signal intensity and the quality being signaled. Modulation of signals to the point that they convey dishonest information about the quality of the signaler is said to represent “cheating.” In this dissertation I will examine the ability of male swamp sparrows to modulate vocal deviation flexibly, and how such modulation affects receiver response.

The third question I will examine is whether vocal deviation is a signal of aggressive intent. Evidence suggests that vocal performance is a signal of male quality, in terms of fighting ability. Vocal performance is correlated with male size and age in swamp sparrows (Ballentine 2009), and in many songbird species, older, larger males tend to win aggressive encounters (Searcy 1979, Richner 1989, Sandell and Smith 1991, Koivula et al. 1993, Yamaguchi and Kawano 2001). Because individuals of high fighting ability are likely to win aggressive encounters, signals of fighting ability can also serve an additional function as signals of aggressive intent, that is, the likelihood that a signaler will attack. Searcy and Beecher (2009) provide three criteria to determine whether signals may be classified as aggressive: demonstrations that the signal increases in aggressive contexts (the "context" criterion), that the signal predicts aggressive escalation by the signaler (the "predictive" criterion), and that receivers respond to the signal (the "response" criterion). I will therefore evaluate the evidence for classifying vocal deviation as an aggressive signal according to these criteria.

The following four chapters consist of empirical studies investigating the role of vocal deviation in aggressive contexts in swamp sparrows. Each study provides insight toward the questions addressed above regarding the adaptive significance of vocal performance. In Chapter 2, I address the use of vocal deviation in male-male signaling and the question of whether vocal deviation is an index signal from the signaler's perspective, by determining whether males are able to modulate vocal deviation according to situational context. The results of this study are discussed with respect to implications for signal honesty. In Chapter 3 I address whether vocal deviation is a signal of aggressive intent. Utilizing data from two experiments, I evaluate the possible relationship between vocal deviation and aggressive escalation, Searcy and Beecher's "predictive" criterion for aggressive signals (2009). In Chapter 4 I continue to examine the use of vocal deviation in male-male signaling and the potential classification of vocal deviation as an aggressive signal—in this case from the receiver's perspective. I test the ability of male receivers to discriminate vocal deviation differences at multiple levels, thereby addressing Searcy and Beecher's "response" criterion for aggressive signals. The final experimental chapter, Chapter 5, consists of an investigation of the male-male signaling function of vocal deviation using speaker occupation experiments. A summary and discussion of all studies is provided in Chapter 6.

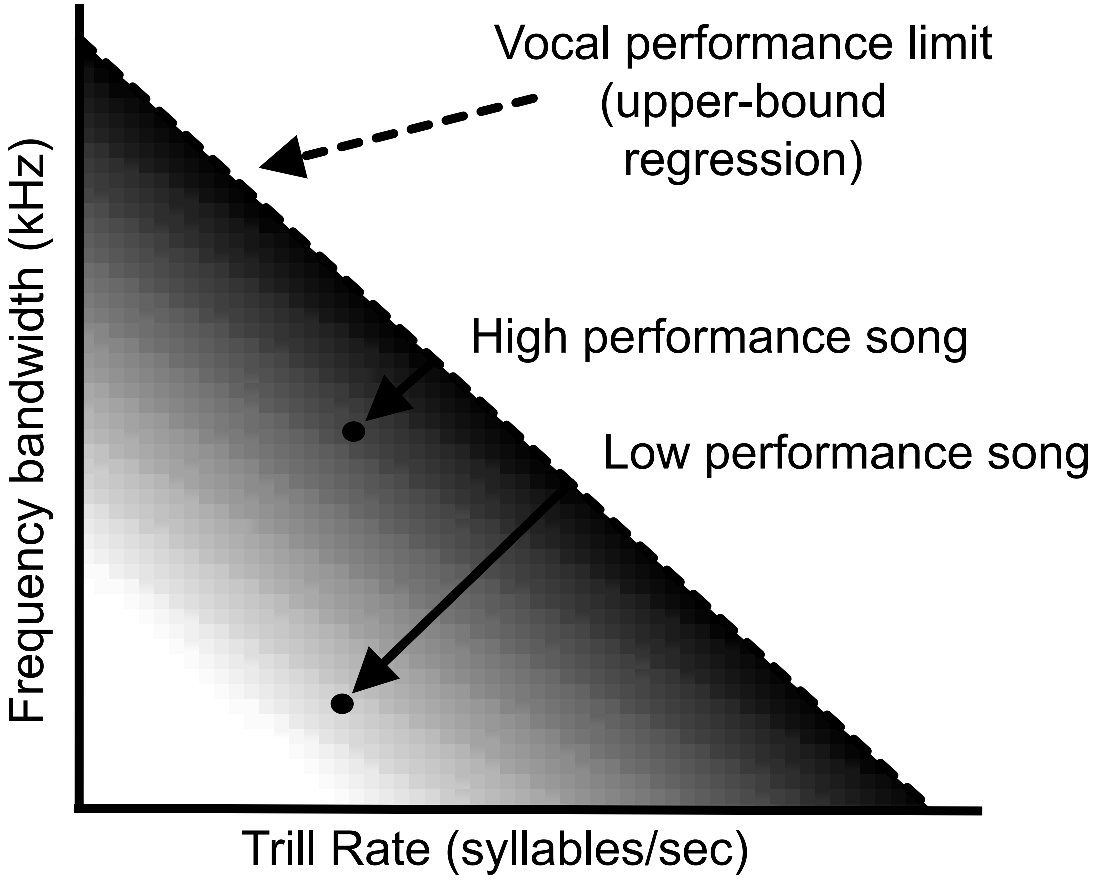

Figure 1.1 Illustration of the triangular distribution of songs in acoustic space. Two song examples are represented by black dots. Low performance songs fall within the white area, while high performance songs are in the grey area closer to the performance limit (dashed line) (after Ballentine et al. 2004).

Chapter 2

Swamp sparrows modulate vocal performance in an aggressive context[1]

Summary

Vocal performance refers to the proficiency with which a bird sings songs that are challenging to produce, and can be measured in simple trilled songs by their deviation from an upper bound regression of frequency bandwidth on trill rate. Here we show that male swamp sparrows (*Melospiza georgiana*) increase vocal performance of individual song types in aggressive contexts by increasing both trill rate and frequency bandwidth. These results are the first to demonstrate flexible modulation by songbirds of this aspect of vocal performance and are consistent with this signal feature having a role in aggressive communication.

Background

In aggressive signaling, receivers should be interested in two attributes of opponents: aggressiveness and fighting ability. Aggressiveness may be encoded in "strategic signals," which all signalers are able to produce (Hurd and Enquist 2005); a likely example is the low amplitude "soft song" produced by some songbirds (Searcy et al. 2006). Fighting ability may be conveyed by "index signals," signals whose performance is constrained by physical ability (Hurd and Enquist 2005). Likely examples include dominant frequency of calls in frogs and toads (Davies and Halliday 1978, Wagner 1989*a*), lowest peak frequency of songs in oropendolas (Price et al. 2006),

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and formant dispersion of roars in red deer (*Cervus elaphus*) (Reby and McComb 2003, Reby et al. 2005).

For songbirds, vocal performance refers to the ability to produce songs that are challenging to sing because of constraints on vocal production mechanisms. A particularly well understood example involves the ability of birds to produce repeated, or "trilled," syllables both rapidly and with a broad frequency bandwidth (Podos and Nowicki 2004*b*). The mechanics of vocal production are expected to produce a tradeoff between trill rate and bandwidth, such that the two measures cannot be maximized simultaneously (Westneat et al. 1993). Podos (1997) demonstrated that, as predicted, the simple trilled songs of sparrows (Emberizidae) exhibit a triangular distribution between frequency bandwidth and trill rate, with maximum observed bandwidth negatively related to trill rate. Given such a distribution, vocal performance can be estimated by the deviation from the upper bound regression of bandwidth on trill rate, with smaller deviations indicating higher performance (Podos 1997). The songs of swamp sparrows (*Melospiza georgiana*) exhibit this negative upper bound relationship, and female swamp sparrows prefer songs with low deviations from the upper bound (Ballentine et al. 2004).

Because females prefer songs of high vocal performance, it seems reasonable that males might also use this parameter to assess aggressive opponents. This hypothesis has been tested in banded wrens (*Pheugopedius pleurostictus*) (Illes et al. 2006) and red-winged blackbirds (*Agelaius phoeniceus*) (Cramer and Price 2007) using territorial playback. In both species, males respond differentially to songs depending on their deviation from upper bound regressions of bandwidth on trill rate. The two species differ, however, in whether they respond more strongly to low deviation songs (Illes et al.

2006) or to high deviation songs (Cramer and Price 2007), making it difficult to conclude which songs represent higher quality males.

This study tests the hypothesis that vocal performance functions in male-male communication using a different approach: by examining whether male swamp sparrows modify vocal performance in aggressive contexts. We examined two mechanisms by which performance could be manipulated. First, in aggressive situations males might choose to sing the highest vocal performance song types in their repertoires. Second, males might modulate the vocal performance of individual song types when producing them in aggressive contexts, by increasing trill rate and/or frequency bandwidth.

Methods

Playback experiments were conducted in a population of swamp sparrows in Crawford County, Pennsylvania, USA between May 17 and June 22, 2007.

To test the prediction that males preferentially sing high performance song types in aggressive signaling, we compared the predominant song types sung during aggressive and control trials. During aggressive trials we simulated an intrusion on a subject's territory using playback of conspecific song from just within his boundaries; during control trials we played songs of white-crowned sparrows (*Zonotrichia leucophrys*), which do not breed in this area. Subjects received control and aggressive treatments on consecutive days (except for two individuals whose trials were separated by three and six days). Treatments were assigned in alternating random order. Playbacks consisted of five minutes of song at a rate of 4 songs/minute. Playback songs were recorded from male swamp sparrows captured in 2005-06 in the study population and from free-living white-crowned sparrows on San Juan Island, WA in 2004. Twenty song exemplars of each stimulus type were used, with each exemplar played to two males. Stimuli were played from a directional speaker on the edge of the subject's territory facing in. The speaker was a Nagra DSM loudspeaker in an open box lined with sound-attenuating foam. Playback stimuli were 82-85 dB 1 m in front of the speaker, and were 24-26 dB lower 1 m behind the speaker.

If the focal male did not sing during the first five minutes, playback was repeated up to three times (maximum of 20 minutes). During aggressive trials, subjects received a mean of 7.5 minutes of playback (range 5-15) and during control trials a mean of 7.75 minutes (range 5-20). If no song was recorded from the focal male in 20 minutes, the trial was abandoned. Songs of focal males were recorded using a Marantz PMD 670 recorder, a RadioShack 33-3001 microphone and a Sony 33 parabolic reflector.

Songs were analyzed using Signal 4.0 software (Engineering Design, Belmont, Massachusetts, USA) following the methods of Ballentine et al. (2004) (256 point transform length, 5.8 ms time resolution, 172.3 Hz frequency resolution). We approached choice of song type in two ways. For the song type sung most often in a trial (the "predominant song"), we measured trill rate and frequency bandwidth for the first ten exemplars of sufficient quality for analysis. Trill rate was measured as syllables/second, averaged across the entire song. Frequency bandwidth was measured as the difference between the maximum and minimum frequencies at -36 dB relative to the peak amplitude frequency. In cases where fewer than ten exemplars were available, we measured as many as possible (mean = 5.7; range = 1-10). Vocal performance was calculated as the orthogonal distance from the upper bound regression line of frequency bandwidth on trill rate, calculated for the Emberizidae by Podos (1997). Vocal performance was averaged across exemplars for statistical analysis. Secondly, we measured average vocal performance for every song type in a male's repertoire, using all song types recorded during playbacks and during additional recording of males singing undisturbed. Songs were ranked within the repertoire according to vocal performance, and a Wilcoxon Signed Ranks test was used to determine whether rank of songs used in the aggressive context differed from the mean rank of the remaining songs in the repertoire.

Modulation of vocal performance during aggressive trials might change the vocal performance rank of a song. To control for this possibility, we did a second analysis of choice of song type, concentrating on males for which we had recordings from a neutral context of the predominant song type given in the aggressive context. To increase the sample of such males, we used additional recordings made while males were singing undisturbed, without any simulated or natural encounters. We then compared vocal performance of the predominant aggressive song type when given in neutral contexts to the performance of other song types given in neutral contexts.

To test for modulation of vocal performance, we concentrated on males that gave the same song type in the aggressive context and a neutral context. We again measured either the first 10 exemplars or as many as were recorded (mean = 7.8; range = 2-10). Vocal performance was measured as above, and averaged for each trial across the ten (or fewer) exemplars. A paired t-test was used to compare vocal performance between contexts.

Results

Song choice

Of the 40 males tested, 31 used only one song type during the aggressive trial, seven used two, and two used three. In all cases, one song type represented over 50% of the songs sung and was designated the predominant song type.

We found no difference in the vocal performance of the predominant song types used in aggressive trials and in control trials (t = -0.28, P = 0.78). When we analyzed trill rate and frequency bandwidth independently, we again found no significant difference between the predominant aggressive and control songs (trill rate: t = -0.09, P = 0.93; frequency bandwidth: t = 0.47, P = 0.64). Comparison of the rank of songs sung in the aggressive context (1.90 ± 0.88) to the average rank of remaining songs in the repertoire (2.09 ± 0.50) also showed no difference (Z = 1.09, P = 0.28).

For 23 males, we recorded the predominant song type used in the aggressive trial in a neutral context as well. The performance of these song types in neutral contexts did not differ from the average performance of the rest of the repertoire (t = 0.016, P = 0.99), nor did the performance rank of these song types differ from the average rank of the rest of the repertoire (Z = 1.44, P = 0.15).

Given a mean repertoire of 3.1 songs in our study population (Ballentine et al. 2004), by chance the predominant song would be the same in the aggressive and control trials 1/3.1 or 32% of the time. In our sample, 8 of 40 males (25%) used the same song type as their predominant song in both trials. The difference from random was not significant (χ^2 = 2.65, df = 1, P = 0.10).

Modulation of Vocal Performance

In the case of song types shared between aggressive and neutral contexts, males increased both trill rate (mean ± SD: aggressive = 7.10 ± 2.68 syllables/sec, neutral = 6.94 ± 2.61; $t = 4.67$, $P < 0.001$) and frequency bandwidth (aggressive = 4960.9 ± 444.4 Hz, neutral = 4870.4 ± 359.6; $t = 2.08$, $P = 0.05$) during the aggressive trial. This resulted in significantly higher vocal performance (smaller deviation) during the aggressive trial (mean ± SD: aggressive = 13.75 ± 4.55, neutral = 14.66 ± 3.90; $t = -2.51$, $P = 0.02$, Figure 2.1).

Discussion

The results confirm our second prediction: males modulate the performance of a given song type in aggressive interactions in the direction that should increase their perceived quality, consistent with the hypothesis that vocal performance functions in male-male interactions. To our knowledge, this is the first demonstration that songbirds modulate deviation from the trill rate/frequency bandwidth upper bound in a functional context.

We have interpreted vocal performance as an index signal. An index is defined as "a signal whose intensity is causally related to the quality being signalled and which cannot be faked" (Maynard Smith and Harper 2003, p. 15); thus modulation of vocal performance might seem to counter the classification of this trait as an index signal. Other well established index signals, however, are modulated in a parallel fashion (Searcy and Nowicki 2005). When interacting with other males, some frogs lower the dominant frequencies of their calls (Wagner 1989*a*, Bee and Perrill 1996), Montezuma oropendolas (*Psarocolius montezuma*) lower the lowest peak frequencies of their songs (Price et al. 2006), and red deer minimize the formant dispersion of their roars (Reby and McComb 2003). These and other examples suggest a general rule that index signals are physically constrained only within limits, with signalers modulating such signals in an adaptive fashion within those limits.

We found no tendency of males to prefer using high performance song types in aggressive contexts. Cramer and Price (2007) found a similar result in red-winged blackbirds. Given that males modulate the performance of individual song types, we do not think this means that males are not trying to maximize vocal performance during aggressive signaling. Instead, this result may indicate that vocal deviation fails to capture all aspects of vocal performance, or that there are other reasons why birds choose to sing particular song types.

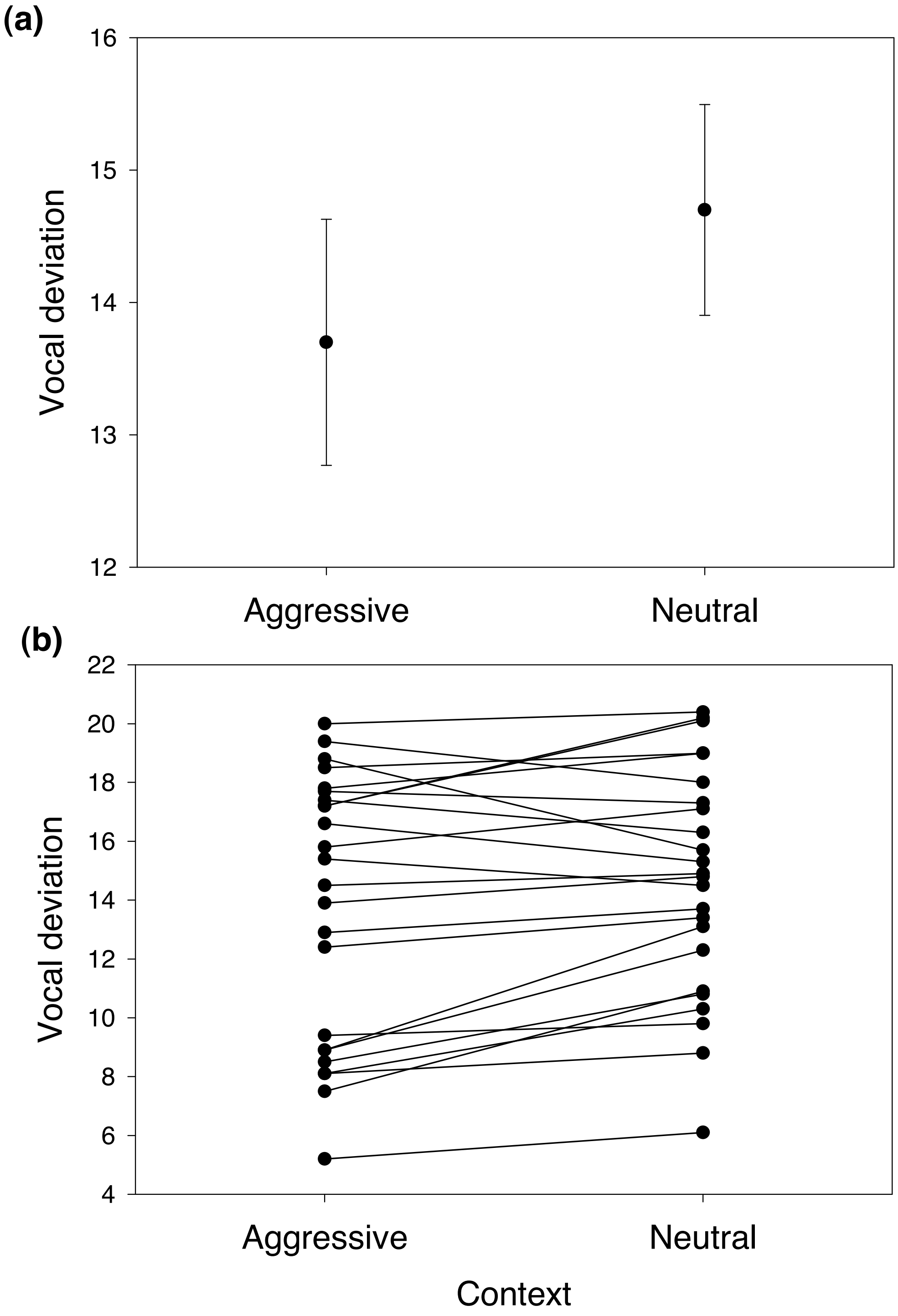

Figure 2.1 Vocal performance for cases in which the same song type was recorded in both aggressive trials and neutral contexts. (a) Means (± SE) of deviation from the upper bound regression of bandwidth on trill rate. (b) Vocal deviations for individual males recorded in both contexts. Note that low deviation equals high performance.

Chapter 3

Vocal performance does not predict aggressive escalation in swamp sparrows, *Melospiza georgiana*[2]

Summary

Vocal deviation is a measure of performance in songbirds that sing a trilled song, based on a tradeoff between the frequency bandwidth of songs and the speed at which song elements are repeated (the trill rate). Because of the difficulty associated with maximizing frequency bandwidth and trill rate simultaneously, vocal deviation is likely an index signal of male quality. In theory, index signals can serve as signals of aggressive intent in addition to signaling quality or resource holding potential (RHP). Here we investigated whether vocal deviation predicts aggressive escalation in swamp sparrows. Recordings and observations from two prior playback experiments were analyzed to address this question. Vocal deviation did not differ between males that attacked a simulated rival and those that did not attack. Vocal deviation was also not correlated with aggressive display behaviors or mean approach distance to a loudspeaker playing conspecific song. Furthermore, modulation of vocal deviation (the increase in performance between a neutral context and an aggressive context) was not correlated with aggressiveness. The results of this study do not support the use of vocal deviation as a signal of aggressive intent, but evidence from previous research suggests that vocal deviation is used in aggressive communication as an index signal of male quality and RHP.

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[2] This chapter will be submitted for publication with authors A.L. DuBois, B. Ballentine, S. Nowicki, and W.A. Searcy.

Background

Signalers might be expected to cheat, or exaggerate signals to incur benefits—especially in cases where signaler and receiver interests are opposed, as in aggressive communication. Mechanisms exist, however, to maintain honesty in animal communication. The honesty of performance signals, for example, is maintained by physical or informational constraints that limit the production of these signals to a subset of signalers (Hurd and Enquist 2005). Performance signals that are subject to physical constraints are termed “index signals.” Index signals are “causally related to the quality being signalled” and thus “cannot be faked” (Maynard Smith and Harper 2003). In aggressive signaling, index signals are best suited to communicate an individual’s quality or resource holding potential (RHP), but they may also communicate aggressive intentions (Searcy and Beecher 2009). Here we examine whether “vocal deviation,” a likely index signal in songbirds, functions as a signal of aggressive intent in swamp sparrows (*Melospiza georgiana*).

Vocal performance refers to the ability of males to produce songs that are physically challenging to sing (Podos 2001, Forstmeier et al. 2002, Ballentine et al. 2004, Cardoso et al. 2009). Vocal performance has been measured in a number of ways; the aspect of vocal performance we focus on here is “vocal deviation.” Vocal deviation is a measure of how closely a song approaches a specific performance boundary defined by the tradeoff in trilled songs between frequency bandwidth and trill rate (Podos 1997). In bird species that sing a trilled song, biomechanical and physiological limitations produce a tradeoff between frequency bandwidth (the range of frequencies encompassed in a unit of song) and trill rate (the speed at which those song units are repeated). This tradeoff occurs because singers are limited in their ability to effect simultaneously the large changes in vocal tract configuration needed to modulate frequency, and to make these changes rapidly to maximize trill rate. Podos (1997) first demonstrated this tradeoff for sparrows of the family Emberizidae. When frequency bandwidth is plotted against trill rate, trilled songs produced by members of the Emberizidae fall into a triangular distribution. Podos calculated an upper bound regression line that represents a performance limit for the population—above which songs cannot be produced. Vocal performance can then be estimated as vocal deviation – the orthogonal distance of the song to that upper bound regression line (Podos 2001). Vocal deviation has since been applied as a measure of performance in species in other families (Draganoiu et al. 2002, Beebee 2004, Illes et al. 2006, Cramer and Price 2007) and orders (Janicke et al. 2008, Juola 2010).

Performance signals in general tend to convey information about signaler quality or RHP. Index signals are honest indicators of quality because production of the signal is physically tied to the quality of interest to the receiver (Maynard Smith and Harper 2003). Vocal signals can serve as indices of size, for example, because of correlations between body size and characteristics of the vocal apparatus that affect signal attributes. The roars of red deer (*Cervus elaphus*) are one example. Vocal tract length determines the spacing of vocal tract resonances or "formants." Individuals with longer vocal tracts produce more closely spaced formants (Reby and McComb 2003). Because of the correlation between vocal tract length and overall body size, the spacing of formants is an index signal of body size. Playback of calls with lower frequency formants, indicative of larger stags, results in increased attentiveness and more, lower roars from receivers, suggesting that receivers attend to formant frequency as a signal of opponent quality (Reby et al. 2005). Similarly, the calls of frogs and toads serve as an index signal of size. Large body size correlates with more massive vocal cords, which results in production of calls with low dominant frequency (Martin 1972). Again, large males tend to win contests (Davies and Halliday 1978, Wagner 1989*a*). Thus, males can use the dominant frequency of croaks as an index signal of size and fighting ability (Wagner 1989*a*).

In addition to signaling RHP, index signals may also serve as aggressive signals by conveying a signaler's aggressive intent, or likelihood of attack. In theory, an index signal might convey aggressive intent because the signal is tied to RHP, and individuals of higher RHP are more likely to attack (Enquist 1985). Alternatively, modulation of an index signal might convey aggressive intent. For example, in the case of frog calls described above, males of some species are able to lower their dominant frequency in aggressive contexts (Wagner 1989*a*, Bee and Perrill 1996, Bee et al. 1999). Male Blanchard's cricket frogs (*Acris crepitans blanchardi*), for example, lower the frequency of their calls (Wagner 1989*a*) to the extent that modulation affects receiver response. When presented with calls that decreased, increased, or remained constant in dominant frequency, males tended to retreat more from calls that decreased in dominant frequency (Wagner 1992). This finding raises the possibility that modulation of dominant frequency serves as a threat because it is associated with aggressive intent.

Various measures of vocal performance in songbirds have been proven to correlate with aspects of male quality such as age and dominance in species such as great tits (Rivera-Gutierrez 2010), tropical mockingbirds (Botero et al. 2009), banded wrens (de Kort et al. 2009), and dusky warblers (Forstmeier et al. 2002). In swamp sparrows, a male’s maximum vocal performance (measured in terms of vocal deviation) is correlated with his age and size (Ballentine 2009). Though the trend has not been explicitly shown in swamp sparrows, in many songbird species, older, larger males tend to win aggressive encounters (Searcy 1979, Richner 1989, Sandell and Smith 1991, Koivula et al. 1993, Yamaguchi and Kawano 2001). Thus, vocal performance likely signals fighting ability or RHP.

Searcy and Beecher (2009) have suggested three criteria to determine whether a signal is aggressive: (1) whether the signal increases in aggressive contexts, the “context criterion,” (2) whether the signal predicts aggressive escalation by the signaler, the “predictive criterion,” and (3) whether receivers respond to the signal, the “response criterion.” Evidence suggests that vocal performance satisfies two of these criteria. Two studies have shown that males increase vocal performance in aggressive contexts, thus satisfying the context criterion. DuBois et al. (2009; Chapter 2) found that male swamp sparrows increase the vocal performance of songs in aggressive contexts by increasing both the trill rate and the frequency bandwidth of their songs. Cardoso et al. (2009) found a similar result in dark-eyed juncos: males increased vocal performance during aggressive singing through their choice of song type. Furthermore, vocal performance appears to satisfy the “response” criterion, as males of several species have been shown to respond differentially to songs of varying levels of vocal performance (Illes et al. 2006, Cramer and Price 2007, de Kort et al. 2009, DuBois et al. 2011; Chapter 4).

This study addresses the “predictive” criterion for establishing an aggressive signal—whether the signal, in this case, vocal deviation, predicts aggressive escalation. We applied such a test using observations and recordings from two prior experiments with swamp sparrows (Ballentine et al. 2008, DuBois et al. 2009; Chapter 2). We tested two predictions of our hypothesis that vocal deviation predicts aggressive escalation: 1) males who attack a taxidermic mount ("attackers") and males who do not attack ("non-attackers") will differ with respect to vocal performance, and 2) vocal performance and/or its modulation will be correlated with aggressive measures (other than attack) that are known to predict subsequent attack.

Methods

Recordings from two previous playback experiments eliciting aggressive responses from swamp sparrows were used for this analysis. Both experiments were conducted on a population of swamp sparrows in Conneaut Marsh, Crawford County, Pennsylvania, USA. The first experiment, which we will hereafter refer to as the "Mount Attack" experiment (Ballentine et al. 2008), examined which vocal and visual displays predict attack in this species. Briefly, male subjects were presented with playback of swamp sparrow song on their territories for 1 minute. Starting with the first playback song, the subject's songs were recorded for five minutes. Then a taxidermic mount of a male swamp sparrow was revealed at the location of the speaker, followed by another 2 minutes of playback song. A microphone was positioned 10-15 cm from the taxidermic mount and connected to one channel of a Sony TC D5M stereo tape recorder to record songs given close to the mount. A Realistic omnidirectional microphone situated in a Sony PBR-330 parabola was plugged into the second channel of the stereo recorder, and held by an observer 15-20 m away from the mount/speaker. This microphone was additionally used to follow and record subject songs. Trials ended at 20 minutes or when the male attacked the taxidermic mount. Attacks were defined as a male either contacting the taxidermic mount or flying directly at the mount, within 1 meter. Several display measures were recorded, including: (1) number of broadcast songs, (2) number of soft songs, (3) bouts of wing waving, (4) song type-switches, and (5) song matches to playback. The mean approach distance of the subject to the speaker/mount was also calculated. For further description of methods, see Ballentine et al. (2008).

Cassette recordings of trials were saved as digital files using Syrinx (J. M. Burt; http://syrinxpc.com) and a Sony TC D5M recorder connected by a stereo cable to a PC. Recordings were then examined visually using Audacity (Version 1.2.6; http://audacity.sourceforge.net/). For the present analysis, only the first five minutes of the trial were used. In each trial, the predominant song type (song type sung most often) was identified, and the trill rate and frequency bandwidth of the first ten exemplars of that song type of sufficient quality for analysis were measured. Trill rate was measured as the number of syllables/second, averaged across the entire song. Frequency bandwidth was measured as the difference between the maximum and minimum frequency at -36 dB relative to the peak amplitude frequency. If fewer than ten exemplars were available, we measured as many as possible (mean = 5.5, range = 1-10). Songs were analyzed using Signal 4.0 digital signal analysis software (Engineering Design, Belmont, Massachusetts, USA) following the methods of Ballentine et al. (2004) (256 transform length, 5.8 ms time resolution, 172.3 Hz frequency resolution). Vocal deviation was calculated as the orthogonal distance from the upper bound regression line calculated for the Emberizidae by Podos (1997), so that performance measurements between the Mount Attack and

Modulation (below) studies could be compared. This measure of "vocal deviation" was averaged across the ten or fewer exemplars for statistical analysis.

Data from the Mount Attack experiment were subsequently analyzed in two ways. "Attackers," those birds who landed on or flew at the mount, and "non-attackers" were compared with respect to vocal deviation, trill rate and frequency bandwidth using two sample t-tests. Additionally, we investigated whether the vocal deviation, trill rate, or frequency bandwidth of the predominant song in the first five minutes of the trial was correlated with any of the display measures or with approach to the speaker. All statistical analyses were conducted using Systat 11.0.

The second experiment used in this study, which we will hereafter refer to as the "Modulation" experiment (DuBois et al. 2009; Chapter 2), originally sought to determine whether males choose songs based on vocal performance and/or whether males are able to modulate vocal performance between aggressive and neutral contexts. In this experiment, male subjects each received two treatments: an aggressive context, in which an intrusion was simulated on the subject's territory using playback of conspecific song, and a control context, in which males received playback of white-crowned sparrow (*Zonotrichia leucophrys*) song. Songs given in response to playback were recorded, as well as the distance of the subject from the speaker during the trial. Trill rate and frequency bandwidth were recorded for the predominant song given in each treatment, and these measures were used to calculate deviation from the Emberizid performance boundary (Podos 1997), as before. Additional recordings of birds singing while undisturbed were also made, and along with recordings from the control trials provided an added source of songs given in a neutral context. Song analysis was completed using

Signal 4.0 software (Engineering Design, Belmont, Massachusetts, USA). For further explanation of methods, see DuBois et al. (2009; Chapter 2).

We examined a potential link between vocal deviation and aggression, which in this study was measured as the mean approach distance to the speaker during a trial. First, we looked for a correlation between vocal deviation of the predominant song sung in the aggressive trial and the approach distance to the speaker during that trial. Furthermore, because vocal performance is a composite measure of two song characteristics, and males are able to modulate both components, trill rate and frequency bandwidth (DuBois et al. 2009; Chapter 2), we also looked for correlations between trill rate and frequency bandwidth and mean approach distance.

Second, 24 of 40 males sang their predominant song type from the aggressive context in a neutral context as well. For these males, we calculated the amount of performance modulation between the aggressive and neutral contexts and determined whether this measure was correlated with approach distance during the aggressive trial. Again, we also looked for any correlations between approach distance and modulation of frequency bandwidth and trill rate of songs independently.

Results

Mount Attack Experiment: A two-sample t-test revealed no difference between attackers and non-attackers with respect to vocal deviation ($t = 0.245$, $P = 0.808$, Figure 3.1a). The trill rate and frequency bandwidth of songs of attackers and non-attackers also did not differ (trill rate: $t = -0.247$, $P = 0.806$, Figure 3.1b; frequency bandwidth: $t = -0.190$, $P = 0.850$, Figure 3.1c). Furthermore, vocal deviation was not significantly correlated with any of the display measures (Table 3.1), including number of broadcast songs, number of soft songs, bouts of wing waving, song type switches, and song type matches. Vocal deviation was also not significantly correlated with mean approach distance to the speaker (Table 3.1). When considered separately, trill rate also was not significantly correlated with any of these display measures or approach distance (Table 3.1). Frequency bandwidth was not significantly correlated with the number of broadcast songs, soft songs, bouts of wing waving, song type switches, or approach distance, but was significantly correlated with song type matches (Table 3.1).

Modulation experiment: Vocal deviations of songs given in an aggressive context and mean approach distance to the speaker were not significantly correlated ($r = -0.219$, $P = 0.103$, $n = 40$). However, the correlation between vocal deviation and approach was nearly significant, and further examination revealed that the trill rate of songs given in an aggressive context was significantly correlated with mean approach distance ($r = 0.439$, Bonferroni $P = 0.005$, $n = 40$). Frequency bandwidth, however, was not correlated with approach ($r = -0.050$, $P = 0.757$, $n = 40$). For males in the Modulation dataset who sang the same song type in both an aggressive and neutral context, the amount of modulation of vocal deviation was also not correlated with mean approach distance ($r = -0.060$, $P = 0.780$, $n = 24$, Figure 3.2a). Modulations of trill rate and frequency bandwidth were also not correlated with mean approach distance (trill rate: $r = 0.192$, $P = 0.368$, $n = 24$, Figure 3.2b; frequency bandwidth: $r = 0.041$, $P = 0.849$, $n = 24$, Figure 3.2c).

Discussion

Males who attacked a taxidermic mount did not differ from males who did not attack with respect to vocal performance. Further analysis of the trill rate and frequency bandwidth of songs of both types of males also revealed no difference between attackers and non-attackers. Therefore, our results do not support our first prediction: that attackers and non-attackers differ with respect to vocal performance.

Vocal deviation was not correlated with any aggressive behavior in either the Mount Attack or the Modulation study. Thus, our second prediction of a correlation between vocal performance and measures of aggressive response was not supported. Only two correlations between performance measures and aggressive behavior were found to be significant in our analysis. The first was between the frequency bandwidth of songs and the number of song type matches in the Mount Attack study. Song type matching does not appear to be a predictor of attack in swamp sparrows (Ballentine et al. 2008), and for songbirds in general, evidence supporting the predictive value of song type matching is lacking (Searcy and Beecher 2009). Furthermore, frequency bandwidth was not correlated with display measures, soft song and wing waves, that are predictors of attack in swamp sparrows (Ballentine et al. 2008). The second significant correlation was between the trill rate of songs and mean approach distance in the Modulation study. Approach distance to the speaker is a strong predictor of attack in swamp sparrows (Ballentine et al. 2008). However, this correlation was not corroborated by the Mount Attack song data. Furthermore, the relationship between trill rate and approach distance is opposite of what was predicted, based on previous studies in this species (DuBois et al. 2009; Chapter 2, DuBois et al. 2011; Chapter 4). Males who sang with *slower* trill rates approached more closely than did males with faster trill rates. Trill rate was also not correlated with any of the other behaviors that predict attack in swamp sparrows, such as bouts of wing waving or soft songs (Ballentine et al. 2008), which weakens the case for a relationship between trill rate and aggressive intent.

Modulation of vocal performance, the increase in performance of a given song type when sung in an aggressive context, was also not correlated with intent, measured as approach distance to the speaker. In other species, the modulation of an index signal does seem to serve as an aggressive intent signal, such as in Blanchard's cricket frogs (Wagner 1989*a*, 1992). In the case of cricket frogs, males are able to modulate dominant frequency to a greater extent than swamp sparrows are able to modulate performance. In fact, male cricket frogs can modulate the dominant frequency of calls enough to affect the outcome of interactions—that is, to cause rivals to retreat from an interaction (Wagner 1992). Swamp sparrows, however, are unable to modulate their vocal performance to the extent that modulation affects receiver response (DuBois et al. 2011; Chapter 4). The small magnitude of modulation, therefore, likely lowers the potential efficacy of vocal performance modulation as a signal of aggressive intent.

Although this study does not support a role for vocal performance as a signal of aggressive intent, it is probable that vocal performance still plays a role in male-male aggressive interactions. Performance signals in general are likely to function in aggressive communicaton primarily as signals of RHP, with at most a subsidiary role as signals of aggressive intent (Searcy and Beecher 2009). As mentioned previously, Ballentine (2009) found that maximum vocal performance was correlated with both age and body mass in swamp sparrows. Older, larger males sing higher performance songs.

This relationship between a male's vocal performance and measures of his quality explains why vocal deviation affects the responses of rival males during territory defense. Male songbirds of several species have been shown to respond differentially to varying levels of vocal performance (banded wrens: Illes et al. 2006, de Kort et al. 2008; red-winged blackbirds: Cramer and Price 2007; swamp sparrows: DuBois et al. 2011; Chapter 4). These studies suggest that receivers are attuned to the vocal performance of other males, and that vocal performance, therefore, is a meaningful signal in male-male communication—despite the lack of information about likelihood of attack.

In summary, male attackers and non-attackers did not differ with respect to vocal deviation. Vocal deviation was not significantly correlated with approach distance to the speaker, or with any behavior predictive of attack. Modulation of vocal deviation was also not correlated with aggressive behavior. Although our current findings do not support a function for vocal performance as a signal of aggressive intent, evidence from other research suggests that vocal performance may still play a role in aggressive communication by serving as an index signal of male quality.

Table 3.1 Correlations between measures of vocal performance (vocal deviation, trill rate, and frequency bandwidth) and display measures from the Mount Attack study (Ballentine et al. 2008). Significance ($P \leq 0.05$) is denoted by *.

	Vocal Deviation			Trill Rate			Frequency Bandwidth		
	n	Pearson Correlation Coefficient	*P*	*n*	Pearson Correlation Coefficient	*P*	*n*	Pearson Correlation Coefficient	*P*
Number of broadcast songs	35	-0.138	0.428	35	-0.019	0.913	35	0.180	0.301
Number of soft songs	35	0.065	0.711	35	-0.225	0.195	35	0.023	0.895
Bouts of wing waving	35	-0.020	0.907	35	-0.214	0.218	35	0.124	0.477
Number of song type switches	25	-0.084	0.690	25	0.093	0.657	25	0.068	0.747
Number of song type matches	35	-0.287	0.095	35	0.028	0.873	35	0.344	**0.043***
Mean approach distance	35	-0.082	0.642	35	-0.006	0.975	35	0.104	0.553

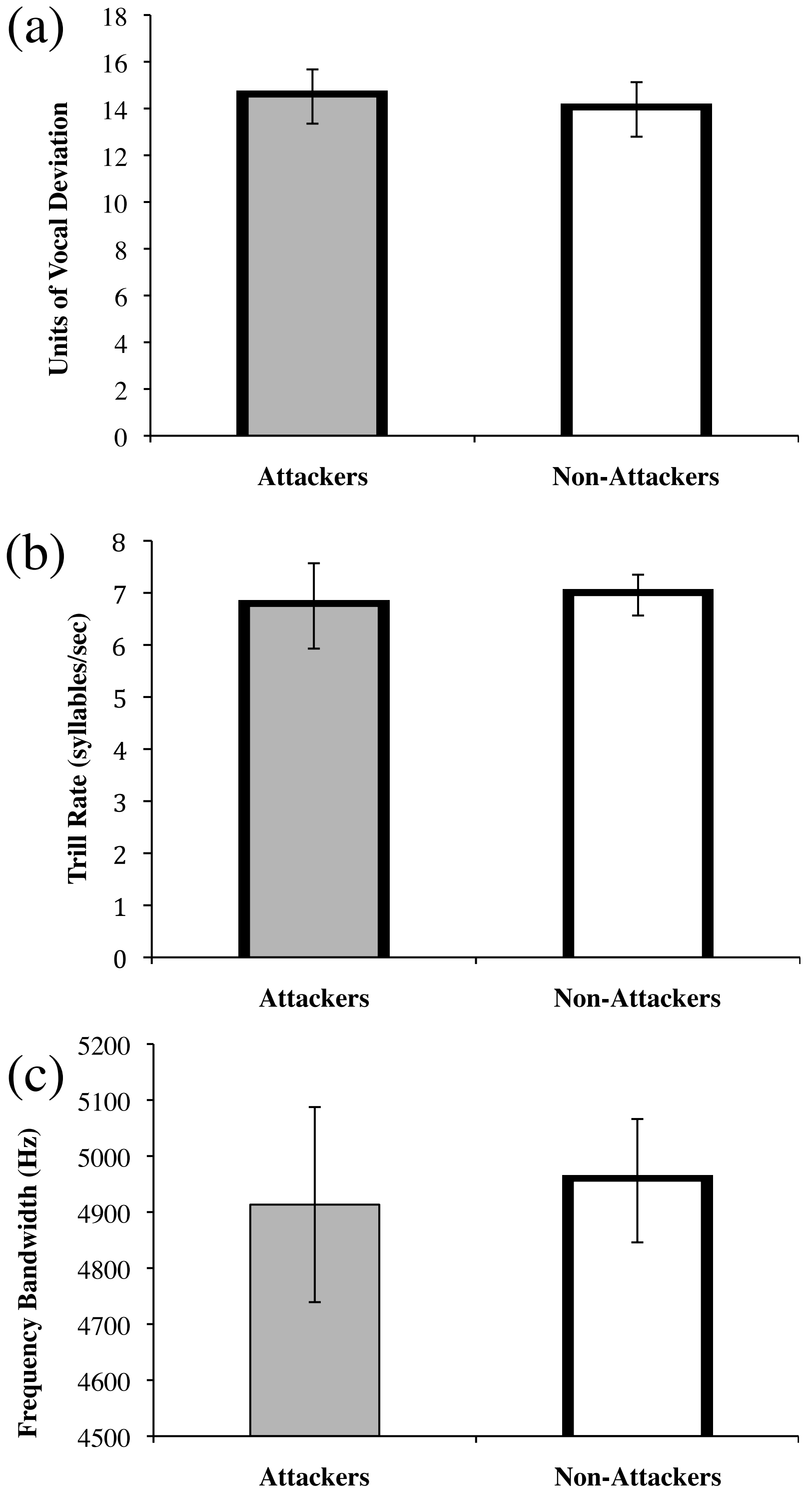

Figure 3.1 Comparison of mean vocal performance measures: (a) vocal deviation, (b) trill rate, and (c) frequency bandwidth between attackers and non-attackers from the Mount Attack study (Ballentine et al. 2008). Bars represent standard error.

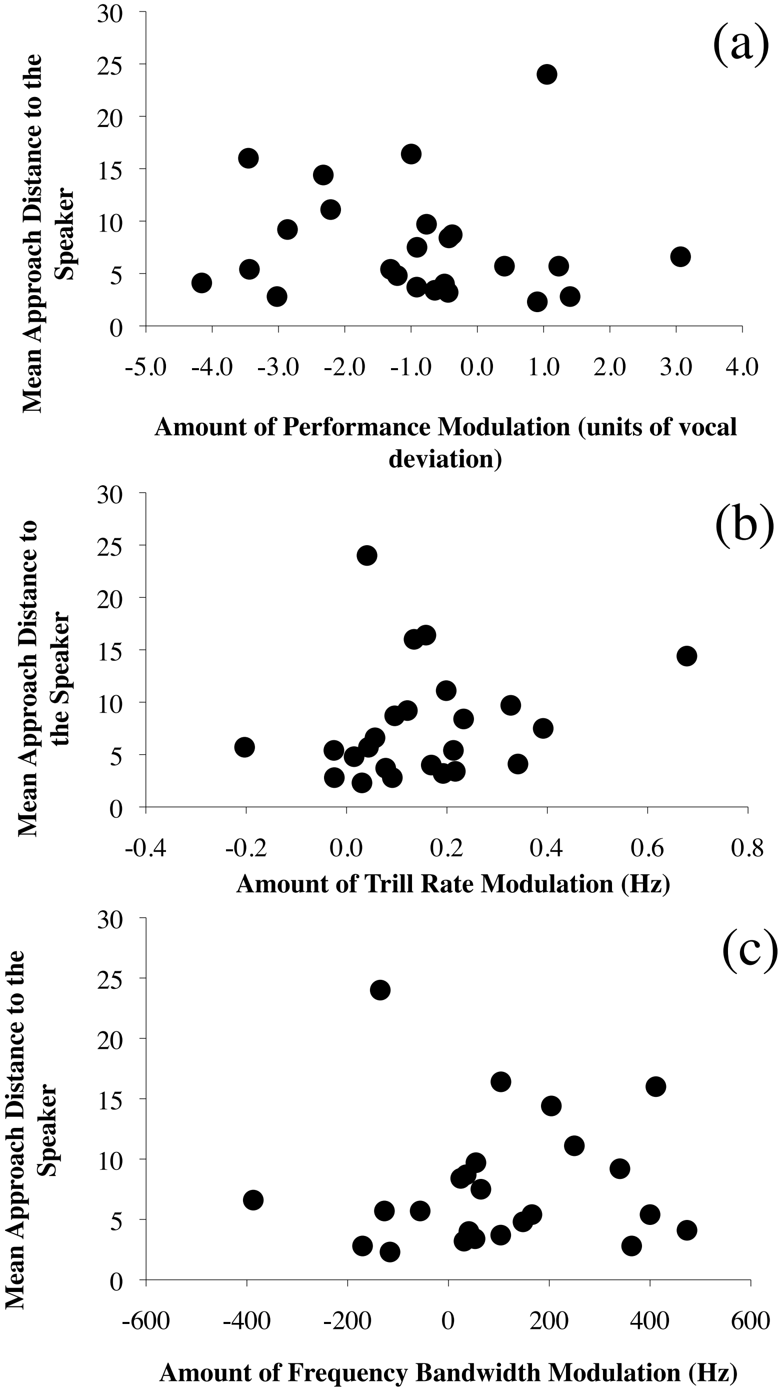

Figure 3.2 Scatterplots of mean approach distance to the speaker modulation of (a) vocal deviation, (b) trill rate, and (c) frequency bandwidth. Lower values for approach distance (along the y-axis) indicate higher aggression. For vocal deviation, (a), more negative values indicate a lower vocal deviation (and therefore better performance) of a song type when sung in an aggressive context than in a neutral context. For trill rate (b) and frequency bandwidth (c), higher values indicate faster trill rates and broader bandwidths of songs, respectively, when sung during the aggressive context, as compared to a neutral context. No significant correlations were detected.

Chapter 4

Discrimination of vocal performance by male swamp sparrows[3]

Summary

In aggressive communication, the interests of signalers and receivers are directly opposed, presenting a challenge to the maintenance of reliable signaling. Index signals, whose production is constrained by physical ability, offer one solution to the reliable signaling problem. Vocal performance, the ability to produce physically challenging songs, is likely such a signal in swamp sparrows. Maximum vocal performance varies between males and is correlated with aspects of quality. However, vocal performance can be modulated in aggressive contexts by increasing the frequency bandwidth and trill rate of songs. This study examines receiver response to 1) differences in performance of the same song types by different signalers and 2) individual modulation of performance between contexts. Results demonstrate that male receivers show differential response to between-male differences in song type performance, but do not show differential response to the smaller scale modulations of performance produced by individuals singing the same song type at different times. This pattern suggests that vocal performance cannot be effectively cheated, and may therefore serve as a good example of an index signal.

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[3] This chapter was published as: DuBois, A.L., S. Nowicki, and W.A. Searcy. 2011. Discrimination of vocal performance by male swamp sparrows. Behavioral Ecology and Sociobiology 65:717-726.

Background

The evolutionary stability of signal reliability is problematic whenever the interests of signalers and receivers are in conflict. In particular, the maintenance of signal reliability is puzzling in aggressive contexts given that the interests of signalers and receivers are in direct opposition. Signals are considered reliable if they convey dependable information about the signaler or its environment that benefits the receiver of the signal (Searcy and Nowicki 2005). In aggressive contexts, receivers typically benefit from information on either the signaler's fighting ability or its aggressive intentions. Signalers would benefit if they could exaggerate signals to intimidate receivers, but if exaggeration becomes sufficiently widespread, then selection will act on receivers to cease responding to the signals, causing the signaling system to break down (Dawkins and Krebs 1978). Mechanisms that maintain signal honesty are therefore crucial for the evolutionary stability of aggressive signaling systems (Grafen 1990). Various mechanisms have been proposed to maintain reliability in aggressive contexts (Vehrencamp 2000), including the possibility of "physical constraints" (Hurd and Enquist 2005). Here we investigated receiver response to a vocal signal – vocal performance – that may be subject to physical constraints in swamp sparrows (*Melospiza georgiana*). We measured the response of male receivers to vocal performance as a test of whether vocal performance functions in aggressive signaling and to explore the mechanisms that maintain the reliability of this signal.

Signals are physically constrained if the mechanism by which the signal is produced determines a fixed relationship between the signal and some characteristic of the signaler. Such signals are termed index signals (Maynard Smith and Harper 2003).

Because the intensity of index signals is causally related to the quality being signaled, they are considered “unfakeable.” Since index signals are tied to physical attributes of signalers, they are likely candidates for conveying information about fighting ability or resource holding potential (Hurd and Enquist 2005). Well-established examples of index signals are few, however. One oft-cited case involves the dominant acoustic frequency of calls in some frogs and toads, which is constrained by size (Davies and Halliday 1978, Ryan 1985, Wagner 1989*a*, 1989*b*). Larger males possess more massive vocal cords, which allow them to produce calls with lower dominant frequencies (Martin 1972). Larger males also tend to win wrestling contests over resources (Davies and Halliday 1978). Because of this relationship between male size, vocal morphology, and the ability to win contests, males of many anuran species may assess opponents using the dominant frequency of calls as an unbluffable signal of size and fighting ability (Wagner 1989*a*). Another likely index signal is the formant dispersion of roars in red deer (*Cervus elaphus*, Reby and McComb 2003, Reby et al. 2005). The length of the vocal tract determines its resonant properties, including the spacing of vocal tract resonances or “formants,” with individuals having longer vocal tracts producing more closely spaced formants (Fitch 1997, Reby and McComb 2003). Because vocal tract length tends to correlate with overall body size due to anatomical constraints, the spacing of formants is a reliable index of body size.

It turns out, however, that signalers can and do exaggerate these ostensibly reliable signals in aggressive situations (Searcy and Nowicki 2005). Some frogs are able to lower the dominant frequency of their calls in response to aggressive playback (Wagner 1989*a*, Bee and Perrill 1996, Bee et al. 1999). Red deer are also able to decrease the formant dispersion of their roars by lowering their larynx and extending their vocal tract (Fitch and Reby 2001). This exaggeration would undermine signal reliability if it occurs at a level salient to receivers, because both red deer and frogs exaggerate their signals to different degrees in different contexts (Wagner 1989*a*, Bee and Perrill 1996, Reby et al. 2005).

Another potential candidate for an index signal is “vocal performance” of birdsong, defined as the ability to sing songs that are physically or physiologically challenging to produce owing to constraints on vocal production mechanisms (Podos 2001, Ballentine et al. 2004, Cardoso et al. 2009, Forstmeier et al. 2002). Vocal performance has been measured in several ways, including vocal deviation (Podos 2001), percentage peak performance (Forstmeier et al. 2002), acoustic density (Cardoso et al. 2009, Holveck and Riebel 2007, Leadbeater et al. 2005), residual intervals, and predicted amplitude (Cardoso et al. 2007, Cardoso et al. 2009). We employ the measure of “vocal deviation” first described by Podos (2001), a measure of the ability to produce repeated notes, or “trills,” both rapidly and with a broad frequency bandwidth. This measure is based on a tradeoff that most likely results from morphological constraints on song production. Sound produced by the syrinx is modified by the vocal tract, which acts as a resonance filter, to allow production of the pure tonal sounds that characterize birdsong (Nowicki 1987). In order to produce pure tones, a bird must modify the configuration of its vocal tract to correspond to the sound frequency produced at the syrinx, specifically by altering bill gape (Nowicki and Marler 1988, Podos and Nowicki 2004*a*). For example, Westneat et al. (1993) demonstrated that sparrows change bill gape to track the frequency of the sounds that they emit, opening the bill wide for high frequency sounds and reducing gape to produce low frequency sounds. Hoese et al. (2000) confirmed that bill gape affects sound production through experiments in which bill movements were constrained. Thus, birds are physically limited by the difficulty of simultaneously making large changes to the angle of their bill (or other elements of the vocal tract) and making these changes rapidly (Podos and Nowicki 2004*b*), and this limitation produces a tradeoff between frequency bandwidth and trill rate.

Podos's (1997) comparative analysis of songs of the Emberizid family of sparrows provided the first evidence for this tradeoff. Podos found that as trill rates of songs increased, the maximal values of frequency bandwidth decreased. When songs are graphed by trill rate against frequency bandwidth, the result is a triangular distribution of songs in acoustic space. An upper bound regression can be used to estimate the performance limit implied by this triangular distribution, and the "vocal deviation" of a song from the regression line can in turn be used to estimate a song's level of performance (Podos 2001). A vocal performance tradeoff measured this way has since been demonstrated for an independent sample of swamp sparrow songs (Ballentine et al. 2004) and for the songs of species outside the Emberizidae, including domesticated canaries (*Serinus canaria,* Draganoiu et al. 2002), yellow warblers (*Dendroica petechia*, Beebee 2004), banded wrens (*Thryothorus pleurostictus*, Illes et al. 2006), and red-winged blackbirds (*Agaeliaus phoeniceus*, Cramer and Price 2007).

In swamp sparrows, maximum vocal performance correlates positively with male age and size (i.e., age and size are negatively correlated with vocal deviation). In a given breeding season, males with higher performance (lower deviation) are older and larger, and males tend to improve their maximum vocal performance between their first and second breeding years (Ballentine 2009). Vocal performance affects female response to song, with females responding preferentially to higher performance songs (Ballentine et al. 2004). Thus, females who choose a high performance singer will likely be pairing with a higher quality male, to the extent that age and size correlate with a male's ability to provide direct and/or indirect benefits to their mates. Signals of size and age are likely also to be important in male-male signaling, because older, larger males tend to win encounters with smaller, younger males in many songbird species (Koivula et al. 1993; Richner 1989; Sandell and Smith 1991; Searcy 1979; Yamaguchi and Kawano 2001). Therefore, vocal performance may be used as an assessment signal in male-male aggressive communication.

One criterion to assess whether a signal is used in male-male aggressive communication is to test males for an aggressive response to the signal (Searcy and Beecher 2009). Illes et al. (2006) found that vocal deviation affected aggressive response in male banded wrens. Males presented with both a high performance and a low performance stimulus tended to approach the high performance stimulus first, though they spent less time overall in close proximity to the high performance stimulus than to the low performance stimulus. In a similar test using red-winged blackbirds, Cramer and Price (2007) also found that males discriminated vocal performance differences, responding to lower performance songs with higher song and flight rates, and by spending more time close to the low performance stimulus. One objective of the present study was to test the hypothesis that male swamp sparrows assess individual differences in vocal performance. That hypothesis predicts that males behaviorally discriminate between two individuals based on typical magnitudes of among-individual differences observed in the population.

Recently, DuBois et al. (2009; Chapter 2) addressed the issue from the signaler's perspective, and found that male swamp sparrows actively increase vocal performance in aggressive situations. When males used the same song type in both an aggressive context and a more neutral one, they sang that song type with a higher performance level (i.e., a lower vocal deviation as measured from the upper bound regression reference line) in the aggressive context. This change was accomplished by increasing both the trill rate and frequency bandwidth of the song. Similarly, Cardoso et al. (2009) found that dark-eyed juncos' (*Junco hyemalis*) increased vocal performance during aggressive singing, although this increase was primarily the result of choice of song type. These examples of individual modulation could be interpreted as "cheating" on an index signal.

Changes in vocal performance produced by individual modulation, however, tend to be small relative to the performance differences seen between males, as well as performance differences between some song types within males. It is important to note here that although it is clear that there are important differences between males in the performance of specific song types, it has not been shown that males differ consistently in performance across their entire repertoires. In testing female swamp sparrows for response to songs differing in vocal performance, Ballentine et al. (2004) used pairs of songs of the same song type obtained from different males, and differing from each other by 5 to 18 units of vocal deviation (as measured from Podos's 1997 Emberizid line, with vocal deviation derived as the orthogonal distance to the reference line). In contrast, individual males in the DuBois et al. (2009; Chapter 2) study were capable of modulating their vocal deviation to a maximum of only 5 deviation units, with most males falling well short of this maximum. Thus male swamp sparrows might be able to detect differences in vocal performance on the order shown between males without being able to discriminate the smaller differences produced by within-male modulation. Accordingly, in this study we not only tested for male discrimination of "between-male" differences in performance, but also tested the hypothesis that within-individual modulation in vocal performance functions as an acoustic bluff. That hypothesis predicts that males would behaviorally discriminate between low and high performance song renditions sung by the same individual.

Methods

Experiments were conducted between 24 April and 9 June 2009 on a population of territorial male swamp sparrows in Conneaut Marsh, Crawford County, Pennsylvania, USA. Territories remain stable during the height of the breeding season, so territorial males can be identified by location; a subset of males ($n = 4$) were color banded as well and none moved during the testing period. Of the total 34 males tested, 11 males were tested in all three experiments, 12 in two experiments, and 11 in one experiment each. No individual was presented with the same stimulus set in more than one experiment.

Experiment 1: Response to Between-male Differences in Vocal Performance

Experiment 1 investigated whether males respond differentially to between-male differences in vocal performance (inter-male discrimination). We employed a single speaker, paired design modified from Cramer and Price (2007). Subjects were presented with stimulus pairings consisting of high and low vocal performance exemplars of the same song type, sung by different males (Figure 4.1). The stimuli used in experiment 1 were the same 20 low and high performance stimulus pairings employed in a study of female preference conducted by Ballentine et al. (2004). These stimuli included 14 unique song types. When the same song type was used more than once, the multiple sets of stimuli were taken from different pairs of males. The mean difference in vocal deviation was 9.9 (range: 5.4-18.1).

Each male subject received a high performance trial and a low performance trial, separated by 48 hours. Stimuli were presented in an alternate random fashion—random for the first male, reverse for the second, random for the third, and so forth.

Playback stimuli were broadcast as WAV files at approximately 89 dB (measured at 1m with a BK Precision 32A sound level meter) using an iPod mini attached to an Advent Powered Partners AV570 speaker (35 W) mounted on a 1m post. Each trial consisted of 6 min of pre-playback observation and recording, followed by observation and recording for 3 min during playback and another 3 min after playback. Playback songs were repeated at a rate of 6 songs/min. Subject songs, as well as spoken narration of behavior and location by an observer (ALD), were recorded using a Marantz 660 solid-state digital recorder and a RadioShack 33-3001 directional microphone mounted in a Sony Parabolic Reflector-330. Behaviors recorded were: the number of broadcast songs sung by the subject, number of soft songs (low amplitude songs associated with aggression, Ballentine et al. 2008), number of flights, and number of wing waves (the visual display most closely associated with attack (Ballentine et al. 2008). The observer also estimated the subject's distance from the speaker at all times (henceforth referred to as approach distance). Flagging markers set at 2 m, 4 m, and 8 m in either direction from the speaker facilitated estimation of approach distance. Distance estimates were recorded on flow sheets divided into 10 sec intervals, from which mean approach distance for each observation period (pre-playback, during playback, and post-playback) was calculated. Males were classified as “within 2 m” (in which case 1 m was used in approach distance calculations for that 10 sec period), “within 4 m” (3m in calculations), “within 8 m” (6 m in calculations), “within 16 m” (12 m in calculations), and “greater than 16 m” (24 m in calculations). To control for variation in a male’s behavior on separate playback days, we calculated the rates of behaviors (per min) for each observation period (pre-, during, and post-playback). We subtracted the rates of each behavior during the pre-playback period from the mean rate of that behavior during and post-playback. Thus, all values used for analysis represent the change in behavior once playback began (Cramer and Price 2007).

To compare subject responses to low and high performance playback in both experiments, we used a principal components analysis (PCA) with changes in broadcast song rate, soft song rate, flight rate, wing waving rate, and approach distance as variables. We used Wilcoxon Signed Ranks tests to compare resultant PCA scores, as well as the subject’s behavioral rates in response to stimuli. Twenty-six males were presented with both high and low performance playback. Behavioral responses of subjects who were tested with playback of the same stimuli were averaged with the response of the other subject to avoid pseudoreplication so that the sample size in the statistical tests is number of stimulus sets (20) rather than number of subjects (26).

Experiment 2: Response to Within-male Differences in Vocal Performance, 1-speaker trials

Experiment 2 investigated whether males respond differentially to two levels of performance modulation of a single simulated rival (intra-male discrimination). We followed the same experimental protocol as in Experiment 1, but replaced the stimuli representing inter-male differences in vocal deviation with digitally manipulated stimuli that simulated intra-male modulation of vocal performance. High and low vocal performance stimuli were artificially created using SIGNAL v. 4.0 software (Engineering Design, Belmont, MA, USA) to mimic a natural level of performance modulation by a single male (mean difference in performance = 4.19, range = 3.02-6.24).

We chose to use digitally manipulated stimuli in experiment 2 (rather than natural recordings as in experiment 1), because we did not have a sufficient number of natural stimulus pairs recorded during the DuBois et al. (2009; Chapter 2) study that met our criteria for this discrimination study. Eighteen males in the DuBois et al. (2009; Chapter 2) study increased their vocal performance in aggressive contexts, with the change in vocal deviation ranging from 0.45 to 5.11. We wished to present vocal performance differences from the upper end of this range. By digitally manipulating songs instead of using natural song pairs, we were able to produce pairs of stimuli identical except for the vocal performance differences, while achieving performance differences in the desired range.

We created 16 stimulus sets, consisting of a base song (low performance), and a test song (high performance) (Figure 4.2). These stimulus sets included 11 unique song types. When the same song type was used more than once, song exemplars were recorded from different males. To create a stimulus set, we began with a natural song exemplar. Exemplars were chosen based on having a broad frequency bandwidth and high recording quality. For each song exemplar, we measured the average syllable length, the average length of time between syllables (average interval), the length of time between notes in the syllable (inter-note intervals), and the maximum frequency of each syllable. To create a base song, we chose a single syllable from the natural song, and digitally inserted silent inter-note intervals of approximately equal length to those of the natural song and then concatenated this control manipulated syllable to create a song of the same trill rate and duration as the natural song. To create a high performance (test) song, we followed the same methods as in the creation of the base song, with two modifications. First, we exchanged the broadest bandwidth note with a corresponding note obtained from a different exemplar of the same syllable type, but one having a broader frequency bandwidth. We then concatenated this manipulated syllable to create a full song, but did so at an increased trill rate from the original. The vocal deviation of each newly created song was measured following the methods of Ballentine et al. (2004), using the upper bound regression line calculated for the Emberizidae by Podos (1997) as a reference. The difference in vocal deviation between the low performance (base) and high performance (test) songs mimicked a natural range of vocal deviation modulation found by DuBois et al. (2009; Chapter 2; mean difference = 4.19, range = 3.02-6.24). As before, the behavioral responses of males who were tested with the same stimulus set were averaged to avoid pseudoreplication so that the sample size in statistical tests is number of stimulus sets (16) instead of number of subjects (26).

Experiment 3: Response to Within-male Differences in Vocal Performance, 2-speaker trials

We performed a second test for behavioral discrimination of within-male vocal performance differences, using a two-speaker discrimination design. This design may provide a more sensitive test of discrimination (Searcy et al. 1995, 1999), at the cost of limiting the number of clearly aggressive response measures that can be associated with each stimulus to one: approach distance. In this design, we placed two matched speakers (Advent Powered Partners AV570) mounted on 1m metal posts on the subject's territory, 12 meters apart. We placed flagging at 3 and 6 m from each speaker in either direction to facilitate estimating the subject's distance from either speaker at all times. We also incorporated a control song for each stimulus set (Figure 4.2). To create a control song, we followed the same protocol as above, but exchanged the note responsible for the maximum frequency of the syllable with the corresponding note in a different syllable with similar or equal maximum frequency to the maximum frequency of the base song. This substitution served as a control for the modifications made to the high performance song. We also kept the trill rate equal to that of the base song. Base and control song pairs were nearly identical with respect to vocal performance (mean difference = 0.17, range = 0.00-0.44). During an initial phase, the base song type was played from both speakers for 42 minutes at a rate of 6 songs/min, with the second speaker offset by 5 sec to prevent song overlap. After this initial phase, both speakers switched to new stimuli, and playback continued for another 6 min. One speaker switched to the low performance (control) song, while the other speaker switched to the high performance (test) song, simulating an increase in vocal performance. The order and location of the high performance song stimulus was balanced across subjects. The territory owner was thus asked to judge which stimulus was more dissimilar to the base song type by approaching one speaker more closely than the other. This design was used successfully to demonstrate stronger discrimination between song types than between song variants in song sparrows (*Melospiza melodia*, Searcy et al. 1999).

During playback, an observer (WAS) noted the distance of the subject from both speakers at all times. This information was recorded in the field on time flow sheets by a second observer (ALD), as in the previous experiments. We used the subject's mean distance to the speaker in the last 6 min before the switch minus his average distance in the 6 min after the switch as a measure of change in approach distance, and compared this measure toward the low and high performance speakers using a Wilcoxon signed ranks test to determine whether subjects discriminated modulation in vocal performance.

Results

Experiment 1: Between-male Discrimination

Principal component analysis reduced five univariate measures of response to two principal components (Table 4.1). Song rate and wing waving rate load highly on PC1, which explains 36.2% of the variance. Soft song rate and approach distance load highly on PC2, (approach distance is negatively correlated, as greater changes in approach are more negative values), which explains 29.4% of the variance. PC1 scores for subjects were significantly greater in response to high performance song (Wilcoxon signed-ranks test, $n = 20$, $Z = -2.58$, $P = 0.01$, Figure 4.3a), as were PC2 scores ($Z = -2.17$, $P = 0.03$, Figure 4.3a).

Responses were greater toward high performance song on all five univariate measures, and the differences were significant for three of these: song rates (*n* = 20: *Z* = -2.58, *P* = 0.01, Figure 4.3b), soft song rates (*Z* = -2.06, *P* = 0.039, Figure 4.3b) and flight rates (*Z* = -2.44, *P* = 0.015, Figure 4.3b). Differences were not significant for wing waving rates (*Z* = -1.22, *P* = 0.22, Figure 4.3b) or approach distance (*Z* = -1.87, *P* = 0.062, Figure 4.3c).

Experiment 2: Within-male discrimination, 1-speaker

Principal component analysis again revealed two principal components (Table 4.2). PC1 was most associated with wing waving rate and explained 37.8% of the variance in response measures, while PC2 was associated with approach distance and explained an additional 29.6%. Comparison of PC1 scores revealed no significant difference between responses to the two stimulus categories (*n* = 16; *Z* = -0.931, *P* = 0.352, Figure 4.4a). Comparison of PC2 scores also revealed no difference (*Z* = -1.45, *P* = 0.148, Figure 4.4a).

Male responses to low and high performance manipulations of song types did not differ with respect to song rate (*n* = 16, *Z* = -0.691, *P* = 0.489, Figure 4.4b), soft song rate (*Z* = -0.525, *P* = 0.60, Figure 4.4b), wing waving rate (*Z* = -1.22, *P* = 0.221, Figure 4.4b), or approach distance (*Z* = -0.982, *P* = 0.326, Figure 4.4c). Flight rate was significantly higher in response to the higher performance song (*Z* = -1.989, *P* = 0.047, Figure 4.4b).

Experiment 3: Within-male discrimination, 2-speaker

The initial playback phase of 48 min was divided evenly into fourteen 3-min time blocks, followed by two 3-min time blocks post-switch. Approach distance toward the two speakers differed only during one of the initial fourteen time blocks (block 11; $Z = -2.05$, $P = 0.041$), but was not significantly different during time blocks 1-10 or 12-14 (Figure 4.5). Thus subjects ($n = 16$) did not show a bias toward either speaker. After the switch to new stimuli, approach was slightly closer to the low performance songs, though the differences were not significant (time block 15: $Z = -0.672$, $P = 0.501$; time block 16: $Z = -1.704$, $P = 0.088$, Figure 4.5). There was no difference in approach between the last 6 minutes pre-switch and first 6 minutes post-switch toward the speaker switching to a higher performance song versus the speaker switching to a control performance level song ($Z = 1.60$, $P = 0.109$, df = 15).

Discussion

Male swamp sparrows discriminated between song exemplars of a single song type, which differed in vocal performance, when the differences in performance were on the level exhibited among different individuals. This result supports our first hypothesis, that males assess individual differences in vocal performance. The difference in PC1 and PC2 scores in the between-male experiment is particularly telling, because PC1 was strongly associated with wing waving rate, while PC2 combined soft song and approach, and these three measures have been shown to predict attack in swamp sparrows (Ballentine et al. 2008). We are thus safe in concluding that aggressive response in this first experiment was stronger toward higher performance songs. Differential response of males to songs differing in vocal performance, in swamp sparrows as well as in other species (Cramer and Price 2007, Illes et al. 2006) suggests that receivers recognize vocal performance as a signal in male-male communication.

Distinguishing potential rivals based on vocal performance may allow males to assess an individual's quality as a competitor, in the same way that females are able to assess a male's quality as a potential mate using vocal performance (Ballentine 2004, Ballentine et al. 2009). While females presumably attend to vocal performance as an indicator of potential direct and indirect benefits, males may be attending to vocal performance as an indicator of potential fighting ability. Maximum vocal performance is correlated with age and size in swamp sparrows, and these attributes have been associated with fighting ability and the ability to win contests against intraspecific competitors in other songbird species (Koivula et al. 1993, Richner 1989, Sandell and Smith 1991, Searcy 1979, Yamaguchi and Kawano 2001). Thus, it is possible that males can garner information about an opponent based on his vocal performance, whether or not any information is conveyed through modulation of this characteristic.

Although we found convincing evidence of discrimination in between-male performance, subjects did not respond differentially to vocal performance differences at the within-male level. Thus, the results failed to support our second hypothesis, that within-individual modulation in vocal performance functions as an acoustic bluff. The only behavioral variable to differ significantly between low and high performance trials in experiment 2 was flight rate. Increased flight rate suggests that males were perhaps slightly more agitated, but flight rate is not likely to be an important aggressive behavior, and none of the other behavioral variables more closely associated with aggression (soft song, wing waving, and approach) differed between trials. The two-speaker assay (experiment 3) also failed to demonstrate discrimination. This method has been used successfully to detect discrimination of other fine scale differences in song variation in a closely related species, the song sparrow (Searcy et al. 1999), but it failed to detect any discrimination of within-male differences in vocal performance in swamp sparrows.

The exhibition of differential response to inter-male differences and an absence of response differences for intra-male modulation found in this study are consistent with the suggestion that vocal performance serves as an index signal. Several species that use index signals are able to modulate these signals (Searcy and Nowicki 2005), suggesting that index signals are only loosely constrained within limits, and that the signal may be modulated adaptively within those limits. For example, Wagner (1989*a*) found that male Blanchard's cricket frogs (*Acris crepitans blanchardi*) lower the dominant frequency of their calls during aggressive interactions. Importantly, the level of modulation of dominant frequency in cricket frogs has been shown to be functionally significant in terms of its effect on receiver response. Male receivers tend to retreat from playback of calls that decrease in dominant frequency more so than from playback calls of constant or increasing frequency (Wagner 1992). This alteration implies that dominant frequency is a signal that can be effectively cheated. In the same vein, red deer stags are capable of modifying the formant dispersion of their roars by actively altering the configuration of their vocal tracts (Fitch and Reby 2001, Reby et al. 2005). Changes in formant dispersion occur at a level salient to receivers, at least in the case of female receivers (Charlton et al. 2007), and are therefore likely to influence the outcome of aggressive interactions (Reby et al. 2005). In contrast to both these examples, swamp sparrow males are able to exaggerate their signal by lowering vocal deviation (DuBois et al. 2009; Chapter 2), but they do not alter the signal sufficiently to affect receiver response, meaning that modulation is unlikely to affect the outcome of an interaction. Swamp sparrows, therefore, may be more strictly constrained in their ability to modulate vocal deviation than are signalers in these other systems. Vocal deviation perhaps provides a better example of an index signal, since it cannot be effectively cheated.

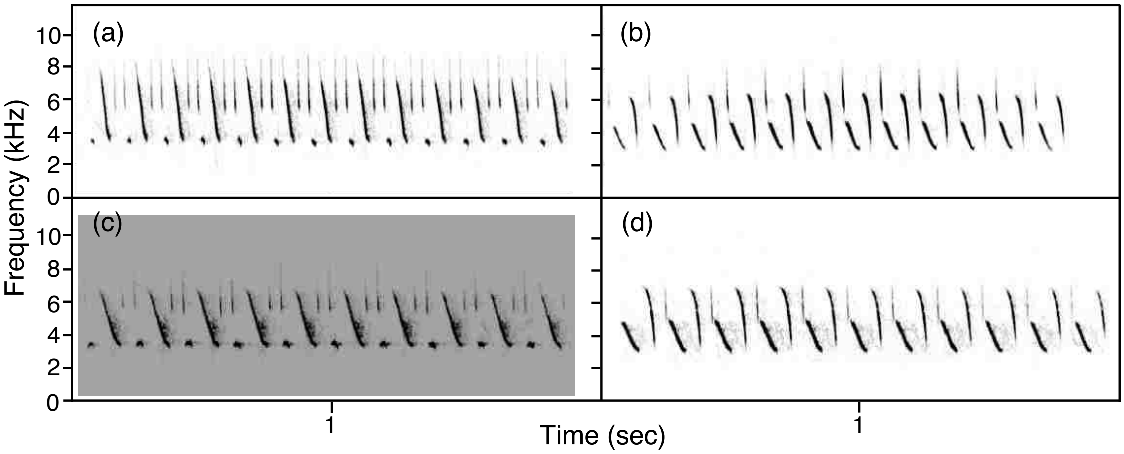

Figure 4.1 Two examples of stimulus pairings used in the between-male discrimination trials (Experiment 1). Spectrograms (a) and (c) constitute one pairing of the same song type sung by two different males, while (b) and (d) are a different pairing. Songs (a) and (b) represent the higher performance (low deviation) renditions of the song type, while songs (c) and (d) represent the lower performance renditions

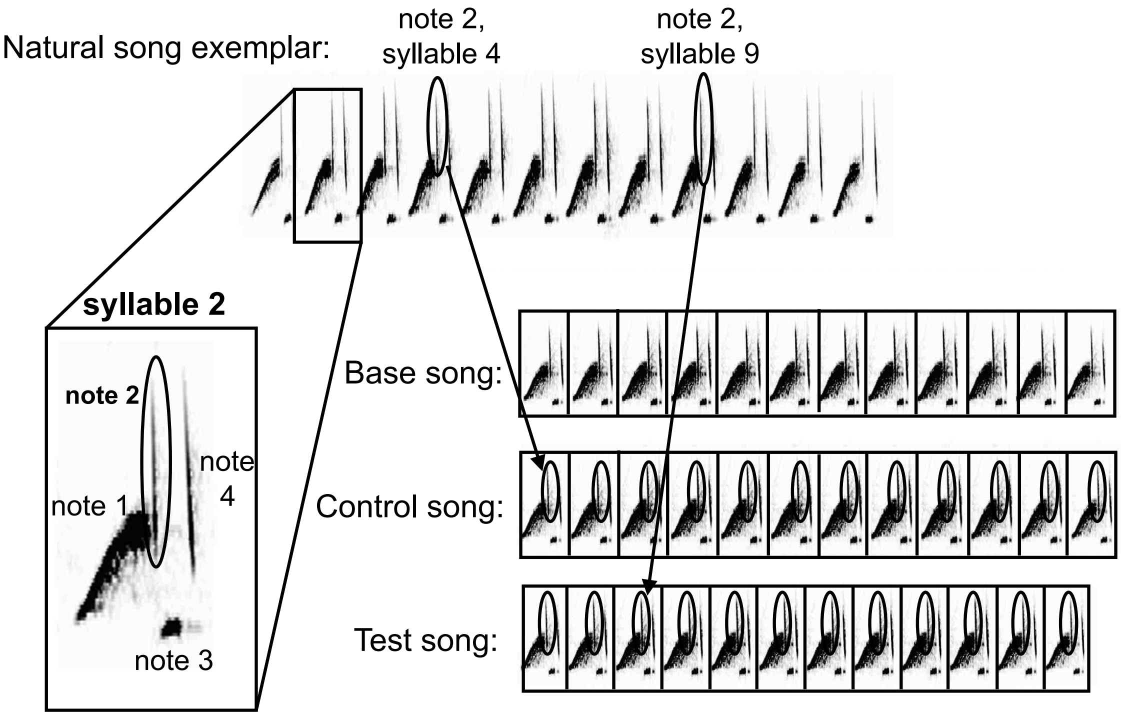

Figure 4.2 Creation of intra-male "modulated" stimuli. To form a base song, a single syllable was chosen from a natural song exemplar. Notes from that syllable were saved into individual time buffers, and reassembled with internote and intersyllable silent intervals equal to the natural song (resulting in equal trill rates). To form the control song, the note responsible for the maximum frequency (in this example, "note 2") of the song was substituted with a note from a different syllable with equivalent frequency bandwidth. Internote and intersyllable silent intervals were again equal to the natural and base song types. To form the test song, "note 2" was substituted with a note with a broader frequency bandwidth, and intersyllable silent intervals were reduced to increase the trill rate of the song.

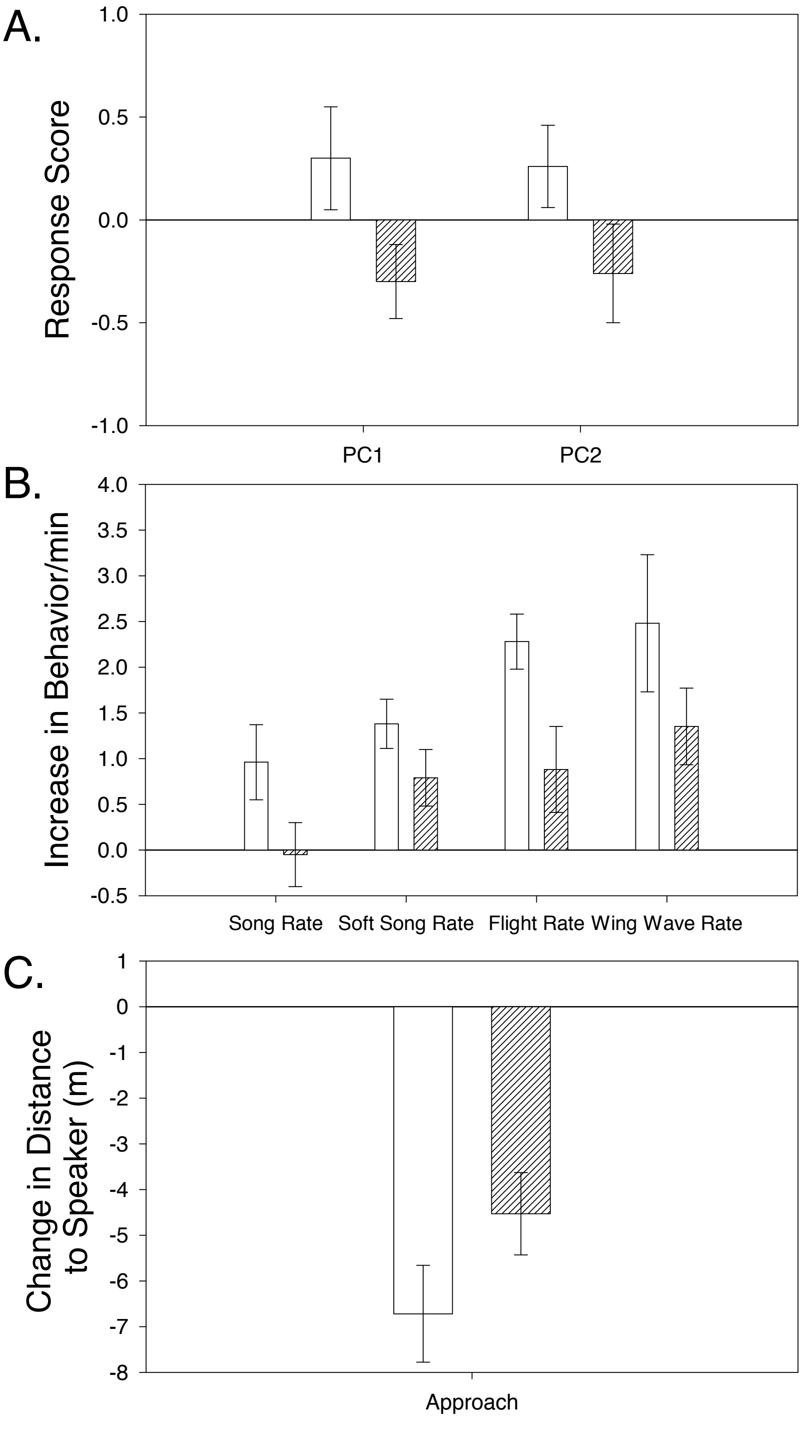

Figure 4.3 Response to between-male differences in vocal performance. A. Mean principal component scores (±SE) in response to high performance (white) and low performance (striped) playback song (*n* = 20); B. Mean (±SE) behavioral responses to playback of high performance and low performance song playback. Values are increases in behavioral rates during and after playback, relative to behavioral rates prior to playback; C. Mean (±SE) change in approach distance. Lower values represent a closer approach to the speaker during and after playback, relative to approach distance prior to playback.

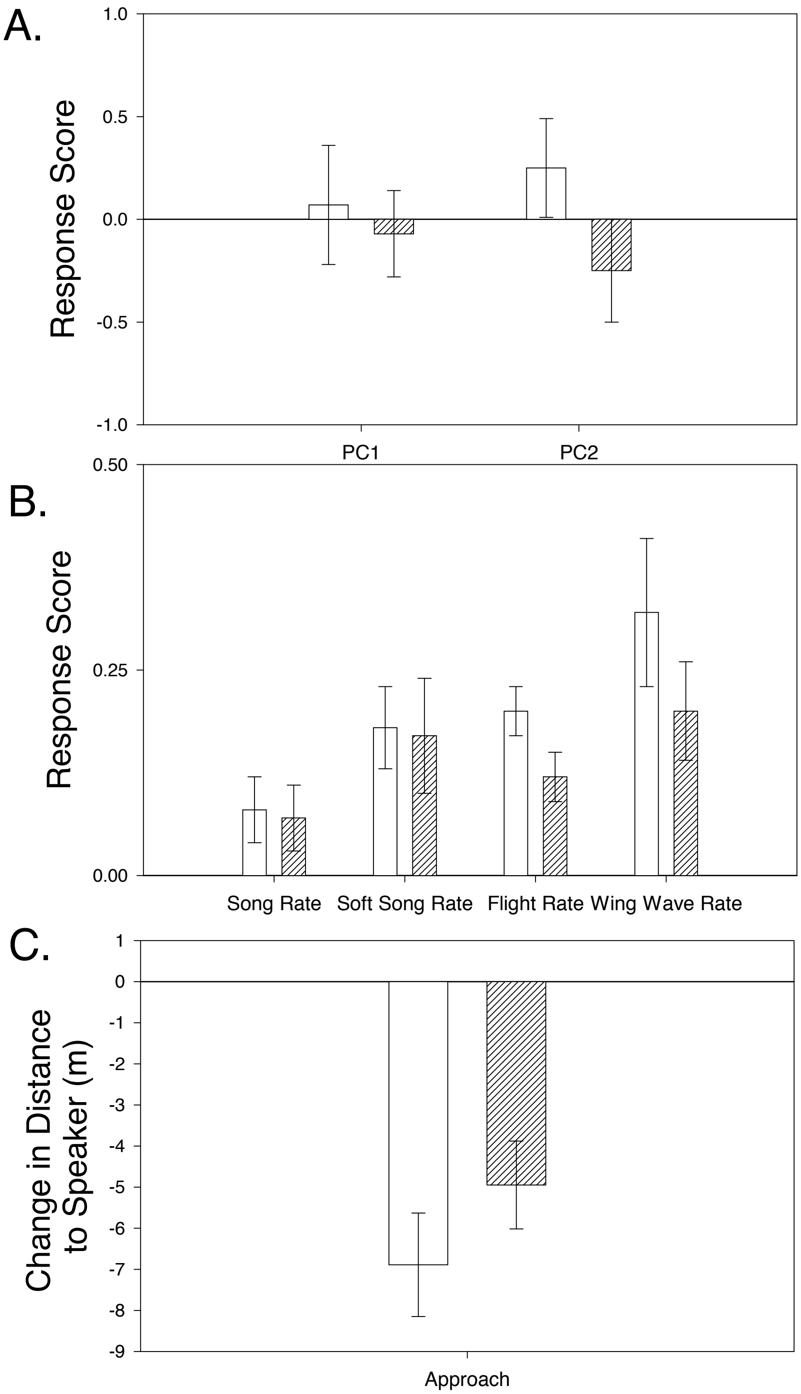

Figure 4.4 Response to within-male differences in vocal performance. A. Mean principal component scores (±SE) in response to higher performance (white) and lower performance (striped) song stimuli (N = 16); B. Mean (±SE) behavioral responses to playback of higher performance and lower performance stimuli. Values are increases in behavioral rates during and after playback, relative to behavioral rates prior to playback; C. Mean (±SE) change in approach distance. Lower values represent a closer approach to the speaker during and after playback, relative to approach distance prior to playback.

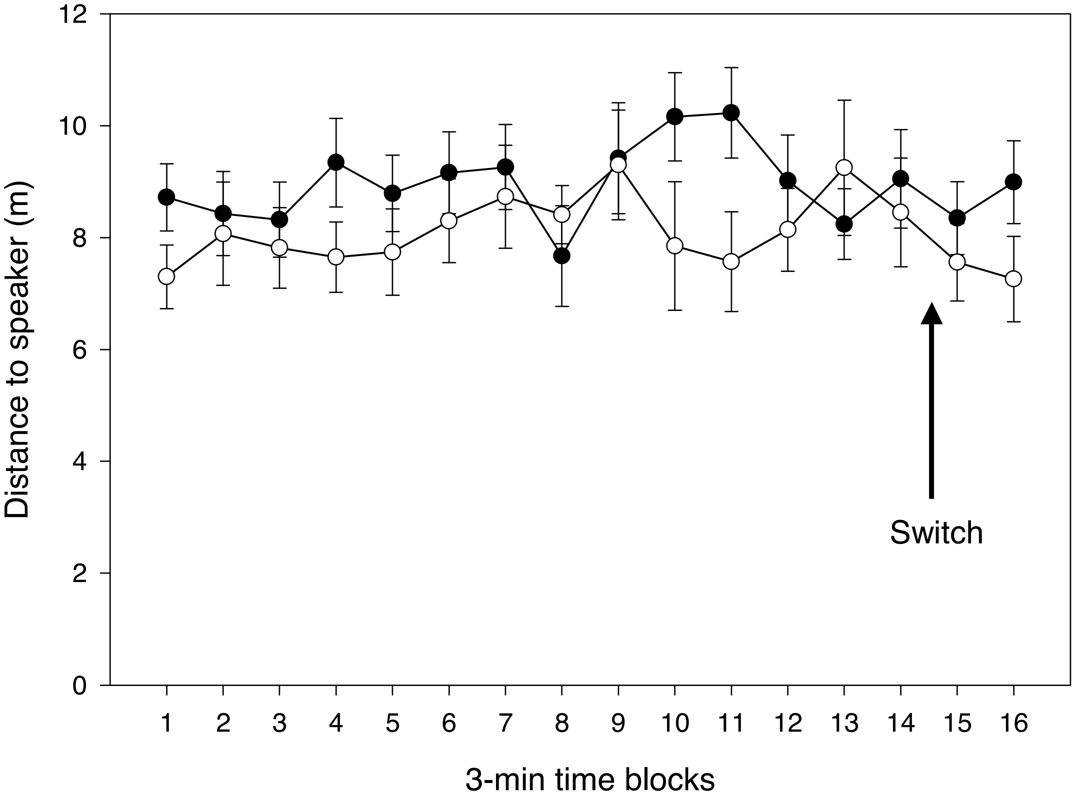

Figure 4.5 Mean approach distance (±SE) to speakers during the two-speaker intra-male discrimination test. One speaker (white circle) switched from a base song type during the habituation phase (time blocks 1-14) to a low performance (control) song playback during the recovery phase (time blocks 15-16). The other speaker (black circle) switched to a high performance (test) song playback. Arrow indicates point at which playback switched from the base song to either the control or test song (N = 16).

Table 4.1 Loadings of response measures on the first two principal components in the between-male discrimination experiment (Experiment 1).

	Loadings	
Response measures	PC1	PC2
Song rate	0.866	-0.028
Soft song rate	0.400	0.729
Flight rate	0.474	0.313
Wing waving rate	0.820	0.143
Approach distance	0.066	-0.905

Table 4.2 Loadings of response measures on the first two principal components in the within-male, 1 speaker discrimination experiment (Experiment 2).

	Loadings	
Response measures	PC1	PC2
Song rate	0.523	0.577
Soft song rate	0.798	0.063
Flight rate	0.380	0.699
Wing waving rate	0.901	0.092
Approach distance	0.155	-0.803

Chapter 5

Investigating the role of vocal performance in territory defense[4]

Summary

Recent evidence suggests that vocal performance is used by males as a signal in territory defense. This evidence, however, comes from indirect tests of signal function—traditional playback studies in which song is presented to a territory owner. We employed a speaker occupation design to directly test the hypotheses that 1) vocal deviation, a measure of vocal performance is used to signal male quality in territory defense and 2) male response to vocal deviation is a conditional strategy based on the relative performance levels of male interactants. We found no difference between intrusion rates onto territories of simulated low and high vocal deviation owners. Intruders and non-intruders did not differ with respect to vocal deviation. The number of cases in which the deviation level of intruders was lower (and therefore of higher performance) than that of simulated owners did not differ from random expectation. We discuss these findings and their implications for the use of vocal deviation as a signal in territory defense.

Background

Darwin (1871) discussed the possibility that birdsong was molded by sexual selection, though he was unable to show explicitly that this was the case. Experimental evidence has since confirmed the use of song as a signal in male-male competition for

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[4] This chapter will be submitted for publication with authors A.L. DuBois and W.A. Searcy.

territories (which are necessary for mating success) and in attracting and courting females (Catchpole and Slater 1995). Fine-scale analyses have additionally revealed that individual components of songs and different modes of singing are used as signals to influence both female preferences and the outcome of male-male competition (reviewed in: Catchpole and Slater 1995, Collins 2004, Searcy and Nowicki 2000). Most studies of the territory defense function of song have, however, provided only indirect evidence that song and song components expedite territory defense, likely due to the difficulties imposed by more direct tests (Searcy and Nowicki 2000). In this study, we examined a component of birdsong, vocal performance, in simulated, naturalistic encounters in swamp sparrows (*Melospiza georgiana*) to test directly whether vocal performance functions as a deterrent to territorial intrusion.

Vocal performance is the ability to produce physically or physiologically challenging song (Podos 2001, Forstmeier et al. 2002, Ballentine et al. 2004, Cardoso et al. 2009). In this study, we focus on a specific aspect of vocal performance, vocal deviation, which measures how closely a song approaches an upper boundary of performance capability that is determined by a tradeoff between trill rate and frequency bandwidth (Podos 2001). In birds that sing a trilled song (a rapidly repeated series of notes or syllables), not all individuals are equally capable of simultaneously maximizing both the trill rate (the rate at which syllables are repeated) and the frequency bandwidth (the range of frequencies encompassed by each note or syllable). This difficulty is due to biomechanical constraints on the vocal tract (Westneat et al. 1993, Hoese et al. 2000) that limit the bird's ability to make the alterations of vocal tract configuration needed to manipulate note frequencies while doing so rapidly to increase trill rate. When songs are graphed by trill rate against frequency bandwidth, they tend to fall out in a triangular distribution, with few or no points in the upper right quadrant representing the combination of rapid trill rate and high frequency bandwidth. Podos (1997) first demonstrated this relationship for the Emberizidae, and calculated an upper-bound regression line that represented a performance limit for the family—above which songs cannot be produced. A song's vocal deviation is its orthogonal distance from that upper-boundary line. Typically, males of overall higher quality are more adept at producing songs with a low vocal deviation (high vocal performance). This has been shown to be the case in the species used in this study, swamp sparrows (*Melospiza georgiana*). Ballentine (2009) found that a male's maximum vocal performance (measured in terms of vocal deviation) is positively correlated with his age and size. Correlations between various measures of vocal performance and male quality have been found in other species as well, including dusky warblers (*Phylloscopus fuscatus,* Forstmeier et al. 2002), banded wrens (*Thryothorus pleurostictus,* de Kort et al. 2009), tropical mockingbirds (*Mimus gilvus*, Botero et al. 2009) and great tits (*Parus major,* Rivera-Gutierrez 2010).

Due to the nature of vocal deviation and its correlation with male quality and resource holding potential, vocal deviation has been classified as an index signal. Index signals are a subset of performance signals whose honesty is maintained by physical constraints. Index signals are considered "unfakeable" because they are "causally related to the quality being signalled" (Maynard Smith and Harper 2003). Index signals thus play a unique role in communication by honestly indicating size, quality, or resource holding potential in competitive interactions across taxa (frogs and toads: Martin 1972, Davies and Halliday 1978, Wagner 1989*a*, 1989*b*; red deer, *Cervus elaphus*: Reby and McComb 2003, Reby et al. 2005; funnel spiders, *Agelenopsis aperta*: Riechert 1978).

Recent evidence suggests that vocal performance, and specifically vocal deviation, plays a signaling role in territory defense. Male swamp sparrows have been shown to modulate their vocal deviation in aggressive contexts. They do so by increasing both the trill rate and frequency bandwidth of songs when challenged by a playback situation, compared to when the same song types are sung in neutral contexts (DuBois et al. 2009; Chapter 2). The level of vocal deviation of playback songs affects aggressive response in male songbirds of several species, (Illes et al. 2006, Cramer and Price 2007, De Kort et al. 2009), including swamp sparrows (DuBois et al. 2011; Chapter 4), supporting the idea that vocal deviation is a signal that is salient to male receivers.

Evidence to date does not, however, directly demonstrate that vocal deviation functions in territory defense. All of the aforementioned results on male response to vocal deviation come from traditional playback studies, which do not directly test whether song traits aid in defense of territories. If song functions in territory defense, it does so by discouraging intrusion by rival males. In traditional playback studies, the aggressive stimulus is presented to a territory owner, rather than to an intruder, and the response measured is approach, rather than repulsion. The data do not, then, provide information regarding whether a signal is effective in deterring territorial intrusions. A more direct test of song function is a speaker occupation experiment (Searcy and Nowicki 2000).

In speaker occupation experiments, a territorial male is removed from his territory and replaced by a loudspeaker. From the loudspeaker, the researcher can broadcast song and compare the number of intrusions to a control treatment or a neutral sound stimulus. The introduction of the speaker allows the researcher to manipulate song characteristics, such as repertoire size, or in our case, vocal deviation (Searcy and Nowicki 2000). The limited number of speaker occupation experiments done to date have shown the effect of song versus no song in deterring territorial intruders (Falls 1988, Nowicki et al. 1998), and also the effectiveness of large compared to small repertoire sizes (Krebs et al. 1978, Yaskukawa 1981). A drawback of this design is that intrusion rates can be very low in territorial songbirds, even in control treatments such as no-song (Nowicki et al. 1998, Searcy and Nowicki 2000), making it difficult to show an effect of experimental treatments in lowering intrusion. To avoid this problem, we have adopted the "simulated intrusion" design, successfully used by Searcy and Nowicki (2006) in a study of soft song in song sparrows. This design uses playback to simulate an interaction between a territory owner and an intruder, and in song sparrows resulted in higher rates of intrusions (Searcy and Nowicki 2006) than seen in a design in which only the owner's songs are played from the territory (Nowicki et al. 1998). Presumably, the simulated interaction between the "owner" and "intruder" stimulates other third party males to intrude.

The objective of this study was to investigate the territorial defense function of vocal deviation. We hypothesized both that vocal deviation is used to signal male quality in territory defense and that male response to vocal deviation (aggression or submission) is a conditional strategy based on the relative vocal deviation levels of the males involved in the interaction. We tested three predictions of our hypotheses: 1) simulated territory owners with low vocal deviation (high performance) would incur fewer intrusions than simulated territory owners with high vocal deviation (low performance), 2) males that intrude on focal territories during trials would have lower vocal deviation than nearby males that do not intrude, and 3) intrusions would be more likely when the vocal deviation of the potential intruder was lower than that of the simulated owner.

Methods

Experiments were conducted May 23 to June 27 2010 in Conneaut Marsh, Crawford County, Pennsylvania on a population of free-living male swamp sparrows. Experiments consisted of paired trials of simulated intrusions on male territories, using a within-subjects design in which both a "low vocal deviation/high performance owner" and a "high vocal deviation/low performance owner" were simulated on each territory. Briefly, male territory owners were removed and replaced with loudspeakers that played synthetic versions of their songs, altered to be of lower or higher vocal deviation, depending on the trial. A second loudspeaker placed on the territory simulated countersinging by an unknown "intruder." Observers then noted whether nearby males intruded onto the focal territory during the simulated interactions.

Territories chosen to serve as experimental replacement territories were carefully mapped to determine boundaries with neighbors. Territory owners were captured using mist nets and banded with a Fish and Wildlife band and a unique color band combination for individual identification. All neighboring territory owners immediately adjacent to the replacement territory were also banded to facilitate identification of intruders.

We recorded the full repertoires of experimental replacement territory owners, as well as all color-banded males who intruded onto experimental territories during trials (unidentified "floater" males could not be recorded). These recordings served as the basis for creation of our experimental stimuli and also allowed us to make comparisons of vocal deviation between males. Males were recorded using a Marantz PMD 660 solid-state digital recorder connected to a RadioShack 33-3001 directional microphone mounted in a Sony Parabolic Reflector-330. We minimized the amount of playback heard by males during recording to avoid any possible effects this playback might have on the vocal deviation of repertoire recordings of territory owners. Playback song was only used when we were unable to record a male's entire repertoire after two attempts on separate days.

We created experimental stimuli to simulate "low vocal deviation territory owners" and "high vocal deviation territory owners." Stimuli consisted of modified versions of the recorded songs of owners, artificially manipulated to decrease and increase vocal performance. Creation of these synthetic songs allowed us to control differences in vocal deviation, while maintaining consistency between stimuli in other non-performance-related song parameters (song length, note types, etc.). Swamp sparrows have been shown to respond to artificially manipulated song, including songs that contain synthetically created notes (Prather et al. 2009; Lachlan *In prep*) and do not discriminate differences between artificially created songs and natural songs, as long as species-specific song characteristics are maintained (Robert Lachlan, unpublished data). To create "low vocal deviation owner" song and "high vocal deviation owner" song to broadcast during simulated intrusions, we chose a good quality recording of one song type from each male's full repertoire, and then manipulated a syllable of that song to create an artificial stimulus song (Figure 5.1). The original trill rate, frequency bandwidth, and vocal deviation of this song were measured using Signal 4.0 digital signal analysis software (Engineering Design, Belmont, Massachusetts, USA). We then manipulated the frequency bandwidth and trill rate of songs to alter vocal deviation. Changes in deviation were based on the natural range of variation observed in a previous study between renditions of the same song type sung by individual males in different contexts (DuBois et al. 2009, Chapter 2; maximum change in vocal deviation: 7.8 units; trill rate: 0.7 Hz, frequency bandwidth: 763 Hz). We selected one syllable of a song to be repeated to create a new stimulus song. Then to manipulate frequency bandwidth, we substituted the note responsible for the maximum frequency in the syllable with a synthetic replacement. Synthetic notes were created using a custom script in Signal, and had similar spectral characteristics to the original note (note type and duration of note were maintained), but differed in maximum frequency. Notes with higher maximum frequency than the original note were used to create low deviation songs and notes with lower maximum frequency than the original note were used to create high deviation songs. To manipulate trill rate, we repeated the syllable at slower or faster rates, depending on whether we were creating the high deviation or low deviation songs. Song length was kept equal to the original song for all stimuli. Synthetic owner songs fell within the natural range of performance modulation (average increase/decrease from original song in vocal deviation: 6.1 units; trill rate: 0.7 Hz; frequency bandwidth: 671 Hz).

To conduct a trial, we chose a focal territory, on which the owner had been color banded and fully recorded and for which all adjacent neighbors had been color banded. We then captured and removed the territory owner using a mist net and, in some cases, playback of swamp sparrow vocalizations. Mist net playback consisted of single note aggressive calls, distress screams, or the owner's song (a different song type than that used for manipulation). We used owner song only in rare cases when the territory owner did not fly into the net on his own or in response to the other forms of playback. To neighbors, playback of unmanipulated owner song should simply sound like the owner is singing on his own territory, and not like an intrusion is occurring. If the territory owner sang in response to playback of his own song, the capture attempt was abandoned because it began to simulate an intrusion on the focal territory. Once a male was captured, he was removed to a cage off-territory and supplied with water, seed, and mealworms for the duration of the trial. In all cases, the male was held for less than 2 hours and then released back onto his territory.

After the male was removed, we placed two playback speakers on the territory to use in simulating an interaction between the territory owner and an intruder. Speakers were placed 5 m apart, and 2 m inside the territory boundary with the focal neighbor—the neighbor sharing the boundary at the simulated intrusion site and thus most likely to intrude. One speaker played either "low vocal deviation owner" song or "high vocal deviation owner" song, depending on the trial, while the other speaker played "intruder song," song sung by an unfamiliar male, of a different song type than owner song, and intermediate in vocal deviation. Songs were repeated at a rate of 5 songs/min, with simulated intruder song and owner song offset by 6 sec to avoid overlap. Intruder song was always played first. Periods of 6 min of playback were alternated with 6 min silent periods, for 1 hr. Stimuli were played as .WAV files from a Marantz PMD 660 solid-state digital recorder connected to a pair of Advent Powered Partners speakers. Playback stimuli were broadcast at 85 dB. Sound level of playback was tested with a BK Precision 732A sound level meter at 1 m from the speaker.

During a trial, two observers stood approximately 12 m from the speakers, positioned to observe all territory boundaries. Observers noted: identity of intruders, beginning and end of intrusions (marked on time flow sheets in the field, divided into 10 sec intervals), songs sung by intruders while on territory, and “deep intrusions” (intrusions greater than 2 m within the territory boundary).

Order of stimulus presentation was alternate random: a coin toss determined which stimulus (low vocal deviation owner or high vocal deviation owner) was presented first on the first replacement territory, then the opposite stimulus was presented on the next replacement territory, then another coin toss determined which stimulus would be used first on the third territory, and so on. The opposing stimulus trial was carried out approximately one week later, although this varied across territories (mean days between trials = 11, range = 6-27). This time between trials was used to ensure that the territory owners had returned to normal behavior, and would be possible to recapture.

To compare intruders and non-intruders to each other and to simulated owners, we measured each male’s maximum vocal performance in terms of vocal deviation (Ballentine 2009). We chose the song type in a male’s repertoire with the lowest vocal deviation, and then measured a maximum of 10 exemplars of sufficient quality for analysis. If fewer than ten exemplars were available, we measured as many as possible (mean = 7, range = 1-10). Trill rate was measured as the number of syllables/second, averaged across the entire song. Frequency bandwidth was measured as the difference between the maximum and minimum frequency at -36 dB relative to the peak amplitude frequency. Songs were analyzed using Signal following the methods of Ballentine et al. (2004) (256 transform length, 5.8 ms time resolution, 172.3 Hz frequency resolution). Vocal deviation was calculated as the orthogonal distance from the upper bound regression line calculated for the Emberizidae by Podos (1997).

Results

We conducted 12 sets of paired trials. At least one intrusion occurred during one or both trials in all but one experimental set. Excluding the two trials conducted on that territory, a mean (± SD) of 5.4 (± 7.4) intrusions occurred per trial. Territorial intrusions were made by a mean of 1.3 (± 1) males per trial, and single intrusions lasted, on average 59 s (± 79 s). Out of a total of 118 intrusions observed during all trials, we successfully identified the intruder by his unique color band combination in 115 cases (97% of all observed intrusions). The remaining three birds were unbanded and suspected to be floaters.

Prediction 1. Low vocal deviation (high vocal performance) will deter intruders: The mean number of individual intruders during a trial was greater during low vocal deviation owner trials, but not significantly so (Table 5.1). Mean number of intrusions during a trial was equal between the two trial types (Table 5.1). The mean duration of intrusions by the adjacent neighbor and the mean total duration of intrusions were greater during the high vocal deviation owner trials, though again, these trends were not significant (Table 5.1). Latency to the first intrusion followed the same pattern as the duration measures, with first intrusions happening sooner during the high vocal deviation owner trial, but not significantly so (Table 5.1). Parametric statistics (paired t-tests) were used despite non-normality of data in order to calculate effect size, but significance does not change if non-parametric equivalents are used (Wilcoxon Sign Rank: non-significant in all cases). Effect sizes (Hedge's *d*) were small for all measures (Table 5.1). A power analysis revealed that a sample size of 88-2654 would be necessary, depending on the measure of intrusion used, to detect a significant difference with power = 0.95 and α = 0.05.

Prediction 2. Intruders and non-intruders will differ in vocal deviation: Intruders and non-intruders did not differ with respect to maximum vocal performance (measured in terms of vocal deviation), frequency bandwidth, or trill rate (Table 5.2). The difference between the trill rate of the maximum vocal performance song of intruders and non-intruders was nearly significant, and this relationship showed a small to medium effect size. However, this effect was in the opposite direction of our prediction (non-intruders had faster trill rates than intruders).

Prediction 3. Intrusions are most likely when intruder vocal deviation is lower than owner vocal deviation: We observed a total of 16 banded males intruding onto 11 separate territories during both low vocal deviation owner and high vocal deviation owner trials (25 unique combinations of intruder/territory/trial type; Table 5.3). In 15 of 25 cases in which a banded male with a fully recorded repertoire intruded onto an experimental territory, the intruding male's vocal deviation was lower (performance was better) than the simulated owner song playing during the trial ($\chi^2 = 1$, df = 1, $P < 0.5$). In 17 cases, the intruder's frequency bandwidth was greater than that of the simulated owner ($\chi^2 = 3.24$, df = 1, $P < 0.1$). However, when we examined trill rate, we found the opposite pattern, that in 15 cases the trill rate of the simulated owner was greater than that of the intruder ($\chi^2 = 1$, df = 1, $P < 0.5$). Chi-squared tests were used to examine trends in vocal performance comparisons between owners and intruders with the caveat that samples were not independent. For all performance measures, observed instances of intruders outperforming owners did not differ from random expectation.

Discussion

We did not find a difference in intrusion between trials with a simulated "low vocal deviation owner" and a simulated "high vocal deviation owner." The data did not, then, support our prediction that low vocal deviation owner song would be more effective at deterring territorial intrusions. While the mean number of intruders was greater during low vocal deviation owner trials, timed variables (duration of adjacent neighbor intrusion, duration of all intrusions, latency to first intrusion) showed a trend toward more severe intrusion during high vocal deviation owner trials. However, these trends were not significant.

The failure to detect an effect of vocal deviation on intrusion may be due to the small size of our sample combined with too-subtle differences between the experimental stimuli used. The sample size for this study was modeled after prior work investigating soft song in a closely related species, the song sparrow (Searcy and Nowicki 2006). The authors of that study investigated the effects on intrusion of soft song (low amplitude song) versus normal, broadcast song. The mean difference between the treatment categories in that study was large enough (23 dB SPL) that the categories were easily discriminated by human observers. Because the stimuli used in the present study varied along a different dimension, it is impossible to compare the degree of difference between the two studies quantitatively. Performance categories used in the present study, however, were more difficult to discriminate, at least for humans, than were the amplitude categories used by Searcy and Nowicki (2006). The differences between original owner song and synthetic low and high vocal deviation versions of that song used as stimuli in this study were on the level of within-individual, natural modulations of performance found by DuBois et al (2009; Chapter 2). Between-individual differences (Ballentine et al. 2004, DuBois et al. 2011; Chapter 4) can be nearly three times the magnitude of the maximum within-individual differences observed by DuBois et al. (2009; Chapter 2). Previously, we showed that male swamp sparrows tested with standard territorial playback can discriminate larger-scale between-male differences in vocal deviation, but that they fail to discriminate within-male performance differences (DuBois et al. 2011; Chapter 4). We chose to use within-individual level differences in the present study, because the illusion that the actual owner is defending the territory in a speaker occupation experiment cannot be maintained if stimuli from multiple males are used to represent the owner. Though our results weigh against the hypothesis that within-male differences in vocal deviation affect intrusion, it may still be true that between-male differences in vocal deviation are large enough to have effects on intrusion.

Regarding our second prediction, that intruders and non-intruders would differ with respect to vocal deviation, we found no differences in vocal deviation, frequency bandwidth, or trill rate between the two groups. We predicted that intruders would have lower vocal deviation because high performance males (in our case, males with low vocal deviation) tend to have higher resource holding potential, and are therefore capable of winning aggressive encounters. However, although males with high resource holding potential may, in theory, be expected to intrude just because they have the ability to do so, index signals of resource holding potential are not necessarily good indicators of aggressive intent. Often, other non-performance-based signals are used to indicate likelihood of attack (Vehrencamp 2000), and it is possible that these other signals, which are not related to vocal deviation, are correlated with a male's propensity to intrude on other territories. A previous study on swamp sparrows supports a separation of signals of performance ability and aggressive intent (DuBois et al. *In prep*; Chapter 3). The vocal deviation of male swamp sparrows in that study was not correlated with their likelihood to attack or with other aggressive behaviors known to predict attack in this species. We suspect that the likelihood that an individual male will intrude on a territory may have more to do with his individual aggressiveness than with his ability to produce low vocal deviation song, and that aggressiveness and performance ability are unrelated characteristics. It may also be the case that differences in ecological circumstances determine a male's tendency to intrude. Whether or not a male has a territory, and whether that territory is of high quality, likely influences a male's likelihood to intrude on another male. If this is the case, and the quality of a male's territory is not correlated with vocal deviation, we would not expect a relationship between vocal deviation and a male's tendency to intrude.

Regarding our third prediction, that intrusions would be more likely when potential intruders were capable of vocally outperforming owners, we did find a very slight trend toward intrusions occurring when intruder performance was better, at least for vocal deviation (60% of cases) and to a slightly greater extent, frequency bandwidth (68% of cases). However, examination of differences in trill rate showed the opposite pattern—in 60% of cases, the trill rate of the intruder was slower, and therefore worse, than that of the owner. Also, three of the 16 male intruders intruded both when their performance was better than the simulated owner and when the simulated owner had higher performance (lower vocal deviation). Similarly, 6 of the intruding males intruded both during the low vocal deviation and high vocal deviation trial of the same male neighbor (Table 5.3). Thus, based on the failure of the data to support either our second or third predictions, we reject our second hypothesis, that intrusion is a conditional strategy based on vocal deviation.

In conclusion, the vocal deviation level of simulated owners did not affect territorial intrusion rates during speaker occupation experiments. Intruding males and non-intruders did not differ in vocal performance measures, nor did males appear to use comparative assessments of vocal deviation when intruding on a territory. We therefore do not believe that intrusion is a conditional strategy based on individual vocal deviation. On the other hand, we are not confident in rejecting our first hypothesis that vocal deviation is used as a signal in territory defense. The negative results found in this study may mean that this hypothesis is incorrect, but they might also be explained by an insensitivity of the experimental design, particularly by our use of within-male level differences in vocal deviation.

Table 5.1 Overview of results from paired t-tests comparing intrusion responses to simulated owners with low and high vocal deviation and effect sizes with associated 95% confidence intervals (CI)

Variable	Mean (± SD) Low Vocal Deviation Trial	Mean (± SD) High Vocal Deviation Trial	*t*	*P*	df	Hedge's *d*	95% CI
Number of intruders	1.42 (± 1.1)	0.92 (± 1.0)	1.32	0.21	11	-0.46	-1.27/0.35
Number of intrusions	4.92 (± 5.6)	4.92 (± 8.8)	0.00	1.00	11	0.00	-0.80/0.80
Duration adjacent neighbor intrusion (s)	108 (± 135)	212 (± 336)	-1.05	0.32	11	0.39	-0.42/1.20
Total duration of intrusion (s)	248 (± 227)	271 (± 382)	-1.17	0.87	11	0.07	-0.73/0.87
Latency to first intrusion (s)	724 (± 965)	408 (± 582)	0.95	0.37	11	0.38	-1.19/0.43

Effect size is presented as unbiased Hedge's *d*, and the 95% CI were calculated based on *d* and sample sizes. (Nakagawa and Cuthill 2007). Effect sizes are considered small, medium, or large if $d \geq 0.2$, 0.5, and 0.8, respectively.

Table 5.2 Overview of results from paired t-tests comparing performance characteristics of songs sung by intruders (those males who intruded onto a neighboring territory during a trial) and non-intruders (adjacent neighbors who did not intrude).

Variable	Mean (± SD) Intruder	Mean (± SD) Non-Intruder	*t*	*P*	df	Hedge’s *d*	95% CI
Maximum vocal performance (units vocal deviation)	8.0 (± 5.8)	7.1 (± 5.5)	0.379	0.71	9	0.15	-0.73/1.03
Mean frequency bandwidth	5516 (± 406)	5471 (± 660)	0.165	0.87	9	0.08	-0.80/0.96
Mean trill rate	8.4 (± 3.0)	9.7 (± 2.5)	-1.237	0.25	9	-0.43	-1.32/0.46

Effect size is presented as unbiased Hedge’s *d*, and the 95% CI were calculated based on *d* and sample sizes. (Nakagawa and Cuthill 2007). Effect sizes are considered small, medium, or large if $d \geq 0.2$, 0.5, and 0.8, respectively.

Table 5.3 Qualitative analysis comparing intruder vocal deviation with that of simulated territory owners. "Intruder" indicates that the intruder sang with better vocal performance (lower vocal deviation), broader frequency bandwidth, or faster trill rate than the simulated owner. "Owner" (in gray) indicates better performance, bandwidth, or trill rate of the simulated owner.

Territory Owner	Trial (Low/High vocal deviation owner)	Intruder	Vocal Deviation	Frequency Bandwidth	Trill Rate
FYGY	High	FKWK	Intruder	Intruder	Intruder
FGGG	Low	YFRY	Intruder	Intruder	Intruder
FOOY	High	FRBR	Intruder	Intruder	Intruder
FGGG	Low	FRBR	Intruder	Intruder	Intruder
FBBW	High	FOBY	Intruder	Intruder	Intruder
FGRB	Low	FKYW	Intruder	Intruder	Intruder
FYWG	High	FWWK	Intruder	Intruder	Owner
BBFK	Low	YFRY	Intruder	Intruder	Owner
FYWG	High	FBKY	Intruder	Intruder	Owner
FGGG	Low	FOOY	Intruder	Intruder	Owner
FYWG	Low	FWWK	Intruder	Intruder	Owner
FYWG	Low	FRRK	Intruder	Intruder	Owner
FRRK	High	FBKY	Intruder	Intruder	Owner
FOOY	High	FBBW	Intruder	Owner	Intruder
FGRB	Low	FYGY	Intruder	Owner	Intruder
FKYW	Low	FGRB	Owner	Owner	Intruder
FOOY	Low	FRBR	Owner	Owner	Intruder
FRBR	High	FWYG	Owner	Intruder	Owner
FOGG	Low	FYWG	Owner	Intruder	Owner
FOGG	Low	FYYO	Owner	Intruder	Owner
FOGG	Low	FBKY	Owner	Intruder	Owner
FOOY	High	FKYK	Owner	Owner	Owner
FBBW	Low	FOBY	Owner	Owner	Owner
FRBR	Low	FWYG	Owner	Owner	Owner
FOOY	Low	FKYK	Owner	Owner	Owner

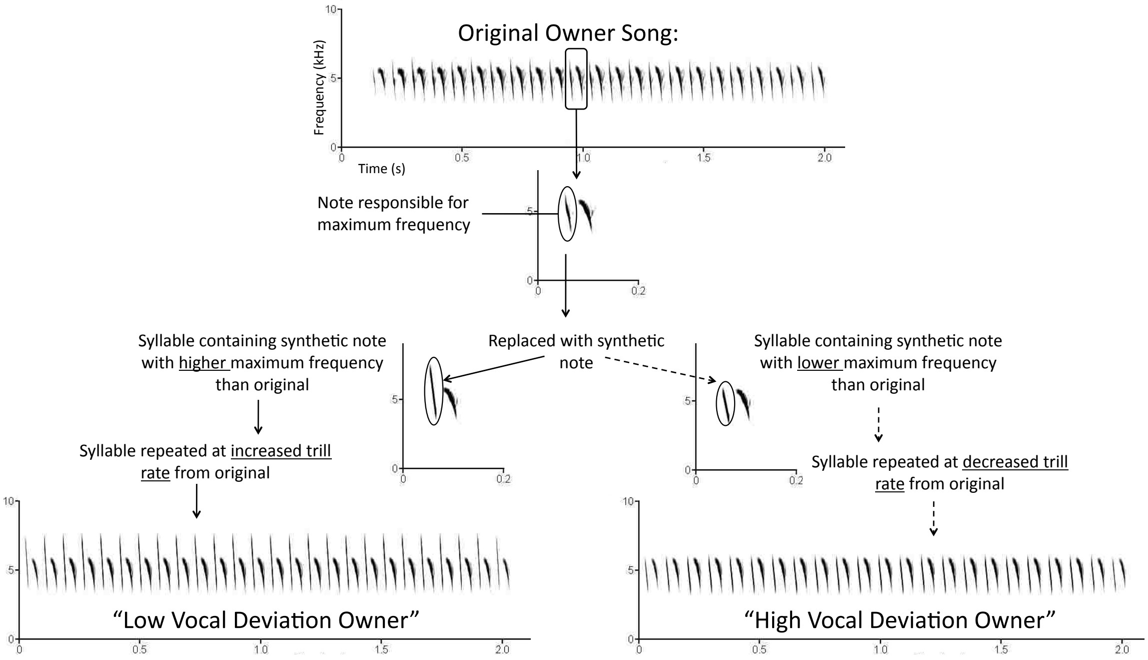

Figure 5.1 Creation of simulated "high performance owner" and "low performance owner" song. A syllable was chosen from an original owner's song. The note responsible for the maximum frequency of the syllable was replaced with a synthetic note of higher or lower maximum frequency than the original to create high and low performance versions of the syllable. Syllables were then repeated at an increased trill rate, in the case of "high performance owner" songs, or a decreased trill rate, in the case of "low performance owner" songs.

Chapter 6

Conclusion

In this dissertation I examined the adaptive significance of vocal performance in songbird communication. More specifically, vocal performance measured as vocal deviation, was investigated with respect to the male-male signaling function of bird song. Four experimental studies conducted on swamp sparrows, *M. georgiana*, addressed three major questions. First, is vocal deviation used as a signal in male-male interactions? Second, does vocal deviation function as an index signal, an honest indicator of male quality? Finally, is vocal deviation used as an aggressive signal, that is, a signal of aggressive intent or likelihood of attack? Studies testing hypotheses related to these questions considered both the signaler and receiver perspectives.

In Chapter 2, "Swamp sparrows modulate vocal performance in an aggressive context," I investigated vocal deviation from the signaler's perspective, by asking whether signalers manipulate vocal deviation in response to changes in signaling context. Males were recorded while singing in both a neutral and an aggressive context. Males were found to be able to modulate their vocal deviation by increasing both the trill rate and the frequency bandwidth of song types when sung in an aggressive context, compared to a neutral one. These changes resulted in an overall decrease in vocal deviation (increase in performance) during aggressive contexts. Modulation of vocal deviation during aggressive contexts suggests that vocal deviation has a signal function in male-male aggressive interactions. Additionally, the increase in performance level between neutral and aggressive contexts satisfies one of the criteria for establishing whether a signal is aggressive—that the signal increases in aggressive contexts (the "context" criterion; Searcy and Beecher 2009). However, the ability of males to modulate vocal performance potentially draws into question the classification of vocal performance as an index signal. The degree of modulation, however, was low, and other "classic" index signals appear to be modulated in a similar fashion (Wagner 1989*a*, Bee and Perrill 1996, Reby and McComb 2003, Searcy and Nowicki 2005, Price et al. 2006). This pattern suggests a general rule that index signals are constrained within limits, but that adaptive modulation of signals may happen within those limits. Evidence from Chapter 2, therefore, supports the use of vocal deviation as a signal in male-male communication and the potential use of vocal deviation as an aggressive signal.

In Chapter 3 I investigated whether vocal deviation satisfies the "predictive" criterion for aggressive signals—the criterion that the signal predicts aggressive escalation by the signaler (Searcy and Beecher 2009). Index signals, in addition to signaling quality or fighting ability, may also be used as aggressive signals in some cases. To investigate whether a signal predicts aggressive escalation, a first step is often to look for an association between the signal and known aggressive behaviors. This was my goal in Chapter 3. Recordings and behavioral observations from two separate studies were analyzed for potential correlations between vocal deviation and behaviors known to be associated with aggressive intent in swamp sparrows. For the analysis, males were classified as either "attackers," because they ultimately attacked a taxidermic mount of a swamp sparrow, or "non-attackers," because they did not attack the mount during the experimental period. Attackers and non-attackers did not differ with respect to vocal deviation. Furthermore, vocal deviation was not correlated with other known aggressive behaviors, such as wing waving or soft singing, nor with approach distance to the speaker, which are all significant predictors of attack in this species. The magnitude of modulation in vocal deviation between neutral and aggressive contexts also did not correlate with aggressive behavior. Because vocal deviation was not associated with aggressive behavior, vocal deviation fails to satisfy the "predictive" criterion for aggressive signals. Evidence from Chapter 3, therefore, suggests that vocal deviation is not used as a signal of aggressive intent, but does not eliminate the possibility that vocal deviation is used in male-male aggressive interactions as an index signal of quality.

In Chapter 4 I addressed the use of vocal deviation in male-male interactions from the perspective of receivers, by asking whether differences in vocal deviation were discriminable by male swamp sparrows. This question was tested at two levels of performance discrimination: between male differences (large scale differences possible between high performance individuals and low performance individuals) and within-male differences (smaller scale differences seen when individual males modulate vocal deviation between contexts). Males were able to behaviorally discriminate large-scale between-male differences, but no behavioral discrimination of finer-scale within-male differences was detected. The finding that males discriminate differences in vocal deviation, and respond more aggressively toward low vocal deviation song, strongly suggests that vocal deviation is used as a signal in male-male aggressive interactions. These findings also suggest that vocal deviation is a good example of an index signal, because although males modulate the signal, they are unable to do so to the point that it affects receiver behavior. Vocal deviation might actually be a better example of an index signal than some others that can be modulated to the extent that modulation affects receiver response (e.g. Wagner 1989*a*, Wagner 1992).

In Chapter 5 I attempted to directly address the adaptive significance of vocal deviation as a signal in male territory defense. Simulated territorial intrusions were conducted to determine whether "low vocal deviation territory owners" were more effective at repelling intruders than were "high vocal deviation territory owners." Intrusion measures did not differ, however, between low and high vocal deviation owner trials. Furthermore, neighboring males who intruded on the experimental territories did not differ from non-intruders in their maximum vocal performance (measured in terms of vocal deviation). The relative vocal deviation levels of intruders compared to simulated owners also did not appear to affect intrusion rates. Despite the negative findings of this study, vocal deviation may still play a role in territory defense. Insensitivity of the experimental design might explain the lack of a difference in intrusions between low and high vocal deviation owners.

Overall, the results of this dissertation support the use of vocal deviation as a signal in male-male interactions. Furthermore, the role of vocal deviation in male-male communication appears to be as an index signal of male quality. Vocal deviation, however, does not appear to serve an additional function as a signal of aggressive intent. Although vocal deviation satisfies the "context" and "receiver response" criteria laid out by Searcy and Beecher (2009), it fails to satisfy the "predictive" criterion for aggressive signals. The use of vocal deviation as a signal in male-male interactions is supported by the findings that signalers actively modulate vocal deviation and that receivers attend to vocal deviation. The classification of vocal deviation as an index signal is supported by outside research demonstrating constraints on vocal performance (Westneat et al. 1993, Hoese et al. 2000) and correlations between vocal deviation and aspects of male quality

(Ballentine 2009). Studies in this dissertation demonstrate that although vocal deviation can be modulated, this modulation capability is paralleled in examples of index signals in other taxa (Wagner 1992, Fitch and Reby 2001, Reby et al. 2005). Furthermore, because males appear not to discriminate within-male differences, modulation cannot alter performance to the extent that it dishonestly affects receiver response.

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